SOME LIFE HISTORY CHARACTERISTICS OF COHO SALMON OF THE KARLUK RIVER SYSTEM, KODIAK ISLAND, ALASKA

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ABSTRACT

This paper contains data on some life history characteristics of the coho salmon of the Karluk River system, Kodiak Island, Alaska: age, fecundity, length, and egg size of adults; and migration characteristics, age, and size of smolts. The greater age at maturity of Karluk coho salmon (4 and 5 years) because of the longer freshwater residence of the juveniles is unique among reported North American stocks and may result in greater freshwater mortality but less marine mortality because the smolts are larger when they enter the ocean. Fecundity of Karluk coho salmon also differs from that reported for other North American stocks in that they are extremely fecund—more similar to Asiatic stocks of the Kamchatka Peninsula.

Coho salmon, *Oncorhynchus kisutch,* are widely distributed along the Pacific coast of North America and occur in commercially harvestable quantities from northern California to northwestern Alaska. About one-third of the total North American commercial catch comes from Alaska waters, where from 1960 to 1968 the average annual catch of 16 million pounds was valued at almost $3.5 million to the fishermen.[2] The amount of biological research on coho salmon in Alaska is small, and published scientific reports on Alaska coho salmon stocks are very few.

In this paper I present data on some life history characteristics of the coho salmon of the Karluk River system. This system is located on the southwest side of Kodiak Island, Alaska, at approximately lat 57° N and long 154° W and includes Karluk Lake, tributaries to the lake, Thumb and O'Malley Lakes, and Karluk River (Figure 1). Information is presented on age, fecundity, length, and egg size of coho salmon adults; and migration characteristics, age, and

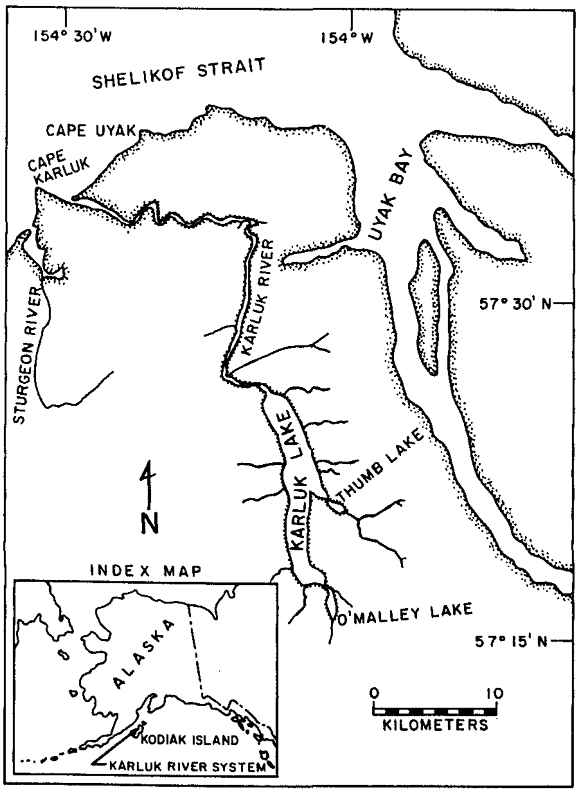

FIGURE 1.—The Karluk River system, Kodiak Island, Alaska.

[1] National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821; present address: National Marine Fisheries Service, Technical Advisory Division, Interior Building, Washington, D.C. 20235.

[2] Nelson, Richard C. 1968. Alaska catch and production, commercial fisheries statistics. Alaska Dep. Fish Game, Stat. Leafl. 17, 29 p. (Unpublished.)

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size of coho salmon smolts. These life history features of Karluk coho salmon are compared with those reported for various coho salmon stocks from other areas on both the Asiatic and North American sides of the Pacific Ocean. In addition, the effect of a prolonged juvenile freshwater residence, a feature unique to the Karluk system, on freshwater and marine survival is discussed. All of the data on Karluk coho salmon were collected incidentally during studies of sockeye salmon, *O. nerka*, the dominant salmon species in the Karluk system; much of the information on other Alaska stocks is from unpublished administrative and progress reports.

Because I intend to discuss differences between coho salmon in the Karluk system and those in other areas, a description of general features of the life cycle of coho salmon stocks is appropriate. Typically, the adults enter streams and rivers from late summer to November and spawn in late fall and early winter. Some Asiatic stocks, however, spawn as late as mid-March (Smirnov, 1960). The progeny emerge as fry in the spring following spawning and reside in rivers or lakes for 1 or 2 years before going to sea as smolts. In some areas the seaward smolt migration begins in late winter (Chapman, 1961; Smoker, 1953), but in most areas it takes place from April to August (Godfrey, 1965). The salmon grow rapidly in the ocean, and the adults return to the streams and rivers to spawn 12 to 18 months later. However, a significant percentage of male coho salmon, particularly in their southern range of distribution in North America (California), mature precociously (6 to 9 months after they enter salt water) and return to spawn the same year that they migrated to sea (Shapovalov and Taft, 1954). These fish are known as jack salmon.

METHODS

The data for adult coho salmon of the Karluk system were obtained from fish from the 1966 escapement that were captured at the adult counting weir or caught by sport fishermen at the outlet of Karluk Lake about 300 yards upstream from the weir site. All fish were measured for length (mideye to fork of tail) with a caliper to the nearest millimeter. Mideye-fork length was used because of morphological changes that occur as the fish matures, particularly the elongation of the snout. Ovaries for fecundity samples were removed from all females and were preserved in 10% Formalin solution for at least 48 hr. The eggs were then hand-counted to get total egg counts. The diameters of some eggs from the fecundity samples were measured. These eggs were removed directly from the ovary, water hardened, and placed in Stockard's solution. The diameters were then measured with a vernier measuring microscope calibrated to 0.01 mm. The ages of adult fish were determined by reading scales that had been taken halfway between the lateral line and the posterior insertion of the dorsal fin.

The data for smolts were obtained from fish captured in 1956, 1965, and 1968 in fyke nets fished on the downstream side of the adult counting weir. Fork lengths were taken to the nearest millimeter with a steel millimeter ruler, and weights were taken to the nearest tenth of a gram on a triple-beam balance. As with the adults, the ages of smolts were determined from scales taken halfway between the lateral line and the posterior insertion of the dorsal fin.

AGE OF COHO SALMON

The average age composition of coho salmon for several systems in northern and southern latitudes of North America and Asia is shown in Table 1. The differences from the northern to southern latitudes in age composition is similar to that noted by Marr (1943) and possibly represent a geographic cline.

The Karluk system had three freshwater age classes,[3] two of which were decidedly predominant (Table 1). The three age classes, 4_3, 5_4, and 6_5, designate fish that went to sea in their third, fourth, and fifth years of life and returned to spawn after being at sea for about 1 year.

[3] Age classes are designated according to the system developed by Gilbert and Rich (1927). A 4_3 coho salmon is in its fourth year of life. It went to sea as a smolt at the beginning of its third year, having spent two growing seasons in fresh water.

TABLE 1.—Age class composition of stocks of coho salmon from North America and Asia, arranged geographically from north to south.

