CHAPTER 4

Sockeye Salmon Life History

In diversity lies the salvation of the species.

Karluk River sockeye salmon and the system they inhabit are unique and complex. With the exception of the much larger Fraser River system, the physical geography of the Karluk River complex is probably as varied as any other sockeye salmon river system in North America.[1] The fish spawn in at least five habitat types ranging from the brackish waters of Karluk Lagoon to the torrential cascades of the lateral streams. They spawn over a long period of time from June to November. There are at least 24 different age groups (combinations of freshwater and saltwater residencies)—more than those identified for any other river system. Some Karluk River sockeye salmon smolts migrate to sea the same summer they emerge from the gravel, while others remain in freshwater for up to five years, at which time they are among the largest smolts reported from Alaska lakes. This unique array of diverse traits selected by a varied physical environment has permitted the Karluk River sockeye salmon to survive a changing total environment. Further, this combination of biological and environmental variability has resulted in the highest density of adult sockeye salmon known.

Sockeye salmon are anadromous, which means they spend part of their early lives in freshwater before migrating to the sea, where they remain for a period before returning to freshwater to spawn. Therefore, some system of age designation is necessary to show what portion of an individual's life is spent in each habitat. The earliest investigators to age Karluk River sockeye salmon and to develop a system that conveys this information were Charles H. Gilbert and Willis H. Rich (1927). In their system, total age is given with the number of years spent in freshwater indicated as a subscript. To obtain the number of years spent in the sea, the subscript is subtracted from the total age. The most common type found in the Karluk River is designated as a 5_3. We will briefly follow this age group through its life cycle.

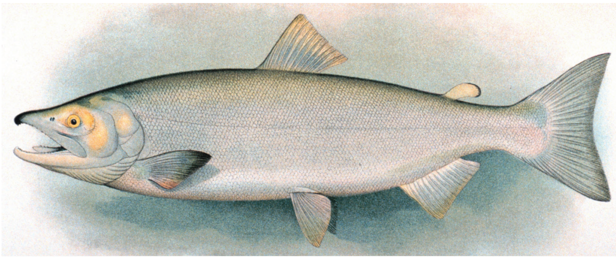
Adult 5_3's return to the mouth of the Karluk River at 5 years of age, swim up the river to Karluk Lake and locate the site of their birth, where they spawn in nests made in the gravel (called redds) and die. The fertilized eggs hatch in the gravel and are now called alevins. In the early spring, the alevins emerge from the gravel after about 10 months. They actively migrate into Karluk Lake as fry, where they feed and grow for a little over two years. Therefore, they remain approximately three years in freshwater from the time when they were deposited as eggs in the redds. In May or June, as smolts they migrate down the Karluk River to the sea. After two years in the ocean this new generation of adults returns to the mouth of the Karluk River, thus completing the cycle. Many variations of this general account occur and are presented in detail in this chapter on life history.

One advantage of the Gilbert and Rich system of age designation is that one can see at a glance the brood year of an individual and predict when the majority of its offspring are likely to return, provided the date of capture is known. Sockeye salmon are often cyclic, and the Gilbert and Rich system is useful in studying this phenomenon. We use the Gilbert and Rich method of expressing sockeye salmon ages in this fisheries research history.

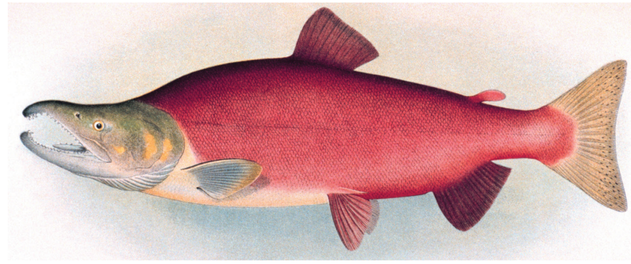
Age Composition of Adults

Age composition of adult Karluk River sockeye salmon was first determined in 1916 by Gilbert and Rich (1927), when scale samples from 382 fish were collected from the seine fishery near Karluk Spit. Subsequently, in 1917, 1919, and 1921, limited numbers of fish from the same source were aged. In 1922, scales from 2,469 fish were aged, but no scales were collected in 1923. Large samples of sockeye salmon scales were generally collected and

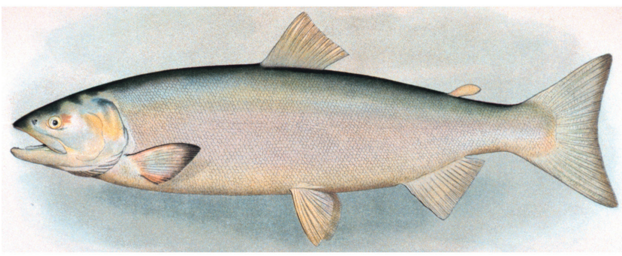
[1] A description of the physical aspects of the Karluk River system is presented in Chapter 1.



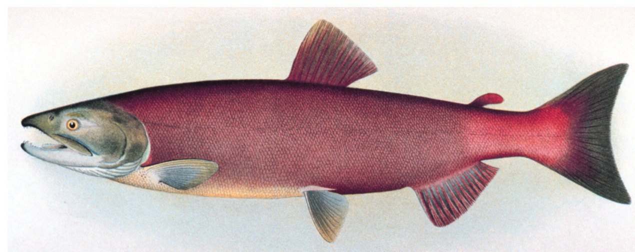
Male sockeye salmon, ocean colors



Male sockeye salmon, spawning colors



Female sockeye salmon, ocean colors



Female sockeye salmon, spawning colors

Ocean and spawning colors of adult sockeye salmon. (Drawings by Albertus H. Baldwin, from Evermann and Goldsborough, 1907.)

aged each year from 1924 to present times (Table 4-1).[2] Length, sex, and, occasionally, weight and fecundity data were also obtained during the sampling process. Between 1964 and 1968, otoliths were collected during the fall sockeye salmon runs because the margins of many late-run scales were badly eroded. These damaged scales resulted in under-assignment of ocean ages. Otoliths were not so affected and would be the preferred structure to use in aging sockeye salmon, except that aging with otoliths is more expensive than aging with scales, and the fish must be killed to obtain the otoliths. It would be a boon to sockeye salmon research if a method were developed that could accurately determine the ocean age without having to kill the fish.

Total age of adults ranged from 2 to 9 years, with 1–5 of those years spent in freshwater as eggs and juveniles and 0–5 years spent in the ocean. Hence, many different age combinations of fresh- and salt-water residencies were possible. A total of 24 different ages have been identified (Table 4-1 and Appendix), including 2_1, 3_1, 3_2, 3_3, 4_1, 4_2, 4_3, 4_4, 5_1, 5_2, 5_3, 5_4, 5_5, 6_2, 6_3, 6_4, 6_5, 7_3, 7_4, 7_5, 8_3, 8_4, 8_5, and 9_5 (Gilbert and Rich, 1927; Barnaby, 1944; Rounsefell, 1958; Barrett and Nelson, 1995). Four of the combinations (3_3, 5_5, 8_3, and 9_5) were reported during one year only with the 9_5 being discovered in 1991 (Barrett and Nelson, 1995) and the 8_3 being first reported in 2009. The 2_1's were reported only three times (1987, 1989, and 2002).

Aging sockeye salmon by reading their scales is as much an art as it is a science. Experienced scale readers sometimes assign different ages to the same fish (Godfrey et al., 1968; Bilton et al., 1983). Hence, one or more of the rare age combinations listed above might not exist in nature, but only in the minds of the scale readers. On the other hand, there may be other valid age combinations that were not present in the samples or identified by the scale readers. Nevertheless, the Karluk River sockeye salmon, with 24 recognized age combinations, exhibit more age variability than any other sockeye salmon system known to us.

The most common age groups of Karluk River sockeye salmon are 5_3, 6_4, and 6_3, listed in descending order of

[2] Table 4-1 is a compilation of data from many investigations. Sampling and analysis methods often differed or were not reported. Some re-calculations were necessary so that all data in this table adhere to the percentage of occurrence format. There may be errors. Therefore, we present this table not as a definitive work, but as a working guide to what we found during our research. If further analysis is desired, we recommend that the original data be located.

Table 4-1
Percentage occurrence of age groups of Karluk River sockeye salmon runs, 1916–2010.[1]

	Age groups																									
	2_1	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_3	8_4	8_5	9_5	Sample		Data source
	0.1	0.2	1.1	2.0	0.3	1.2	2.1	3.0	0.4	1.3	2.2	3.1	4.0	1.4	2.3	3.2	4.1	2.4	3.3	4.2	2.5	3.4	4.3	4.4	size	Remarks	(taken or adapted from)
1916						0.3	0.5				85.1	1.0			2.9	10.2									382	Fall run	Gilbert and Rich, 1927
1917		0.3	0.1		0.4	0.3				0.9	82.4	0.3			5.3	9.5			0.1						758	[2]	Gilbert and Rich, 1927
1918																											
1919						1.0	1.9			1.9	81.6				7.8	5.8									103	Fall run	Gilbert and Rich, 1927
1920																											
1921										0.9	88.2				5.2	5.2			0.5						211	Fall run[3]	Gilbert and Rich, 1927
1922					0.2	0.8	1.1	0.3		0.6	59.3	1.3	0.1		32.2	4.0	tr		0.1						2469	Total run[3]	Barnaby, 1944
1923																											
1924				tr		0.4	3.2	0.4		0.4	76.0	3.2			5.4	10.5			0.5						5132	Total run[3]	Barnaby, 1944
1925		0.2			tr	0.9	5.2			0.2	66.8	2.3			8.3	15.8	tr		0.3						5513	Total run[3]	Barnaby, 1944
1926		0.1			0.3	2.6	0.5	tr		0.9	81.1	0.2			6.0	7.6	tr		0.6	0.1		tr			8172	Total run[3]	Barnaby, 1944
1927		tr			tr	0.1	2.1	tr		7.9	70.8	2.7			9.6	6.1	tr		0.5	0.2			tr		4963	Total run[3]	Barnaby, 1944
1928					tr	0.4	0.2			tr	56.9	0.4			32.8	9.0			0.3	tr					4247	Total run[3]	Barnaby, 1944
1929					tr	1.0	0.2			0.8	34.8	0.3			26.0	35.1		0.5	tr	1.3					1602	Total run[3]	Barnaby, 1944
1930						tr	4.0			0.6	51.5	11.9			14.5	16.0		tr	1.5	tr					3617	Total run[3]	Barnaby, 1944
1931		tr			tr	0.9	0.5			0.3	49.8	3.0			6.4	38.1	0.1	tr	0.9	tr					7258	Total run[3]	Barnaby, 1944
1932					tr	1.0	0.9			0.8	48.2	2.1			4.5	38.6			3.2	0.7					4700	Total run[3]	Barnaby, 1944
1933					tr	0.5	0.4			2.0	52.3	1.3			13.1	27.9	tr	tr	1.3	1.2					3867	Total run[3]	Barnaby, 1944
1934						0.7	0.2			1.7	32.0	1.0			35.7	25.7	tr		2.9	0.1			tr		6551	Total run[3]	Barnaby, 1944
1935			tr		0.1	2.7	4.2			2.0	24.1	5.4		0.2	19.7	32.8	0.5	0.1	6.2	1.9		tr	0.1		7152	Total run[3]	Barnaby, 1944
1936		tr			tr	0.5	1.3	tr		2.2	69.9	3.2		tr	6.2	13.1	tr	0.1	2.5	1.0		tr	tr		7093	Total run[3]	Barnaby, 1944
1937			tr			0.6	2.2			1.0	68.0	1.8			7.6	16.6	0.2	tr	0.8	0.1			1.0			Total run[3]	Rounsefell, 1958
1938						2.6	0.6			1.5	59.9	0.2			16.4	16.7	tr	tr	1.0	1.1			tr			Total run[3]	Rounsefell, 1958
1939			tr			0.1	0.7			1.7	29.4	3.2			45.1	12.3	0.2	0.1	6.6	0.4		0.1	tr			Total run[3]	Rounsefell, 1958
1940					tr	0.6	0.6		x	0.2	33.0	5.1		tr	23.8	32.0	0.1	0.3	3.9	0.3		tr	tr			Total run[3]	Rounsefell, 1958
1941						0.4	0.8			0.4	51.2	2.4		x	11.8	29.1		0.2	3.5	0.2		tr	tr			Total run[3]	Rounsefell, 1958
1942					0.1	0.8	2.2			0.9	52.9	0.9			10.2	24.2		0.1	7.6				0.1			Total run[3]	Rounsefell, 1958
1943					0.5	0.6	0.9			2.0	55.0				23.0	14.2			3.6	0.1		0.1				Total run[3]	Rounsefell, 1958
1944		0.1	tr		0.1	0.8	0.3			3.5	56.5	1.0		tr	25.5	8.9		0.2	3.1	0.1		0.1	tr			Total run[3]	Rounsefell, 1958
1945			tr			0.9	0.2			9.5	19.8	0.1		tr	49.9	13.4		0.3	5.8	0.1		0.2	tr			Total run	Rounsefell, 1958
1946			0.1		tr	0.8	0.2			3.4	18.3	1.1		0.1	31.7	30.5		1.0	12.3	0.3		0.1	tr			Total run	Rounsefell, 1958
1947			tr			0.8	2.9			2.1	26.6	4.9			26.2	30.7		0.1	5.4			0.2				Total run	Rounsefell, 1958
1948						0.1	0.5			0.5	71.1	0.1			8.9	14.2		0.2	4.3	0.1						Total run	Rounsefell, 1958
1949						0.1	0.3			0.1	52.3	0.1			20.2	20.2	tr	0.1	6.0	0.3		0.1	tr			Total run	Rounsefell, 1958
1950							0.1				29.1	0.4			47.1	11.2		0.1	11.8	0.1			tr		2705	Total run	[4]
1951							2.0			0.2	23.8	0.6		0.1	15.9	54.8	0.1	0.2	0.8	1.7					1910	Total run	[4]
1952						0.3	1.8			0.5	52.3	3.1			5.2	12.0			22.1	x						Total run	[5]
1953					tr	0.4	0.8			0.1	52.3	0.5			9.8	28.4			6.3	x			x			Total run	[5]
1954						0.6	0.4			0.7	47.0	2.1			12.9	34.7			2.1	x			x			Total run	[5]
1955						0.1	1.1				17.3	2.2			15.1	58.7			5.4	0.1						Total run	[5]

Table 4-1 (cont.)
Percentage occurrence of age groups of Karluk River sockeye salmon runs, 1916–2010.[1]

	Age groups 2_1	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_3	8_4	8_5	9_5	Sample		Data source
	0.1	0.2	1.1	2.0	0.3	1.2	2.1	3.0	0.4	1.3	2.2	3.1	4.0	1.4	2.3	3.2	4.1	2.4	3.3	4.2	2.5	3.4	4.3	4.4	size	Remarks	(taken or adapted from)
1956						x	4.6			tr	49.1	3.4			21.2	19.9	x		1.7	x			x		3236	Total run[6]	[7]
1957			tr			0.1	5.1			0.1	52.4	3.3			13.3	24.0			1.7						3670	Total run[6]	[7]
1958						0.2	4.2				42.6	9.1		0.1	5.4	36.0	0.1		2.1	0.2					2080	Total run[6]	[7]
1959							1.5			0.1	51.5	3.5			10.0	28.9			4.6	0.1					3185	Total run[6]	[7]
1960			tr			tr	1.5			tr	44.4	0.7			13.9	37.3			2.2						>3914	Total run[6]	[7]
1961			0.1			1.2	7.6			1.4	44.4	1.8			16.2	23.1		0.1	4.1	0.1					1760	Total run[6]	[7]
1962			0.1			0.1	2.6			1.1	78.3	0.5		0.1	9.9	6.2			1.2						2237	Total run[6]	Gard and Drucker, 1963
1963						0.7	0.5			0.1	41.2	1.7			20.5	19.2			16.1						2022	Total run[6]	Gard and Drucker, 1965
1964						0.4	0.8			0.2	50.8	4.1			9.5	32.1		tr	1.2	0.9					2410	Total run[6]	Gard and Drucker, 1966a
1965										0.4	26.0	2.6			8.3	59.4		0.1	3.3						1712	Total run[6]	Gard and Drucker, 1966b
1966							0.1				14.0	0.8			6.7	72.2		0.1	3.6	2.5					2233	Total run[6]	Drucker and Gard, 1967
1967							0.7				29.1	0.3			13.5	44.4			11.4	0.5					1758	Total run[6]	Drucker, 1968
1968			0.1			0.1	5.2			0.1	51.7	2.2			11.0	23.4		0.1	5.9	0.3					1702	Total run[6]	Drucker, 1970
1969			0.2				1.6				47.9	3.5			11.4	31.8			2.8	0.7					995	Fall run	[7]
1970						0.3	0.7			0.4	45.6	1.5			9.4	41.0		0.2	0.9						1054	Total run	Blackett and Davis, 1971
1971							1.3			2.1	41.0	0.2			45.4	9.1			0.8						471	Total run	Blackett, 1973
1972																											
1973						1.0	1.7			1.0	60.1				21.3	11.7			2.7				0.3		291	Spring run	ADFG, Kodiak
1974						1.9	1.3				45.6	1.3			31.0	7.6			11.4						158	Spring run	ADFG, Kodiak
1975			0.5			0.5	3.4			1.0	5.4	3.4			20.6	60.3	2.5		2.0	0.5					204	Spring run	ADFG, Kodiak
1976			0.6			12.8	13.4				33.1	0.6			4.1	32.6			2.3	0.6					172	Spring run	ADFG, Kodiak
1977			1.5			3.9	3.6			3.0	66.3				13.7	4.8			3.3						335	Spring run	ADFG, Kodiak
1978			0.4			2.6	9.4			5.7	52.1	0.4			26.0	1.1			2.3						265	Spring run	ADFG, Kodiak
1979																											
1980						5.5	1.5			11.0	24.8				55.2				2.0							Total run[3]	White, 1985
1981						1.8				7.8	47.8	0.9			24.0	12.2			5.5							Total run[3]	White, 1985
1982						2.8				3.2	39.9	0.4			48.8	1.2			3.7							Total run[3]	White, 1985
1983						1.3	6.6			2.8	67.3	0.1			21.0	0.8			0.1							Total run[3]	White, 1985
1984						1.6	7.3			2.2	54.3	1.0			15.6	16.5			1.5						1134	Total run[3]	White, 1985
1985			0.1			1.2	3.3			1.1	65.3	0.9			9.0	17.4			1.4						2336	Total run[3,6]	Barrett and Nelson, 1995
1986			tr		0.1	0.4	0.7			0.3	52.7	0.5			20.1	16.9		tr	8.4						1383	Total run[3,6]	Barrett and Nelson, 1995
1987	tr	0.1			0.4	1.3	2.5			2.8	47.6	0.6			29.7	7.9		0.1	7.1						3086	Total run[3,6]	Barrett and Nelson, 1995
1988						0.7	2.4			2.3	51.7	0.5			27.5	9.3		0.1	5.6						2446	Total run[3,6]	Barrett and Nelson, 1995
1989	tr	0.1			0.1	3.1	0.3			3.3	46.9	0.1		tr	35.8	6.8			3.6						2739	Total run[3,6]	Barrett and Nelson, 1995
1990		0.3			0.5	0.9	0.3			1.5	45.1	0.4			35.3	10.9		0.2	4.5						2959	Total run[3,6]	Barrett and Nelson, 1995
1991		0.2	tr		0.8	1.2	0.4		tr	1.2	38.5	0.5			33.7	17.6		0.1	5.9					tr	2948	Total run[3,6]	Barrett and Nelson, 1995
1992		0.2	0.2		0.1	0.7	0.8			0.5	21.6	2.2			14.5	52.3		0.1	6.7	0.1					2746	Total run[3,6]	Barrett and Nelson, 1995
1993		0.4	0.1		0.4	1.1	2.2			1.0	23.8	1.7		tr	5.3	53.5		0.1	10.1	0.2		tr	tr		3252	Total run[3,6]	Barrett and Nelson, 1995
1994		0.8	0.1		0.6	3.0	0.6			1.3	37.9	1.1			9.7	36.0	tr	0.1	9.3	0.2		tr	0.2		2973	Total run[3,6]	Barrett and Nelson, 1995
1995		0.1	0.5		0.3	2.7	1.6			3.9	41.9	0.8			21.2	20.0		tr	6.9			0.1	0.1		2545	Total run[3,6]	Nelson and Swanton, 1996

Table 4-1 (cont.)

Percentage occurrence of age groups of Karluk River sockeye salmon runs, 1916–2010.[1]

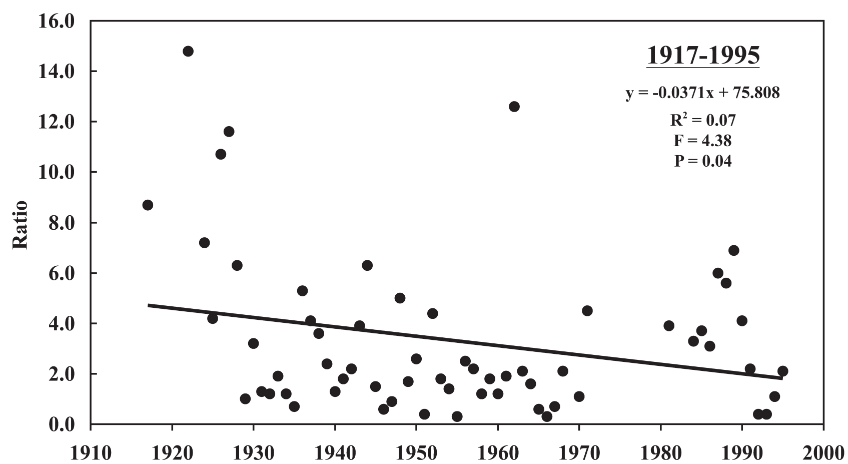
	Age groups																							Sample		Data source
	2_1	3_1	3_2	3_3	4_1	4_2	4_3	4_4	5_1	5_2	5_3	5_4	5_5	6_2	6_3	6_4	6_5	7_3	7_4	7_5	8_3	8_4	8_5	9_5			
	0.1	0.2	1.1	2.0	0.3	1.2	2.1	3.0	0.4	1.3	2.2	3.1	4.0	1.4	2.3	3.2	4.1	2.4	3.3	4.2	2.5	3.4	4.3	4.4	size	Remarks	(taken or adapted from)
1996		tr	0.2		tr	1.3	1.3			11.0	42.9	0.9		0.1	19.3	12.8		tr	9.2	0.7		tr	0.4		1204	Spring run	ADFG, Kodiak
"			0.3			0.8	1.3			1.7	66.6	0.9		tr	10.3	15.7			2.4	0.2			tr		1340	Fall run	"
1997			0.3		0.1	0.9	4.7			3.4	13.6	3.9			33.0	21.0	0.2	0.1	18.3	0.2			0.4		1199	Spring run	ADFG, Kodiak
"			tr		0.7	0.8	3.9			2.8	13.0	1.1		tr	43.6	19.4		0.1	14.2	0.2					1410	Fall run	"
1998			0.1			2.4	2.0			2.1	61.4	0.6			11.6	15.8		tr	3.3	0.7					1747	Spring run	ADFG, Kodiak
"		0.2			0.2	3.6	0.6			1.7	60.1	0.2			11.1	20.2		0.1	1.9	0.1			tr		1185	Fall run	"
1999						4.0	2.3			7.2	51.3	0.3			22.3	6.1		0.1	6.4				tr		1543	Spring run	ADFG, Kodiak
"		0.1	0.1		0.3	4.9	0.9			1.7	61.4	0.1		tr	20.2	7.5		0.1	2.8			tr			1748	Fall run	"
2000						0.4	1.1			5.9	41.6	0.6		0.1	32.6	9.7		0.3	7.6	0.1		tr			1207	Spring run	ADFG, Kodiak
"			0.1			0.5	tr			0.3	53.9	0.8			24.2	16.7			3.6						753	Fall run	"
2001			0.1		0.3	0.6	1.8			0.3	39.5	0.4			38.3	13.0		0.1	5.3	0.3		tr			1259	Spring run	ADFG, Kodiak
"			tr			0.2	2.5			0.1	32.4	0.3			44.8	14.8		0.1	4.7	0.1					1258	Fall run	"
2002			0.1			0.7	3.2			1.1	37.5	0.5			34.5	13.5		0.2	8.4	0.1		0.2			1525	Spring run	Foster and Witteveen, 2003
"	tr					0.1	3.9			tr	57.0	2.2			17.3	16.1		tr	3.3	tr		tr			1571	Fall run	"
2003			0.1			1.9	3.5			0.7	64.4	0.5			16.0	7.7		tr	5.1			0.1			1388	Spring run	Foster, 2004
"		tr	tr			1.6	2.6		0.1	0.2	58.0	0.5			16.9	14.8			5.2			tr	0.1		1870	Fall run	"
2004						1.2	0.5			4.3	54.7	1.3		0.1	21.3	13.2	0.1		3.0			0.2	tr		695	Spring run	Foster, 2005
"					0.5	0.9	tr			1.2	61.2	0.5			11.8	21.8			1.9				0.1		554	Fall run	"
2005			tr			0.6	1.2			0.6	42.1	1.1		tr	36.3	15.2			2.8						1594	Spring run	Foster, 2006
"			tr			0.3	0.6			0.1	57.6	0.3		tr	16.8	22.9			1.4			tr			1742	Fall run	"
2006						1.0	2.4			0.2	45.5	1.2		tr	23.0	16.4			10.2						1210	Spring run	Foster, 2007
"			tr		0.5	0.6	2.2			0.5	23.2	0.7			51.3	9.6			11.5				tr		1605	Fall run	"
2007		0.2			0.1	0.5	1.9			1.5	14.2	0.3			55.7	10.4		0.1	15.1	0.1		tr			1169	Spring run	Foster, 2008
"		tr	tr		0.2	0.3	0.2			0.9	25.4	0.1			42.3	15.8		0.4	14.0	0.1		tr	tr		1933	Fall run	"
2008			0.2		0.1	0.1	0.3			0.8	20.2	0.4		0.1	38.8	7.9		2.1	27.8	0.3		1.0			531	Spring run	Foster, 2009
"		1.2	tr		0.1	0.7	0.2			0.6	14.0	0.8		0.1	54.6	8.8		4.5	13.0			1.4			773	Fall run	"
2009						8.8	1.8			1.4	24.8	6.8		0.1	23.0	23.1	0.9	1.0	7.1		0.1	1.1	0.1		1018	Spring run	Foster, 2010
"			tr			0.1	0.6			0.2	4.6	3.3			4.7	81.7	0.1	tr	4.5	tr	tr	0.1	tr	tr	1247	Fall run	"
2010			0.9		tr	18.6	6.4			3.1	17.3	5.2			6.3	39.4		tr	1.8	0.8					1155	Spring run	Foster, 2011
"			tr			0.5	0.6			0.2	20.1	0.2			2.2	70.7			1.8	3.3			0.2		1255	Fall run	"

[1] A trace (tr) means that the percentage occurrence was less than 0.05% and an x means that the age group was present, but the percentage occurrence was unknown.
[2] Spring (33%) and fall (67%) runs.
[3] Karluk River spawners were included in the samples used for aging.
[4] Anonymous. Adult age composition data. NARA, Anchorage, AK.
[5] Walker, Charles E. 1956. Age analysis of the Karluk red salmon runs, 1922, 1924-1936, and 1952-1955. Unpubl. report. Located at FRI, University of Washington, Seattle.
[6] Total age composition was weighted by size of spring and fall escapements.
[7] Drucker, Benson. ca. 1969. Length frequency distribution by major age group for male and female sockeye salmon in spring, fall, and total escapements to Karluk Lake, 1956-1969. BCF, ABL Unpubl. tables. Located in personal papers of Richard Gard, Juneau, AK.

importance (the long term averages of 6_4 and 6_3 are similar). This ranking was first reported by Gilbert and Rich (1927) during their analysis of scale samples in 1916. Subsequent investigators have corroborated the usual predominance of 5_3 fish, even though 6_4 and 6_3 age groups were the most abundant in some years (Barnaby, 1944; Rounsefell, 1958; Owen et al., 1962; Gard and Drucker, 1965). Considering the years 1916–2009, the 5_3 age group was most numerous in 64 years, the 6_4 group in 12 years, and the 6_3 group in 12 years (Table 4-1). The fourth most abundant age group was 7_4, which occasionally (e.g. 1952) appeared in larger numbers than the 6_3 or 6_4 age groups.

