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Distribution, Abundance, and Growth of Juvenile Sockeye Salmon, *Oncorhynchus nerka,* and Associated Species in the Naknek River System, 1961-64

ROBERT J. ELLIS

SEATTLE, WA
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ROBERT J. ELLIS[1]

ABSTRACT

The Naknek River system contains eight interconnected and generally biologically discrete basins, each with a different ratio of spawning grounds to rearing area for sockeye salmon, *Oncorhynchus nerka*, and different densities of juvenile sockeye salmon and associated species of fish. Juvenile sockeye salmon and other pelagic species were sampled with tow nets at night. Sockeye salmon were the most common and abundant species in all basins, followed by threespine sticklebacks, ninespine sticklebacks, and pond smelt. Eighteen other species of potential competitor or predator fish were present.

In the summers of 1961 to 1963, juvenile sockeye salmon in the pelagic areas had a characteristic pattern of abundance for the entire system: abundance (catch per tow) of age 0 increased from early summer to midsummer and then declined to late August. The abundance in late August varied about threefold and, in general, was independent of variations in the number of parents from 1960 to 1963.

In July the abundance of age 0 fish in each basin was proportional to the amount of known contiguous spawning ground, but by late August this relation no longer existed. This change was at least partly due to migration of the age 0 fish—generally from basins of greater abundance of fish to those of lesser abundance. The larger and faster growing fish were the first to migrate. Not all basins were involved in these migrations.

The production of sockeye salmon smolts in the Naknek system is relatively stable. At least three major factors probably contribute to this stability: (1) the presence of several major spawning units or races in widely separated spawning grounds of different types, (2) the presence of several connected lakes, and (3) the migratory behavior of juvenile sockeye salmon during their first summer.

A mechanism which prevents the population of juvenile sockeye salmon from exceeding some upper limit is not apparent in the Naknek system. A reduction in growth in areas of high density was not apparent in the Naknek system in 1961-64 and apparently did not occur in 1957-65. Many kinds of predators on juvenile salmon are present but probably are not limiting production of smolts.

The data on abundance and growth of juvenile sockeye salmon and the distribution of the escapement and spawning grounds indicate that it should be possible to increase the production of sockeye salmon in the Naknek system. Two of the major basins, North Arm and Brooks Lake, which constitute about 35% of the system, are now producing juveniles at very low levels. North Arm appears to suffer from too little spawning area, whereas Brooks Lake appears to have adequate spawning area but too few spawners.

Three factors in the biology of juvenile sockeye salmon of the Naknek system are of special significance to the managers of the resource and should be investigated in any effort to enhance the production of sockeye salmon in the Naknek system: (1) the abundance of smolts each spring is fairly constant for the system as a whole and not closely related to the abundance of the parents or, from 1961-64, even to the original abundance of age 0 fish; (2) the apparent growth of juvenile sockeye salmon and potential competitor species is not related to the abundance of these fish in any lake of the Naknek system; and (3) two major lakes, constituting about 35% of the rearing waters, do not receive age 0 sockeye salmon from other basins and are supporting relatively few sockeye salmon.

The question of what escapement of adult sockeye salmon is needed to ensure full production of juveniles is considered. The present study indicates that escapements in the range of 600,000 to 1,000,000 fish, as recommended by other studies, would probably fully use the present combination of spawning and rearing areas without danger of overburdening the food supply.

The Naknek River system—the Naknek River and tributary lakes—is one of several major producers of sockeye salmon, *Oncorhynchus nerka*, in Bristol Bay, Alaska. The annual commercial value of the catch of sockeye salmon from the Naknek system has varied in recent years from a few hundred thousand to more than a million dollars, and the ultimate goal of fishery research here is to stabilize the production at the higher or even increased levels. As biologists learn more of the life history of sockeye salmon, it becomes increasingly evident that although most stocks (races) have the same general life history, each stock has unique characteristics that are determined by the biological and physical environments in which each stock evolved. It is the interaction between these characteristics and the environment that makes some stocks more productive than other stocks in the same year and some years more productive than other years for the same stock.

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The sockeye salmon of the Naknek system have the general freshwater life history common to most stocks of the species. Adults return to fresh water in early summer, ascend the system through rivers and lakes, and spawn in gravel of streams or lake beaches. The embryos overwinter in the gravel, and young salmon emerge and enter the littoral areas of the lakes in spring. The juvenile salmon soon move out into the pelagic areas where they feed on zooplankton for 1 or 2 summers before going to the ocean as smolts in the spring. In the Naknek system, smolts are yearlings (age I); 2-year-olds (age II); or, rarely, 3-year-olds (age III). Each lake in the Naknek system has its own unique combination of physical features and assemblage of other species of fish associated with the young sockeye salmon.