Area	Percent coho salmon in age class—											Reference
	2_1	2_2	3_1	3_2	3_3	4_1	4_2	4_3	5_3	5_4	6_5	
North America												
Nome River, Alaska	--	--	--	29.4	--	--	--	70.6	--	--	--	Godfrey (1965)
Unalakleet River, Alaska	--	--	--	37.9	--	--	--	62.1	--	--	--	Godfrey (1965)
Yukon River, Alaska	--	--	--	55.6	--	--	--	44.4	--	--	--	Godfrey (1965)
Yukon River, Alaska	--	--	--	38.7	--	--	--	58.1	--	3.2	--	Gilbert (1922)
Cook Inlet River, Alaska	--	--	--	40.0	--	--	--	60.0	--	--	--	Godfrey (1965)
Resurrection Bay, Alaska	--	--	--	30.3	--	--	--	68.8	--	0.9	--	Logan (1963,[1] 1964[2])
Bear Creek, Alaska	--	--	--	27.1	--	--	--	71.1	--	1.8	--	Logan (1964)[2]
Dairy Creek, Alaska	--	--	--	[3]83.3	--	--	--	16.7	--	--	--	Logan (1964)[2]
Mendenhall River, Alaska	--	--	--	12.0	8.0	--	--	80.0	--	--	--	([4])
Hood Bay Creek, Alaska	--	--	--	46.5	--	--	--	47.5	--	6.0	--	Armstrong (1970)
Karluk River, Alaska	--	--	--	--	--	--	--	56.9	--	41.7	1.4	Present study
Sashin Creek, Alaska	--	--	--	18.0	--	--	--	77.0	--	5.0	--	Crone (1968)
Port Herbert, Alaska	--	--	--	20.0	--	--	--	76.0	--	4.0	--	Crone (1968)
Stikine River, Alaska	--	--	--	45.2	--	--	1.0	51.9	1.9	--	--	Godfrey (1965)
Chignik River, Alaska	--	--	--	23.2	--	--	--	72.4	--	4.4	--	Israel (1933)
Ketchikan River, Alaska	--	--	--	70.8	--	--	--	29.2	--	--	--	Godfrey (1965)
Quatsino Bay, British Columbia	--	2.0	--	95.0	--	--	3.0	--	--	--	--	Godfrey (1965)
Fraser River, British Columbia	2.6	--	0.7	96.5	--	--	0.2	--	--	--	--	Godfrey (1965)
Georgia Strait, British Columbia	1.5	0.6	0.4	97.1	--	--	0.4	--	--	--	--	Godfrey (1965)
West coast, Vancouver Island, British Columbia	1.3	--	0.6	97.5	--	--	0.4	0.2	--	--	--	Godfrey (1965)
Langara Island, Georgia Strait, British Columbia	0.1	0.1	0.2	97.9	Tr.	0.1	0.7	0.9	--	--	--	Pritchard (1940)
Columbia River, Wash.	--	6.1	--	83.9	0.3	--	--	9.7	--	--	--	Marr (1943)
Waddell Creek, Calif.	--	18.4	--	81.6	--	--	--	--	--	--	--	Shapovalov and Taft (1954)
Asia												
East coast of Kamchatka, USSR:												
Kamchatka River	--	1.2	--	55.7	--	--	--	43.1	--	--	--	Godfrey (1965); Gribanov (1948)
Lake Ushki	--	Tr.	--	4.3	Tr.	--	--	92.9	--	2.8	--	Gribanov (1948)
Kyrganik River	--	Tr.	--	93.6	Tr.	--	--	6.4	--	--	--	Gribanov (1948)
Paratunka River	--	Tr.	--	57.4	Tr.	--	--	42.6	--	--	--	Gribanov (1948)
Avachin Gulf, Solevarka Bay	--	Tr.	--	80.2	Tr.	--	--	19.8	--	--	--	Gribanov (1948)
Kalyger River	--	Tr.	--	27.5	Tr.	--	--	72.5	--	--	--	Gribanov (1948)
West coast of Kamchatka, USSR:												
Kikhchik River	--	Tr.	--	100.0	Tr.	--	--	--	--	--	--	Gribanov (1948)
Bolshaya River	--	--	Tr.	69.3	Tr.	--	--	30.1	--	--	--	Godfrey (1965); Gribanov (1948); Semko (1954)
Ozernaia River	--	--	Tr.	100.0	Tr.	--	--	--	--	--	--	Gribanov (1948)
Kukhtui River (Okhotsk)	--	--	--	32.8	--	--	--	67.2	--	--	--	Godfrey (1965)

[1] Logan, Sidney M. 1963. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1962-63, Vol. 4: 175-194, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[2] Logan, Sidney M. 1964. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 133-151, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[3] The high percentage of age 3_2 fish is atypical and not representative of Resurrection Bay streams. Dairy Creek juveniles are reared in a brackish water lagoon rather than in the stream itself, resulting in 1-year smolts. (Personal communication, Sidney Logan, Area Management Biologist, Alaska Department of Fish and Game, Soldotna, Alaska, March 15, 1971.)
[4] Collected by author in 1966.

Fifty-seven percent of the Karluk fish had migrated in their third year and 42% in their fourth year; only 1% had migrated in their fifth year (Table 1). Although the freshwater residence of fish in the Karluk escapement varied from 2 to 4 years, Karluk coho salmon, like those in all other systems, returned to spawn after being at sea for 12 to 18 months.

The presence of large numbers of fish (42%) that had spent 3 years in freshwater residence (age class 5_4) is unique to the Karluk system. Fish of age class 5_4 have been found in other Alaska river systems, i.e., the Yukon River (Gilbert, 1922), Resurrection Bay and Bear Creek (see footnotes 1 and 2, Table 1), Hood Bay Creek (Armstrong, 1970), Sashin Creek and Port Herbert (Crone, 1968), and Chignik River (Israel, 1933); but the proportion of 5_4 fish in the total runs to these systems is small—usually less than 5% (Table 1).

The age composition of stocks of coho salmon from systems on the Kamchatka Peninsula, USSR, is similar to that of coho salmon in the northern areas of the west coast of North America. The main age classes are 3_2 and 4_3 (Table 1). The ratio of one age class to the other varies, however, from year to year and from area to area (Gribanov, 1948; Semko, 1954).

An additional comparison of the age composition of coho salmon from northern to southern latitudes is shown in Figure 2, which gives the percent age composition of the major age classes from five geographical areas along the west coast of North America. In California, the southern limit of the range of coho salmon, the major age class is 3_2, but jack salmon (age 2_2) contribute significantly to the runs. The 3_2 age class is still dominant in Washington, but the number of jack salmon is less and 4_3 fish are starting to appear. North of Washington to central British Columbia, more than 95% of the fish are age 3_2, and there are only traces of other age classes, mainly the 4_3 class. From central British Columbia and northward through Alaska, the primary age class is 4_3; 3_2 fish are the secondary class and 5_4 fish are found in small numbers. In Alaska, the increase in total age is the result of juvenile coho salmon residing an additional year in fresh water before migrating to sea. Possible exceptions to the dominance of the 4_3 age class in Alaska are the Ketchikan River, Dairy Creek, Yukon River, and Karluk River systems (Table 1). In the first three river systems, 3_2 fish are the dominant age class and 4_3 fish the secondary class. The sizes of the samples from these systems were small, however (less than 25 fish). In the Karluk system, although 4_3 fish were dominant, 5_4 fish rather than 3_2 fish were the secondary age class (Figure 2).