The age composition varied throughout the season in Karluk River sockeye salmon. Gilbert and Rich (1927), in analyzing 1922 scale data, found that the 6_3 group was abundant in the spring run, but diminished as the summer progressed. The 6_4 group was initially present in low numbers, but increased in abundance later in the spring run and especially in the fall run. The 5_3 age group was abundant throughout the season. Further, Rounsefell (1958) reported that older ocean-aged fish (age groups 6_2, 7_3, 7_4, and 8_4) generally returned early in the season, whereas older freshwater-aged fish (age groups 6_5 and 7_5) usually returned late in the season. Exceptions to this generalization were the 8_5, 3_1, and 4_1 age groups.

Long-term changes in freshwater age composition may also have occurred in the Karluk River sockeye salmon. Barnaby (1944) presented graphical evidence that indicated little or no change in ocean age, but a decrease in 3-freshwater fish and an increase in 4-freshwater fish in most of the returns from the 1922 and the 1924–29 escapements. He suggested that a shortage of phosphorus in Karluk Lake might have caused a decrease in phytoplankton, resulting in decreased growth of sockeye salmon juveniles. This reduced growth might have caused the juveniles to remain in Karluk Lake for an extra year. Unless the relationship changed, he predicted that the majority of the fish in the Karluk sockeye run would be 4-freshwater, whereas formerly the 3-freshwater age group was dominant. To test whether or not this trend continued to present times, we regressed the ratio of percentage occurrence of the



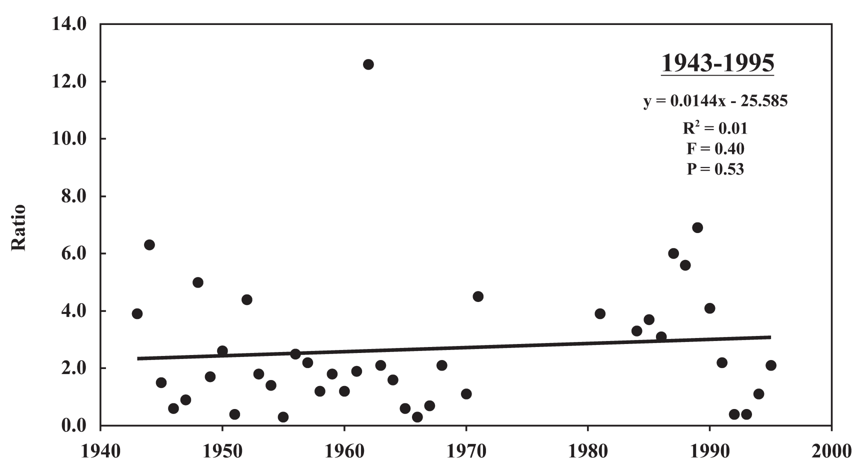


Figure 4-1. Ratio of age group 5_3 to 6_4 in Karluk River sockeye salmon (See Table 4-1 for sources of data by year. Data for 1919, 1921, and 1969 are not included in the analysis because no spring-run samples were taken in those years).

two major age groups (5_3 and 6_4) on year, from 1917 to 1995. Over the entire period, the ratio declined significantly ($P = 0.04$), but the regression for the 1943–95 period was not significantly different ($P = 0.53$) from zero (Fig. 4-1). A cursory scan of Table 4-1 suggests that the 6_4 age group may replace the 5_3 group when the latter are in low numbers. It is likely that cycles in freshwater ages may be found that are similar to those reported by Schmidt et al. (1998) for total age.

Size at Return

Size at return is an important life history aspect of Karluk River sockeye salmon. Although lengths of tens of thousands of adult sockeye salmon have been measured over the years, less weight data have been collected. Most references to the weight of adults are from the early years of the fishery, and many of these are anecdotal (Table 4-2). During the 1884–1931 period, Karluk River sockeye salmon averaged about 3.0 kg in weight, with a range of 2.0 to 4.5 kg. Females were somewhat smaller than males, and there may have been a slight downward trend in weight during the period. If we assume that 3.0 kg is a valid average weight (which is questionable), Karluk River sockeye salmon would rank among the heavier North American populations (Burgner, 1991). Chignik sockeye salmon adults averaging 3.2 kg are the largest and Columbia River sockeye averaging 1.6 kg are the smallest.

Sockeye salmon that spend 0 (actually a few weeks) or 1 year at sea are called “jacks,” “grilse,” or “Arctic salmon.” All 0-ocean jacks and most 1-ocean jacks are males. Zero-ocean jacks are in age groups 3_3, 4_4, or 5_5, and they are the smallest returning adults, ranging from only 301 to 338 mm in average mideye-fork length during the 1916–26 period (Table 4-3). The 3_3 and 5_5 types were seen only once, but 4_4’s occurred on three occasions. One-ocean jacks (age groups 2_1, 3_2, 4_3, 5_4, and 6_5), with the exception of the rare 2_1’s, appear more regularly, with the 4_3’s and 5_4’s occurring most years. Most of these are small, averaging from 399 to 532 mm in mideye-fork length (Table

Table 4-2
Early references concerning weight of adult sockeye salmon in the Karluk River.

Observer	Year	Avg. weight (kg)	Fish per case	Remarks
Petroff (1884)	1884	4.5		Sockeye salmon not specifically identified.
Bean (1891)	1888	3.2–3.6	13	“Individuals of 15 lbs [6.8 kg] are occasionally seen, but they
	1889	3.2–3.6	12	are uncommon.”
Luttrell (1898)	1893		14	
Moser (1899)	1896		12	“. . . the early run usually consists
	1897		12	of fish from 14 to 15 and even as high as 17 to the case, but as the season advances they come down to 12 . . . the general average is probably 5½ pounds [2.5 kg] in weight.”
Moser (1902)	1900		13.6–13.9	
Kutchin (1904)	1903	2.0		“. . . this season the fish were remarkably small . . . commonly they run about 6 pounds [2.7 kg].”
Kutchin (1905)	1904		20	[Normally] “the common average of 13 or 14.”
Evermann and Goldsborough (1907)	1903	2.6 males 2.1 females		Males averaged 64.0 cm. Females averaged 60.7 cm.
Baker[1]	1922		13.5–14.5	
Gilbert and Rich (1927)	1925	2.8 5_3 males 2.4 5_3 females		
	1926	2.8 5_3 males 2.5 5_3 females 2.9 6_3 males 2.5 6_3 females 2.8 6_4 males 2.5 6_4 females		
Rich and Ball (1931)	1931		14	Used 14 fish/case to determine number of fish caught from case pack data.

[1]Letter (12 December 1922) from Shirley A. Baker, Assistant Agent, USBF, Cordova, AK, to Commissioner of Fisheries, Washington, DC. Located at NARA, Anchorage, AK.

Table 4-3
Mean mideye-fork length (mm) for male jack sockeye salmon, Karluk Lake, 1916–26 (derived from Gilbert and Rich, 1927).

Year	Male sample size	Mean length by age group for total run						
		3_3	4_4	5_5	3_2	4_3	5_4	6_5
1916	148	—	—	—	—	482	546	—
1917	363	—	—	—	399	—	505	—
1919	45	—	—	—	—	534	—	—
1921	96	—	—	—	—	—	—	—
1922	1175	—	313	338	—	494	502	514
1924	2513	301	322	—	—	482	525	—
1925	2548	—	—	—	—	512	526	—
1926	3523	—	310	—	—	464	524	551
Grand mean		301	315	338	399	495	521	532

4-3). The shortest of the 1-ocean jacks were the 3_2's, which spent only two years in freshwater, and the longest were the 6_5's, which spent five years in freshwater; this shows that some growth occurs during each year spent in freshwater.

Jacks arrive in the Karluk River predominantly toward the end of the run season. A large run of 4_3 jacks is often a harbinger of a large run of 5_3's, as well as a large total run the following year. A good example of this association occurred when a 5.2 percentage occurrence of 4_3 jacks in 1925 was followed by an 81.1 percentage occurrence of 5_3's and a run of 4,918,000 fish in 1926. Similar associations were evident in 1961–62 and 1984–85 (Table 4-1, Figs. 1-2, 1-3).

Two-ocean fish were longer than 1-ocean fish. For the 1916–26 period, total runs of 2-ocean fish from age groups 5_3 and 6_4 averaged 603 and 611 mm in length, respectively (Table 4-4). Fish from age groups 4_3 and 5_4 averaged only 495 and 521 mm in length, respectively (Table 4-3). Growth during the second year at sea averaged 108 mm for the 5_3 fish and 90 mm for the 6_4 fish. It should be pointed out that we don't know how long the 5_3's and 6_4's were one year prior to their capture, and we can only assume they were the lengths of the 4_3's and 5_4's.

Table 4-4
Mean mid-eye-fork length (mm) by major age group for male sockeye salmon in spring, fall, and total runs, Karluk Lake. The 1916–26 data were derived from Gilbert and Rich (1927)[1] and the 1956-69 data were compiled by Benson Drucker.[2]

Year	Sample size	Spring run				Fall run				Total run			
		5_3	6_3	6_4	7_4	5_3	6_3	6_4	7_4	5_3	6_3	6_4	7_4
1916	148	—	—	—	—	606	611	599	—	—	—	—	—
1917	363	—	—	—	—	—	—	—	—	611	635	624	658[3]
1919	45	—	—	—	—	620	658	628	—	—	—	—	—
1921	96	—	—	—	—	619	621	611	—	—	—	—	—
1922	1175	558	—	—	—	592	—	—	—	587	600	588	532[3]
1924	2513	582	—	—	—	617	—	—	—	603	619	612	635
1925	2548	573	—	—	—	614	—	—	—	605	609	612	634
1926	3523	589	612	581	—	624	643	628	—	611	621	619	631
Grand mean		576	612	581	—	613	633	616	—	603	617	611	618
1956	485	501	562	534	581	543	560	547	592	512	561	542	584
1957	841	511	561	513	576	542	572	551	590	522	563	541	578
1958	752	498	541	490	534	547	576	549	574	529	558	535	565
1959	707	526	557	504	547	543	556	547	572	537	557	530	548
1960	1326	510	558	521	551	534	571	548	562	514	558	537	551
1961	475	526	557	520	562	548	576	571	597	532	560	552	571
1962	664	532	561	512	559	553	588	558	—	545	567	522	559
1963	825	520	568	508	552	519	577	531	574	520	575	527	573
1964	489	512	549	507	558	545	538	553	—	518	549	512	558
1965	248	512	553	499	544	542	577	562	570	525	558	548	545
1966	430	524	556	516	554	556	—	569	582	531	556	544	558
1967	553	517	571	526	559	553	593	566	593	531	576	547	564
1968	401	513	567	538	576	548	596	566	628	518	569	552	582
1969	172	—	—	—	—	548	579	554	579	—	—	—	—
Grand mean		516	558	514	558	544	574	555	584	526	562	538	564

[1] From 1916 through 1921 the fish were measured in inches. These were converted to mm by multiplying inches by 25.4. Also, all the lengths measured from 1916 to 1926 were snout-fork lengths. These were converted to mideye-fork lengths using the equation in Hartman and Conkle (1960:55) modified for mm. This was $Y = 23.9 + 0.924X$.
[2] Drucker, Benson. ca. 1969. Length frequency distribution by major age group for male and female sockeye salmon in spring, fall, and total escapements to Karluk Lake, 1956-1969. U.S. Department of the Interior, FWS, BCF, Biological Laboratory, Auke Bay, AK. 27 unpubl. tables.
Copy in the personal papers of Richard Gard, Juneau, AK.
[3] Only one fish was measured.

In like manner, 3-ocean fish were longer than 2-ocean fish. During the 1916–26 period, 6_3 and 7_4 fish averaged 617 and 618 mm in length, respectively (Table 4-4). A comparison of these groups to the 5_3's and 6_4's shows that the 6_3's grew 14 mm and the 7_4's grew only 7 mm during their third ocean year; both growth increments were much less than those for the second ocean year. Taft (1930) also reported little growth of 6_3's and 7_4's during their last year at sea. As pointed out in the previous paragraph, we assume that one year prior to their return the 6_3's and 7_4's were the lengths of 5_3's and 6_4's.

Male sockeye salmon from the Karluk River are usually longer than females. This difference is clearly evident in Figure 4-2 where 2-ocean males were significantly ($P<0.01$) longer than 2-ocean females in 1962 (Gard and Drucker, 1963). However, if there is a large number of jacks such as occurred in 1968 (Fig. 4-3), females may average significantly ($P<0.05$) longer than males. In that year, 8% of the sample was composed of jacks.

Season of return has a profound effect on length. For the 1956–69 period, mean lengths of the major age groups of fall-run males were longer than those for spring-run males (Table 4-4). Similar differences oc-

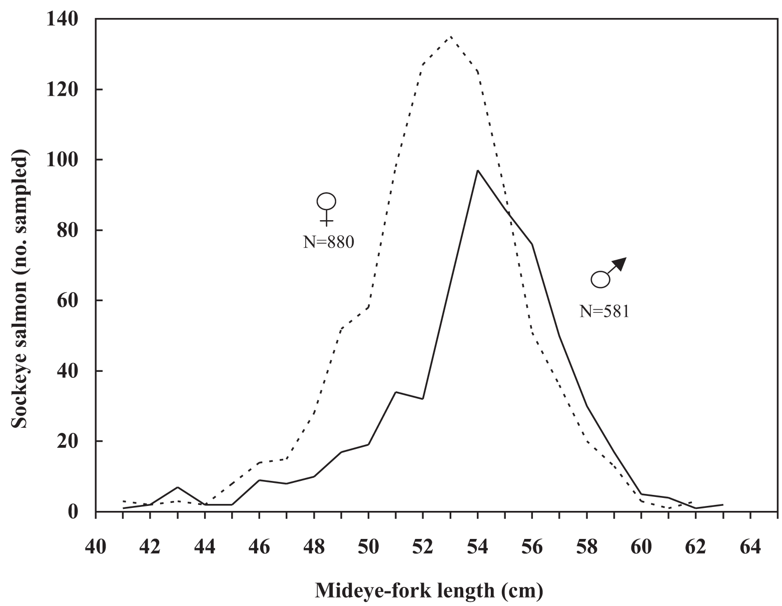


Figure 4-2. Length frequency of 2-year ocean male and female sockeye salmon sampled at the Karluk River weir, 1962 (from Gard and Drucker, 1963).

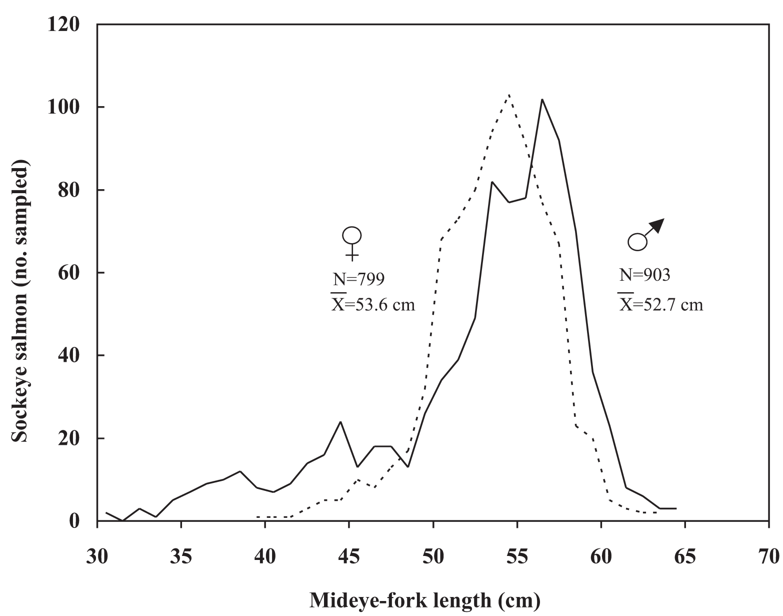


Figure 4-3. Length frequency of male and female sockeye salmon sampled at the Karluk River weir, 1968 (from Drucker, 1970).

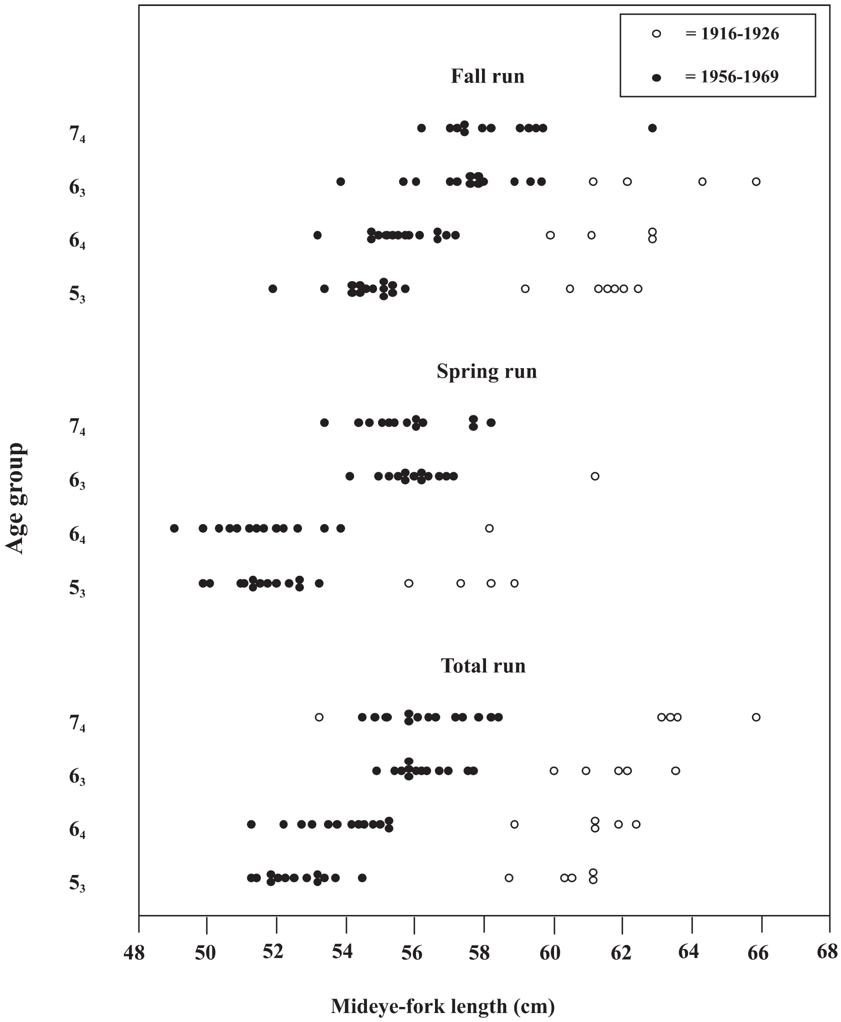


Figure 4-4. Mean mideye-fork lengths by major age group for male sockeye salmon in spring, fall, and total runs to Karluk Lake for individual years of the 1916–26 and 1956–69 periods (data are from Table 4-4).

curred during the 1916–26 period between spring and fall age groups 5_3, 6_3, and 6_4 (Table 4-4).

Gard et al. (1987) found that fall-run females from Karluk River weir and various spawning grounds were significantly (t-test; $P < 0.01$) longer than spring-run females in 1962 and 1963 when the samples were not stratified into age classes. In 1965, when the comparisons were made with 2-ocean females only, fall-run fish were longer than spring-run fish, although the lengths of spring- and fall-run fish from terminal streams did not differ significantly (t-test; $P > 0.05$). This was attributed to small sample sizes.

There appears to have been a substantial decrease in size of Karluk River sockeye salmon between the 1916–26 period and the 1956–69 period (Table 4-4). The grand mean lengths of the major age groups decreased a minimum of 54 mm in the total run of 7_4's, to a maximum of 77 mm in the total run of 5_3's. There was no overlapping of mean lengths for individual years although the single 7_4 fish measured in 1922 was shorter than the mean for any 7_4 sample from the more recent period and may have been an error. These differences are quite apparent from the plots of 1916–26 mean lengths (open circles) and 1956–69 mean lengths (solid circles) for the major age groups and runs (Fig. 4-4). In a comparison of average lengths of spring-run Karluk River sockeye salmon from early (1925–41) and recent (1973–95) years, Martinson (2004) also found a size reduction over time. Similarly, Ricker (1982) reported that between 1950 and 1980 most areas of British Columbia registered small decreases in size of sockeye salmon.

The most significant findings concerning the size of returning sockeye salmon adults were: 1) differences in length from various spawning grounds and between spring and fall runs were evidence supporting the existence of subpopulations (see Chapter 5), and 2) size was primarily determined by the length of stay in the ocean. Gilbert and Rich (1927) first showed that fish spending the shortest time in the sea should have the shortest lengths, and fish spending the longest time in the sea should have the longest lengths, and 3) that size also varied with freshwater age, sex, and from year-to-year.

Sex Ratio

In the past, it has been generally assumed that there should be as many males as females on the spawning grounds to assure fertilization of all eggs. However, Barnaby (1944) reported that in the 1923–33 returns of sockeye salmon to Karluk Lake, the average occurrence of males was only 43% despite a 50% average occurrence of males in the smolt out-migration for the 1925–34 period. Part of this decrease between the smolt and adult stages was attributed to selection of males by a gill-net fishery off the mouth of the river, but part of the decrease was unexplained. With reference to the earlier years of the same data, Gilbert and Rich (1927) concluded that "This is an unusual condition among red salmon races and appears the more remarkable from the fact that, aside from the grilse, every important year class shows a deficiency of males." In fact, a preponderance of females is neither "unusual" nor "remarkable"; Foerster (1968:116) presents a table of sex ratios from eight British Columbia sockeye systems for the years 1950–58 that generally shows an excess of females. We now know that a modest excess of females may not be harmful with respect to degree of egg fertilization because Mathisen (1962) demonstrated that one male can effectively fertilize the eggs of up to 15 females. However, the suggestion by some that "surplus" males be selectively harvested could be detrimental as a surplus of males would help buffer females from bear predation (see Chapter 10) and would increase lake fertilization (see Chapter 7).

A more recent series of data (1956–68) shows a male-dominated sex ratio for six years and a female-dominated sex ratio for seven years (Table 4-5). Hence, there has been a shift from total female dominance to an almost even split between the sexes since Barnaby's period. Usually when males are substantially more numerous than females, as in 1958, 1961, and 1968, jacks are in abundance (Table 4-1).

As we have seen with length, sex ratio is also closely associated with ocean age. Barnaby (1944) reported that the percentage occurrence of males decreases with increased ocean residence with 100% males in the 0-ocean group and only 35–38% in the 3-ocean group. In the 2-ocean group, which includes the usually abundant 5_3's and 6_4's, the percentage occurrence of males ranges from 32% to 62%. This group has the most balanced sex ratio.

Table 4-5
Sex ratios of adult sockeye salmon in the spring, fall, and total escapement, Karluk Lake, 1956–69.[1]

Year	Spring escapement (male : female)	Fall escapement (male : female)	Total escapement[2] (male : female)
1956	1 : 0.96	1 : 0.83	1 : 0.90
1957	1 : 1.04	1 : 0.89	1 : 0.95
1958	1 : 0.93	1 : 1.25	1 : 1.13
1959	1 : 1.23	1 : 0.95	1 : 1.04
1960	1 : 0.91	1 : 0.89	1 : 0.90
1961	1 : 1.10	1 : 1.19	1 : 1.14
1962	1 : 0.87	1 : 0.68	1 : 0.74
1963	1 : 1.20	1 : 1.33	1 : 1.28
1964	1 : 1.27	1 : 0.95	1 : 1.05
1965	1 : 0.86	1 : 0.84	1 : 0.84
1966	1 : 1.73	1 : 0.97	1 : 1.08
1967	1 : 1.00	1 : 0.78	1 : 0.85
1968	1 : 1.26	1 : 1.04	1 : 1.12
1969	[3]	1 : 0.83	[3]

[1] Drucker, Benson. ca. 1969. Length frequency distribution by major age group for male and female sockeye salmon in spring, fall, and total escapements to Karluk Lake, 1956-1969. U.S. Department of the Interior, FWS, BCF, Biological Laboratory, Auke Bay, AK. 27 unpubl. tables. Copy in the personal papers of Richard Gard, Juneau, AK.
[2] Ratios weighted by escapement size.
[3] Weir washed out.

Upstream Migration

Length of time required for the upstream migration of the spring and fall subpopulations of Karluk River sockeye salmon varies markedly. Both groups pass through the fishery off the mouth of Karluk River and enter the river at Karluk Spit (Fig. 1-4) in two large, distinct waves. The vanguard of the early run arrives at the spit in mid May, and the first fish of the fall run arrive there sometime in July depending on conditions. The first 3 km of the river constitute a lagoon and the fish swim through the lagoon and thence up the river proper for another 34 km before reaching Karluk Lake and its spawning grounds.