The National Marine Fisheries Service (formerly the Bureau of Commercial Fisheries) has conducted research on the Naknek system since about 1940, but intensive work on juvenile sockeye salmon and associated species of fish began in 1961. A principal objective of this research has been to define some of the details of the life history of the juvenile sockeye salmon in the system. The results of the research on juvenile sockeye salmon through 1962 were presented in a report that summarized all available information on the major sockeye salmon systems of southwestern Alaska (Burgner et al., 1969).

I continued the work on juvenile sockeye salmon and associated species in the Naknek system, and in this report I analyze the data collected from 1961 through 1964. First is a description of the general distribution and relative abundance of all species of fish in the system, based on sampling with several types of gear. This is followed by a discussion of the abundance of juvenile sockeye salmon and a few associated species in the habitats where these fish are most abundant—the pelagic areas. Next is the account of the migrations of young-of-the-year (age 0) sockeye salmon from lake to lake in two areas. Changes in average lengths and length-frequency distributions are then used to determine relative growth in the lakes of the system. The significance of predators in controlling the numbers of juvenile sockeye salmon in the Naknek system is considered next. Finally, all of the available information is marshaled and summarized to consider for the fishery manager what factors seem to be limiting the production of sockeye salmon in the Naknek system and what might be done to increase production.

THE STUDY AREA

The freshwater environment of sockeye salmon includes the spawning grounds of streams or lake beaches, followed briefly by the open waters of the spawning streams or beaches, and then the littoral areas of the lakes for a few days or weeks and the pelagic areas of the lakes for several months, followed, again briefly, by the outlet river as the juveniles go to the ocean as smolts.

The Naknek system (Fig. 1) consists of four major connected lakes—Coville, Grosvenor, Naknek, and Brooks—and the outlet stream, Naknek River, which connects the lakes to the ocean. Naknek Lake contains four distinct basins and a large shallow outlet

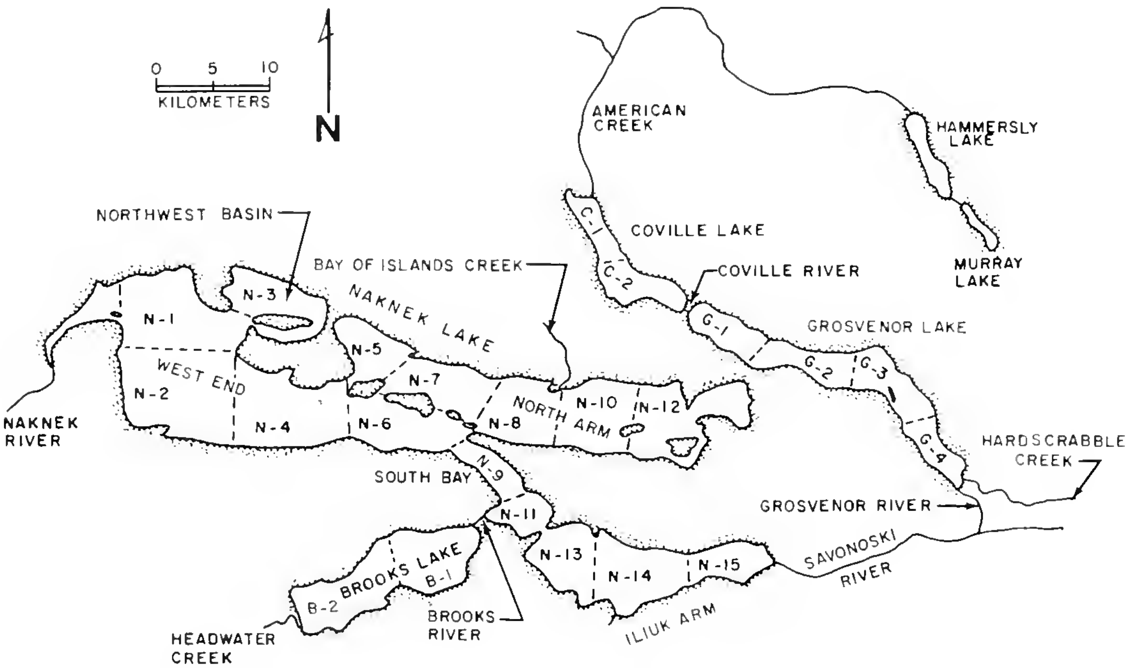

Figure 1.—Naknek River system, Bristol Bay, Alaska, showing sampling units where juvenile sockeye salmon were studied from 1961 to 1964.

portion, each of which I treat as an entity—Iliuk Arm, South Bay, West End, North Arm, and Northwest Basin. Two small lakes at relatively high elevations, Hammersly and Murray, receive small numbers of adult sockeye salmon, but were not part of this study.