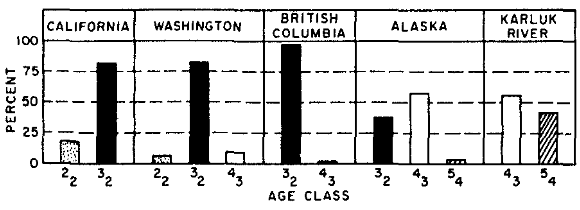

FIGURE 2.—Average age composition of coho salmon runs along the west coast of North America by geographical area (minor age classes omitted).

The presence of older fish (5_4) in northern latitudes may be a result of the juveniles being reared in lakes rather than rivers. Typically, coho salmon spawn in rivers or tributaries to rivers and the emerging fry reside in these areas until they migrate to sea. In contrast, in some Alaska river systems where 5_4 fish are part of the run (Table 1 and Figure 2), the juveniles migrate from spawning grounds to lakes before migrating to sea. It appears that some of the juveniles that reside in lakes (lake type) go to sea at an older age than those that reside in rivers (river type).[4]

NUMBER AND SIZE OF EGGS

In this section, information is presented on fecundity (number of eggs contained in a female) as a function of latitude and length, the relative numbers of eggs in right and left ovaries, and egg size in relation to length and fecundity. Fecundity and factors related to it form the basis for determining the reproductive potential of a spawning stock and subsequent survival from egg to young. Knowledge of variations in fecundity and egg size is of increasing importance in fish stocking and fish rehabilitation programs. Size of egg may be useful in predicting the condition, or hardiness, of developing fry. Because the fecundity of fish differs among geographic areas, the reproductive potential must be determined for each stock.

FECUNDITY AS A FUNCTION OF LATITUDE

The average fecundity for both North American and Asiatic stocks of coho salmon is considerably higher in fish from northern latitudes than in those from southern latitudes (Table 2 and Figure 3). Coho salmon from Alaska river systems (with the exception of the two small samples from Port Herbert and Sashin Creek)

[4] Personal communication, 1969, Charles J. DiCostanzo, Chief, Salmon Investigations, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821.

TABLE 2.—Average fecundity of coho salmon stocks from North American and Asiatic river systems, arranged geographically from north to south.

Area	Latitude	Average number of eggs	Reference
North America			
Swanson River, Alaska	61° N	3,378	Engel (1966)[1]
Bear Creek, Alaska	60° N	4,115	Lawler (1963,[2] 1964[3])
Dairy Creek, Alaska	60° N	4,177	Engel (1965),[4]; Lawler (1963)[2]
Karluk River, Alaska	57° N	4,706	Present study
Pasagshak River, Alaska	57° N	4,510	Marriott (1968)[5]
Sashin Creek, Alaska	56° N	2,868	Crone (1968)
Port Herbert, Alaska	56° N	2,565	Crone (1968)
Namu River, British Columbia	54° N	3,002	Foerster and Pritchard (1936)
Fraser River, British Columbia	53° N	3,152	Foerster and Pritchard (1936)
Nile Creek, British Columbia	49° N	2,310	Wickett (1951)
Cultus Lake Hatchery, British Columbia	49° N	2,300	Foerster and Ricker (1953)
Port John, British Columbia	49° N	2,313	Hunter (1948)
Cowichan River, British Columbia	48° N	2,329	Neave (1948)
Oliver Creek, British Columbia	48° N	2,267	Foerster (1944)
Beadnell Creek, British Columbia	48° N	2,789	Foerster (1944)
Seattle, Wash.	47° N	3,141	Allen (1958)
Minter Creek, Wash.	47° N	2,447	Salo and Bayliff (1958)
Fall Creek, Alsea River, Ore.	44° N	1,983	Koski (1966)
Scott Creek, Calif.	37° N	2,336	Shapovalov and Taft (1954)
Asia			
East coast of Kamchatka, USSR:			
Ushki Hatchery	56° N	5,282	Gribanov (1948)
Kamchatka River	56° N	4,883	Gribanov (1948)
Paratunka River	53° N	4,350	Gribanov (1948)
West coast of Kamchatka, USSR:			
Bolshaya River	53° N	4,638	Semko (1954)
Sakhalin Island, USSR:			
Tymi River	52° N	4,570	Smirnov (1960)

[1] Engel, Larry J. 1966. Egg-take investigations in Cook Inlet drainage and Prince William Sound. *In* Federal aid in fish restoration, 1965-66 progress report, Vol. 7: 109-116, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[2] Lawler, Robert E. 1963. Silver salmon egg taking investigations in Cook Inlet drainage. *In* Dingell-Johnson project report, 1962-63, Vol. 4: 161-173, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[3] Lawler, Robert E. 1964. Egg take investigations in Cook Inlet and Prince William Sound. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 123-132, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[4] Engel, Larry J. 1965. Egg take investigations in Cook Inlet drainage and Prince William Sound. *In* Dingell-Johnson project report, 1964-65, Vol. 6: 155-163, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[5] Marriott, Richard A. 1968. Inventory and cataloging of the sport fish waters in southwest Alaska. *In* Federal aid in fish restoration, 1967-68 progress report, Vol. 9: 81-93. Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

are more fecund than coho salmon from more southerly areas in North America (Figure 3). Stocks of coho salmon from Asiatic river systems are extremely fecund, even more so than North American stocks in more northerly latitudes. The high fecundity of Karluk River coho salmon more closely resembles the fecundity of Asiatic stocks than North American ones.

Contrary to these findings for coho salmon, Rounsefell (1957) suggests that for the genus *Oncorhynchus*, salmon in southern latitudes may be more fecund than those in northern latitudes because of ". . . the higher age at maturity, and therefore slower growth rates, from south to north." Rounsefell found that the amount of time juvenile sockeye salmon spent in fresh water had no effect on fecundity, but the amount of time the adults spent at sea did have an effect: adult sockeye salmon that spent 2 years at sea had higher fecundity counts than fish of the same size that spent 3 years at sea. With coho salmon, however, the greater age at maturity is not due to increased time in the ocean but to increased time in fresh water.