There is general agreement that spring-run fish require about 7 days to make the passage, but average travel time for the fall run is longer and ranges from 10 to 28 days (Gard, 1973).[3] Reasons why fall-run fish re-

[3] 1) Rutter, Cloudsley Louis. 1903. Field observations by Cloudsley Rutter on his Karluk work of 1903. Unpubl. notes. 48 p. Copy provided courtesy of Mark R. Jennings (Davis, CA) and located in Box 130, Barton Warren Evermann papers, Library Special Collections, California Academy of Sciences, San Francisco, CA.
2) Simon, Robert J., Jack Lechner, Martin F. Eaton, Peter B. Jackson, and Louis A. Gwartney. 1970. Kodiak area management annual report, 1970. ADFG. Unpubl. report. Located at ASA, Juneau, AK.

quire more time than spring-run fish are that 1) pink salmon are abundant in the fall in even years and they impede the progress of the sockeye salmon by their physical presence, and 2) a fairly high flow of water is required to permit salmon to ascend the shallow Karluk River. Sufficient flows are present throughout the spring run because of snow melt, but adequate flows during the fall run require rain, which is sporadic until mid September.

During the early part of the fall run, fish often enter the lagoon, mill around for a few days, and return to the sea apparently to await better conditions. Unlike other salmon, sockeye tend to form schools in the lagoon. After a good rain an entire school of many thousands may head upstream in a group, leaving the lagoon nearly devoid of fish temporarily. The range in fall travel time from 10 to 28 days, reported in different studies, may also be due to fluctuations in rainfall, or it may depend on where in the lagoon the tagged fish are released. Both Gilbert[4] and Barrett and Nelson (1994) found that it requires an average of about 10 days in the fall for salmon to travel from the Karluk Spit area to the lower weir. That distance is essentially the length of the lagoon, which is over 3 km long. Tagged fish released near Karluk Spit will require more time to reach the lake than fish released near the upper end of the lagoon.

Spawners arrive at the upper weir in two large waves, repeating their pattern of arrival at the river mouth. The first fish of the spring run enter the lake in mid May. Daily escapements build to a peak in mid June and decrease to a few fish in mid to late July. The fall run then commences, tops out between late August and late September and declines to a few fish by November. After reaching the lake, the spring-run fish spend 3–5 weeks migrating and maturing before they appear on the spawning grounds, whereas the fall-run fish require only 1–3 weeks. Spring-run fish may spend a longer time in the lake because they are not as mature as fall-run fish when they enter the lake. Timing of the spring run is precise and hence predictable within a few days from year-to-year and timing of the fall run is imprecise and unpredictable as a result of stream flow and pink salmon escapement patterns. More detail is given in Chapter 6. We do not know what routes the groups of spawners take during their migrations from the lake outlet to their respective spawning grounds.

[4] 1) Letter (18 August 1925) from Ray S. Wood to Fred R. Lucas. 2) Letter (11 September 1925) from Ray S. Wood to Fred G. Morton. Both located at NARA, Anchorage, AK.

Sexual Dimorphism

When sockeye salmon arrive at Karluk Spit they are streamlined and silvery. There are no large dark spots on the back or fins, but rather, a fine black stippling. The dorsal surface is greenish blue grading into a darker blue on top of the head. The gums are lightly pigmented. Both sexes are of similar coloration and form, the main difference being that the snout and jaw of the males are somewhat longer than those of the females. At this stage of maturation a Karluk River sockeye salmon has the appearance of a generalized salmonid. Most of the fish entering the lake during the spring run and a few that enter during the fall run appear as described.

As the season progresses, there is a remarkable change in color and form. These changes become evident toward the end of the spring run when a subtle reddening of the body and elongation of the snout and jaw of the males are evident in fish entering Karluk Lake. The rate of change increases during the fall run. By the time the fish from both runs reach the spawning grounds they appear as follows: Males have bright red backs, somewhat darker red sides, and red adipose, anal, and dorsal fins. Their heads and opercula are green. Spawning males acquire a hump between the head and dorsal fin, become laterally compressed, and develop elongate, hooked lower jaws and snouts with enlarged upper teeth. Females have a coloration similar to males except that their sides are darker. The form of females is much the same as at sea, but their abdomens become enlarged and there is a slight elongation of snout and lower jaw.

Fry and smolts have uniform bluish-green backs and silvery sides with 8–12 short, oval parr marks. No dark spots are on the dorsal fin.

Spawning

Spawning Habitat

At least five distinct spawning grounds are used by Karluk River sockeye salmon. These are 1) lateral streams such as Cottonwood and Salmon creeks, 2) terminal streams such as Thumb and O'Malley rivers, 3) lake beaches especially near the mouths of Thumb and O'Malley rivers, 4) Karluk River below the lake outlet, and 5) Karluk Lagoon at the mouth of Karluk River (Figs. 1-4, 1-5). Most lateral streams are short, shallow, narrow, swift, and steep with thin rubble and gravel substrates except in short stretches above their mouths which are similar to terminal streams. Two lateral

Table 4-6
Physical characteristics of representative spawning habitats of sockeye salmon of the Karluk system (from Owen et al., 1962).

Type and location of spawning area	Area utilized (m^2)	Length utilized (m)	Mean gradient (%)	Streamflow (m/sec)	Streamflow (m^3/sec)	Type of gravel
Lateral streams						
Grassy Point Creek	1,363	427	5.26	0.77	0.41	Shallow gravel of all sizes
Cottonwood Creek	2,425	396	4.13	0.35	0.14	thickly interspersed with
Others	12,935	—	—	—	—	rubble and small boulders.
Total	16,723					
Terminal streams						
Upper Thumb, East Fork	26,422	2,865	0.70	0.85	2.23	Uniform fine gravel and sand.
Others	40,719	—	—	—	—	
Total	67,141					
Outlet River (Karluk)	252,845	4,663	0.2[1]	0.55	18.21	Uniform fine gravel interspersed with pockets of sand in lower reaches.
Karluk Lake Beaches	—	—	—	—	—	Rubble, some rocky
Thumb, O'Malley areas	12,542[2]					outcrops.

[1] Mean gradient estimated.
[2] Area utilized estimated.

streams, Little Lagoon and Spring creeks, are so different from the others that they could be considered a class by themselves: Little Lagoon consists of a pond a few meters back from the lake, fed by little streams. Spring Creek is composed of a few interconnected ponds fed by springs and small streams. The terminal streams are longer, deeper, wider, slower, with less gradient than lateral streams and possess thick, gravel substrates. Upper Karluk River is similar to the terminal streams except that it is wider and has a greater volume flow. Beach spawning areas are generally in deeper, slower moving water than tributary or outlet streams and have a rubble substrate. The Karluk Lagoon spawning area is unique in that it is in brackish water near the head of the lagoon. It may be the only sockeye salmon spawning area in the world in brackish water.[5] Finally, there are a few creeks that empty into Karluk River between the lake outlet and the lagoon that accommodate some spawning sockeye salmon. These are Silver Salmon, Katzenjammer, and Barnaby creeks.

Physical data related to spawning are presented in Table 4-6, which is reprinted from Owen et al. (1962). Total spawning area for the Karluk River system is estimated to be 349,251 m^2. Using this area and the 1955–62 average escapement of 334,000, we determined that an average of 9,543 spawners per hectare were accommodated. This density of spawners is much higher than that for Bristol Bay river systems for which comparable data are available. The Kvichak River system with 4,557 spawners per hectare had the second highest spawning density (Burgner et al., 1969, Tables 12, 15). Terminal streams at Karluk Lake have about four times as much spawning area as lateral streams and the upper 4.8 km of Karluk River have three times as much spawning area as do all the tributary streams together (Owen et al., 1962). However, sockeye salmon may not spawn effectively in the lower part of the 4.8 km stretch because the substrate there is seemingly compacted, fine material under the top several cm of gravel.[6]

[5] Letter (5 January 1994) from Len Schwarz, ADFG, Division of Sport Fish, Kodiak, AK, to Kevin Delaney, ADFG, Division of Sport Fish, Anchorage, AK. Located at ADFG, Kodiak, AK.

Timing and Distribution of Spawners

Distribution of spawners in the tributaries was determined by weekly or biweekly stream surveys. In 1963 spawning occurred between about 1 July and 1 November (Fig. 4-5). The peak of the spring run was about 19 July and the peak of the fall run was about 14 September with the midseason low on 15 August. Ninety-one percent of the lateral stream spawners were from the spring run while terminal stream spawners were from both runs. Canyon Creek and O'Malley River accommodated both runs. Upper Thumb River was occupied by the spring run and Lower Thumb River by the fall run. Most of the lake beaches were used by fall spawners. Although the prime beach spawning areas were near the mouths of Thumb and O'Malley rivers, some beach spawning occurred near lateral stream mouths during the spring run. Upwelling usually was present at

[6] Wilmot, Richard L. Auke Bay, AK. 1996. Personal commun.

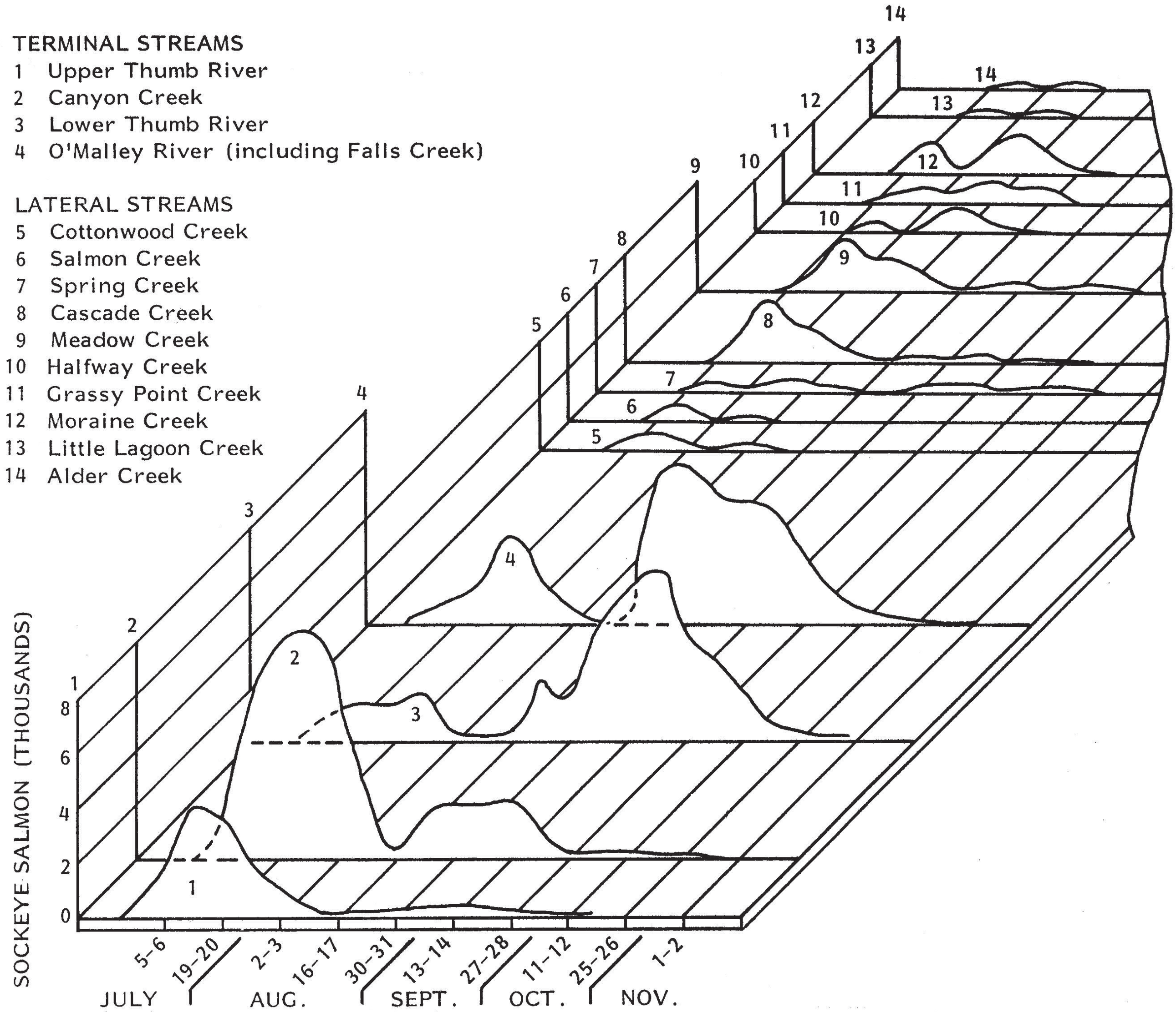


Figure 4-5. Timing and distribution of sockeye salmon on the spawning grounds by weekly stream survey counts, Karluk Lake, 1963 (from Gard and Drucker, 1965).

favored beach spawning sites. Ten percent of the total escapement spawned in Upper Karluk River below the former weir site during late spring and fall runs (Gard and Drucker, 1965). Temporal and spatial distributions of spawners in 1963 were similar to those in 1957, 1958, and 1959 (Owen et al., 1962) and in 1962 and 1964 (Gard and Drucker, 1963, 1966a). This general pattern has existed as far back as 1922.[7]

Spawning Process

After arriving at their natal spawning grounds, mature sockeye salmon initiate the spawning process. The following sequence of events is for Wood River sockeye (Mathisen, 1962), but it generally applies to Karluk River sockeye salmon as well. The female selects a site and starts to dig a nest. She is joined by a male who may help some with the digging and fights off other males who may take up "satellite" positions nearby. Digging is accomplished when the female turns on her side and rapidly flexes her body back and forth. Gravel and sand are lifted from the nest by suction and the current carries the particles away. There are periods of rest when she tests the nest with her anal and pectoral fins. The excavated nest is oblong and measures about 76 × 51 cm with the long dimension parallel to stream flow.

When the nest is ready, the dominant male and female lie side by side quivering with their mouths

[7] Rich, Willis H. 1922 notebook. Location of original notebook unknown; copies at NARA, Anchorage, AK, and ABL Library, Auke Bay, AK.

agape while eggs and sperm are released simultaneously. The spawning act takes 10–12 seconds, and during this period a satellite male may dart in and also release sperm. Fertilization occurs rapidly with an efficiency of nearly 100%. The female then digs on the upstream side of the nest to bury the eggs quickly. She now rests for several hours before excavating another nest nearby and repeats the process until 3–7 nests are completed, each accommodating 500–1,100 eggs. Finally, she covers the batches of eggs with gravel to a depth of 15–23 cm and guards the completed redd until near death.

Longevity of spawners on the spawning grounds was determined at Grassy Point Creek, a lateral stream at Karluk Lake (Gard and Drucker, 1966a). Maximum longevity (time through the weir to time of disappearance) decreased from 14 to 9 days and average longevity decreased from 3.8 to 1.5 days as the season progressed. Salmon entering the creek later in the season were more mature and a progressive decline in longevity would be expected.

Many factors affect the success of spawning, but spawner density may be the most significant. As spawner density increases, egg retention in the bodies of the females, superimposition in the spawning gravels, competition for spawning sites, and mortality of eggs in the gravel also increase. The Karluk River system, with a density of 9,543 sockeye salmon per hectare of spawning area, accommodates the largest known density of spawning sockeye in Alaska (computed from information in Tables 12 and 15 in Burgner et al., 1969).

What is there about Karluk sockeye salmon or the environment they inhabit that permits such a high density? First, the total run is divided into two approximately equal, well-separated runs that extend over a four month period. Second, within each major run there is wave spawning. This may be seen best in the run configurations for the lateral streams (Fig. 4-5). Division into runs and waves within runs ensures that only a portion of the total escapement is on the spawning grounds at any one time. Third, spawners in Karluk lateral streams tolerate each other in closer proximity (<1 m² per pair) than do spawners in many other systems. Hartman et al. (1964) suggest that abundant boulders on the bottoms of Karluk lateral streams block the vision of neighboring pairs of spawners, giving them a sense of privacy not present in streams with substrates of uniform gravel. Finally, during years with large escapements, spawners go farther upstream and spawn over a longer period of time than they do in years with smaller escapements.

Although high densities of spawners at Karluk seem to function well during most years, there are limits. In 1926, when there was a huge escapement of 2.5 million sockeye salmon, many females died unspawned. Willis H. Rich observed this event and was so appalled by the waste that he fertilized some eggs from newly-deceased females, planted them in the gravel, and later determined that some of the eggs survived at least the early stages of development.[8]

Fecundity and Egg Size

Fecundity (number of mature eggs per spawning female) is an important life history characteristic. It is an essential element in calculating freshwater survival rates and is used in hatchery operations and in documenting the existence of subpopulations.

Mean fecundity of Karluk sockeye salmon females has been estimated for about 100 years. One of the earliest records was in 1900 when Moser (1902) said that the average fecundity of Karluk hatchery females was 3,000. With reference to a collection made between 5 August and 5 September 1903, Chamberlain (1907:101) stated: "The sockeye carries between 2,500 and 4,000 eggs, an average, perhaps of 3,500." The maximum range of average fecundity for the Karluk system that we found was from 2,145 at Cottonwood Creek to 3,792 at O'Malley River, both counts being obtained in 1965 (Gard et al., 1987). By themselves, the counts mentioned above are of limited value because fecundity varies with size and ocean age of females, with season and year, and with location.

The number of eggs contained in any female is closely related to its length. Therefore, a mathematical expression relating these variables is necessary when fish of different lengths are compared. Smith (1947) and Vladykov (1956) reported that the relationship is curvilinear in salmonids that mature over a wide range of lengths, but since sockeye salmon mature over a narrow size range, a linear equation adequately describes the relationship (Forester and Pritchard, 1941; Rounsefell, 1957; Gard et al., 1987). Therefore, we use linear regression techniques in this report.

That fecundity is related to size of sockeye salmon was reported by Gilbert and Rich (1927): "It is apparent

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

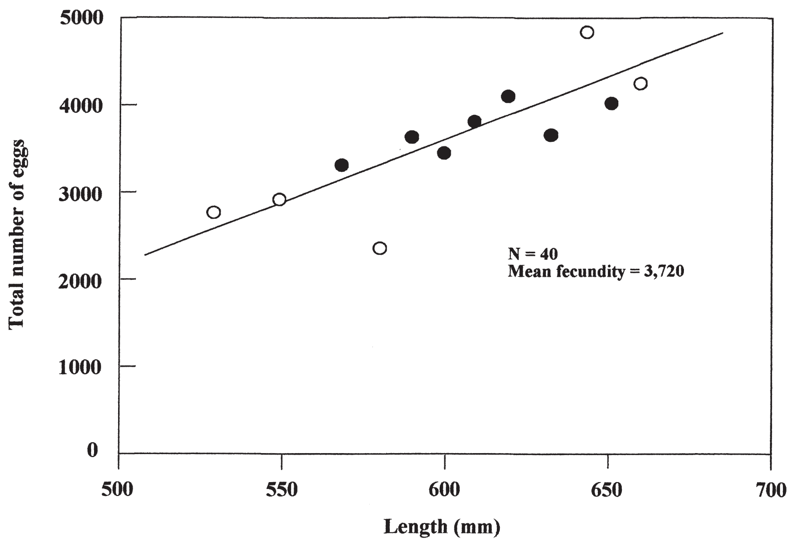


Figure 4-6. Number of eggs in Karluk River sockeye salmon taken on 15 September 1926. Solid circles are mean values for several individuals; open circles are data for single individuals (from Gilbert and Rich, 1927).

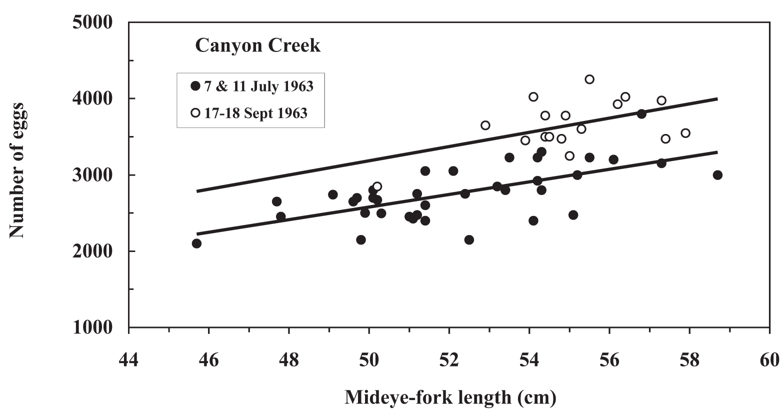


Figure 4-7. Relation of egg content to length of sockeye salmon sampled at Canyon Creek, a terminal tributary of Karluk Lake, July and September 1963 (from Gard and Drucker, 1965).

that the larger females have the greater number of eggs, the relationship being such that a difference of 1 centimeter in the length of the fish is accompanied, on the average, by a difference of 150 in the total number of eggs." Included in their report is the first graph known to us of the regression of total number of eggs on length for Karluk sockeye salmon. Data points and a regression line fitted by eye are shown (Fig. 4-6). Thus, Gilbert and Rich established the format which was followed by subsequent studies of Karluk sockeye salmon fecundity. For example, the regressions of fecundity on length for the 1963 spring and fall samples from Canyon Creek clearly show the dependence of fecundity on length (Fig. 4-7).

To the extent that fecundity is related to size and size is related to ocean age (demonstrated earlier in this chapter), fecundity is also related to ocean age. For example, 2-ocean females are longer and have more eggs than 1-ocean females and 3-ocean females are longer and have more eggs than 2-ocean females (Table 4-7). However, if fecundities of Karluk fish of the same length are compared, younger 2-ocean fish have more eggs than older 3-ocean fish (Rounsefell, 1957:458). He attributed this to the fact that the younger fish are faster growing than the older fish.

Fecundity also varies with season. Between 1963 and 1965 and in 1968, each fall sample of females from the Karluk River weir had a higher mean fecundity and length than each respective spring sample (Table 4-8). Similar differences were evident between spring and

Table 4-7
Reproductive potential of the 1958 escapement at Karluk Lake by age group (Hartman and Conkle, 1960).

Age group	Number of females[1]	Mean mideye-fork length (cm)	Mean fecundity	Potential egg deposition
4_3	814	43.5	1674	1,363,000
5_4	2,471	43.8	1717	4,243,000
5_3	60,872	51.4	2810	171,050,000
6_4	53,601	51.3	2796	149,868,000
6_3	8,695	54.3	3227	28,059,000
7_4	2,186	53.8	3155	6,897,000
Total				361,480,000

[1]Based on a sample of 2108 sockeye salmon from the 1958 experiment.

Table 4-8
Mean mideye-fork length, fecundity, and regression data for sockeye salmon from the Karluk River weir and Grassy Point Creek, a lateral tributary of Karluk Lake (1962, 1963, and 1965 data from Gard et al. (1987), 1964 data from Gard and Drucker (1966a), 1966 data from Drucker and Gard (1967), 1967 data from Drucker (1968), and 1968 data from Drucker (1970)).

Sample site and year	Run	Number of females	Mean mideye-fork length (cm)	Mean fecundity	Intercept (a)	Slope (b)	F[1]
Karluk River Weir							
1963	Spring	44	52.4	2834	−5,791	164.5	
1963	Fall	58	54.3	3435	−7,375	199.1	
1964	Spring	49	52.3	2756	−1,563	82.5	
1964	Fall	70	53.7	3526	−2,399	110.4	
1965	Spring	14	51.5	2811	−6,337	177.5	
1965	Fall	144	54.5	3618	−10,860	265.7	
1968	Spring	23	51.5	2880	−848	72.3	
1968	Fall	48	53.9	3313	−3,530	126.9	
1963–65, 68	Spring						1.52[2]
1963–65, 68	Fall						3.23[3]
Grassy Point Creek							
1962	Spring	30	50.5	2197	−3,879	120.3	
1963	Spring	31	49.1	2225	−4,390	134.7	
1964	Spring	30	48.8	2268	−3,234	113.4	
1965	Spring	30	48.2	2264	−4,633	143.1	
1966	Spring	30	49.3	2332	−2,996	108.1	
1967	Spring	30	50.7	2291	−3,982	123.8	
1968	Spring	30	50.4	2617	−5,001	151.2	
1962–68	Spring						3.94[3]

[1] F statistic from analysis of covariance, which tests the hypothesis that a single line fits all data.
[2] = not significant.
[3] = significant at $P < 0.01$.

fall samples from the spawning grounds (Fig. 4-7), and these differences were used to document the existence of subpopulations (Gard et al., 1987).

Year to year changes in fecundity occur. Fecundity of fall-run samples from the Karluk River weir from 1963–65 and 1968 and of samples from Grassy Point Creek from 1962–68 varied significantly among years (F; $P < 0.01$) (Table 4-8). Also, long-term increases in fecundity of similar-sized sockeye salmon from the Karluk River weir occurred between 1940 and 1965 (Fig. 4-8). In contrast to increase in fecundity, average size of females probably decreased between 1940 and 1965 because, as we have shown earlier, it decreased between the 1916–26 and 1956–68 periods (Fig. 4-4). The reasons for these seemingly contradictory trends are not clear. However, Svärdson (1949) stated that increase in fecundity may be an indication of overfishing and decrease in size is a common response to the exploitation of any animal because the largest individuals are usually the preferred targets.

Egg size within spawning populations in the Karluk River system increases with length of females. The first reference to egg size was by Fassett in 1910 who stated: "The red-salmon eggs at Karluk are reported to be very variable in size, and a big difference is said to be noted between those of the early, or "spring," run and those of the later, or "fall," run. The fall fish are themselves larger,

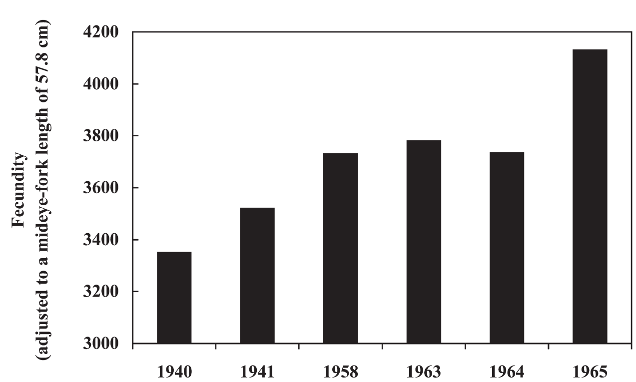


Figure 4-8. Karluk River sockeye salmon fecundity, 1940–65. All data were obtained at a weir in the Karluk River for the spring and fall runs combined. The 1940 and 1941 data are derived from Rounsefell (1957), the 1958 data are from Hartman and Conkle (1960), and the 1963–65 data are from Gard and Drucker (unpubl.).