The basic bathymetry and limnology of the lakes of the Naknek system have been determined. The total surface area and the areas within the 5-m contour, selected as the arbitrary limit of the pelagic area, for each lake or basin and the sampling units within each lake or basin are itemized in Table 1. The limnology of these lakes was intensively studied in 1961 and 1962, and details of the chemistry and productivity were summarized and compared with other western Alaska lakes (Burgner et al., 1969). In general, the lakes of the Naknek system are deep and oligotrophic and have a pH of about 7.2 and alkalinity of about 26 ppm. Maximum summer surface temperatures reach 12° to 16°C, and although thermoclines occasionally occur, they usually last only a few days.

Each lake of the Naknek system has several spawning grounds that are used by sockeye salmon, but neither the extent of the spawning grounds nor the numbers of spawners in the escapements (the adult salmon that escape the fishery and enter fresh water to spawn) are uniformly proportional to the size of the lakes (Table 2). In Table 2 the various types of stream spawning grounds have been combined for each lake (the few known beach spawning areas are not significant). The distribution of spawners among the several lakes each year is variable and only occasionally proportional to the amount of spawning ground contiguous to each lake. For example, American Creek (Coville Lake) has about one-third of the system's spawning ground, but from 1959 to 1963 it received from 10% to 60% of the escapement.

Table 1.--Total surface area, area within 5-m contour, percent of each lake deeper than 5 m, and percent of system total deeper than 5 m for lakes of the Naknek River system.

Lake and sampling area	Total surface area (km²)	Area within 5-m contour (km²)	Percent of each lake deeper than 5-m: Contribution of each area	Percent of each lake deeper than 5-m: Total lake	Percent of system total deeper than 5 m
Coville Lake[1]					
C-1	9.3	1.1	5.4	--	0.2
C-2	24.1	19.2	94.6	--	2.9
Total	33.4	20.3	100.0	60.8	3.1
Grosvenor Lake					
G-1 and 2	30.9	27.9	42.3	--	4.2
G-3 and 4	42.3	38.1	57.7	--	5.7
Total	73.2	66.0	100.0	90.0	9.9
Iliuk Arm					
N-15	19.2	18.2	20.3	--	2.7
N-14	33.3	32.4	36.1	--	4.8
N-13	41.1	39.1	43.6	--	5.8
Total	93.6	89.7	100.0	95.8	13.3
South Bay					
N-11	15.6	11.9	17.8	--	1.8
N-9	16.2	15.2	22.8	--	2.3
N-6	42.6	39.8	59.4	--	5.9
Total	74.4	66.9	100.0	89.9	10.0
West End					
N-4	56.0	50.8	31.4	--	7.6
N-2	81.0	74.8	46.3	--	11.2
N-1	81.4	36.1	22.3	--	5.4
Total	218.4	161.7	100.0	74.0	24.2
North Arm (all units combined)	181.5	162.1	--	89.3	24.2
Northwest Basin					
N-3	40.8	28.7	--	70.3	4.3
Brooks Lake					
B-1 and 2	74.9	74.6	--	99.6	11.1
System total	790.2	670.0	--	84.8	--

[1] In 1963 and 1964 Coville Lake was divided into more sample areas; the percent of the surface area in water deeper than 5 m in each sampling area was: 1963--C-1 = 5.30, C-2U = 55.86, C-2M = 28.58, C-2L = 10.26; 1964--C-1 = 10.67, C-2 = 31.50, C-3 = 35.37, C-4 = 11.77, C-5 = 10.66.

Table 2.--Area of potential spawning grounds, numbers of spawners in escapements, and numbers of smolts produced by each brood year for lakes of the Naknek River system, 1959-63.

Lake or basin	Surface area (km^2)	Area of potential spawning grounds (ha)	Area per unit lake area (ha/km^2)	Spawners in escapement (thousands)				
				1959	1960	1961	1962	1963
Coville Lake	33.4	111.0	3.32	1,000	--	218	85	80
Grosvenor Lake	73.2	[1]29.6	0.40	--	--	--	[2]35	--
Iliuk Arm	93.6	34.3	0.37	--	--	--	--	--
South Bay	74.4	[3]5.5	0.07	150	40	4	72	54
West End	218.4	147.8	0.68	--	--	([4])	75	200
North Arm	181.5	7.5	0.04	22	--	6	8	--
Northwest Basin	40.8	0.7	0.02	--	--	--	--	--
Brooks Lake	74.9	18.0	0.24	10	12	8	27	[5]10
System total[6]	790.2	354.4	0.45	2,231.8	828.4	351.1	723.1	905.4
Total smolts produced[6] by brood year (millions)	--	--	--	13.0	16.7	11.1	12.1	20.8