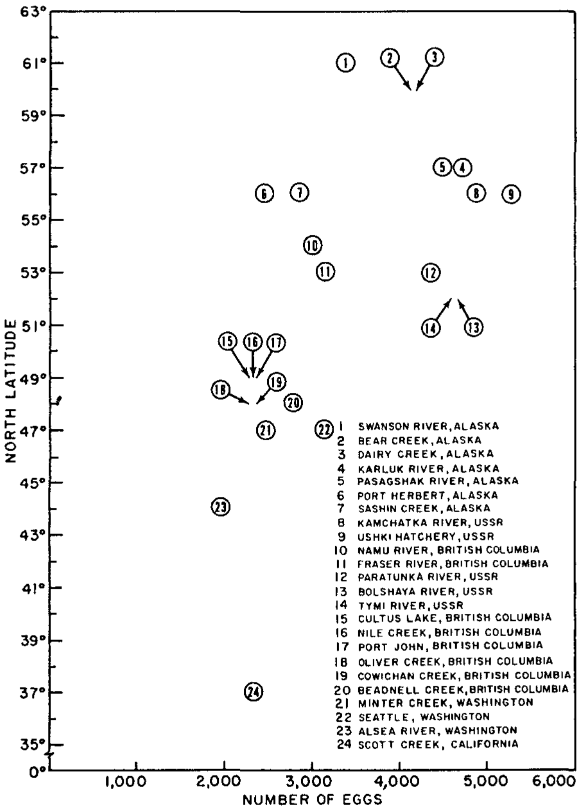

FIGURE 3.—Average fecundity of various stocks of coho salmon from North America and Asia.

FECUNDITY AS A FUNCTION OF LENGTH

The presence of a positive relation between fecundity and length in the genus *Oncorhynchus* is well known (Gilbert and Rich, 1927; Foerster and Pritchard, 1941; Allen, 1958; Hartman and Conkle, 1960). For fish in general, the relation of fecundity to length is logarithmic ($\hat{Y} = aX^b$) over a wide range of lengths. For salmon, however, the narrow range in length at maturity permits this relation to be described adequately by a straight line of the form $\hat{Y} = a + bX$ (Foerster and Pritchard, 1941; Rounsefell, 1957).

I counted the total number of eggs in 49 coho salmon from the Karluk River and calculated the relation between number of eggs and mideye-fork length by the method of least squares. The result may be expressed by the equation $\hat{Y} = -7{,}503.55 + 195.51X$, where $\hat{Y}$ is the estimate of number of eggs and X is the mideye-fork length of female salmon (Figure 4). The mean number of eggs for the sample was 4,706 (range 1,724 to 6,906); the mean length was 62.1 cm (range 46.6 to 69.8 cm).

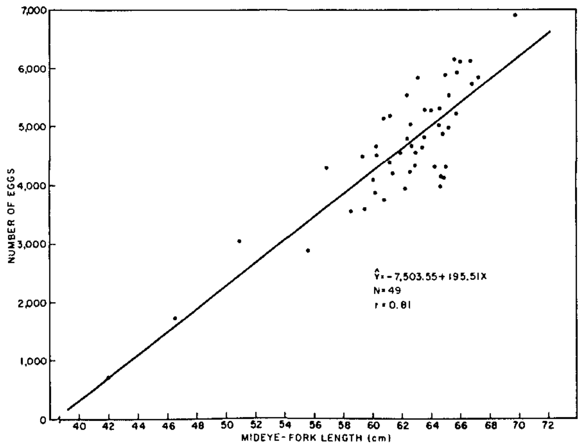

FIGURE 4.—Relation of fecundity to length of coho salmon sampled at Karluk weir, 1966.

It is difficult to determine if the high fecundity of coho salmon of the Karluk system (Figure 3) is due to greater fecundity per unit length or simply to the fact that coho salmon from Karluk are very large. The average lengths of female coho salmon from various spawning streams along the Pacific coast of North America are quite variable and do not seem to follow any set geographic pattern (Table 3). Moreover, Karluk fish were measured from mideye to fork of tail, and direct comparisons of lengths with coho salmon from other areas are difficult to make because of variability in the types of measurements used. For instance lengths reported from areas other than Karluk include tip of snout to fork of tail (fork length), tip of snout to tip of tail (total length), and tip of snout to base of tail (standard length).

TABLE 3.—Average lengths of female coho salmon from river systems along the Pacific coast of North America and Asia, arranged geographically from north to south.

Area	Average length				Reference
	Fork	Total	Standard	Mideye-fork	
	cm	*cm*	*cm*	*cm*	
North America					
Yukon River, Alaska	63.4	--	--	--	Gilbert (1922)
Swanson River, Alaska	62.0	--	--	--	Engel (1966)[1]
Resurrection Bay, Alaska	67.2	--	--	--	Logan (1965)[2]
Dairy Creek, Alaska	72.8	--	--	--	Engel (1965)[3]
Brooks River, Alaska	--	58.8	--	--	([4])
Karluk River, Alaska	--	--	--	62.1	Present study
Sashin Creek, Alaska	70.5	--	--	--	Crone (1968)
Port Herbert, Alaska	67.8	--	--	--	Crone (1968)
Namu River, British Columbia	--	69.0	--	--	Foerster and Pritchard (1936)
Fraser River, British Columbia	--	64.0	--	--	Foerster and Pritchard (1936)
Seattle, Wash.	63.4	--	--	--	Allen (1958)
Minter Creek, Wash.	--	--	62.1	--	Salo (1955)
Columbia River, Wash.	74.6	--	--	--	Marr (1943)
Deer Creek, Oreg.	70.7	--	--	--	Koski (1966)
Flynn Creek, Oreg.	69.4	--	--	--	Koski (1966)
Needle Branch, Oreg.	67.6	--	--	--	Koski (1966)
Scott Creek, Calif.	66.3	--	--	--	Shapovalov and Taft (1954)
Waddell Creek, Calif.	63.9	--	--	--	Shapovalov and Taft (1954)
Asia					
East coast of Kamchatka, USSR:					
Kamchatka River	60.9	--	--	--	Gribanov (1948)
Kyrganik River	68.1	--	--	--	Gribanov (1948)
Kalyger River	61.0	--	--	--	Gribanov (1948)
Avachin Gulf	55.4	--	--	--	Gribanov (1948)
Paratunka River	59.4	--	--	--	Gribanov (1948)
West coast of Kamchatka, USSR:					
Kikhchik River	58.6	--	--	--	Gribanov (1948)
Bolshaya River	57.4	--	--	--	Gribanov (1948)
Ozernaia River	62.6	--	--	--	Gribanov (1948)

[1] See footnote 1, Table 2.
[2] Logan, Sidney M. 1965. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1964-65, Vol. 6: 129-145, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[3] Lawler, Robert E. 1964. Egg take investigations in Cook Inlet and Prince William Sound. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 123-132, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[4] Eicher, George J., Jr. The effects of laddering a falls in a salmon stream. National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska, 5 p. (Unpublished.)

NUMBER OF EGGS IN RIGHT AND LEFT OVARIES

The numbers of eggs in the right and left ovaries of the genus *Oncorhynchus* are usually quite variable. Rounsefell (1957) noted that although the rate of maturation of eggs from Karluk Lake sockeye salmon was the same in both ovaries of the same fish, the number of eggs in each ovary varied. Eguchi and his co-workers (Rounsefell, 1957) found no significant differences in the numbers of eggs in the two ovaries in chum salmon, *O. keta*, in Japanese waters. Helle (1970) found the same lack of a significant difference in a sample of pink salmon, *O. gorbuscha*, from Olsen Bay, Alaska, in 1963. Sockeye salmon from Brooks Lake, Alaska, in 1957 and 1958 and from Karluk Lake in 1958 had more eggs in the left ovary than in the right (Hartman and Conkle, 1960). At Bare Lake, Alaska, sockeye salmon had more eggs in the right ovary than in the left (Nelson, 1959).