Table 4-9
Average size of eggs in the largest and smallest sockeye salmon females in spawning ground samples from Karluk Lake, 1965 (Gard, unpubl. data).

					Average volume of eggs (cm^3)	
Spawning ground	Run	Mideye-fork length (mm)	Number of eggs	Total volume of eggs (cm^3)	Largest females	Smallest females
Grassy Point Creek	Spring	559	3214	360	.1120	
		413	1414	130		.0919
Meadow Creek	Spring	557	2682	370	.1380	
		461	1905	190		.0997
Cottonwood Creek	Spring	542	2833	350	.1235	
		419	1586	100		.0632
Canyon Creek	Spring	567	3517	390	.1109	
		463	2697	190		.0704
Upper Thumb River	Spring	583	3653	460	.1259	
		482	2425	260		.1072
O'Malley River	Fall	607	4826	500	.1036	
		488	3226	300		.0930
Lower Thumb River	Fall	571	5168	520	.1006	
		493	2363	260		.1100
Thumb Beach	Fall	587	3809	490	.1286	
		477	2764	305		.1103

and have larger eggs, the eggs are more regular in size, and are in greater number."[9] Actual sizes of eggs in the largest and smallest females from several spawning ground samples obtained in 1965 were determined.[10] With the exception of the sample from Lower Thumb River, the largest female in each sample had larger eggs than the smallest female in each sample (Table 4-9). Mathisen (1962) and Bilton (1971) respectively found increased egg size or weight in larger sockeye salmon from the Bristol Bay and Skeena River system streams.

To summarize fecundity relationships for the Karluk River system, mean fecundity varies widely among years and spawning areas with a maximum range of 2,145 to 3,792. Also, fecundity (and egg size) increases with length of fish and between the spring and fall runs. When fish of the same length are compared, younger ocean-age fish are more fecund than older ocean-age fish and there has been a long-term increase in fecundity since 1940.

Egg Deposition

Two expressions of egg deposition are commonly used. One is potential egg deposition (PED) which is the total number of eggs carried into the river system or a segment thereof in the bodies of the females. The second term is actual egg deposition (AED) which is the number of eggs actually deposited in the spawning gravel. To calculate the PED of a given area one must have the number of spawning females, the length frequency distribution of the females, and the equation expressing the regression of number of eggs on length. Usually this information is obtained at a weir. Fecundities for each length or length group are calculated from the regression equation and are multiplied by the numbers of fish in each length group. The sum of these products is the PED.

The method most used today to determine the AED is hydraulic egg pumping. After spawning is completed, many randomly-selected points are successively surrounded by a 0.1 m^2 wire screen and an air/water mixture is pumped into the enclosed gravel dislodging buried eggs which are washed by the current into an attached net. The eggs are enumerated, and an average egg density is calculated and multiplied by the total spawning area giving the AED.

Early investigators were aware of the tremendous number of eggs coming into the Karluk system each year and how few of these survived to the adult stage. Alln[11] calculated that egg to adult mortality was 99.77%. Some of that mortality had to be taking place among the developing eggs in the gravel and Barnaby made the following suggestion:

[9] Fassett, H. C. 1910. Report on the salmon hatchery operated by the Alaska Packers Association on Karluk Lagoon, Kadiak Island, Alaska. Unpubl. report. 25 p. Located at Alaska Historical Collections, Alaska State Library, Juneau, AK.
[10] Gard, Richard. Auke Bay, AK. Unpubl. data.

[11] Memo (6 April 1927) by M. Alln [Possibly Henry D. Aller or Alan C. Taft?] Located at NARA, Anchorage, AK.

[Concerning the Karluk River sockeye salmon, 1933] By visiting the spawning grounds and digging up nests of eggs laid down during the summer we can find out how these early eggs are developing, how soon they hatch out, when they emerge from the gravel and what natural enemies, if any, they have to contend with at this early stage of their life-history.[12]

There was little response to this suggestion until the 1950s when methods answering two questions were explored. The first question was how many eggs are buried in the gravel of a given spawning area? One method tested was the egg deposition survey which entailed digging holes with a shovel at sites located randomly and catching and counting the excavated eggs in a net. Another method involved the use of an oil drum with the bottom removed. The purpose of the drum was to delineate an area of gravel which was excavated and the eggs enumerated. A third method employed the use of a hydraulic pump and a circular wire screen which has already been described. The first two methods proved to be unsatisfactory, but the egg pumping system gave estimates of the number of eggs in the gravel (AED) as well as ancillary information.

The second question asked was what was the fate of predetermined batches of eggs? To answer that question, various types of egg cartridges, cages containing a known number of live eggs, were buried in the gravel of several tributaries and removed periodically for evaluation. Additionally, adult pens, bottomless cages placed on unseeded gravels and supplied with one pair of mature sockeye salmon each, were installed in four tributaries to determine egg retention, egg deposition, and total eggs recovered from individual females. Considerable data were obtained, but neither method was satisfactory and both were discontinued after 1958 in favor of hydraulic egg pumping of randomly selected points.

Some interesting results were obtained from the various methods used in 1958. Conkle et al. (1959) pumped eggs in several 0.9 m^2 sample plots located in two lateral streams (Grassy Point and Cottonwood creeks) and one terminal stream (Upper Thumb River). They found that eggs in the terminal stream were buried 23–46 cm deep while those in the lateral streams were only 5–18 cm deep, reflecting the deeper more uniform gravels in the terminal stream. Although their data were not statistically significant at $P = 0.05$ because of small sample sizes, they estimated that 470 live eggs per female were deposited in the terminal stream as compared to 312 and 370 live eggs per female in the lateral streams.

They suggested that the lower number of eggs deposited per female in the lateral streams was due to higher densities of spawners, shallower redds, and greater superimposition. The adult pen studies revealed that egg retention was variable ranging from 0 to 110 eggs per female, and that many more eggs were recovered from about half the pens than were estimated to be in the bodies of the enclosed females. Clearly, eggs were being washed into the pens from spawning activity upstream. In both adult pen and egg pumping studies, survival of eggs that got buried in the gravel was quite high, ranging from 68 to 99%.

The next hydraulic pumping at Karluk Lake was done at Grassy Point Creek in 1964 by Gard and Drucker (1966a) and was continued through 1968 (Drucker, 1970). There were two major differences in the procedure since the initial program in 1958: 1) the area of each sampling point was reduced from 0.9 m^2 to 0.1 m^2 and 2) the number of points sampled was increased substantially from 16 to 220 in 1964–66 and 100 in 1967–68 when a stratified sampling scheme was used (for details of methods used see Gard and Drucker, 1966a, b; Drucker, 1968). A weir was installed at the mouth of Grassy Point Creek each year to obtain number and length frequency of females and the regression of fecundity on length so that the potential egg deposition could be calculated. An example of the calculation of the PED in 1964 is shown in Table 4-10.

Table 4-10
Potential egg deposition of sockeye salmon spawning in Grassy Point Creek, 1964 (Gard and Drucker, 1966a).

Length group (cm)	Females in weir sample	Estimated eggs per female	Females spawning	Potential egg deposition
38	1	1108	46	50,968
39	—	—	—	—
40	—	—	—	—
41	1	1447	46	66,562
42	—	—	—	—
43	2	1672	92	153,824
44	2	1785	92	164,220
45	3	1898	138	261,924
46	11	2011	505	1,015,555
47	12	2124	551	1,169,773
48	19	2236	872	1,949,792
49	22	2349	1009	2,370,141
50	14	2462	643	1,583,066
51	3	2575	138	355,212
52	5	2687	230	618,010
53	4	2800	184	515,200
54	1	2913	46	133,998
Total	100	—	4592	10,408,245

[12] Barnaby, J. Thomas. 1933. Work contemplated during the fiscal year 1933. Karluk red salmon investigation, fiscal year, 1933. Unpubl. report. 2 p. Located at NARA, Anchorage, AK.

Table 4-11
Production and survival of sockeye salmon eggs and fry in Grassy Point Creek, 1961-68
(modified from Drucker, 1970, Table 10).

Brood year	Female spawners	PED[1]	AED[2]	PED to AED survival (%)	Average monthly survival rate (2.5 months—PED to AED) (%)	Fry produced	PED to fry survival (%)	AED to fry survival (%)	Average monthly survival rate (7.5 months—AED to fry emergence) (%)
1960	2593	5,699,414[3]	—	—	—	657,370	11.5	—	—
1961	4619	10,152,562[3]	—	—	—	311,773	3.1	—	—
1962	5767	11,938,235	—	—	—	173,472	1.4	—	—
1963	3393	7,475,400	—	—	—	241,925	3.2	—	—
1964	4592	10,408,245	1,487,838	14.3	45.9	410,591	3.9	27.6	84.2
1965	3024	7,096,314	1,053,680	14.8	46.5	451,284	6.4	42.8	89.3
1966	4630	10,525,111	1,299,905	12.4	43.3	344,144	3.3	26.5	83.8
1967	1395	3,133,939	729,643	23.3	55.8	138,646	4.4	19.0	80.1
1968	1895	4,739,059	143,028	3.0	24.6	38,809	0.8	27.1	84.0
						Average	= 4.2		

[1] PED = potential egg deposition.
[2] AED = actual egg deposition.
[3] Based on mean fecundity from 1962.

For the years 1964–68 the survival between PED and AED ranged from 3.0% to 23.3% (Table 4-11). These figures indicated a heavy loss during this period. One or more of the following factors could have caused this loss: retention of eggs by females, washing away of eggs before being buried, superimposition, predation by bears or other animals, and adverse environmental conditions in the gravel. The highest survival (23.3%) was in 1967 when the escapement was restricted to a low 1,395 females. Low spawner density would have resulted in less wave spawning and superimposition and a lower percentage of dead eggs to live eggs (only 6% in 1967 compared to 22–37% during the three previous years). Also, mean egg retention was only 28 eggs per female in 1967 compared to 97 eggs per female in 1968, the only other year for which comparable information was available. Since competition between spawners was minimal in 1967, the females undoubtedly selected the best spawning sites. During 1968, females were also restricted to a low number (1,859), but contrary to expectations, survival from PED to AED was only 3%, the lowest of the five years of study. Drucker (1970) attributed that low survival to extreme predation by subadult brown bears. These bears seemed to prefer to prey on Grassy Point Creek salmon, despite the occurrence of much higher concentrations of salmon in nearby streams.

Incubation

Although considerable effort was expended in the 1950s and 1960s to understand the developmental processes occurring during the incubation period for Karluk sockeye salmon, comparatively little was discovered. Reasonable estimates of actual egg deposition and fry abundance were obtained for some tributary streams, but what occurred between those two points in time was largely conjecture.

It is generally accepted that once the fertilized eggs are in the gravel they are comparatively safe from predators and environmental extremes. Hence survival from AED to fry emergence should be high. Between 1964 and 1968 at Grassy Point Creek, PED to AED survival ranged from 3 to 23% whereas AED to fry emergence[13] survival increased to 19–43% (Table 4-11). Viewed on a monthly basis, average monthly survival rates between PED and AED varied from 25 to 56% whereas comparable survival rates between AED and fry emergence varied from 80 to 89%. Clearly, survival was better after the eggs were in the gravel.

Temperature is usually considered to be the most important environmental factor that determines the rate of development of sockeye salmon embryos. Further, Brannon (1987) reported that temperature units (degree days) required for Fraser River sockeye embryos to develop to the yolk absorption stage varied greatly at different incubation temperatures with many more temperature units required in warmer than in colder waters. This adaptation would tend to synchronize the time of fry emergence from various spawning grounds within a river system so that most of the fry would enter the lake at a time when feeding and survival conditions were optimal.

Hartman et al. (1967) suggested that optimal feeding conditions occurred at Karluk Lake in spring when

[13] Details of fry population estimation are presented in the Fry Emergence and Migration section.

water temperatures rose and plankton bloomed, but Koenings and Burkett (1987b) reported that macroplankter production for the 1980–83 period was highest from September through November. Adults returning to two Karluk tributaries, Canyon and Meadow creeks, in 1962 spawned in two distinct runs and their fry emerged the following spring and summer in two well-separated waves (Gard and Drucker, 1965). There was no tendency for a synchronized emergence of Karluk fry due to a compensatory mechanism operating during the incubation period as was observed by Brannon (1987) for Fraser River fry. If the timing of macroplankton blooms reported by Koenings and Burkett (1987b) occurred consistently over past years, then the late-emerging fry from Canyon and Meadow creeks entered the lake at a propitious time for feeding, but the early-emerging fry did not. Still, the spring run of adults and their early-emerging offspring have existed for at least 100 years, so some selective force other than food supply must also have been operating.

Fry Emergence and Migration

In 1897 Moser (1899) gave a description of sockeye salmon alevin behavior prior to emergence: ". . . . The young with the sac could be seen by taking up a handful of gravel from the bottom. Upon being released they wriggle back in the gravel again." Though he may not have used these terms, what he described was negative phototaxis, positive geotaxis, and thigmotaxis which respectively mean a penchant for darkness, upright orientation on the substrate, and the touch of surrounding gravel. Moreover, if Moser had noted the orientation of the alevins in the gravel with respect to the current, he probably would have seen them facing upstream (positive rheotaxis) (Bams, 1969). These are behavioral responses that pre-emergent fry or alevins exhibit prior to emergence and which must change (or at least weaken) before emergence will occur.

Fry destined to migrate to Karluk Lake originated from many spawning areas. In 1963, fry descending tributary streams were counted at nets near the mouths of Grassy Point Creek (two nets) and Meadow and Canyon creeks (three nets each). The nets were installed in early April and fished until catches became very low. Each night the nets were fished from 1900 to 0700 hours. The nets were emptied every one or two hours, depending on conditions, until 0200 and again at 0700.

To estimate populations, a mark and recapture program was conducted. Samples of fry were periodically stained with Bismarck Brown, released 100 m upstream from the sample sites, and recaptured and enumerated in the nets (Gard and Drucker, 1963, 1965). In addition to the 1963 investigation, fry were also counted in a similar manner in 1961–62 and 1964–68 in Grassy Point Creek, 1962 in Meadow Creek, and 1964 in Canyon Creek. In 1964 fork lengths of fry migrating from Grassy Point and Canyon creeks were also measured.

Timing and direction of sockeye salmon fry migrating to Karluk Lake varied with the situation. Most fry in the lake tributaries migrated downstream at night (Gard and Drucker, 1963; Hartman et al., 1967). By contrast, most fry emerging from the upper Karluk River migrated upstream during the day in large schools near the stream banks. Some may have migrated directly to sea and others may have remained in the river as far downstream as Barnaby Ridge before heading upstream (Raleigh, 1967; Gard et al., 1987).[14] Further, Walker reported that the upstream migrating fry moved in two well-separated waves, the first occurring in May to the early part of June and the second from the latter part of July to the end of August.[15] The diel timing of emergence of Karluk fry is not known, but we assume it was mainly at night because Heard (1964) reported that most sockeye fry in the Brooks River, Alaska, emerged at night and few fry were seen in tributaries of Karluk Lake during the day.

Seasonal timing of fry migration varied among spawning grounds and, as reported earlier, appeared to be related to the timing of spawning of the parents. In 1963, fry migrated from Grassy Point Creek in one wave from early April to late June whereas fry migrated from Canyon and Meadow creeks in two distinct waves between early April and late July (Fig. 4-9). In 1962, the parents of the Grassy Point Creek fry spawned in one wave between July and late August, while the parents of the Canyon and Meadow Creek fry spawned in two waves between early July and October. Apparently the two waves of fry in Canyon and Meadow creeks were derived independently

[14] 1) Bevan, Donald E. 1951. Karluk Lake stream surveys, 1948–1951. FRI, University of Washington, Seattle. Unpubl. report. 45 p.
2) Walker, Charles E. 1954. Karluk young fish study, 1950–1954. FRI, University of Washington, Seattle. Unpubl. report. Both located at FRI Archives, University of Washington, Seattle, WA.

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

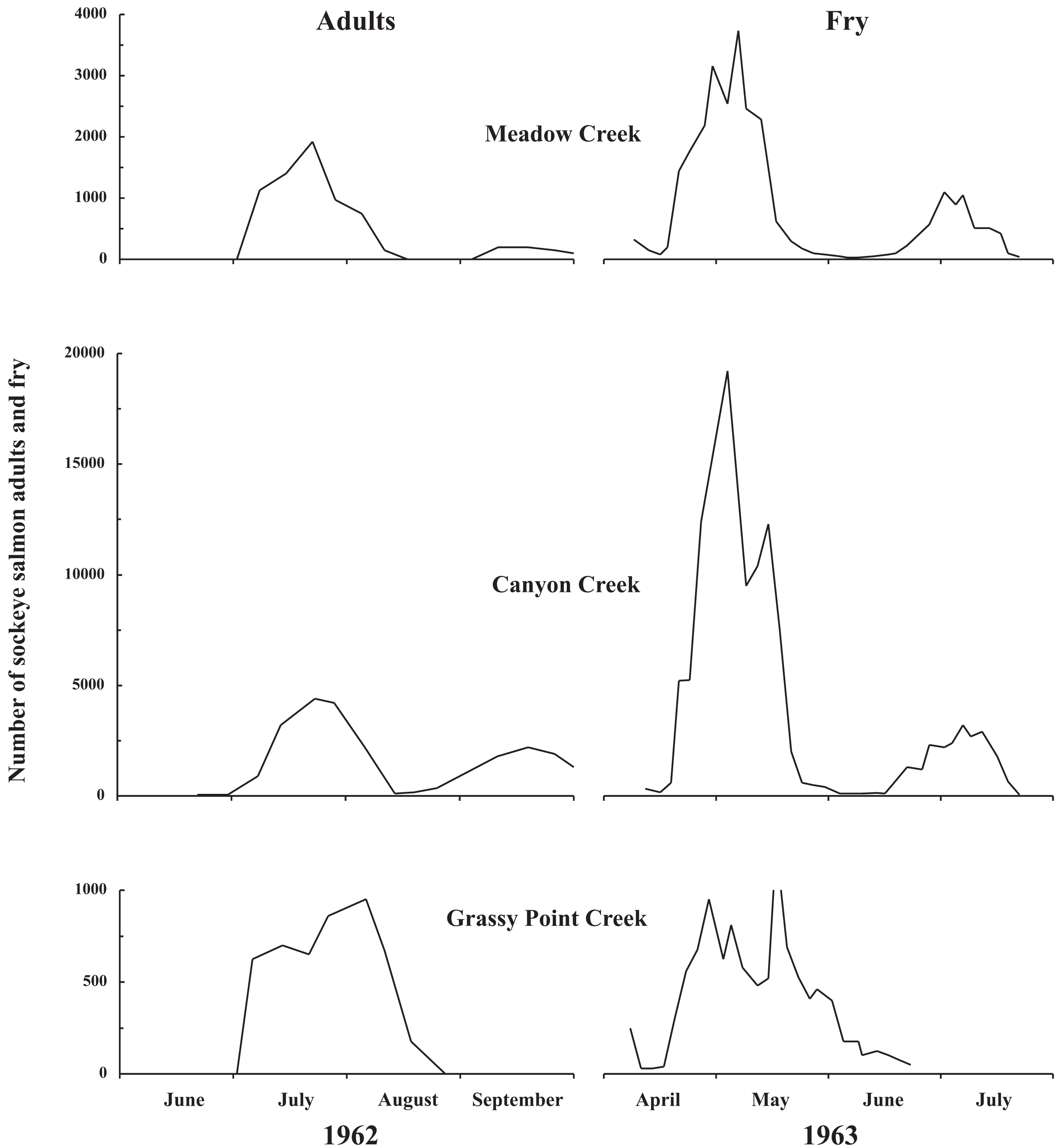


Figure 4-9. Relation between time of sockeye salmon parent spawning in 1962 and time of fry migration in 1963 in three tributaries of Karluk Lake. Fry catches shown are total numbers caught nightly (adapted from Gard and Drucker, 1965, Fig. 20).

from the two waves of spawners. Differences in abundance of parents and offspring in the two waves and differences of about 60 days between the peaks of abundance of the parent and offspring curves support this view (Fig. 4-9). It is not known if the parents of the two groups of fry hatched in the upper Karluk River also spawned in two waves.

In general, the timing and pattern of fry migration have been consistent from year to year. The best example of this is for Grassy Point Creek where beginning and ending dates for the migration varied only a few days during eight years of study (1961–68). Another seasonal phenomenon occurring each year was that as the season progressed and the period of darkness decreased, the daily migration period shortened and shifted to later in the evening (Drucker, 1970).

It was likely that most fry in the lateral streams emerged and migrated to the lake during the same night because these streams were relatively short and most stained fry released 100 m upstream reappeared at the nets within four hours. Any fry that did not reach the lake during the night they emerged probably behaved similarly to fry in Hidden Creek, a tributary to Brooks Lake. During the day, those fry remained in protected areas near stream banks in schools, became positively rheotactic, and proceeded toward the lake the following night singly or in small groups while facing downstream (Hartman et al., 1962).

Several fry migrations occurred into or within Karluk Lake. The early wave of fry from the tributary streams entered the lake in April and May, immediately formed schools in littoral areas, and became positively phototactic and rheotactic (Hartman et al., 1967). Rheotactic behavior may have been the mechanism that ensured the fry remained in the lake during the rearing period (Hartman et al., 1962). This early group of fry was soon joined by the first wave of fry from the trunk river in May and early June[16] and by fry hatched above Thumb and O'Malley lakes (Burgner et al., 1969). Apparently, in late July and August most of this assemblage of young-of-the-year fish moved offshore to limnetic areas, as did progeny from beach spawners, as well as late-emerging fry from tributary streams and the Karluk River.[17] Drucker also reported a gradual vertical migration of all ages of juvenile sockeye from surface waters (0–3 m) to subsurface water (3–6 m) between July and September and associated this shift with cooling of surface waters in the fall.[18] Kyle (1990) found similar horizontal and vertical shifts in juvenile populations in Karluk Lake between July and September 1986. Although Pella (1968) found a distinct diel vertical migration of juvenile sockeye in July in Lake Aleknagik, Alaska, this has not been confirmed at Karluk Lake. Finally, Drucker reported that many young-of-the-year migrated from Thumb and O'Malley basins of Karluk Lake to the Weir basin from which the trunk river flows. Navigation by young-of-the-year sockeye within the lake was likely enabled by the utilization of celestial and magnetic cues (Quinn, 1980, 1982a; Quinn and Brannon, 1982).

Some feeding by migrating fry in the spawning streams occurred before they reached the lake. This was especially evident in upper Karluk River where average length of the first wave of fry was 28 mm and that of the second wave was 46 mm.[19] To increase 18 mm in length, the latter group of fry had to be feeding intensively. Chamberlain (1907:31) stated: "Small fingerlings taken in Karluk River May 22 [1903] were feeding on crustacea, insects, and insect larvae." Also, Walker reported for young-of-the-year in upper Karluk River: "Coho fingerling, and to a less extent, red fingerling have been found to contain small reds."[20] Cannibalism, as we will discuss later, may occur among Karluk sockeye.

Feeding by fry has also been documented in tributary streams. Rabe made the following observations at lower Canyon Creek or the O'Malley River in 1956: "Found young of the year (?) stickleback in mouth of dead red migrant in trap."[21] Further, Chamberlain (1907) stated that 11 of 87 fry caught in Spring Creek on 14 July 1903 were feeding and contained insects, larvae, and crustaceans. These fry averaged 41 mm in length and must have been feeding for some time because newly-emerged fry are much shorter. Chamberlain reported catching few fry in other spawning creeks on 16 July and 27 July. There may be a tendency for fry to remain in Spring Creek to feed because it has a series of ponds in which planktonic animals may be in greater abundance than they are in streams lacking ponds.

During their migration to Karluk Lake, sockeye fry, in turn, became the prey of other species. Barnaby counted about one dozen fry in a Dolly Varden stomach from a tributary at the south end of the lake.[22] Further, Dolly Varden 9 to 18 cm long from Thumb, Karluk, and O'Malley rivers contained 6 to 30 sockeye fry.[23] Walker also examined coho fingerlings from the Karluk River that had eaten sockeye fry and concluded that "In summary, it would seem that the [sockeye] fry at the time of

[16] See footnote 15.

[17] 1) 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.
2) 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.

[18] See footnote 17.

[19] See footnote 15.

[20] See footnote 15.

[21] Rabe, Fred. 1956 notebook (15 August). Found at NARA, Anchorage, AK.

[22] Barnaby, J. Thomas. 1934 notebook. Found at NARA, Anchorage, AK.

[23] See footnote 15.

emergence and shortly thereafter do undergo considerable predation . . .” Some of the references to Dolly Varden may have included Arctic charr because earlier authors sometimes referred to all charr as Dollies. In a brief food habit study of 18 American mergansers, *Mergus merganser*, and red-breasted mergansers, *Mergus serrator*, Gard found that six individuals from the O'Malley and Karluk rivers contained salmonid fry, some being identified as sockeye salmon.[24] Burgner et al. (1969) mentioned three other species present at Karluk Lake which were known to prey on migrating sockeye salmon fry in other river systems. These were rainbow trout, Arctic terns, *Sterna paradisaea*, and Bonaparte's gulls, *Larus philadelphia*. These species probably ate some migrating sockeye fry at Karluk Lake, but this has never been documented. In any event, migrating sockeye fry at Karluk Lake experienced substantial predation by various species.

Egg to Fry Survival

Survival between potential egg deposition (PED) and fry emergence varied between spawning areas, seasons, and years. For the brood year 1962, PED to fry survival rates of the spring runs to Grassy Point and Meadow creeks (lateral streams) were 1.4% and 2.5%, respectively, whereas survival of the spring run to Canyon Creek (terminal stream) was 8.5% (Tables 4-11, 4-12). Similarly, for the brood year of 1963, the PED to fry survival rates of the spring runs to Grassy Point and Canyon creeks were 3.2% and 11.9%, respectively (Tables 4-11, 4-12). Therefore, survival in terminal streams seems markedly better than it is in lateral streams. As pointed out earlier, terminal streams are slower and deeper than lateral streams and possess a thicker, more uniform gravel bed, characteristics that should provide a superior environment for egg survival. Also, predation by bears on unspawned female sockeye should be less in terminal streams because the deeper water provided better opportunities for escape. Egg to fry survival for the fall run to Meadow Creek for the brood year 1962 was 5.9% while survival for the spring run was only 2.5% (Table 4-12). Better survival for the fall run was expected because bear predation on unspawned adults and superimposition of eggs by subsequent spawners decreased as the season progressed.