[1]Includes Hardscrabble Creek; does not include beach spawning areas.
[2]Hardscrabble Creek weir count.
[3]Includes Brooks River, which commonly has three waves of spawning activity.
[4]Salmon were observed spawning in the West End in 1961, but the number is not known.
[5]Field Reports, 1962 and 1963, Brooks Lake Field Station, Natl. Mar. Fish. Serv. Auke Bay Fish. Lab., Auke Bay, AK 99821.
[6]Stewart, Donald M. (editor). 1969. 1967 Bristol Bay red salmon smolt studies, Appendix D, Table 2, p. 64. Alaska Dep. Fish Game, Inform. Leafl. 134.

METHODS AND EQUIPMENT

Sampling Units

For sampling, the lakes were divided into units, generally on the basis of surface area. Each unit was designated by a system of letters and numbers (N-1, N-2, C-1, C-2, etc.—Fig. 1). Coville Lake was further divided in 1963 and 1964, and the designations of the sampling units were changed (see Fig. 2). The original objectives were to establish units of about equal size that were small enough to reveal possible gradients in biological attributes and few enough to permit sampling with a limited effort. As the study progressed some units were further divided and others combined.

Types of Gear

Several types of gear were used to sample fish and many revisions were made throughout the 4 yr of the study.

Pelagic areas were sampled with tow nets similar to those used by Johnson (1956) and Burgner (1958). Two types of tow nets were used. The first, which was used in all 4 yr, had a round metal hoop 3 m (10 ft) in diameter with an attached cone-shaped mesh bag about 7.6 m (25 ft) long. It was connected to two boats by bridles and steel cables retrieved by a gasoline-powered winch (1961 and 1962) or by ropes retrieved by hand (1963 [in part] and 1964). The second net, which was used only for some collecting in 1964, had a 2.7-m-square (9 ft) opening and was towed by ropes and retrieved by hand.

Tow netting was usually done between 2200 and 0200, or in general from sunset to sunrise. Two kinds of tows were made: (1) surface tows (0 to 3 m) with the center of the net 1.4 or 1.5 m from the surface; and (2) deep tows (3 to 6 m) with the center of the net 4.1 or 4.5 m from the surface. To produce a "standard" tow, the net was pulled through the water over a 457 m (1,500 ft) course in about 6 min 15 sec for a surface tow and 6 min 45 sec for a deep tow. Most tows were of the surface type in 1961, but in 1962, 1963, and 1964, a sequence of tows — one surface, two deep, and one surface — was used.

Field crews selected the specific track to be towed on any night within an area; the general objective was to tow near the middle of a sampling area. When one considers that the crews depended on outlines of hills and mountains and running time for orientation, the selection of specific sampling tracks must be considered as random, with bias toward the center of the sampling area.

Littoral areas were sampled with beach seines, generally in water less than 3 m deep. Two types of nylon seines were used. One was 31 m (100 ft) long; the center 6 m was 1 m high and had four meshes per inch (2.5 cm), and the balance was 1.2 m high and had two meshes per inch. The other seine was 40 m (130 ft) long and 3 m high; the center 9 m of the web had four meshes per inch and the balance had two.

Pelagic and littoral areas were also sampled with floating box traps in 1962 and 1963. The box portion of the trap was about 1.2 m (4 ft) square in cross section by 1.8 m (6 ft) long; wings extended 4.5 m from the box and the lead was 15 m long. The box and wings had four meshes per inch and the lead had two. To separate fish entering from each side, the box had a lengthwise partition connected to the lead.

A small otter trawl (gulf-type shrimp try-net) was used sporadically throughout the system. The wings had a spread of about 9 m and were about 1 m high. The net was cotton and had two meshes per inch in the wings and body and four meshes per inch in the tail.

Gill nets were also fished sporadically. The sizes varied from a 1.3-cm (½-inch) bar to a 10-cm (4-inch) bar. Small nets were nylon and large ones were cotton or linen.

Rivers and streams were sampled with small and large fyke nets. The small nets were 1 m (3 ft) square with 1.2-m (4-ft) wings and were made of nylon web with eight meshes per inch. The large nets were 1.2 m square or 1.2 m wide by 1.5 m high and had 1.8-m wings. The large nets were nylon web with two meshes per inch in the wings and body and four meshes per inch in the tail and cod end. The cod end of the net was often replaced with a 20.2-cm (8-inch) diameter flexible hose connected to a floating livebox. With this arrangement several thousand juveniles could be collected without many being killed.