I compared the numbers of eggs from the right and left ovaries of Karluk River coho salmon (Table 4) by means of a t test for paired observations. The differences between the numbers of eggs in the right and left ovaries were significant ($t = 2.60$; df $= 31$; $P = 0.05$). In 31 fecundity samples, 71% had more eggs in the right ovary than the left. I could not find comparable information on comparisons between the numbers of eggs in the ovaries of coho salmon from other areas.

TABLE 4.—Numbers of eggs in right and left ovaries from coho salmon collected at the outlet to Karluk Lake, 1966.

Sample number	Mideye-fork length (cm)	Number of eggs		
		Right ovary	Left ovary	Total
1	50.9	1,640	1,403	3,043
2	61.4	2,265	1,918	4,183
3	65.0	3,005	2,876	5,881
4	56.9	2,213	2,083	4,296
5	62.7	2,322	2,337	4,659
6	65.6	3,001	3,147	6,148
7	69.8	3,559	3,347	6,906
8	64.7	2,258	1,884	4,142
9	62.6	2,546	2,501	5,047
10	60.2	2,433	2,220	4,653
11	59.3	2,243	2,225	4,468
12	60.2	2,331	2,161	4,492
13	62.3	2,481	2,283	4,764
14	61.2	2,620	2,539	5,159
15	60.1	2,067	2,000	4,067
16	63.5	2,581	2,221	4,802
17	64.5	2,473	2,546	5,019
18	67.2	2,604	3,233	5,837
19	60.2	2,044	1,813	3,857
20	65.2	2,824	2,697	5,521
21	64.0	2,608	2,659	5,267
22	65.1	2,491	2,501	4,992
23	66.0	2,926	3,174	6,100
24	62.9	2,266	2,280	4,546
25	65.8	3,047	2,878	5,925
26	64.6	2,726	2,579	5,305
27	63.6	2,721	2,563	5,284
28	66.7	3,104	2,997	6,101
29	63.1	2,981	2,843	5,824
30	61.9	2,176	2,125	4,301
31	64.8	2,340	2,521	4,861
Average	63.0	2,545	2,469	5,015

RELATION OF EGG SIZE TO LENGTH AND TO FECUNDITY

The average diameter of eggs obtained from the fecundity samples from Karluk River was plotted against the length of the female coho salmon from which the samples were taken (Figure 5) to determine if there was a relation between the size of a female and the size of her eggs. The size of eggs increases as they mature, and so the eggs used had to be in the same stage of maturation. I therefore selected only females beginning to show secondary sexual characteristics and containing eggs that could not be readily expressed from the body cavity. For 25 females the eggs varied in size from 4.92 to 6.88 mm (mean 6.11 mm); lengths varied from 50.4 to 69.8 cm (mean 62.0 cm). No relation was found between the size of the egg and the length of the fish. Allen (1958) in his studies of coho salmon in Green River, Wash., also found no relation.

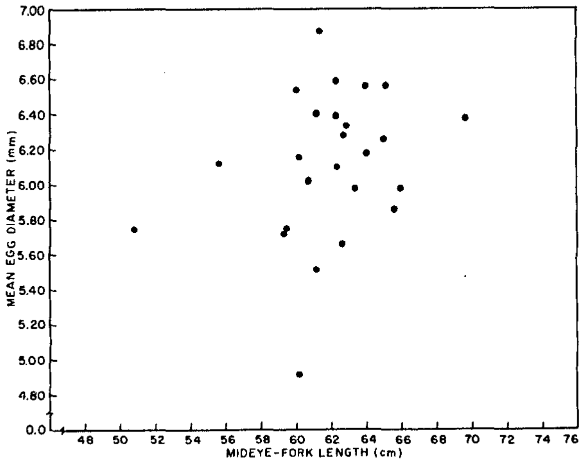

FIGURE 5.—Relation of mean egg diameter to mideye-fork length of female coho salmon, Karluk River, 1966.

The average diameters of eggs were plotted against number of eggs in individual fish to determine if a relation existed between the fecundity of a female and the size of her eggs (Figure 6). For 24 females, the egg diameter ranged

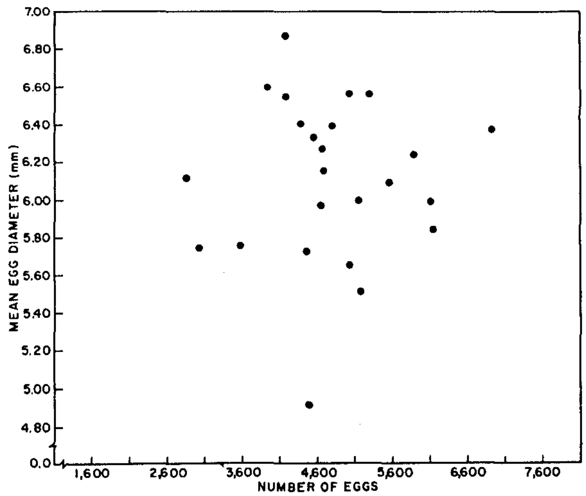

FIGURE 6.—Relation of mean egg diameter to number of eggs in female coho salmon, Karluk River, 1966.

from 4.91 to 6.87 mm (mean 6.11 mm); fecundity ranged from 2,855 to 6,906 (mean 4,766). No relation was found: eggs from a female with low fecundity were not necessarily large, nor were those from a female with high fecundity necessarily small. Allen (1958) reported similar findings.

Unlike the general relation that exists between fecundity and length (i.e., larger fish are more fecund), the size or fecundity of the females I sampled apparently had no relation to the size of the eggs. Large, fecund females had a wide range of egg sizes (Figure 5). Thus, the larger number of eggs in large females may be due to a larger body cavity that allows more eggs to develop rather than to the fish having smaller eggs.

COHO SALMON SMOLTS

Smolts of coho salmon, like those of other salmon that live for a while in fresh water before migrating to sea, migrate seaward at a particular season and under particular light intensities. This migration and the associated environmental factors and information on age and size of migrating smolts are discussed in this section.

SEASONAL MIGRATION

Coho salmon juveniles reside in Karluk Lake for 1 to 4 years before they migrate to sea as smolts. From 1961 to 1967 the migration began in mid-May and was usually over by early July (Figure 7).