In a summary of 37 observations from five sockeye streams in British Columbia and one in Kamchatka,

Table 4-12
Calculated survival rates of sockeye salmon fry in Meadow and Canyon creeks (Gard and Drucker, 1965, 1966a).

Creek (run)	Brood year	Females	PED[1]	Fry	PED to fry survival (%)
Meadow (spring)	1962	6,259	15,993,648	402,971	2.5
Meadow (fall)	1962	528	1,766,104[2]	104,993	5.9
Canyon (spring)	1962	9,456	26,152,260	2,213,200	8.5
Canyon (spring)	1963	11,740	30,974,260	3,676,244	11.9

[1] PED = potential egg deposition.
[2] Estimated figure (see Gard and Drucker, 1965:37).

Foerster (1968:140) calculated an average PED to fry survival of 10.6% (Range 1.8–19.3%). An average of the 13 survival rates for Karluk streams presented in Tables 4-11 and 4-12 was 5.5% (Range 1.4–11.9%). These data are not strictly comparable, but it appears that sockeye egg to fry survival at Karluk is less than that in many other streams. However, this difference could have been the result of differences in methods used or the timing and location of sampling. We have already pointed out the considerable temporal and spatial diversity of egg-to-fry survival rates at Karluk Lake. If the Karluk survival rates had been obtained for the progeny of fall-run sockeye to terminal streams only, the average rate might have been as high as (or higher than) that for the British Columbia and Kamchatka streams.

Life in the Lake

Although there is general agreement that some limiting factor in freshwater is preventing Karluk sockeye from recovering from their present low level, just what that factor is and how it is operating is open to debate. However, a growing cadre of investigators now believe that something relating to the production or availability of food for sockeye juveniles in the lacustrine environment is responsible.

Food and Feeding

Because sockeye salmon are anatomically equipped to eat zooplankton and because Willis Rich recognized the linkage between decomposing adult carcasses and phytoplankton/zooplankton production in Karluk Lake in 1926, subsequent investigators of juvenile foods have concentrated on availability of zooplankton. In

[24] Gard, Richard. 1965. Merganser Food Habits Study, 1965. Unpubl. data. 1 p. Located at NARA, Anchorage, AK.

Table 4-13
Numerical analysis of the net plankton catches for Karluk, Thumb, and O'Malley lakes, 1927 (adapted from Juday et al., 1932, Table 12).

Location and date	Depth (m)	Average number of organisms per liter of water							
		Cladocera	Copepoda	Nauplii	Rotifera	Protozoa	Blue-green algae	Green algae	Diatoms
Karluk Lake Station 1									
19 July	0–125	1.0	8.7	30.5	244.0	11	273	2,928	4,457
31 July	0–125	1.3	1.9	32.3	257.0	1,279	445	28,561	4,802
13 Aug.	0–125	0.7	4.0	47.0	214.0	543	241	1,547	553
24 Aug.	0–125	2.5	12.6	53.4	106.0	729	65	3,679	542
13 Sept.	0–125	2.1	15.3	37.7	29.3	43	9	3,681	226
Thumb Lake									
21 July	0–10	29.5	29.1	24.1	370.0			3,896	1,375,370
3 Aug.	0–10	160.0	33.8	4.6	405.0		31,172		985,825
12 Aug.	0–10	4.2	13.4	0.9	58.2	355			889,000
26 Aug.	0–10	17.8	5.0	0.9	133.0	195			55,134
16 Sept.	0–10	5.0	0.9	1.4	456.0	178		355	309,906
O'Malley Lake									
23 July	0–10	1.2	11.8	6.9	386.0		129		36,040
10 Aug.	0–10	5.0	12.9	5.5	167.0			3,896	502,650
24 Aug.	0–10	2.7	1.8	8.3	147.0	782	7,820	1,564	133,466
14 Sept.	0–10	6.0	1.8	1.0	180.0		1,760	782	145,445

the first such study, Juday et al. (1932) analyzed plankton hauls taken from three locations in Karluk Lake and one location in Thumb and O'Malley lakes. Sampling was done at various depths between mid July and mid September during 1927–30. Results for Karluk station 1 (mid-lake) and for Thumb and O'Malley lakes for 1927 are presented (Table 4-13). The Cladocera were represented in Karluk and Thumb lakes by *Bosmina* and *Daphnia* and in O'Malley Lake by *Bosmina* and *Chydorus.* In all three lakes Copepoda were represented by *Diaptomus* and *Cyclops* and rotifers were the dominant multicellular zooplankter group in all the samples. Protozoans, principally *Epistylis* and *Vorticella,* were found in abundance in Karluk Lake, but in lesser numbers in Thumb and O'Malley lakes. Green algae and diatoms were the dominant elements of the phytoplankton with the blue-green algae playing a minor role. Phytoplankters were most abundant above 20 m where photosynthetic activity was greatest. Although there was considerable variability, most multicellular zooplankter groups occurred in relatively large numbers in July or early August, declined in mid August and increased in late August or September (Table 4-13). No sampling was done after 16 September.

Following Juday et al. (1932) came a remarkable study by Hilliard (1959a) which did not initially receive the attention it deserved. Hilliard conducted a phytoplankton study at Karluk Lake between 20 June 1956 and 22 November 1957 and found that diatoms were the dominant phytoplankters throughout the year, reaching a maximum of 70,975 individuals per liter on 15 October 1956. He also noted, almost as an aside, that one zooplankter, *Cyclops scutifer* (= *C. columbianus*), averaged 0.6 organisms per liter in the summer, but increased to 11 organisms per liter in the fall and early winter, an 18 fold increase! Even more astonishing was that on 8 December 1956 (two days before lake freeze-up), the maximum number of 101 individuals per liter was counted. Juday et al. (1932) reported a 4-year copepod maximum of 37.6 on 7 September 1929. Hence, Hilliard discovered the second annual plankton bloom at Karluk Lake which was one of the major revelations in Karluk research history. As Juday et al. (1932) sampled plankton between 9 July and 13 September only, it is no surprise that Hilliard (1959a:142) concluded: "It is apparent from the available data that sampling over such a limited period (2 months in summer) can give misleading concepts of plankton populations." If Juday et al. (1932) had noted the hints of a second plankton bloom apparent in their data (Table 4-13), they might well have continued sampling into October thus discovering this later bloom at that time.

It was 28 years before the importance of Hilliard's 1959 discovery of a second plankton bloom at Karluk Lake in fall and winter was recognized and corroborated with further sampling (Koenings and Burkett, 1987a, b). These two investigations found that in terms of zooplankton abundance the fall-winter plankton bloom was much larger than the spring plankton bloom (Fig. 4-10). The implications of this discovery of two plankton blooms imposed on early and late fry emergences were enormous and raised many questions such

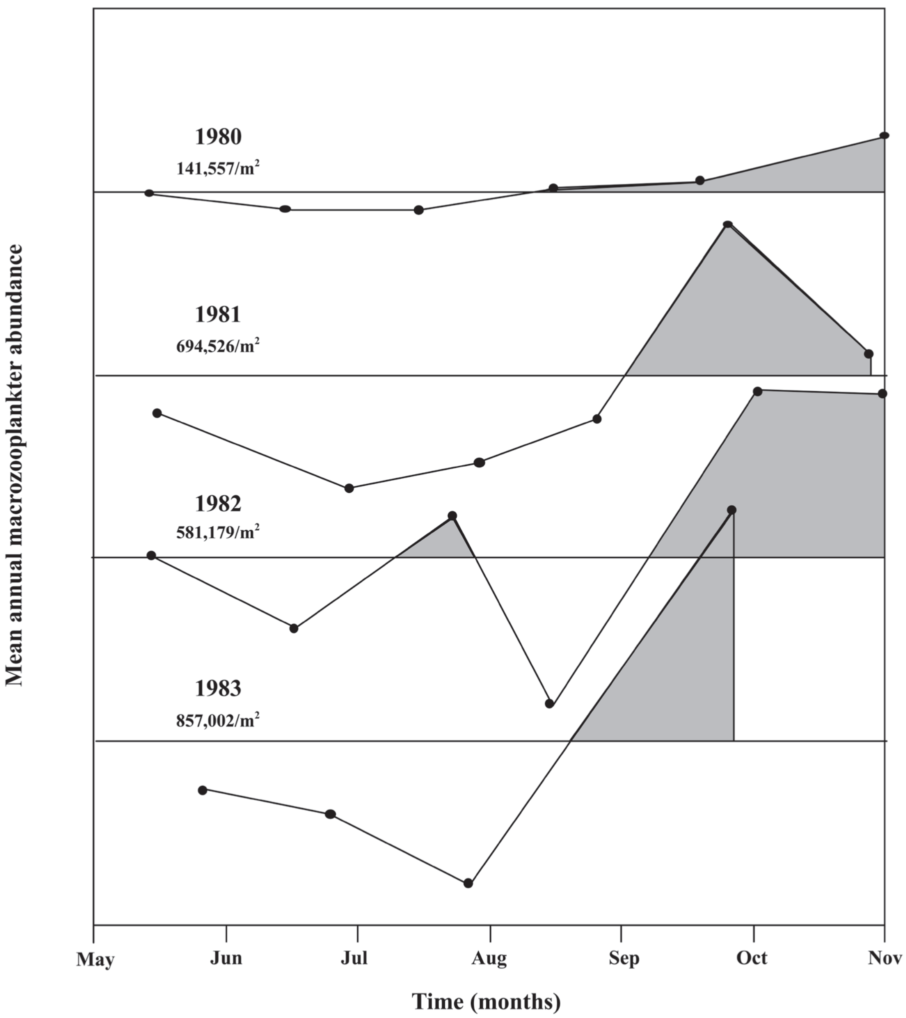


Figure 4-10. The seasonal (May–October) timing of macrozooplankter production at three stations in Karluk Lake over the 1980–83 period (from Koenings and Burkett, 1987b). Solid horizontal lines indicate mean density over the season; individual points within a year show the actual density estimates.

as: Were the two plankton blooms in synchrony with the two fry emergences? Was the larger late plankton bloom the reason why the progeny of fall-run adults survived better than the progeny of spring-run adults? If the plankton blooms and fry emergences were out of synchrony, did this explain why the Karluk runs did not respond to attempts to increase their numbers? The answers to some of these questions were dealt with elsewhere, but the first question to be answered here is: What were juvenile sockeye salmon eating in the lake?

Feeding in the Littoral Zone

We have located few references for juvenile feeding in the littoral zone of Karluk Lake and nearby Bare Lake. On 18 July 1935 Barnaby made beach seine hauls at Camp Island and found "Reds feeding mainly on cladocerans, some copepods, one had flies in its stomach".[25] Further, while discussing stickleback behavior, probably from the littoral areas of Karluk and Bare lakes, Greenbank and Nelson (1959:555) stated: "Juvenile red salmon have been found with sticklebacks in their mouths or stomachs . . ." In August at Bare Lake, Robert F. Raleigh found that on a volumetric basis a sample of juvenile sockeye stomachs contained 55% insects (mostly Diptera), 35% debris, and 10% fish remains (sticklebacks and salmonids).[26] Finally, Nelson (1959) found that the diet of juveniles taken in Bare Lake between May and September 1955 was mainly chironomids. Thus, on the basis of these limited observations, juvenile sockeye salmon in littoral areas of Karluk Lake appeared to eat a combination of zooplankton, insects, and sticklebacks in summer. Chapter 7 provides further details.

[25] Barnaby, J. Thomas. 1935 notebook. Located at NARA, Anchorage, AK.

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

Table 4-14
Comparison of percent composition of the major macrozooplankton taxa found in sockeye fry gut contents (Ri) and vertical net tows (Pi) expressed as an electivity index (E). The index has a range of −1 to +1. Positive values indicate active selection, zero indicates random selection, and negative values indicate avoidance or inaccessibility. (Data provided by ADFG Commercial Fish Division, Central Region, Limnology.)

	Bosmina	Ovigerous *Bosmina*	*Daphnia*	Ovigerous *Daphnia*	*Cyclops*	Ovigerous *Cyclops*	*Diaptomus*	Ovigerous *Diaptomus*
Ri	40.81	8.36	3.88	0.02	45.01	0.44	1.46	0.01
Pi	14.64	2.54	4.89	1.06	72.2	0.22	4.45	0
E	0.47	0.53	−0.12	−0.96	−0.23	0.33	−0.51	1

Feeding in the Limnetic Zone

The importance of knowing what juvenile Karluk sockeye eat in the limnetic zone was not recognized until 25 stomachs from the Thumb, O'Malley, and main basins were collected on 21 September 1994 and preserved for later analysis.[27] Because no plankton samples were obtained on that date, mean densities of macrozooplankton seined from O'Malley and main basins on 30 August and 11 October were used for comparison with the contents of the stomachs. The plankton was sampled in the water column with a vertical net tow down to 50 m or the bottom, whichever came first. Percentage composition of the major macrozooplankters in the stomachs and the environment (net tows) were determined and combined as Ivlev's electivity indices. An electivity index is calculated from the equation $E = (r_i - p_i)/(r_i + p_i)$, where r_i = the percentage composition of the prey item in the stomachs and p_i = the percentage composition of the same prey item in the environment. Positive values indicate active selection by the predation, zero indicates random selection, and negative values indicate avoidance or inaccessibility.

Results of the study are summarized in Table 4-14. The most frequent prey species in the stomachs in descending order of importance were *Cyclops, Bosmina,* ovigerous *Bosmina,* and *Daphnia,* whereas the most frequent prey species in the net tows were *Cyclops, Bosmina, Daphnia,* and *Diaptomus*. However, the electivity indices show that ovigerous *Bosmina* were highly selected (0.53) followed by *Bosmina* (0.47), while ovigerous *Daphnia* (−0.96) and *Diaptomus* (−0.51) were avoided or inaccessible. A comparison of weighted mean body size of all prey items from the stomachs and the net tows showed that juveniles, on the average, selected larger prey than existed in the environment. The juveniles ranged in length from 48 to 113 mm. Although four of the juveniles measured over 100 mm in length and were probably capable of consuming smaller fish, no fish were found in the guts.

Cannibalism

Juvenile sockeye are usually plankton eaters, but occasionally they eat fish. Because there are up to five different ages of young sockeye in Karluk Lake at any one time, there has been considerable speculation that older (and larger) individuals may prey on younger (and smaller) individuals. One of the first references to cannibalism at Karluk was by Henry C. Fassett, who inspected the hatchery in 1900, and was quoted by Moser (1902) as stating: "Owing to the cannibalistic tendencies of the larger fry, the young with the egg sac still attached are kept by themselves." Also, Walker, with reference to the Karluk River, reported: ". . . red fingerling have been found to contain small reds."[28] One of the most compelling bits of information suggesting cannibalism in young Karluk sockeye was the tracing through the food chain of unique marine nitrogen isotopes in the bodies of decomposing adult sockeye (Kline, 1992). Specifically, the proportion of marine nitrogen isotopes present in pre-smolts increased during the fall and winter (Kline, 1993). This change suggested a diet shift from zooplankton to cannibalism on smaller sockeye and possibly predation on sticklebacks as well. Associated with this presumed diet change was a marked increase in size of pre-smolt juveniles. Chapter 7 gives more details. Verification of this hypothesis is presently impossible because there has never been a fall and winter study of juvenile food habits. Such a study is needed if we are to understand the mechanism by which increased escapements would

[27] Data provided by ADFG Commercial Fisheries Division, Central Region, Limnology.

[28] See footnote 15.

Table 4-15
Frequency of occurrence of items in stickleback stomachs from littoral areas of Karluk Lake (adapted from Greenbank and Nelson, 1959, Table 9). Numbers in parentheses are ranges of numbers of organisms per stomach.

Food	Date: 4 June 1948	7 June 1948	13 June 1948	25 July 1948	7 July 1949	9 Aug. 1949	13 Sept. 1949	Total
Number of stomachs with food	11	23	50	15	68	25	25	217
Number of stomachs with:								
Chironomids	7 (4–14)	10	9		31	2	3	62
Other insects	1				4			5
Copepods *(Diaptomus, Cyclops)*	10 (11–20)	23	22	9 (1–71)	59 (1–276)	24	25	172
Cladocera *(Daphnia, Bosmina)*	3	20		13 (1–182)	31	23	25	115
Ostracods	3 (1)	2	2	5 (1–22)	9 (1–134)	1	1	23
Rotifers	2	13	24		1	1		41
Clams					2			2
Stickleback eggs		1		5 (1–38)	23 (5–58)	1		30

result in larger smolts, smolt outmigrations, and returns of adults.

Potential Competitor Species

Fish species with food habits overlapping those of juvenile sockeye salmon in Alaskan lakes include threespine and ninespine sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*), pond smelt, *Hypomesus olidus*, and pygmy whitefish, *Prosopium coulteri* (Burgner, 1991). Of these, only the threespine and ninespine sticklebacks are present in Karluk Lake and the ninespine stickleback is rare. This leaves the threespine stickleback as the only species that might be a competitor with juvenile sockeye salmon for food or space.

Many biologists have mentioned the possibility of competition for food between sticklebacks and juvenile sockeye salmon in Karluk Lake (Greenbank and Nelson, 1959; Blackett, 1973).[29] Unfortunately, food habits data for juvenile sockeye are scarce, but those which are available appear earlier in this chapter. Hence, stickleback food habits only will be covered here. Barnaby examined some stickleback stomachs captured at Camp Island on 18 July 1935 and reported that they contained stickleback eggs, copepods, and Cladocera.[30] In 1948 and 1949, Greenbank and Nelson (1959) examined 217 stickleback stomachs and found that copepods, Cladocera, and chironomids (larvae and pupae) were the most frequent groups present (Table 4-15). The most important genera of copepods were *Diaptomus* and *Cyclops* as were *Daphnia* and *Bosmina* of the Cladocera. No sockeye fry or eggs were found in the stickleback stomachs. A comparison of stickleback food habits shown in Table 4-15 with juvenile sockeye food habits (Table 4-14) indicates considerable commonality. Although overlapping of food habits does not prove competition exists, it is a prerequisite for that to occur.

To determine if juvenile sockeye salmon and sticklebacks competed for food, Richard Wilmot and associates conducted a study in Karluk, O'Malley, and Thumb lakes from 1985 to 1988.[31] In that investigation, a low-level dam was constructed across O'Malley River to prevent mature sticklebacks from migrating from Karluk

[29] 1) Morton, Mark. ca. 1942. No Title. Unpubl. report. 3 p. Located at NARA, Anchorage, AK.
2) McIntyre, John D. 1980. Further consideration of causes for decline of Karluk sockeye salmon. USFWS. National Fisheries Research Center, Seattle (18 September 1980). Unpubl. report. 29 p. Located at USFWS, National Fisheries Research Center, Seattle, WA.

[30] See footnote 25.

[31] 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, AK. Unpubl. report. 20 p. Copy from Jim Finn, USFWS, Anchorage, AK.

Lake to O'Malley Lake to spawn while allowing free passage of sockeye salmon. A dam was not constructed across Thumb River and therefore sticklebacks had free access to Thumb Lake which served as a control. Growth rates of sticklebacks and young-of-the-year sockeye in the two lakes were determined. Results were that density of sticklebacks in O'Malley Lake was reduced 50% by the weir, and growth of both young sticklebacks and sockeye salmon in O'Malley Lake increased in comparison to growth of these species in Thumb Lake. Wilmot et al. concluded that competition for food existed between sticklebacks and young sockeye salmon in the Karluk Lake system (Chapter 8 provides details).[32]

Predation on Sockeye Salmon in Freshwater

Adult sockeye are known to be the prey of brown bears, red foxes (*Vulpes fulva*), bald eagles, river otters (*Lontra canadensis*), and various species of gulls (*Larus*). The most important of these predators is the brown bear. The percentage of spawners killed by bears in streams with natural escapements ranged from 2% to 74% (average, 43%) in twelve studies (Table 10-2). However, the percentages of bear-killed fish that were unspawned ranged from less than 1% to 31% (average, 11%). Therefore, bear predation on sockeye salmon adults was confined mainly to spawned out fish and had little effect on the succeeding generation (see Chapter 10 for details).

Many animals are known to prey on sockeye salmon eggs during the spawning period at Karluk Lake. Perhaps the most important are the Dolly Varden and Arctic charr whose stomachs often contain sockeye eggs when the adults are spawning nearby. The only question is how many of the eggs would have survived if they had not been consumed by the charrs? Although Moser (1899) reported that charr took eggs as they were deposited, most observers believed that the vast majority of the eggs consumed had washed away before they were buried or were dislodged by late spawners and probably would not have survived (DeLacy, 1941; Foerster, 1968; Morton, 1982). Other animals known to prey on sockeye eggs are coastrange sculpins (Greenbank, 1966), coho salmon,[33] various species of gulls (Morton, 1942),[34] and mallard ducks, *Anas platyrhynchus*.[35] Many of the eggs ingested by birds are drifting eggs although glaucous-winged gulls, *Larus glauceacens*, may walk over nests to dislodge eggs (Moyle, 1966) or peck the bellies of mature female sockeye to stimulate extrusion of eggs (Willson and Halupka, 1995).[36]

During the incubation period, total mortality is high, averaging 71% for the 1964–68 period (Table 4-11). Mortality may have been caused by unfavorable environmental conditions, superimposition, or by intragravel predators such as leeches and oligochaete worms. Heavy infestations of leeches and oligochaetes as well as broken sockeye egg shells were found in egg cartridges buried in Cascade Creek during the 1952–53 incubation period.[37] No one has documented predation by leeches or oligochaetes on sockeye eggs or alevins and it is not known if the embryos were alive or dead when they were presumably eaten. Still, the evidence suggests that predation occurred. Earp and Schwab (1954) reported considerable predation by leeches, *Piscicola salmositica*, on pink salmon alevins in a Washington state salmon hatchery.

Newly emerged Karluk sockeye fry have generally been considered to be vulnerable to predation by several species of birds and fish, the most notable being Dolly Varden and Arctic charr. During the first 50 years of sockeye research a few scattered observations of predation on fry by the two charrs appeared in the literature, accompanied by a great deal of conjecture, until Allan C. DeLacy and William M. Morton examined over 5,000 charr stomachs mainly from Karluk Lake (Tables 9-2, 9-3). DeLacy (1941) and Morton (1982) demonstrated that the two charr preyed little on sockeye fry. For the next 40 years analysis of generally small numbers of charr stomachs from the lake and lake outlet indicated that the lake outlet and the upper Karluk River were likely areas to find significant charr predation on fry if, indeed, it existed. Accordingly, John D. McIntyre, Richard Wilmot, and others examined 1,279 mostly Dolly Varden stomachs collected in the spring between 1982 and 1986 and counted 10,032 sockeye fry (Table 9-3). There was intense predation by Dolly Varden on sockeye

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[32] See footnote 31.

[33] Smith, Seymour P. 1927 notebook (27 August). Located at NARA, Anchorage, AK.

[34] 1) Gilbert, Charles H. 1921 notebook. Original at Stanford University Libraries, Department of Special Collection and University Archives, Palo Alto, CA, and a typed summary of Gilbert's survey of Karluk Lake, 8–13 August 1921, at NARA, Anchorage, AK. 2) Morton, William M. 1941 notebook. Original notebook in personal papers of Robert S. Morton, Portland, OR. 3) Freeman, Arthur. 1948 notebook. Original notebook in personal papers of Arthur Freeman, Indianapolis, IN. 4) Gard, Richard. Personal observation.

[35] Gard, Richard. Personal observation.

[36] Armstrong, Robert H. Juneau, AK, Personal commun.

[37] Letter (3 August 1954) from [Phil Nelson] to Carl [Abegglen]. Located at NARA, Anchorage, AK.

fry for several weeks each spring in the upper Karluk River, but this has not been documented elsewhere in the Karluk Lake system or during other seasons. Other predators on sockeye fry were coho and sockeye fingerlings.[38] Also, Gard found that American mergansers and red-breasted mergansers from the upper Karluk and O'Malley rivers contained some sockeye fry.[39]

There is little evidence of predation on sockeye salmon juveniles during their residence in the limnetic waters of Karluk Lake. This may be because few of their most formidable predators, large Dolly Varden and Arctic charr, are present or because observation and sampling methods are more difficult in offshore waters. Examination of a few hundred stomachs of small Dolly Varden taken in the limnetic zone in May showed insects to be the predominant food and sockeye fingerlings to be present in only one stomach.[40] Diving predators, such as Bonaparte's gulls and Arctic terns, probably take some juveniles. Even if the predation intensity is light in the limnetic zone of Karluk Lake, total predation could be substantial because most Karluk juveniles spend 1–3 years in this zone.

Limited quantitative evidence of charr predation on sockeye salmon smolts exists, but there is considerable observational evidence. Morton (1982) examined four Dolly Varden stomachs from the lower Karluk River in 1939 and 1940 that contained 1–10 smolts and Shuman[41] examined one stomach from the lake outlet that contained six smolts (Table 9-3). Many biologists, including the senior author, have witnessed a mass of smolts "boiling" at the river surface immediately upstream from the outlet weir at night while large fish, assumed to be Dolly Varden, cruised below (Hartman et al., 1967).[42] It is likely that the Dolly Varden were feeding on the smolts and the presence of the weir created an unnatural condition that exacerbated the predation. Gard and Drucker (1963) observed no predation by Dolly Varden on sockeye smolts at the lake outlet or below the weir, although both species were present in these locations. However, in upper Karluk River in early June 1984 (nine years after the weir was moved far downstream), large salmonids were observed rushing through schools of smolts and apparently feeding on them.[43] This apparent predation was not verified and quantified by stomach analysis. It should be mentioned that heavy predation of Arctic charr on sockeye smolts has been documented where the Agulowak River enters Lake Aleknagik in the Wood River system (Rogers et al., 1972; Meacham and Clark, 1979). Some 13,000–14,000 charr were estimated to have eaten 3–4 million smolts in 1971. The solution was to confine the charr temporarily in pens during the smolt outmigration. The information presently available for the Karluk River system does not indicate that charr predation on smolts is of the magnitude of that present in the Wood River system. However, only a thorough study of predation by Dolly Varden on smolts in the outlet area and at the site of the present weir near the river mouth when both species are present will determine the role, if any, of a weir and the extent of the predation in the absence of a weir.

Although there is good evidence that young stickleback and young-of-the-year sockeye salmon compete for food and that the young of both species are preyed on significantly by charrs, it is questionable that control of charrs would result in an increased abundance of sockeye. Perhaps, as was suggested by Greenbank and Nelson (1959), charr control would result in an increased abundance of sticklebacks followed by greater competition between sockeye and sticklebacks and a lesser abundance of sockeye. In other words, sticklebacks may act as a buffer against depletion of sockeye by charr predation (see Chapter 9 for details).

Residence Time and Growth

Karluk smolts migrated to sea after spending 1–5 years in fresh water (Table 4-1). This corresponds to 0–4 freshwater growing seasons because the first 10 months were spent in the gravel as eggs or alevins. A 5-year range of residence time in fresh water was unique and may be the longest range known. Only a few fish (age groups 2_1, 3_1, 4_1, 5_1, as designated by the Gilbert-Rich system) migrated to sea after one year and had almost zero freshwater growth. A somewhat larger number (age groups 5_5, 6_5, 7_5, 8_5) went to sea after five years, but the vast majority migrated after three or four years (Table 4-1). Moser (1899) made what may have been the

[38] See footnote 15.

[39] See footnote 24.

[40] USBF. 1938–1943. Monthly report of activities, 1938–1943. U.S. Fisheries Biological Station, Fish and Wildlife Service Biological Station, and Section of Alaska Fishery Investigations, Seattle, WA. Unpubl. report (21 Apr–20 May 1940). Located at NARA, Anchorage, AK.

[41] Shuman, Richard F. 1948 notebook. Located at NARA, Anchorage, AK.

[42] Duncan, T. O. 1955 notebook (21 June). Located at NARA, Anchorage, AK.

[43] 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 at ARLIS, Anchorage, AK.

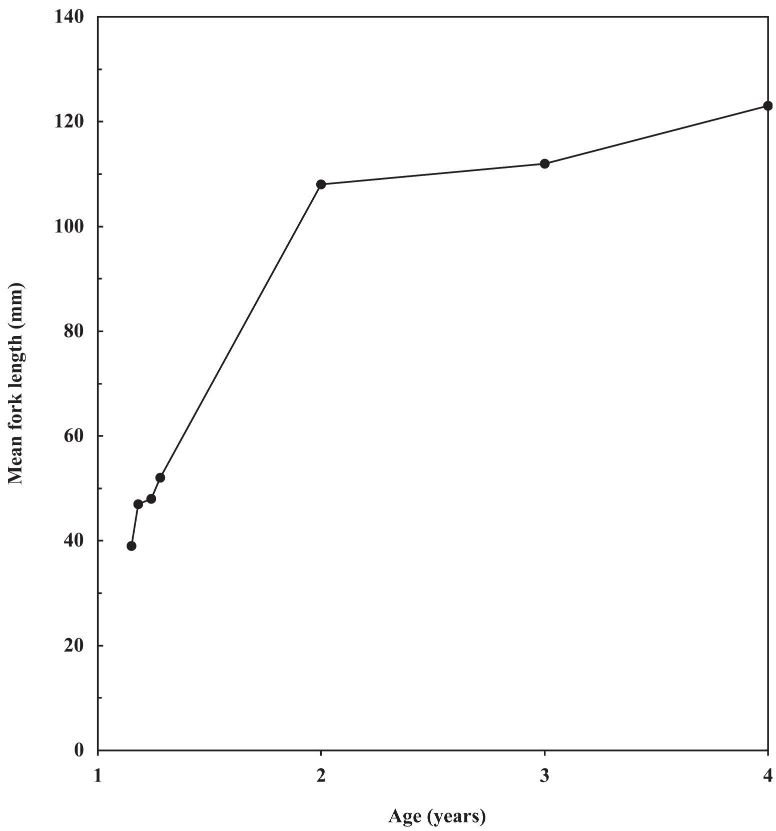

Figure 4-11. Mean lengths of 1-year Karluk sockeye salmon juveniles and 2–4 year smolts from 1962. Lengths of juveniles were obtained from littoral samples (Gard and Drucker, 1963, Fig. 13) and lengths of smolts were obtained from Drucker (1970, Table 21). Age is designated by the Gilbert-Rich system.

first reference to the fact that most sockeye juveniles spent considerable time in fresh water before migrating to the sea: "So far as can be learned, it is a year from this time, [i.e. time of emergence] or the following spring or summer—two years from the time of the arrival of the parent fish—before the young proceed to salt water . . ." Growth influenced duration of time spent in fresh water. Older age groups migrated earlier in the season than younger age groups (Gard and Drucker, 1965) and larger smolts in each age group tended to migrate earlier than smaller smolts (Barnaby, 1944). In addition to age, other factors that determined growth included distribution and abundance of food, water temperature, length of growing season, and density of juveniles.

Although adult sockeye varied greatly in size from about 325–635 mm in mideye-fork length (Gard et al., 1987), newly-emerged fry varied only moderately in size. In 1950, fry seined from littoral areas of Karluk Lake (Island, Long, and Tree points and Thumb Beach) between 31 May and 14 June ranged from 24 to 30 mm in total length.[44] Later that summer, from the shore of Thumb Lake, Walker measured "newly emerged" fry that averaged 26 mm in total length. Walker continued to measure fry in early May 1951 and again reported total lengths from 24 to 30 mm for fry collected from Little Lagoon, Canyon Lagoon, Karluk River, the outlet of Thumb Lake, and lower Thumb River.[45] In April and May 1964, fork length of migrating fry from Grassy Point Creek and the first wave from Canyon Creek averaged 28.9 and 29.8 mm, respectively (Gard et al., 1987). Regardless of natal area, it appeared that newly-emerged Karluk fry varied only 6 mm in length, i.e. from 24 to 30 mm and had an average size of about 27 mm.

A definitive presentation of Karluk sockeye salmon growth in freshwater could not be made with the data available, but an approximation of a growth curve was constructed by plotting mean lengths of 1-year juveniles from littoral areas and of 2–4 year smolts collected in 1962 (Fig. 4-11). The first juvenile sample was measured in late June 1962 and averaged 39 mm in length. The juveniles grew fast for about two weeks, after which there was an apparent pause during July. This temporary flattening of the growth curve was probably the result of the recruitment of small, newly-emerged fry from the late run. Fast growth of juveniles resumed in late 1962. Age 2-, 3- and 4-year smolts for the 1962 outmigration aver-

[44] See footnote 15.

[45] See footnote 15.

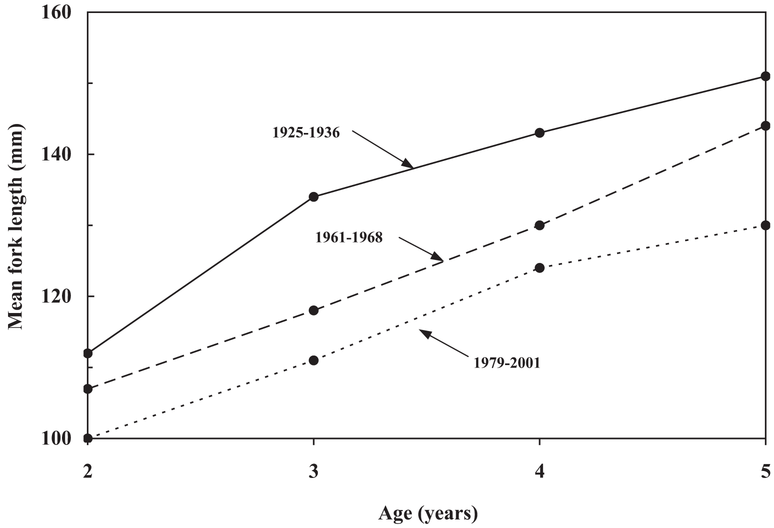

Figure 4-12. Mean length of Karluk Lake sockeye salmon smolts, 1925–2001. Data from Barnaby (1944, Table 27), Drucker (1970, Table 21), Burgner (1991, Table 8), and Schrof and Honnold (2003, Appendix M.12). Age is designated by the Gilbert-Rich system.

aged 108 mm, 112 mm, and 123 mm, respectively. On the basis of these figures, there was a 69 mm growth between age 1 and 2, a 4 mm growth between age 2 and 3, and an 11 mm growth between age 3 and 4. The resulting growth curve was similar to many growth curves as there was a large increase in length between ages 1 and 2 followed by lesser growth between ages 2 and 4.

Earlier in this chapter, we pointed out that adult male sockeye from years 1916–26 were much longer than those from years 1956–69. A similar difference appeared early in the life history of Karluk sockeye. After the 1925–36 period, smolts of all ages and both sexes became progressively shorter during the 1961–68 and 1979–2001 periods (Fig. 4-12). These graphs were constructed by averaging smolt lengths from several outmigrations and, therefore, approximated true growth better than the graph in Figure 4-11 which was based on juvenile and smolt lengths from only one year. However, the mean lengths determined for age groups 2–4 in both Figures 4-11 and 4-12 were too long because the largest individuals in these age groups migrated first and some individuals remained in the lake after each outmigration. Mean lengths of the 5-year smolts in Figure 4–12 were not so biased because all 5-year smolts of the same year class migrated during the same year.

Compared to the expressions of growth described above, a potentially better method would have been back calculating fish sizes at earlier annuli from fish length at time of capture and appropriate scale measurements. With this method, growth of ages 2 through 4 would not have been exaggerated, but finding the proper relationship between body and scale growth was problematical. Barnaby (1932) employed the back calculation method using adult mean lengths and scales from some age groups, but to our knowledge, no one has attempted this recently. A current growth study utilizing back calculation of all age groups and coordinated with a food habits/supply study would be valuable because an accurate expression of freshwater growth and adequate food habits information are not available.

Smolt Outmigration

Before sockeye salmon parr (juveniles) residing in a lake can become functional inhabitants of the sea (smolts), a number of transformations must occur. They must change in color, shape, activity, and, perhaps most importantly, in their ability to tolerate saltwater. Their color becomes more silvery and their bodies become slimmer and more streamlined. Orientation to the current changes from positively rheotactic to generally negatively rheotactic. Osmoregulatory ability changes as their salt glands develop. These changes are brought about by a complex interaction of endogenous and exogenous factors which are summarized in Burgner (1991). Apparently, the primary controlling force in the parr-smolt transformation is an endogenous rhythm in hormone production (Hoar, 1965, 1976; Wedemeyer et al., 1980; Groot, 1982). Environmental factors, especially increasing photoperiods and temperatures, influence the innate hormonal rhythm only after the parr reach a threshold size (Groot, 1982). While these processes are going on, Karluk smolts leave the limnetic areas of the lake, migrate to the trunk river, and continue for 37 km to the sea.

History of Karluk Smolt Observations

Over the past 115 years there have been many references to sockeye salmon smolt migrations in the Karluk River.

Interpretation of some observations was difficult because the term "fry" was used when smolts were probably being observed. Hence, occasionally we were obliged to make arbitrary decisions as to which life history stage was under consideration. For convenience, the 115-year time span was divided into four sections: Early Smolt Observations: 1889–1920, Smolt Observations: 1921–41, Smolt Observations: 1942–69, and Smolt Observations: 1970–2004.

Early Smolt Observations: 1889–1920

Early smolt observations were made from lake and stream banks, supplemented with information from fish acquired with dip nets, traps, and seines. As early as 1889, Bean (1891) reported: "Mr. Charles Hirsch informed me that in March or April the Karluk River is solid full for a whole month of salmon fry going down to sea." Most progeny of spring-run adult sockeye emerge from April to late June and a few of them migrate directly to sea, but the river would hardly be "solid full." Further, Hirsch could not have been observing the early wave of upper Karluk River fry or the smolt run from the lake because neither would have been present in the Karluk River until May. Perhaps the fry observed were not sockeye. Whatever the correct explanation, this observation was of interest because it was the first documentation of young salmon migrating down the Karluk River to the sea.

Several years later, Rutter reported that during May and June salmon fry were abundant in Karluk River from the lake to the estuary.[46] In one seine haul, he identified 40 sockeye fry and 2 fingerlings. On 1 July he set a trap in the river just above the estuary and caught many young of various species including 5 sockeye fingerlings 9–10 cm long. Rutter may have been the first investigator to use traps. Moving down to the estuary on 24 July, Rutter seined 21 sockeye fry and 11 fingerlings 10–14 cm long. The fry may have come from the hatchery which was then operating on the lagoon, and the fingerlings were probably part of the smolt migration from Karluk Lake.

Chamberlain (1907) [reporting on Rutter's 1903 field work] fished a downstream trap at the lake outlet several days in June, apparently during daylight only. Although he caught salmon fry and "parrs" (smolts?), he concluded that there was ". . . but a slight movement of sockeye fry from the lake." He was fishing during the right month to catch the smolt outmigration, but as we now know, most of the smolts migrate at night. Chamberlain also observed many sockeye fry and small fingerlings in the upper Karluk River throughout May and June and dipnetted some fingerlings that averaged nearly 5 cm in length. These fingerlings may have emanated from the second wave of upper Karluk River fry which were feeding in the river prior to migration to the lake.

Passage of 80–130 mm smolts through the lagoon was described by Fassett: "When the migration of these fry [smolt] is on they are seen about the seining beaches on the outside of the spit in tremendous numbers and are hauled in with every sweep of the seine. It is not thought there is much loss on this account, however, as they readily escape through the meshes of the nets."[47] Sporadic visits were made to the Karluk River system from 1911 through 1920, but there were no observations of smolts recorded.

Smolt Observations: 1921–41

Smolt observation and sampling were greatly enhanced by the installation of an adult counting weir in the lower Karluk River just above the lagoon in 1921. This weir, operated under the general supervision of Charles H. Gilbert, was tended each summer season through 1941 and provided a structure above which large numbers of migrating smolts often held temporarily, thus facilitating sampling. A seine was passed around a school of fish, the ends of the seine were pulled to each side of a gate in a holding pen, and the fish were induced to enter the pen by continuing to draw in the ends of the seine (Barnaby, 1944). Between 1921 and 1941 seasonal timing of the smolt outmigration was determined precisely at the weir and samples were collected for weighing, measuring, and age determination. Additionally, during the 1926–36 period between 40,000 and 57,000 smolts seined at the weir were marked annually by the removal of the adipose and one pelvic fin and released below the weir. Recovery of marked fish was done in subsequent years (through 1939) at the canneries and at the weir.

Willis Rich and, subsequently, Joseph Barnaby supervised the smolt marking program. The marking was initiated to serve as a check on age determinations from scales and to enable the calculation of ocean and freshwater mortalities and number of smolts.[48] Further, Taft emphasized that determining smolt numbers was a central goal of the smolt marking program.[49] Although

[46] See footnote 3.

[47] See footnote 9.

[48] USBF. ca. 1930s. Marking experiments. Unpubl. report. 2 p.Located at NARA, Anchorage, AK.

[49] 1) Taft, Alan C. ca. 1928. Karluk red salmon investigations—1927–1928. Unpubl. report. 35 p.
2) Taft, Alan C. ca. 1929. Investigations concerning the red-salmon runs to the Karluk River, Alaska. II. 1927–1928. Unpubl. report. 57 p. Both reports located at NARA, Anchorage, AK.

a smolt population estimate was made for 1926,[50] the main use of the smolt marking was to determine ocean survival (Barnaby, 1944). Gilbert and Rich may not have published the 1926 smolt estimate or produced subsequent estimates because they discovered weaknesses in the method or because they concluded that population estimates for smolt migrations one or more years in the past were not useful.

Smolt Observations: 1942–69

Throughout the 1942–69 period, smolts were collected most years at weirs located at the Portage and at about 300 m below the lake outlet to obtain timing, age, weight, and length data. Smolt age data in the 1930s indicated that there was a change in the amount of time smolts were spending in freshwater and one question under investigation was whether or not the trend was long-term. A second matter to be resolved was the development of a smolt population estimation method that applied to the current year.[51] During the 1950s efforts were made to determine smolt population size by the use of traps or fyke nets in conjunction with marking and recapturing, with minimal success. The most promising of these efforts was in 1958 when eight traps were spaced across the river and fished in a Latin-square design. Unfortunately, the smolts swam between the traps and, although revisions to the design seemed satisfactory, high water washed out the structure before it could be thoroughly tested (Conkle et al., 1959). In 1960 the Latin-square design was developed further and in 1961 a satisfactory estimate of the smolt outmigration was determined. This method with minor modifications was used in determining smolt population estimates through 1969 at the lake outlet weir where the river was 43.9 m wide. Every 3.6 m across the weir was an A-frame, and between every two frames was a trapping site. All fish entering this 3.6-m span were funneled into the winged fyke net. Wire screening was tacked to both sides of the A-frames to prevent smolts from going between the frames and escaping the fyke nets. Two nets were always in position; one net was fishing, the other, with the cod end off, was standing by at the next site to be fished. The Latin-square sampling design was set up to fish randomly 12 sites, each for a 2-hour period each day. At the end of every 12-day period, each site had fished a total of 24 hours. Estimates of the smolt outmigration were computed for each 12-day period by multiplying the total catch by 12. Some modifications to this method were made in 1963 and subsequent years (see Gard and Drucker, 1965 for details). The only serious problem with this method was when the weir washed out, which it did in 1969.

Smolt Observations: 1970–2004

After 1969, smolt observations were made sporadically through 1997. From 1979 to 1982 Sonar was used to enumerate smolts at the "King Hole" located about 4 km below the lake outlet (White 1988b). Chatto,[52] in 1983, and Wilmot and Finn,[53] in 1984, estimated smolt populations using a Canadian fan trap (incorporating mark and recapture) located about 1.5 km below the lake outlet. White (ADFG, ca. 1988), in response to a question concerning both smolt counting methods, said "nothing worked very well," but Chatto thought the fan trap method produced a satisfactory smolt population estimate.[54] Age and length data were also determined at both locations. From 1989 or 1990 to 1996, Steve Honnold and Steve Schrof used hydroacoustic estimates of juvenile populations in Karluk Lake before and after smolt outmigrations to calculate smolt population estimates. This was not successful.[55] The Canadian fan trap was used again in the upper Karluk River in 1991 and 1992 by Lorne White and Steve Honnold to produce acceptable smolt estimates.[56] Finally, in 1997 size and age of smolts were determined at the present weir location just upstream from the lagoon. No smolt investigations were conducted in 1998.

Timing of Smolt Migrations

Seasonal timing of the beginning of smolt migrations through the outlet and lagoon weirs was fairly consistent from year to year. During the 1922–36 period smolts arrived at the lagoon weir between 21 May and 1 June with an average arrival date of 26 May, whereas during

[50] 1) Letter (18 November 1927) from Willis H. Rich, USBF, Stanford University, CA, to C. H. Gilbert, Washington, DC. 2) USBF. 1928. Marking experiments with seaward migrants. Unpubl. report. 5 p. Letter and report located at NARA, Anchorage, AK.

[51] 1) FWS. 1946. Biological investigations in relation to the management of the Karluk sockeye salmon fishery. Unpubl. report. 5 p.
2) Letter (26 February 1953) from Clinton E. Atkinson, Chief, Pacific Salmon Investigations, Seattle, WA, to Regional Director, FWS, Juneau, AK. Report and letter found at NARA, Anchorage, AK.

[52] Chatto, Tony. 1984. Karluk Lake sockeye smolt enumeration, 1983. USFWS, Kodiak National Wildlife Refuge, Kodiak. Unpublish. report. 20 p. Located at Kodiak National Wildlife Refuge files, Kodiak, AK.

[53] Wilmot, Richard, and Jim Finn. Personal commun. 1998.

[54] Chatto, Tony. Kodiak, AK, Personal commun. 1996.

[55] Honnold, Steve. Kodiak, AK. Personal commun. 1998.

[56] See footnote 55.

Table 4-16
Seasonal and diel timing of Karluk smolt migration through the weirs at the lagoon and lake outlet.

Year	First smolt seen	Last smolt seen	Diel timing (%) Day (0400–2000)	Night (2000–0400)	Data source
Weir near Karluk Lagoon					
1922	27 May	8 July			[1]
1923	25 May	16 June			[2]
1926	Late May	Late July			[3]
1927	1 June	22 June			[4]
1931	21 May	18 June			[5]
1932	25 May	7 Aug			[6]
1934	21 May	15 June			[7]
1936	28 May	24 June			Bower, 1937
Average	26 May	29 June			
Weir at lake outlet					
1950	21 May				[8]
1958	26 May				[9]
1961	26 May	30 June	22	78	Gard and Drucker, 1963
1962	17 May	22 June	23	77	Gard and Drucker, 1963
1963	18 May	7 July	4	96	Gard and Drucker, 1965
1964	18 May	7 July	8	92	Gard and Drucker, 1966a
1965	15 May	16 July	9	91	Gard and Drucker, 1966b
1966	18 May	2 July	25	75	Drucker and Gard, 1967
1967	18 May	29 June	14	86	Drucker, 1968
1968	17 May	25 June	35	65	Drucker, 1970
1969	25 May				[10]
Average	20 May	2 July	18	82	

[1] Lucas, Fred R. 1924. Summary of red salmon census for the season of 1922 at Karluk Alaska. USBF. Unpubl. report. 5 p. Located at NARA, Anchorage, AK.
[2] Lucas, Fred R. 1924. Report of the red salmon census at Karluk Alaska during the season of 1923. USBF. Unpubl. report. 4 p. Located at NARA, Anchorage, AK.
[3] Hungerford, Howard H. 1926. Report of operations at Karluk Weir (Lower) season of 1926. USBF. Unpubl. report. 4 p. Located at NARA, Anchorage, AK.
[4] Letter (16 June and 2 July 1927) from Ray S. Wood, Foreman In Charge, USBF, Karluk, AK, to H. H. Hungerford, Warden, USBF, Kodiak, AK. Located at NARA, Anchorage, AK.
[5] Wood, Ray S. 1931. Report of the Karluk River weir, 1931. USBF, Karluk, AK. 10 Unpubl. report. Located at ABL Library files, Auke Bay, AK.
[6] Letter (4 Ocotber 1932) from JTB [Joseph Thomas Barnaby], Temporary Assistant, Seattle, WA, to Willis H. Rich, Stanford University, CA. Located at NARA, Anchorage, AK.
[7] Turner, Charles. 1934. Report of operations, Kodiak-Afognak Dist., 1934. USBF. Unpubl. report. 49 p. Located at ABL Library files, Auke Bay, AK.
[8] FWS. 1943-1952. Monthly reports of the Alaska Fishery Investigations. Unpub. reports. Located at NARA, Anchorage, AK.
[9] Conkle, Charles Y. 1958. Karluk Lake field reports (27 April-21 June 1958). BCF, Karluk Lake, AK. 3 Unpubl. report. Located at NARA, Anchorage, AK.
[10] BCF. 1969. Karluk Lake Station 1969 Record Book. Data notebook. Located at NARA, Anchorage, AK.

the 1950–69 period smolts arrived at the outlet weir between 15 May and 26 May with an average arrival date of 20 May (Table 4-16). If there had been no inherent change in timing between the two periods, it took an average of about six days for the migrants to travel the 32 km between the outlet and lagoon weirs at a rate of 5.3 km/d. Withler (1952) reported that sockeye smolts traversed a 13 km stretch of the Babine River at an average rate of 4.2 km/d during a 4-year study. In the Columbia River above Bonneville Dam sockeye smolts averaged 19–40 km/d when they were released 565–645 km above the dam, and 3 km/d when released 32 km above the dam (Anas and Gauley, 1956). Foerster (1968) stated that the speed of travel depends largely on the velocity of the current and the character of the flow, i.e. smolts travel more slowly when they pass through turbulent water, which always occurs at weirs. Many observers, including the senior author, have witnessed large schools of smolts approach a weir, turn and head upstream while moving laterally, and eventually pass quickly through the weir tail first. Upon reaching smooth water they turn downstream and swim with the current.

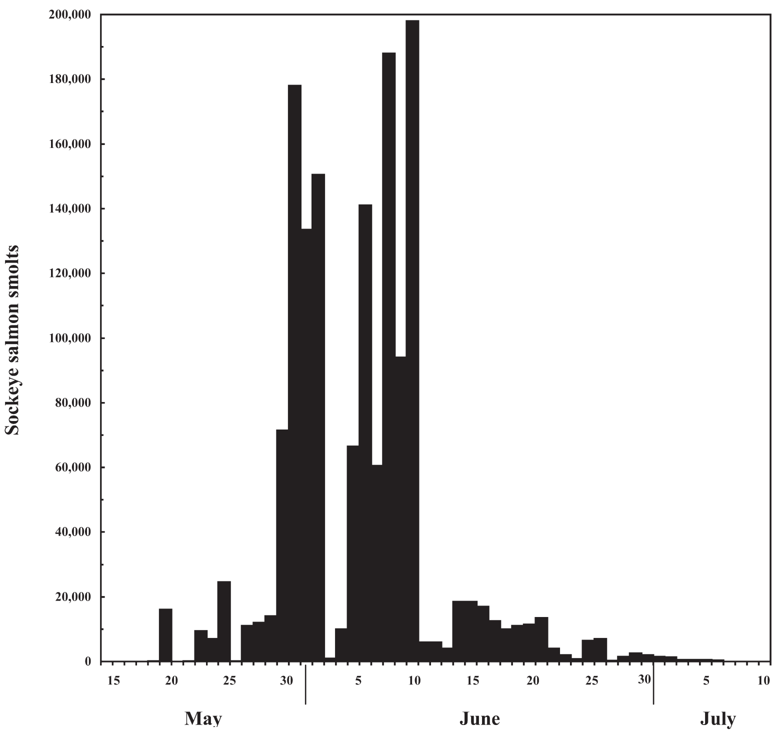

Figure 4-13. Daily estimated sockeye salmon smolt outmigration at Karluk Lake, 1963 (from Gard and Drucker, 1965). Daily totals run from 1900 of one day to 1900 of the next day.

The migration termination dates of Karluk sockeye smolts varied greatly from 15 June to 7 August (Table 4-16). Part of this variability was due to sampling irregularity because sometimes nets were removed immediately after the height of the migration while at other times they were tended for several weeks thereafter. The information we have indicated that smolts migrated in small numbers well into the summer.

A typical smolt migration pattern at the lake outlet is shown in Figure 4-13. In 1963 the smolts arrived at the outlet weir on 18 May, increased by 30 May to high numbers which were maintained through 10 June, and then dropped erratically to very low numbers by 7 July. The tails of the migration pattern were unequal, with the descending tail being twice as long as the ascending tail.