Although most coho salmon migrate in the spring (Hamilton and Andrew, 1954; Taft, 1934; Gharrett and Hodges, 1950; Semko, 1954), several exceptions do exist. In the Paratunka River, Kamchatka Peninsula, the migration extends from the end of May to the end of August (Gribanov, 1948); in several streams in Oregon it extends from late winter to May (Chapman, 1961); in some streams in western Washington it runs from early winter to late spring (Smoker, 1953); and at Waddell Creek, Calif., small numbers of atypical migrants migrate in the fall and early winter (Shapovalov and Taft, 1954). The

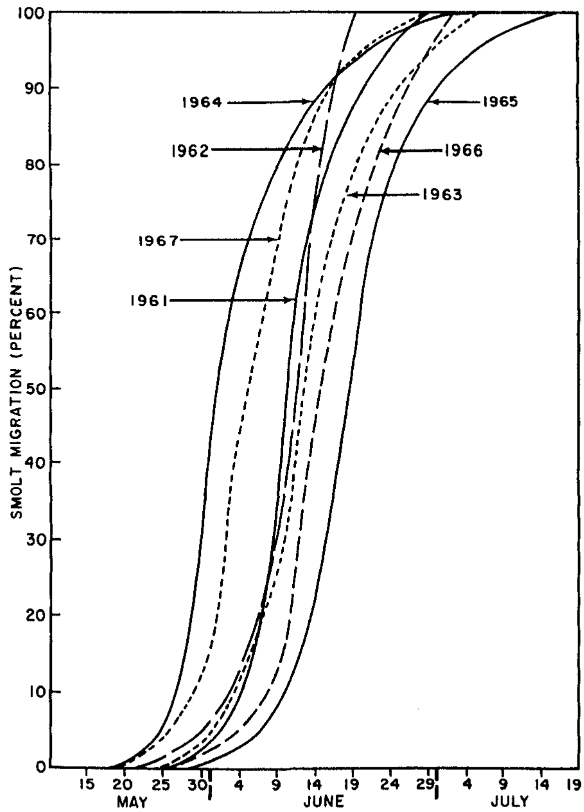

FIGURE 7.—Cumulative seasonal migration of coho salmon smolts from Karluk Lake, 1961-67.

number of coho salmon smolts involved in the early or late parts of these migrations, however, represents only a small percentage of the total number of smolts in each migration.

The warming of the water after the ice breaks up is of major importance in initiating the seaward migration of smolts. Hartman, Heard, and Drucker (1967) found this to be a major factor in the migration of sockeye salmon in lakes of southwestern Alaska; and Logan (see footnote 2, Table 1) found that the coho salmon smolt migration in Bear Lake, Alaska, did not start until the ice cover on the lake was gone and the water temperature had risen to 4.2° C. Ninety percent of the Bear Lake coho salmon smolts had migrated to sea when water temperatures ranged between 5° and 13.3° C. Coho salmon smolts apparently migrate over a greater temperature range than sockeye salmon, whose migration generally ends when water temperatures reach about 10° C (see footnote 2, Table 1).

At Karluk Lake, for each year from 1961 to 1968 (excluding 1964) the date by which 50% of the coho salmon smolts had migrated was later than the comparable date for sockeye salmon smolts (Table 5). The difference in time of the two migrations ran from 6 to 19 days (average 11 days). Not only did more of the coho salmon smolts migrate later than the sockeye salmon smolts, but the coho salmon smolts usually migrated during a period of relatively warmer water, when the abundance of migrating sockeye salmon smolts had greatly diminished. Similarly, Foerster and Ricker (1953) found that the coho salmon smolt migration in Cultus Lake and Sweltzer Creek, British Columbia, always followed the sockeye salmon smolt migration by about 10 days.

Although the seasonal timing of the outmigration of coho salmon smolts may vary from system to system, it is relatively consistent within a particular system. When time of migration is plotted against latitude, a definite south to north cline in time of migration becomes evident (Figure 8). Coho salmon smolts migrate later in the season in northerly systems than in more southerly ones. More than a month separates the midpoint of smolt migration from the central coast of California (lat 37° N) to the Gulf of Alaska (lat 60° N). This relation also applies for the Asiatic side of the Pacific Ocean.

DIEL PATTERN OF MIGRATION

The transformation of juvenile coho salmon from either lake- or stream-type residents to smolts is associated with avoidance of light and increasing nocturnal activity (Hoar, Keenleyside, and Goodall, 1957; Hoar, 1958; Smirnov, 1960).

TABLE 5.—Dates by which 50% of the coho and sockeye salmon smolts migrated from Karluk Lake, 1961-68.

Year	Sampling period	50% migration date	
		Coho salmon	Sockeye salmon
1961	May 25 to June 29	June 10	June 2
1962	May 17 to June 21	June 10	May 29
1963	May 18 to July 6	June 12	June 6
1964	May 17 to July 6	June 2	June 3
1965	May 16 to July 16	June 18	June 6
1966	May 18 to July 2	June 15	June 4
1967	May 18 to June 29	June 5	May 27
1968	May 17 to June 26	June 12	May 24

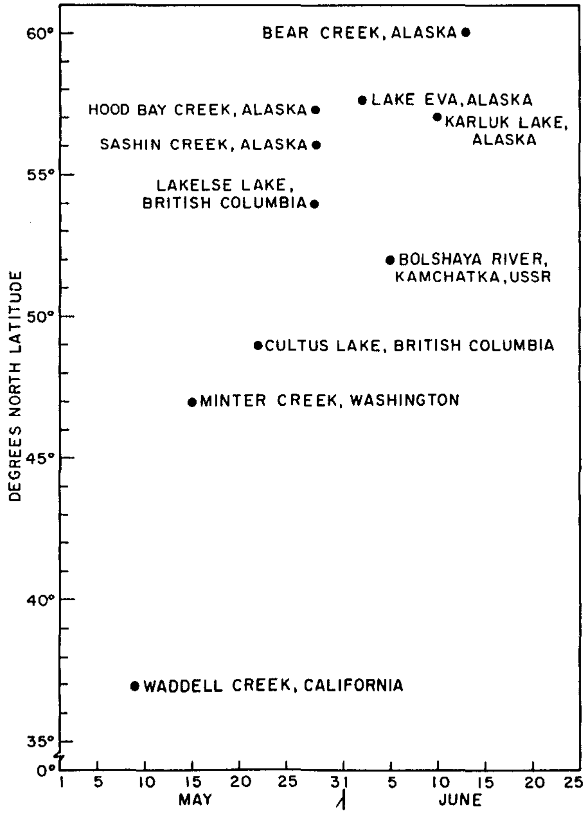

FIGURE 8.—Average date when 50% of the coho salmon smolts had migrated from river and lake systems along the Pacific coast of North America and Asia.

Although most of the migration of smolts to salt water occurs during the darkest hours of the night, some occurs during the daytime. At Karluk Lake, for instance, during some years almost 40% of the coho salmon smolts migrated in the daytime—between 0600 and 1800 hr (Figure 9). In other coho salmon rivers, the percentage of smolts that migrate seaward during daylight is quite variable. In the Bolshaya River in Kamchatka, during the years 1944-47, 6.3 to 50.0% of the age 1 smolts[6] and 8.8 to 73.2%

[6] Fish that go to sea in their second year.

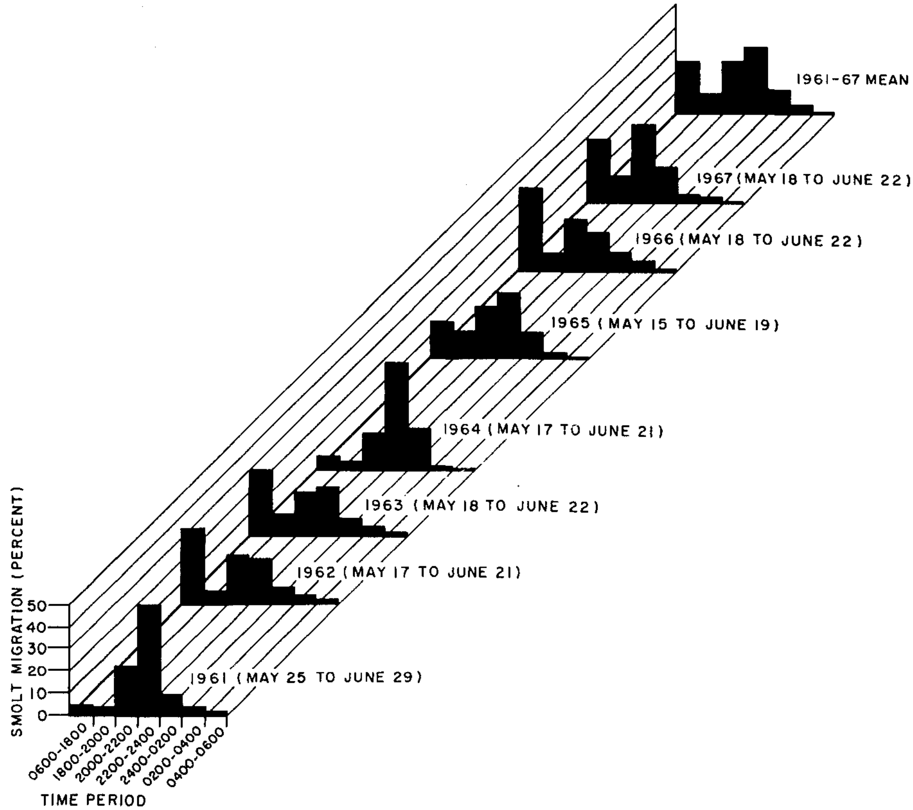

FIGURE 9.—Migration of coho salmon smolts by time period from Karluk Lake for the years 1961-67.

of the age 2 smolts migrated in daylight (Semko, 1954.) At Bear Creek, Alaska, 49.8% of the smolts migrated between 0400 and 2000 hr in 1962 (see footnote 1, Table 1), and 16% migrated between 0900 and 1700 hr in 1964 (see footnote 2, Table 3).

AGE

In 1956, 1965, and 1968, scale samples taken from seaward-migrating coho salmon smolts at the Karluk Lake weir revealed that the dominant ages were 2 and 3 and that the age composition was similar between years (Table 6).

The freshwater age composition determined from the scales of adults collected in 1966 was strikingly similar to the age composition of seaward-migrating smolts in 1965—smolts that produced the adults in 1966 (Table 6). The only group missing from the adult scale sample but present in small numbers in the smolt scale samples was age 1 (fish that went to sea in their second year of life). Fish from this age class could have been missing in the returning adults

TABLE 6.—Freshwater age composition of Karluk Lake coho salmon as determined from smolt and adult scale samples.

Freshwater age	Percent composition			
	From smolt scales			From adult scales
	1956	1965	1968	1966
1	1.4	3.0	3.0	--
2	44.5	51.5	48.5	56.9
3	49.1	43.9	42.5	41.7
4	4.9	1.5	6.0	1.4

because (1) they had poor ocean survival because of their small size; (2) the young overwintered in the river and migrated as age 2 smolts the following year; or (3) the young never migrated at all.

SIZE

Only lengths were measured in 1956, and lengths and weights were taken in 1965 and 1968. A summary of average size data by age class is presented in Table 7. Average lengths for comparable age classes were greater in 1968 than in 1956 and 1965. Average weights, with the exception of age 3 fish, were less in 1968 than 1965. Differences in lengths and weights between smolts for the two comparable years (1965 and 1968) are reflected in the condition factor (K), or coefficient of condition, which indicates the relative well-being of the fish. In 1965 all age groups had K values greater than 1.0000; the range was 1.0544 to 1.3695. In 1968 all K values were under 1.0000; the range was 0.9187 to 0.9600.

Information on the size of coho salmon smolts from other spawning systems is presented in Table 8. This table gives information for natural or "wild" populations and not for artificially hatched or reared stocks. Karluk Lake coho salmon smolts were generally as large as smolts of the same age from other areas or larger.

POSSIBLE EFFECTS OF INCREASED FRESHWATER RESIDENCE ON SURVIVAL OF COHO SALMON

The extended period of freshwater residence resulting in coho salmon smolts of age 3 occurs in many systems but seems to be significant only at Karluk.

It is interesting to hypothesize what effect a prolonged freshwater residence has on the annual return of adult coho salmon at Karluk Lake. Is an increased freshwater residence advantageous or disadvantageous to survival of each year class? What effect is there on marine survival of coho salmon if they take up ocean residence at an older age and consequently a larger size?

One means of answering these questions is to examine freshwater and marine survival rates for coho salmon from other areas. Survival from egg to smolt (fresh water) and smolt to returning adult (marine) are shown in Table 9 for some areas in California, Oregon, Washington, and British Columbia. Both freshwater and marine survival for age 1 smolts from these areas are quite variable: 0.13 to 12.00% and 3.77 to 11.79% respectively. The survival data in Table 9 pertain to stocks in which the smolts were primarily age 1 when they migrated to sea, and the application of these data to more northern stocks in which the smolts are mostly older and larger when they migrate must be done with caution.

The small population of age 2 smolts from Sweltzer Creek in British Columbia (Table 9) is of interest because these fish are more comparable to Karluk smolts, in that they may possibly have had a period of lake residence. Marine survival of these older, larger fish was high. Of 72 fin-clipped migrating age 2 smolts, 19 (26%) returned 5 or 6 months later as 3_3 fish (Foerster and Ricker, 1953). Although marine survival for these age 2 smolts might have been lower if they had spent another year in the ocean, it

TABLE 7.—Average length, weight, and condition factor of coho salmon smolts by age from Karluk Lake, 1956, 1965, and 1968.

Age	1956			1965			1968		
	Length	Weight	Condition factor	Length	Weight	Condition factor	Length	Weight	Condition factor
	mm	*g*		*mm*	*g*		*mm*	*g*	
1	106.8	--	--	112.5	19.5	1.3695	114.8	13.9	0.9187
2	139.7	--	--	136.3	28.2	1.0544	140.1	26.4	0.9600
3	151.1	--	--	141.7	30.7	1.0790	160.4	38.5	0.9329
4	165.4	--	--	177.0	63.9	1.1523	181.8	56.2	0.9353

TABLE 8.—Average fork lengths of coho salmon smolts of ages 1 to 4 from river and lake systems along the Pacific coast of North America and Asia, arranged geographically from north to south.