Another way to express seasonal timing of smolt migrations was to determine the date by which 50% of the fish had migrated. The average date so calculated for Karluk smolts migrating through the outlet weir during the 1961–68 period was 1 June. Comparable dates for 16 other sockeye river systems ranged from 25 April at Cultus Lake in the extreme south to 1 July for Taslina Lake in the extreme north (Hartman et al., 1967). A plot of average dates by which 50% of the smolts had migrated against latitude revealed a close correlation between these variables, with the point representing Karluk smolts lying near the middle of the latitudinal and seasonal ranges (Hartman et al., 1967).

Diel timing of departure of Karluk smolts from the lake was mostly at night (Table 4-16). Sixty-five to 96% of the smolts passed through the outlet weir between 2000 and 0400 hours during the 1961–68 period. However, some migration always occurred during the day, the highest being 35% in 1968 (Table 4-16). Kerns (1961), Burgner (1962), Groot (1965), and Hartman et al. (1967) have also reported that sockeye smolts migrated mostly at night.

Changes in age and size of Karluk smolts occurred as the season progressed. Barnaby (1944) reported that older age groups tended to migrate earlier than younger age groups. This was clearly evident when mean age composition of the abundant 3- and 4-year smolts from

Table 4-17
Mean age composition of Karluk sockeye salmon smolt outmigration by seasonal time period, 1962-68.[1]

	Total outmigration (%)			
Age	1st time period (15–29 May)	2nd time period (27 May–10 June)	3rd time period (8–22 June)	4th time period (21 June–15 July)
5	0.5	0.8	0.5	0.0
4	58.9	43.5	21.7	14.9
3	38.8	52.1	74.4	74.4
2	1.8	3.6	3.4	10.4

[1]Compiled from BCF Karluk Lake Station Record books 1962–68 located at NARA, Anchorage, AK.

Table 4-18
Estimated numbers of sockeye salmon smolts in outmigrations from Karluk Lake.

Year	Smolt outmigration	Agency	Sampling location	Method used	Reference
1961	1,694,761	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1963
1962	1,434,864	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1963
1963	1,539,599	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1965
1964	1,561,105	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1966a
1965	1,469,307	BCF	Outlet weir	Fyke net and Latin square	Gard and Drucker, 1966b
1966	1,080,950	BCF	Outlet weir	Fyke net and Latin square	Drucker and Gard, 1967
1967	1,358,237	BCF	Outlet weir	Fyke net and Latin square	Drucker, 1968
1968	3,641,665	BCF	Outlet weir	Fyke net and Latin square	Drucker, 1970
1979	1,001,000	ADFG	4 km below outlet	Sonar	White, 1988b
1980	1,687,200	ADFG	4 km below outlet	Sonar	White, 1988b
1981	2,041,900	ADFG	4 km below outlet	Sonar	White, 1988b
1982	821,200	ADFG	4 km below outlet	Sonar	White, 1988b
1983	941,500	USFWS	1.5 km below outlet	Fan trap and mark-recapture	[1]
1984	1,074,000	USFWS	1.5 km below outlet	Fan trap and mark-recapture	Schrof and Honnold, 2003
1991	4,700,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	Holland and McKean, 1992
1992	3,700,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	McNair and Holland, 1993
1999	1,066,534	ADFG	1.5 km below outlet	Fan trap and mark-recapture	Schrof and Honnold, 2003
2000	1,676,702	ADFG	1.5 km below outlet	Fan trap and mark-recapture	Schrof and Honnold, 2003
2001	3,740,268	ADFG	1.5 km below outlet	Fan trap and mark-recapture	Schrof and Honnold, 2003
2002	1,300,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak
2003	2,200,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak
2004	2,300,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak
2005	1,500,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak
2006	1,200,000	ADFG	1.5 km below outlet	Fan trap and mark-recapture	ADFG, Kodiak

[1] Chatto, Tony. 1984. Karluk Lake sockeye smolt enumeration, 1983. USFWS, Kodiak National Wildlife Refuge, Kodiak, AK. Unpubl. report. 20 p. Located at USFWS, Kodiak National Wildlife Refuge files, Kodiak, AK.

the 1962–68 period were compared (Table 4-17). Four-year smolts decreased from 58.9% of the outmigration during the first time period to only 14.9% during the fourth time period, while 3-year fish increased from 38.8% in the first time period to 74.4% in the last time period. The youngest fish sampled (age 2) increased from 1.8% to 10.4% as the season progressed. Data for the 5-year fish were not clear-cut, but not one was found in the latest period. During the outmigration season larger smolts often migrated earliest. This was partly because the older fish that migrated earliest were larger, but even within one year class the larger fish migrated earlier (Barnaby, 1944).

The external stimulus that triggered smolts in the appropriate physiological condition to migrate was primarily increasing water temperature, with its attendant effect on ice breakup. However, wind velocity and direction and photoperiodism may also have been involved (Foerster, 1968; Hartman et al., 1967; Burgner, 1991).

Abundance of Smolts

During the 1961–2006 period estimated numbers of sockeye smolts that migrated from Karluk Lake varied widely from 821,200 in 1982 to 4,700,000 in 1991 (Table 4-18). However, during the first seven years of this period (1961–67) estimated smolt numbers were fairly constant, averaging about 1,500,000 fish (Table 4-18). Then in 1968, the smolt outmigration was estimated to be 3,642,000; this was the result of excellent freshwater survival because the parent generations in 1964 and 1965 were not particularly large. These smolts did not survive well at sea because all age groups were short (Drucker, 1970) and the expected large adult returns in 1970 and 1971 did not materialize (Figs. 1-2, 1-3). Other years of interest were 1991 and 1992 when an estimated 4,700,000 and 3,700,000 smolts, respectively, migrated (Table 4-18). These large smolt outmigrations were probably, in part, the result of fertilization of Karluk Lake between 1986 and 1990 although sockeye populations increased simultaneously in nearby unfertilized sockeye systems (see Chapter 7).

The series of smolt numbers presented here is exceedingly important to our understanding of the life history of Karluk sockeye because it, in conjunction with adult counts, permits us to determine total freshwater and marine survival rates. These will be discussed in subsequent sections of this chapter.

Survival in Fresh Water

Survival between the potential egg deposition and smolt migration stages of Karluk sockeye salmon varied from

Table 4-19
Survival of sockeye salmon at Karluk Lake during the freshwater phase of the life cycle. Brood years 1958-61 are from Gard and Drucker (1966b) and brood years 1962-65 are from Drucker (1970).

Brood Year	Escapement	Potential eggs deposited[1]	Smolts produced	Total freshwater survival (%)
1958	303,914	468,000,000	1,853,000	0.40
1959	493,589	803,000,000	2,001,000	0.25
1960	387,434	682,000,000	1,906,000	0.28
1961	329,596	485,000,000	1,143,000	0.24
1962	623,013	1,174,000,000	1,116,000	0.10
1963	452,910	623,000,000	682,000	0.11
1964	537,863	845,000,000	2,354,000	>0.28
1965	386,096	724,000,000	2,455,000	>0.34
			Average	0.25

[1] Including estimates for the Karluk River spawners below the weir.

0.10% to 0.40% (average, 0.25%) for fish spawned between 1958 and 1965 (Table 4-19). The figure listed for brood year 1964 (0.28%) would have been slightly higher had an estimate of the 5-year migrants been made in 1969. Additionally, the figure for brood year 1965 (0.34%) would have been considerably higher had the 4- and 5-year migrants been enumerated in 1969 and 1970. Although 5-year smolts were rare, 4-year smolts were second in abundance in most years. Unfortunately, the weir washed out in 1969 and smolt estimates were not made for many years thereafter. Barnaby (1944) calculated that egg to smolt survival for Karluk sockeye ranged from 0.45% to 0.90% depending on whether a 2:1 or a 4:1 ratio of return to escapement was assumed. The egg to smolt survival rates for the 1958–65 brood years (Table 4-19) were probably more realistic than those calculated by Barnaby (1944) because the former were not based on any assumptions except those that applied to the estimation of egg and smolt abundances, whereas the latter were based on hypothetical ratios of return to escapement and an unreasonably high average fecundity of 3,700 eggs (see Gard et al., 1987, Table 2). In a summary of eight other sockeye river systems, Foerster (1968:313–324) reported freshwater survival rates averaging 2.3%. Freshwater survival of Karluk sockeye averaging 0.25% was less than that in many other sockeye systems, one reason being that Karluk juveniles remained in the lake for a longer period of time.

Near Shore Sea Life

Few observations have been recorded of the early sea life of Karluk sockeye juveniles in the near shore and estuarine environments. The information presented here was obtained incidentally from beach seining for adults in the ocean off Karluk Spit or within Karluk Lagoon (Chamberlain, 1907). Although large-mesh seines were used, some juveniles were usually caught in each haul. On 8 June 1903, 67 young sockeye averaging 181 mm in length (range, 123–207 mm) were measured. An examination of 20 stomachs revealed that the sockeye were feeding mainly on small crustaceans, but not on fry of any species. In a similar manner, 30 young sockeye composed of 12 males averaging 136 mm (122–156 mm) and 18 females averaging 139 mm (125–164 mm) were collected on 3 July. Most of these had been feeding on small crustaceans, some contained pteropods, and two had some small blennies and sticklebacks. Small sockeye were present in the cannery seines outside the spit throughout the canning season, but none of the larger individuals observed in June were collected after 3 July. One haul within the lagoon on 24 July captured many young sockeye 30–145 mm in length and Chamberlain surmised that the smaller fish were from the hatchery and the larger fish were smolts from the lake. All were feeding on crustaceans and insects. Masses of intestinal worms were present in many of the fish.

A summary of smolt information follows: 1) Karluk smolts migrated to sea after 1–5 years in the lake. A 5-year residence in fresh water was unique and may be the longest known. 2) Timing of the smolt migration was fairly consistent from year to year. Smolts arrived at the outlet between 15 May and 26 May (average date 20 May) which was about six days earlier than they arrived at the lagoon. 3) Larger (and often older) smolts tended to migrate earlier than smaller smolts. 4) Estimated numbers of smolts migrating from the lake varied from 821,000 in 1982 to 4,700,000 in 1991. The large outmigration in 1991 may have been the result of lake fertilization in prior years. 5) Karluk smolts have become progressively shorter over the years. Much of this decrease came between 1903 and the 1925–36 period when they lost 34–37 mm in length. 6) The main food of young sockeye in the lake and at the river mouth was small crustaceans.

Life in the Ocean

Distribution and Migration in Offshore Waters

After leaving the Karluk River and adjacent shores, the majority of the juveniles moved to offshore feeding areas where they remained for 1–4 years before returning to spawn. The exact timing of the offshore migration was questionable, but Hartt and Dell (1986) presented a time series of maps showing that catches of juvenile sockeye off

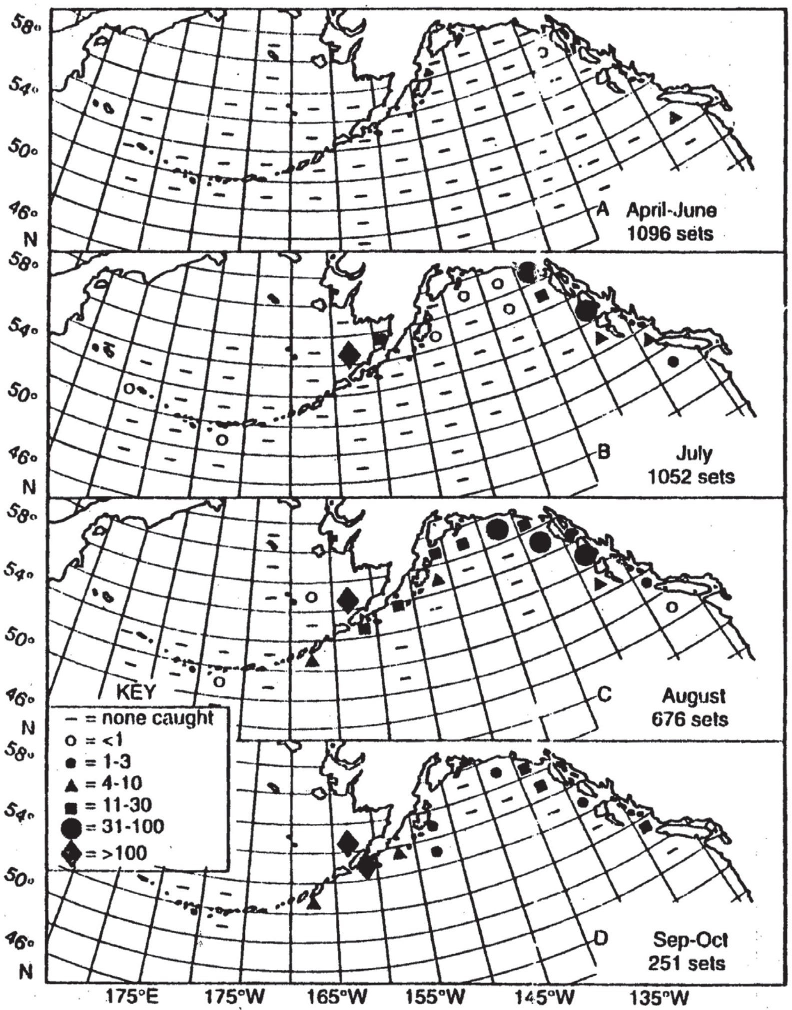

Figure 4-14. Mean catch per seine set of juvenile sockeye salmon by area and by time period; 3075 sets, 1956–70 (from Hartt and Dell, 1986, Fig. 3).

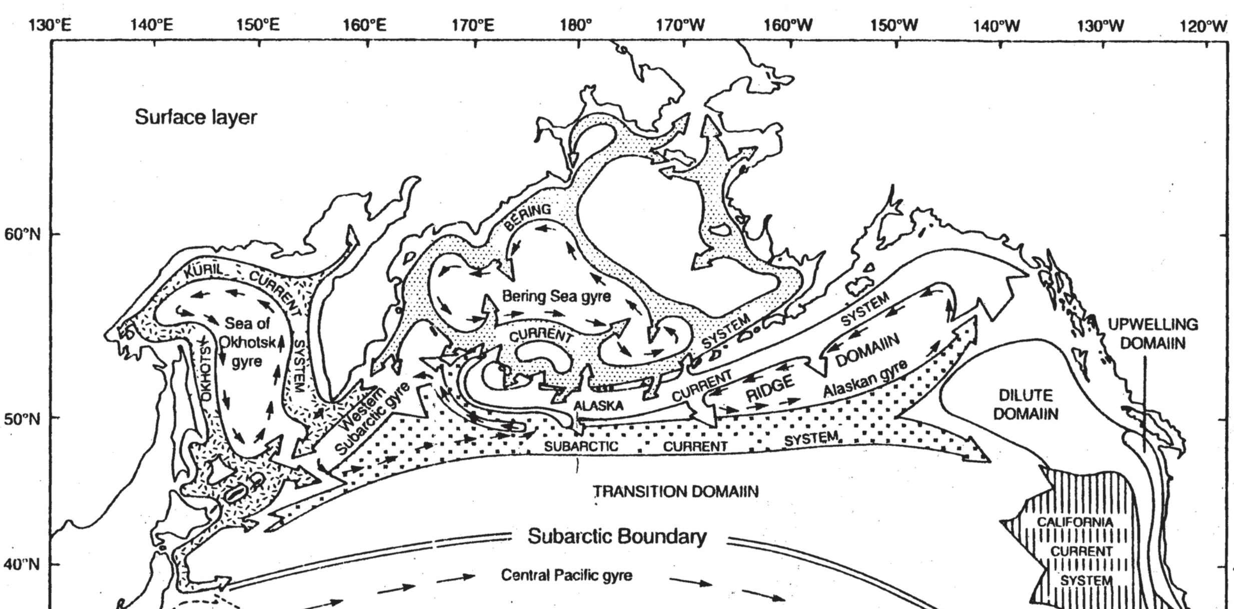

Figure 4-15. Schematic diagram indicating extent of surface layer domains and current systems in the Subarctic Pacific Region (from Favorite et al., 1976, Fig. 41).

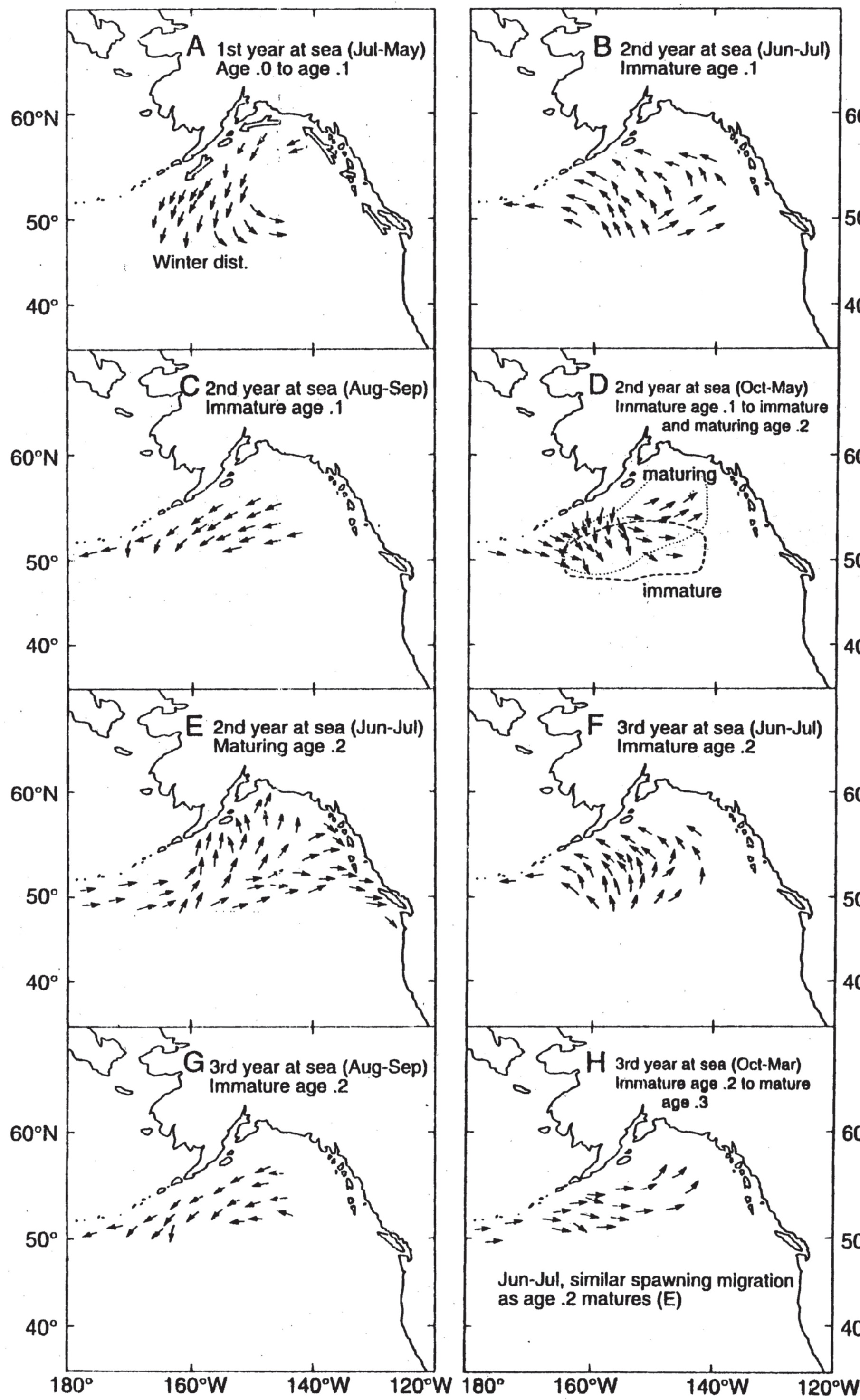

Figure 4-16. Model of migration of northeastern Pacific sockeye salmon (from French et al., 1976, Fig. 94).

Kodiak Island were largest between August and October (Fig. 4-14). Many of the sockeye in those catches were from northeastern Pacific rivers to the east or south of Kodiak Island, but some were surely from the Karluk River. The series of maps showed a northwest movement of eastern Pacific stocks followed by a southwestern movement during which the Karluk juveniles joined the others.

Several circular current systems known as gyres (Fig. 4-15) occur in the North Pacific Ocean and adjacent seas, and these gyres are often bounded by large masses of relatively stable water known as domains (Favorite et al., 1976). On the northern border of the Alaska gyre is the Alaska Current System into which the eastern Pacific sockeye stocks swim during their northwestern migration. This

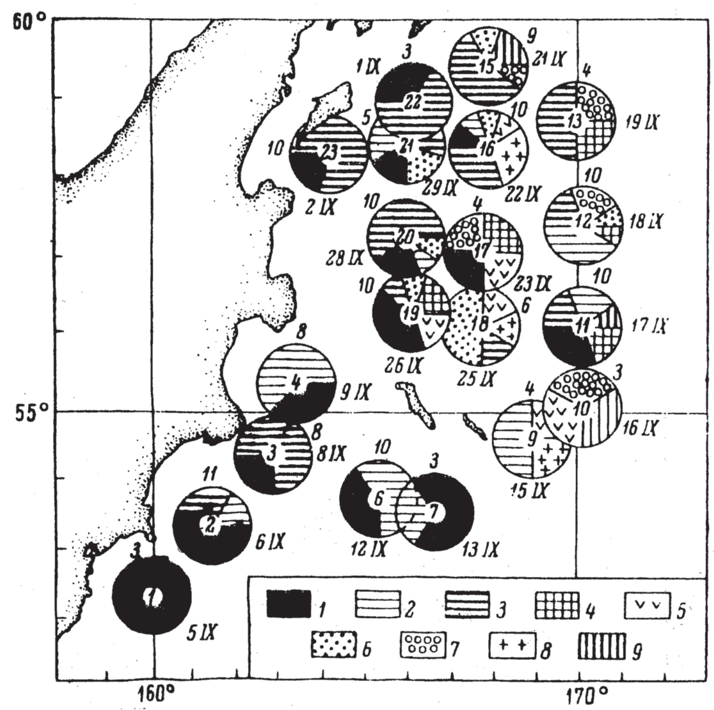

Figure 4-17. Distribution of local populations of sockeye salmon in the Commander Islands area of the Pacific Ocean and of the Bering Sea in September–October 1966 (from Konovalov, 1975, Fig. 104). (Key: 1 = population of Lake Kurilskoe; 2 = population of the Kamchatka River; 3 = undetermined populations of the NW coast of Kamchatka Peninsula; 4 = population of Lake Karluk; 5 = population of the Naknek River; 6 = population of the Wood River; 7 = population of the Egegik River; 8 = population of the Ugashik River; 9 = undetermined populations of Bristol Bay.)

system assists these stocks as well as the Karluk juveniles during their southwestern journeys and beyond.

French et al. (1976) described a generalized, circuitous migration of the northeastern Pacific stocks associated with the Alaska gyre (Fig. 4-16). A tagging experiment (Neave, 1964) suggested that some Karluk fish joined the northeastern Pacific stocks in this repetitious journey. Any mature 1-ocean Karluk fish (mainly age groups 4_3 and 5_4) returned to the natal river after one complete circle of the gyre (Fig. 4-16, Map B). Most Karluk fish, however, remained in the gyre a second year and returned to their spawning grounds principally as age groups 5_3 and 6_4 (Map E). Still other maturing Karluk fish (age groups 6_3 and 7_4) remained a third year in the gyre (Map H), and a few 4-ocean individuals repeated the process once again.

As is often the case with biological systems, the process described above was an oversimplification. Using presence of diagnostic parasites and scale characteristics to identify natal rivers, Konovalov (1975) found that Karluk sockeye seined in spring and early summer of 1963–66 occurred from 48–50°N and from 172°E to 172°W. That placed them somewhat south of the Aleutian chain and straddling the 180° meridian (Fig. 4-14). However, when seining was done in September and October 1966 east of Kamchatka, he found relatively large numbers of immature Karluk sockeye from 55°N to nearly 59°N and from 166–170°E (Fig. 4-17; Table 4-20). These fish, located well into the Bering Sea and only about 150 km off Kamchatka, were about 2,200 km from their natal river as measured along the most direct route—considerably farther than had previously been reported. They were accompanied by sockeye from Kamchatka and Bristol Bay. Commenting on that discovery, Konovalov (1975:236) stated: "In view of the relatively large number of fish (9 specimens) of this population caught, we may consider the feeding areas of sockeye of Lake Karluk as having shifted in relation to their spawning body of water on Kodiak Island somewhat to the west." The migration path followed by Karluk sockeye from their natal river to Kamchatka and return was a mystery. However, a working hypothesis is that they could follow the Alaska Current System from the Karluk River to about the 180th meridian, then turn north through an Aleutian Island pass into the Bering Current System which they could follow to near Kamchatka (Fig. 4-15). On the return, they could ride the Bearing Sea Current to the southeast, turn south through an Aleutian Island pass, and swim to the Subarctic Current System which would transport them to their natal river.

In additional to currents, temperature and salinity characteristics of oceanic water masses may influence sockeye distribution and migration. A copious literature addressing these topics exists, but effects on Karluk sockeye are not specifically mentioned. Generalities that may be made are that sockeye prefer colder water than do other species of Pacific salmon, and that temperature definitely influences their distribution and migration whereas salinity rarely has such an ef-

Table 4-20
Number of specimens of immature sockeye salmon of some local populations of different complexes in the catches of the northwestern part of the Pacific Ocean in September-October 1966 (From Konovalov, 1975, Table 51).

Drift number	Coordinates		Kamchatkan complex				Bristol Bay complex					Pacifico-Alaskan complex
	N Latitude	E Longitude	Lake Kurilskoe	Lake Azabachie	Kamchatka River	Eastern Coast	Wood River	Naknek River	Egegik River	Ugashik River	Kvichak River	Lake Karluk
1	52°20′	160°00′	3	–	–	–	–	–	–	–	–	–
2	53°20′	161°20′	6	–	1	4	–	–	–	–	–	–
3	54°20′	162°46′	2	–	2	4	–	–	–	–	–	–
4	55°20′	163°23′	3	3	2	–	–	–	–	–	–	–
6	53°42′	165°20′	4	5	1	–	–	–	–	–	–	–
7	53°32′	166°40′	2	–	1	–	–	–	–	–	–	–
9	54°35′	168°58′	–	1	1	–	–	1	–	1	–	–
10	55°02′	170°10′	–	–	–	–	–	1	1	–	–	1
11	56°07′	170°07′	3	–	2	2	–	1	–	–	–	2
12	57°27′	170°10′	–	1	3	2	1	–	2	–	–	2
13	58°43′	170°10′	–	–	–	2	–	–	1	–	–	1
15	59°27′	167°54′	–	1	1	3	1	–	1	–	2	–
16	58°23′	167°52′	1	–	1	3	1	1	–	3	–	–
17	57°05′	167°50′	1	–	–	–	–	1	1	–	–	1
18	56°05′	167°48′	–	–	1	–	3	–	–	1	–	–
19	56°18′	166°10′	4	–	–	1	1	2	–	–	–	2
20	57°16′	166°00′	2	–	1	4	1	1	–	–	–	1
21	58°25′	166°00′	1	2	1	–	1	–	–	–	–	–
22	59°01′	166°10′	1	–	1	1	–	–	–	–	–	–
23	58°19′	164°10′	2	1	2	5	–	–	–	–	–	–

fect. Two or more physical factors may operate in concert, but no single environmental element wholly determines the distribution or migration of sockeye salmon. For a thorough discussion of these topics see Burgner (1991:70–83).