Area and year	Age 1	Age 2	Age 3	Age 4	Reference
	mm	*mm*	*mm*	*mm*	
North America					
Hood Bay Creek, Alaska					
1968	83.0	96.0	--	--	Armstrong (1970)
1969	79.0	91.0	--	--	Armstrong (1970)
Karluk River (Karluk Lake), Alaska					
1956	106.8	139.7	151.1	165.4	Present study
1965	112.5	136.3	141.7	177.0	Present study
1968	114.8	140.1	160.4	181.8	Present study
Bear Creek, Alaska					
1962	106.3	118.7	150.8	--	Logan[1]
Sweltzer Creek (Cultus Lake), British Columbia					
--	110-120	--	--	--	Foerster and Ricker (1953)
1939	--	291.6	--	--	Foerster and Ricker (1953)
Minter Creek, Wash.					
1940	[2]96.3	--	--	--	Salo and Bayliff (1958)
1953	[2]99.7	--	--	--	Salo and Bayliff (1958)
Deer Creek, Oreg.					
1960	88.7	--	--	--	Chapman (1961)
Flynn Creek, Oreg.					
1960	88.1	--	--	--	Chapman (1961)
Waddell Creek, Calif.					
1933	113.5	--	--	--	Shapovalov and Taft (1954)
1934	113.3	--	--	--	Shapovalov and Taft (1954)
1935	113.1	--	--	--	Shapovalov and Taft (1954)
1936	116.6	--	--	--	Shapovalov and Taft (1954)
1937	114.8	--	--	--	Shapovalov and Taft (1954)
1938	112.4	--	--	--	Shapovalov and Taft (1954)
1939	112.4	--	--	--	Shapovalov and Taft (1954)
1940	109.5	--	--	--	Shapovalov and Taft (1954)
1941	103.1	--	--	--	Shapovalov and Taft (1954)
Asia					
Bolshaya River, Kamchatka, USSR					
--	85.0	130.0	--	--	Semko (1954)

[1] Personal communication, Sidney M. Logan, Fishery Biologist, Alaska Department of Fish and Game, May 3, 1967.
[2] Primarily age 1 fish.

TABLE 9.—Average freshwater and marine survival for coho salmon from various streams along the Pacific coast of North America, arranged geographically from north to south.

Streams	Percent survival: Fresh water: Egg to age 1 smolt	Percent survival: Marine: Age 1 smolt to adult	Reference
Nile Creek, British Columbia	1.40	6.00	Wickett (1951)
Hooknose Creek, British Columbia	1.30	11.79	Godfrey (1965)
Sweltzer Creek, British Columbia	[1]0.13	8.07	Foerster and Ricker (1953)
Sweltzer Creek, British Columbia	[2,3]0.33	--	Foerster and Ricker (1953)
Sweltzer Creek, British Columbia	--	[4]26.39	Foerster and Ricker (1953)
Minter Creek, Wash.	3.22	3.77	Salo and Bayliff (1958)
Deer Creek, Oreg.	12.00	--	Chapman (1961)
Waddell Creek, Calif.	1.35	4.95	Shapovalov and Taft (1954)

[1] Before piscivorous fishes were controlled.
[2] After piscivorous fishes were controlled.
[3] Geometric mean.
[4] Age 2 fish only.

nevertheless was considerably higher than for any of the age 1 smolts.

In the absence of knowledge of survival rates for the more northern populations of coho salmon, an examination of the effect of increased freshwater residence on sockeye salmon, the dominant species of salmon in the Karluk system, is of value. Sockeye salmon juveniles at Karluk Lake have long been known to reside in the lake a year or more longer than do sockeye salmon in other areas (Gilbert and Rich, 1927). In most Alaska systems, sockeye salmon smolts migrate at the beginning of their second or third year of life, but at Karluk Lake most sockeye salmon smolts migrate at the beginning of their third or fourth years. Possibly the factor(s) responsible for the 1-year holdover of juvenile sockeye salmon in the lake may also be responsible for the holdover of juvenile coho salmon.

Freshwater survival of sockeye salmon at Karluk Lake is extremely poor, but marine survival is good. During the late 1920's and early 1930's, freshwater survival was less than 1% and ocean survival was about 21% (Barnaby, 1944). In recent years, freshwater survival has dropped to less than 0.5% and ocean survival has increased to about 40%.[6] Ricker (1962) modified Barnaby's data by applying a marking mortality factor derived from his Cultus Lake studies and determined that the older, larger smolts have greater marine survival and that Barnaby's original estimate of 21% survival was too low. Average marine survival by freshwater age for the years 1926 and 1929-33 were as follows: age 1 smolts, 18.3%; age 2, 27.4%; age 3, 34.2%, and age 4, 33.3%. Ricker attributed the high ocean survival to the large size of the smolts when they entered salt water. The larger size of the sockeye salmon smolts at the time of seaward migration, however, is offset by a greater total freshwater mortality due to their prolonged stay in the lake.

I have shown that in the more northern latitudes coho salmon usually reside a minimum of one extra year in fresh water before they migrate to sea. Generally, a longer period of freshwater residence will result in greater freshwater mortality but lower marine mortality because the fish are larger when they enter the ocean. Most likely, as with Karluk Lake juvenile sockeye salmon, an extra year in the lake for juvenile coho salmon probably results in a greater total freshwater mortality. Total marine mortality, however, may be less for coho salmon than for sockeye salmon because the coho salmon generally spend less time at sea before returning to spawn (12 to 18 months rather than 24 to 30 months).

[6] Unpublished data on file at National Marine Fisheries Service Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821.

SUMMARY AND CONCLUSIONS

Both the freshwater and total ages of adult coho salmon increase from southern to northern latitudes. In California, the southern portion of the coho salmon's range, fish of ages 3_2 and 2_2 are in the majority, but in the northern areas, ages 4_3 and 3_2 predominate. Karluk coho salmon, however, are unique, in that although age 4_3 fish are still the primary age class, the age 3_2 fish are replaced by age 5_4, so that age 5_4 fish account for 42% of the run. In no other North American or Asiatic coho salmon stock for which information is available is such a large percentage of the run composed of 5_4 fish.

The increase in total age of coho salmon from south to north is associated with the increased time the juveniles spend in fresh water. The small numbers of age 5_4 fish in several Alaska stocks may represent juveniles that live in lakes rather than rivers.

Fecundity generally increases from south to north, and Karluk coho salmon are the most fecund of any North American stock and closely parallel the highly fecund Asiatic stocks from the Kamchatka Peninsula. In Karluk coho salmon, there is a relation between number of eggs and length but no relation between egg size and length or egg size and fecundity. Egg counts are significantly higher in the right ovary than in the left.

Coho salmon smolts generally migrate after the ice breaks up and the water warms. In North America, the migration is earlier in southern latitudes than northern ones. The coho salmon migration at Karluk Lake is primarily nocturnal, although some daytime migration does occur.

A prolonged freshwater residence by juvenile coho salmon in Karluk Lake should result in a greater total freshwater mortality, but the resulting larger smolts should have a lower total marine mortality. Coho salmon at Karluk may have an even lower marine mortality than sockeye salmon, in part because the coho salmon spend less time at sea.

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