Vertical Distribution

A few studies have been conducted on vertical distribution of salmon at sea. Manzer (1964) reported that sockeye were caught down to a depth of 61 m in the Gulf of Alaska, but most were caught in the upper levels. He also found that they tended to be caught closer to the surface at night. During an investigation in the northwestern Pacific Ocean and Bering Sea, Machidori (1966) reported that immature and maturing sockeye were mostly in the upper 10 m and that they were somewhat shallower at night. The efficient Japanese high-seas gill net fishery set gear down to a depth of only 8 m (Fukuhara, 1971) and their longline salmon fishery placed gear a scant 1–2 m below the surface. Finally, French et al. (1976) reported that 90% of the sockeye caught in vertical gill nets in the northeastern Pacific Ocean were in the top 15 m and that none were caught below 30 m. After reviewing these observations, Burgner (1991) concluded that salmon generally occurred in near-surface waters. Because two of the investigators reported that sockeye were caught closer to the surface at night, a diel vertical migration may have occurred. Pella (1968) presented conclusive evidence of a diel vertical migration in juvenile sockeye in Lake Aleknagik. It would seem likely that planktivorous fish such as sockeye salmon would have a diel vertical migration pattern in both fresh and salt water because plankton has long been known to exhibit such movements.

Rates of Travel

Rates of travel of sockeye at sea vary greatly with stage of maturity, distance to be covered, and season. They are usually determined by tagging fish at a certain location and noting how long it takes them to reach a second location. For example, maturing sockeye traveled along the north coast of Kodiak Island from Uganik Bay to Karluk River at a mean rate of 8 km/day (Rich and Morton, 1930) whereas maturing salmon traveled from the Aleutian Islands to Bristol Bay at an average rate of 43 km/day (Hartt, 1966). The Bristol Bay fish had to travel a much longer distance. Hartt (1966) also reported that the rate of travel of maturing Bristol Bay sockeye increased as the season progressed and that immature fish moved more slowly than maturing individuals. Gard (1973) also found that the rate of travel of maturing sockeye migrating up the upper Karluk River increased from 2 km/day to 6 km/day between 1 August and 1 October.

Migration Mechanisms

One of the great mysteries of the biological world is how salmon navigate on the high seas and find their way back to their natal streams. A number of hypotheses have been proposed to explain this phenomenon, but the most likely explanation is the salmon's perception of celestial and magnetic cues, accompanied by their ability to translate this information into a workable navigational system. Several studies have demonstrated that sockeye fry and smolts utilize celestial and magnetic cues during their migrations in lakes (Groot, 1965; Brannon, 1972; Quinn, 1980; Quinn and Brannon, 1982). However, that sockeye use celestial and magnetic cues to navigate in the open ocean where the distances traveled may be 3,000–4,000 km has not been documented. To navigate in this manner, the sockeye would have to know the time of season and day and approximately where they are and where they are to go. With these considerations in mind, Quinn (1982b) proposed that salmon navigate at sea using a map based on inclination and declination of the earth's magnetic field, a celestial and magnetic compass, and a calendar which is in effect a seasonal clock. Day length is the most likely environmental factor that drives the clock.

If Quinn's model is correct, there is a close similarity between the methods used by sockeye and humans (prior to satellite navigation) to navigate on the high seas: Sockeye would have a map; humans have a nautical chart. Sockeye would have an internal magnetic compass which gives them horizontal and vertical information; humans have an external magnetic compass which gives them a horizontal course. Sockeye would have a biological clock; humans have a chronometer; sockeye would estimate the elevation of the sun by eye; humans use a sextant to do the same. Finally, sockeye would integrate within their brains the information they perceive to give them a geographical position; humans use a nautical almanac, a sight reduction table, and a position plotting sheet for that purpose.

Near the end of their return home, the sockeye switch from their high seas navigational system to a near shore olfactory system as they can smell their natal river. This ability was imprinted upon them before they migrated to sea as smolts (Hasler et al., 1978).

Food and Growth

In contrast to the paucity of food habit studies for juvenile sockeye in Karluk Lake, considerable feeding information has been acquired in the northeastern Pacific Ocean and the Bering Sea for sockeye of various stocks. In a summary of stomach analysis information from many areas presented by Foerster (1968) and French et al. (1976), Burgner (1991) stated: "Euphausiids, hyperiid amphipods, small fish, and squid were the groups most frequently listed as main food items, with copepods, pteropods, and crustacean larvae listed as of lesser importance. The fish included lantern fish (Myctophidae) and juvenile cod (Gadidae) in the central North Pacific Ocean. In the eastern Bering Sea, juvenile sockeye (aged-0) fed on larval capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), and herring (*Clupea harengus pallasi*)."

The northeastern Pacific Ocean, including the Alaska Current and Ridge systems, is known to be a favored Karluk sockeye feeding area (Fig. 4-15). In the eastern Alaska Current, Le Brasseur (1966) found that fish followed by euphausiids were the most important foods in mature sockeye stomachs, whereas the immature sockeye stomachs contained amphipods and euphausiids in equal amounts. Although no stomachs were examined, McAlister et al. (1969) reported immature sockeye concentrated in autumn in the Ridge Domain where there was an abundance of euphausiids. Because the areas sampled by Le Brassure and McAlister et al. are adjacent and high concentrations of euphausiids were found in the stomachs and in the environment, feeding was probably associated more with availability than with preferences for specific organisms.

The western Bering Sea off Kamchatka is another known feeding area for Karluk sockeye. Andrievskaya (1957) found that sockeye stomachs from this area contained 60% euphausiids, 28% young fish, and 13% copepods, plus some young squids, crab larvae, pteropods, and insects. He also examined sockeye stomachs from just south of the western Aleutian Islands and reported that copepods were dominant (53%) followed by euphausiids, amphipods, pteropods and young fish in equal proportions.

Some contradictory and unusual discoveries were reported by investigators of sockeye food habits. Both Le Brasseur (1966) and Dell (1963) reported differences in food preferences by maturity stages of sockeye with euphausiids being more favored by immatures. However, Ito (1964) and Andrievskaya (1957) found no food preference by maturity stage. Additionally, Andrievskaya reported that sockeye contained a significantly less volume

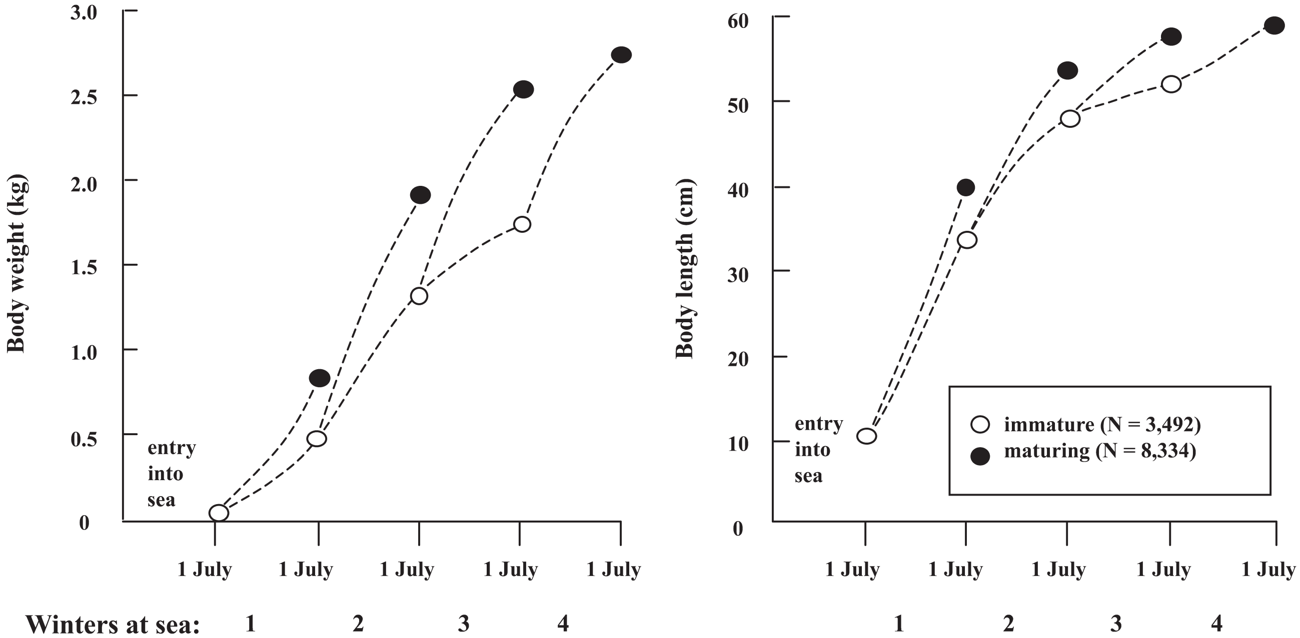

Figure 4-18. Estimated mean body weights and lengths of sockeye salmon on 1 July (Lander et al., 1966, in French et al., 1976, Fig. 36). Connecting lines indicate related stages, not actual growth.

of food than did pink or chum salmon even though their diets were similar. Perhaps pink and chum gorge themselves more than sockeye do because the former generally spend less time feeding before they spawn.

Size and Growth at Sea

There is little specific information on size and growth at sea for Karluk sockeye, but there is some general information for combined stocks (Fig. 4-18). Growth in length is greatest during the first year at sea and decreases progressively each year thereafter, whereas growth in weight is greatest in the second year followed by sequential decreases. At a given age, maturing fish are larger than immature fish. Also, male sockeye are larger than females by the spring of their second winter at sea and remain longer until death (Lander and Tanonaka, 1964).

It was formerly thought that little sockeye growth occurs in winter and early spring, but French et al. (1976) present average lengths of combined stocks from the North Pacific and Bering Sea which shows that growth continues through most of the year (Fig. 4-19). Appreciable growth occurred between September and winter and between winter and April.

Indirect evidence of seasonal trends in growth of Karluk sockeye in the sea comes from scales. The most common Karluk age group is the 5_3 which indicates that the fish spent 3 years in freshwater and 2 years in the ocean (Fig. 4-20). Moving out from the center (focus) of the scale we see the first two annuli, the area where the circuli are close together, which occurred in freshwater. These two annuli formed during the winter in the lake. After annulus 2 the fish went to sea and the circuli are wide apart and numerous, indicating a long period of fast growth. During the first winter at sea annulus 3 was formed and was followed by a second period of strong growth terminated by annulus 4, after which there was some spring growth before the fish returned to the natal river. Bilton and Ludwig (1966), after examining sockeye scales from the Gulf of Alaska collected in January and February, concluded that the annual ring was probably formed between November and January and, on the average, was completed in January. Therefore, if body growth slowed down during the formation of the annual ring, the slow growth was for a relatively short period of time.

Survival in the Ocean

Total ocean survival of Karluk sockeye has been determined by marking smolts and recording the presence of marked adults in future runs and by estimating the number of migrating smolts and determining the number of returning brood year adults. For both methods, numbers of fish in the catch and escapement had to be determined, as well as appropriate age structures. See Barnaby (1944) and Gard and Drucker (1966a, b) for further details. These ocean survival rates included some time in freshwater because the weirs where enumeration or marking were conducted were 6–37 km from the sea.

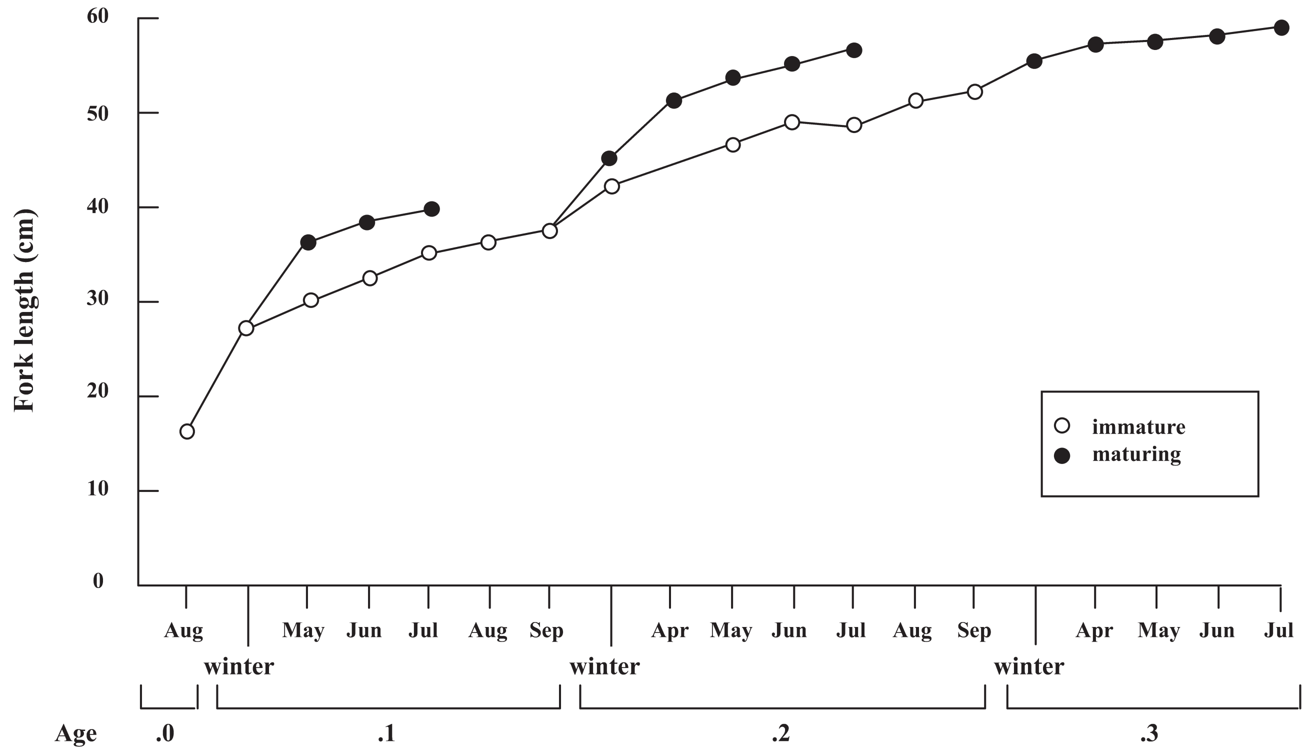

Figure 4-19. Average fork lengths of sockeye salmon taken at sea by ocean age and time periods (from French et al., 1976, Fig. 40). Data from gillnet catches, combined sexes, and for all areas in the North Pacific Ocean and Bering Sea.

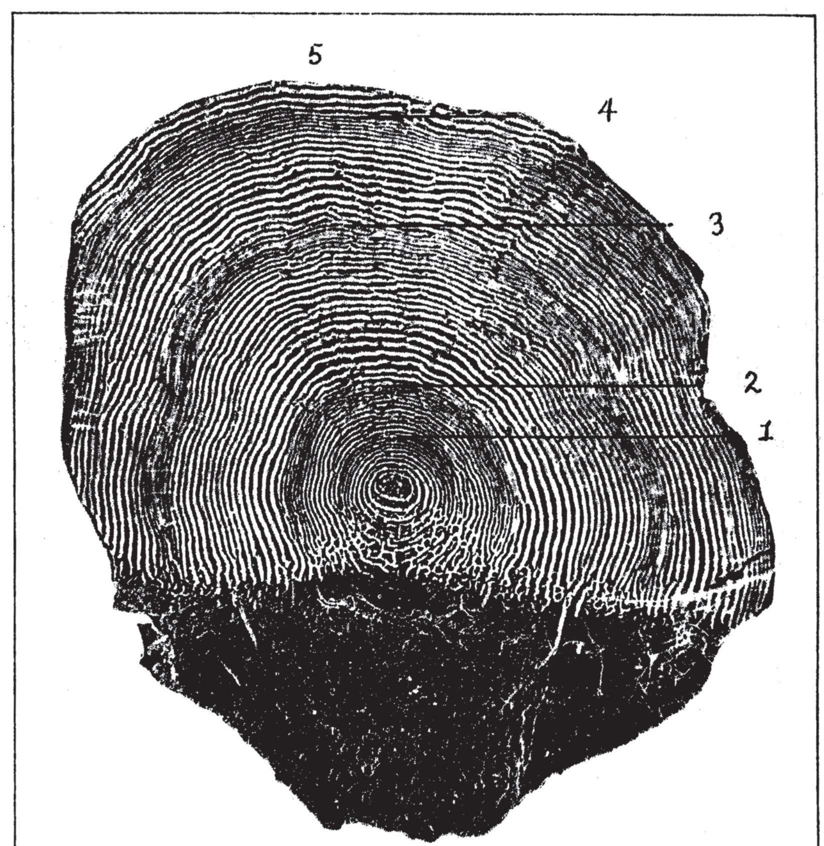

Figure 4-20. Scale from an age 5_3 male sockeye salmon taken on 9 June 1924 at the lower Karluk River weir (from Gilbert and Rich, 1927).

Table 4-21
Marine survival of sockeye salmon from Karluk Lake (from Drucker, 1970).

Smolt migration year	Number of smolts (1,000s)	Returning adults (1000s) by year								Survival (%)
		1962	1963	1964	1965	1966	1967	1968	Total	
1961	1694	28.1	418.0	82.6	0.4				529.1	31.2
1962	1444		17.6	631.6	66.1	0.7			716.0	49.6
1963	1540			36.8	469.5	71.1			577.4	37.5
1964	1561				14.0	656.5	129.5	0.3	800.3	51.3
1965	1469					6.8	408.1	78.9	>493.8	>33.6
1966	1082						5.4	379.0	>384.4	>35.5
									Average	>39.8

The first ocean survival rates for Karluk sockeye were determined by Barnaby (1944). He marked migrating smolts at the Lagoon weir by removing the adipose fin and one or both of the ventral fins and recovering the marked returning adults from canneries on Karluk Spit and at Larsen and Uyak bays. Ocean survival rates so determined for smolt migration years 1926 and 1929 through 1933 were 20.8% (incomplete), 22.3%, 21.0%, 23.6%, 20.5%, and 20.5%, respectively, with a 6-year mean of 21.4%. These survival rates were unusually uniform and high when compared to a 6–17% variation for five years of data from Chilko Lake or a 2–18% variation for 18 years of data from Cultus Lake (Ricker, 1962, Fig. 1).

When Barnaby combined all his data into 3-freshwater and 4-freshwater groups, he found that respective ocean survival rates were 17.4% and 25.7%. That would suggest that older (and also longer) smolts survived better in the ocean than did younger (and shorter) smolts. However, any survival advantage enjoyed by the older fish in the ocean could have been offset by increased freshwater mortality that resulted from spending an additional year in the lake. In an evaluation of six sockeye populations from North America and Siberia, Ricker (1962, Fig. 1) also demonstrated that ocean survival rate generally increased in larger smolts.

Although Barnaby recognized that there may have been differential mortality between marked and unmarked fish, he did not correct his survival rates accordingly because he did not believe the differences would be very great and because marked fish held in tanks for several days did not display ill effects. However, Ricker (1962) believed that delayed mortality due to marking may have occurred and corrected Barnaby's survival rates using information obtained at Cultus Lake by Foerster (1934, 1936, 1937). These corrections resulted in increased ocean survival of 3-freshwater Karluk fish from 17.4% to 27.4% and of 4-freshwater fish from 25.7% to 34.2%.

Recent ocean survival rates of sockeye (1962–83) for nine Alaskan lakes including Karluk combined with those from Ricker (1962, Fig. 1) indicated that a polynomial curve described the relationship between smolt length and marine survival better ($P < 0.001$, F-test) than a straight line (not significant) (Koenings and Burkett, 1987a, Fig. 8). Marine survival increased with increasing smolt length to about 110 mm, leveled off, and then decreased after a length of about 130 mm. Also, ocean survival rates of many sockeye populations have increased on the average during the past 30–50 years. This was especially evident for Karluk Lake where sockeye marine survival rates between 1961 and 1966 ranged from 31.2% to 51.3% (Table 4-21) and in later years up to about 60% (Koenings and Burkett, 1987a).

Harvest

Sockeye salmon have been harvested in the Karluk River for over 200 years. In 1785–86 a party of Russians, Aleuts, and Alutiiq established a post on the Karluk River and harvested salmon from the river to produce dried and salted fish for native fur hunting parties and for local use. These activities continued sporadically until the United States purchased Alaska from the Russians and three salting operations were founded in 1867. Three years later, the Alaska Fur Trading Company and Alaska Commercial Company entered the sockeye salting business which increased in succeeding years. Karluk River was becoming an important sockeye salmon processing center and Bean (1887) stated: "Karluk River, on the west side of Kodiak Island, furnishes more salt salmon than any other Alaska stream, about sixteen hundred barrels having been secured there during the season of 1880 by two firms." Additionally, Captain Bowen told Bean that at least 100,000 salmon were caught and dried.

Commercial fishing at Karluk is often considered to have started in 1882 when the first cannery was constructed on Karluk Spit by Oliver Smith and Charles Hirsch; it was subsequently known as the Karluk Packing Company in 1884. This cannery was followed by two others constructed on Karluk Spit, another just west of the Karluk River mouth, and a fourth at Larsen Bay in 1888. Still another cannery was built on the Spit in 1889, bringing the total to five canneries (Gilbert and Rich, 1927, Table 1). The result of this rapid expansion of processing capacity was over production of canned salmon in 1888–89.

There were many restrictions relating to permissible fishing gear and areas open to fishing. All salmon fishing was conducted within Karluk Lagoon and River through 1888, but in 1889 beach seining in ocean water outside the river mouth was begun. Karluk River and Lagoon were closed to commercial fishing in 1918. Gill nets, purse seines, and stationary and floating traps were all used at various times in the commercial Karluk salmon fishery; restrictions came and were sometimes rescinded later. Purse seines and floating traps were prohibited in 1924, with the seines being legalized in 1933. However, in 1946 seines were disallowed within 500 yards of the Karluk River mouth. Fish traps were prohibited in the Kodiak Region for commercial fishing in 1958 and after statehood were ruled illegal for virtually all of Alaska in 1960.

Sockeye salmon catches for the Karluk River have varied enormously since the inception of the fishery in 1882, from a high of nearly 4 million in 1901 to lows of only a few thousand in 1955 and 1971–73 when the fishery was closed due to low escapements, and again in 1989 when the *Exxon Valdez* oil spill occurred (Fig. 1-2). Let us examine the changes in catch that occurred by mostly 10-year periods (Table 4-22). From 1882 to 1890 the fishery grew rapidly from about 60,000 to over 3 million fish (average 1.3 million). During 1891–1900 the fishery reached its zenith with a mean catch of 2.5 million and this was followed by another decade with large harvests that averaged 2.2 million fish. Thereafter, the numbers decreased progressively despite a huge catch of 2.4 million in 1926. It appeared that the fishery bottomed out during the 1950s because a modest increase occurred in the 1960s (average, 226,000), but the 1970s were a disaster with a mean of only 120,000 taken. During the 1980s numbers improved somewhat, but the average catch doubled to 575,000 in the 1990s and 555,000 in the 2001–10 period. Various theories that attempt to explain the decline and recovery of the catch (and run) are discussed in Chapter 11.

Table 4-22
Average catch of Karluk River sockeye salmon by 10-year periods. (See Fig. 1-2 for data sources.)

Years	Average catch
1882–1890	1,332,277
1891–1900	2,503,987
1901–1910	2,205,012
1911–1920	1,342,631
1921–1930	974,198
1931–1940	799,054
1941–1950	487,353
1951–1960	144,710
1961–1970	226,164
1971–1980	120,131
1981–1990	273,916
1991–2000	575,025
2001–2010	555,420

Cyclic fluctuations in abundance of sockeye occurred in a number of rivers and were apparent in catches from Karluk during the earlier years of the fishery. Excluding the earliest years through 1895 when the fishery was building up to consistently high catches, 5-year cycles began to appear (Fig. 1-2). The 1896 catch was high and was followed by a somewhat lower catch in 1897, a low catch in 1898, a still lower catch in 1899, and a high catch again in 1900. This pattern with minor variations repeated itself during four successive cycles, but it started to weaken with the 1921 cycle when the catch in the second year was the lowest of the five (Gilbert and Rich, 1927, Fig. 7). Thereafter, the 5-year cycles disappeared and never returned. It was reasonable to expect that a 5-year cycle would develop at Karluk because the majority of the fish mature at five years of age, i.e. if catch and escapement are generally proportional, a high catch one year should be followed by a high catch five years hence. The mechanism involved in maintaining cycles could be cannibalism by a large year class on subsequent year classes or interactions between the spring and fall runs. Karluk Lake, with up to five year classes of juveniles present at any one time, would be a likely situation where cannibalism could be involved. Other possibilities for interaction between year classes could be depletion of their food supply by the dominant year class, or depletion of oxygen in the spawning gravels, caused by abundant decomposing eggs deposited by the dominant year class, thus lowering survival of subsequent year classes (Ricker and Smith, 1975). Obviously, some changes occurred within Karluk Lake that caused the cycles to disappear and may also be responsible for the depletion of the runs.

Conclusion

Much has been learned during the past years of study about the life history of the unique and diverse Karluk sockeye salmon. However, there is one important aspect about which we know virtually nothing. This is the food habits of the rapidly-growing pre-smolts in the lake during the late fall and winter and the potential food then available. The proportion of marine nitrogen isotopes present in pre-smolts increased sharply at that time and this change was possibly from cannibalism on younger sockeye or predation on sticklebacks (Kline, 1993; Kline and Goering, 1993). Only a fall and winter food habits study will verify or disprove this hypothesis.