Angling with sport fishing gear was used to supplement other sampling methods.

Measurements of Fish

Sockeye salmon juveniles and associated species were usually measured for fork length (tip of snout to fork of tail) to the nearest millimeter and weighed (drained weight) to the nearest higher gram. The fish were usually preserved in 10% Formalin for at least 48 h, but less than 1 wk, before being measured or weighed. Sockeye salmon smolts and recently emerged fry were measured alive, but anesthetized; the fry were measured for total length (tip of snout to tip of tail in normal extension).

The preserved juvenile sockeye salmon were also routinely weighed by 3-mm size groups on a triple beam balance. Length and weight data were combined to yield "condition factors." These condition factors were somewhat variable but usually well above 1.0000 for all fish from all lakes. No utility was seen in the condition data and the weight data will not be considered in this report.

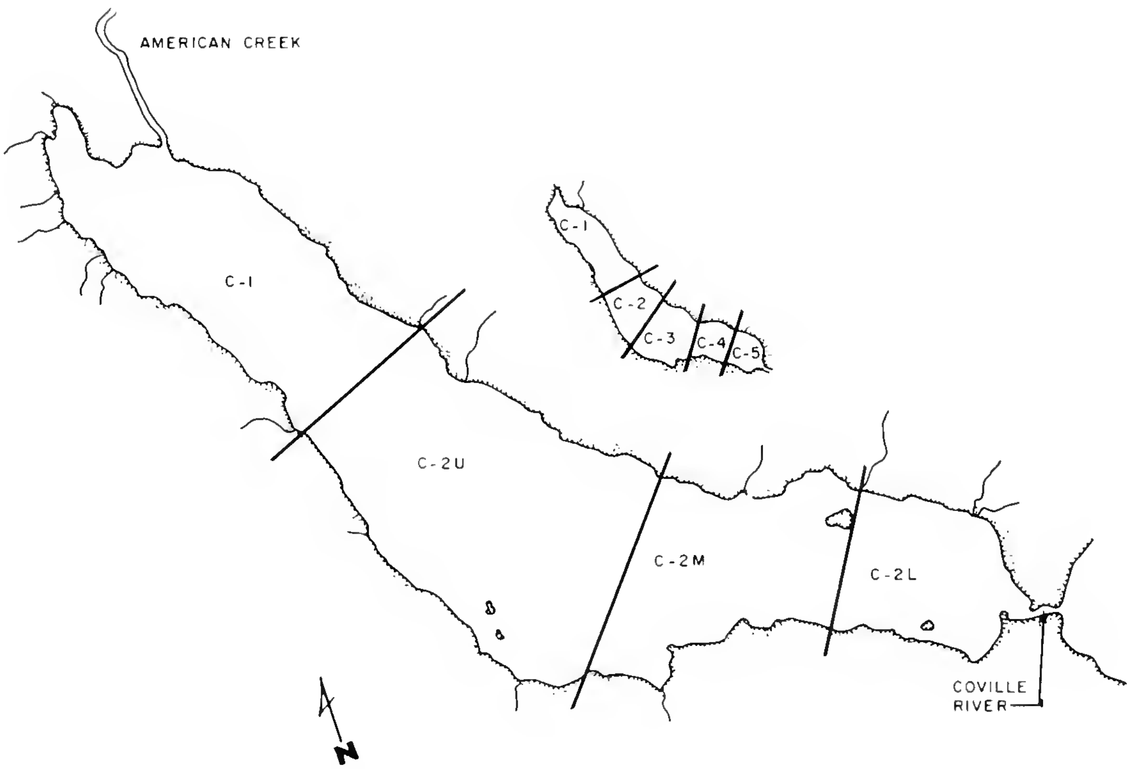

Figure 2.—Coville Lake, Naknek River system, showing units where juvenile sockeye salmon were sampled with tow nets in 1963 (lower) and 1964 (upper).

GENERAL DISTRIBUTION AND ABUNDANCE OF ALL FISH SPECIES

Although the principal subject of this study was juvenile sockeye salmon, data were collected on all species of fish encountered because of probable interactions among the species. Earlier work (Johnson, 1956) had indicated that juvenile sockeye salmon were readily available to tow nets in summer in the pelagic portion of the freshwater rearing areas and our effort was concentrated on this gear and habitat. We sampled with other gear in other habitats, however, to learn more of the biology of all the species present.

The greatest effort with all types of gear was in 1962; the results for that year are summarized in Table 3 to give a general picture of the distribution and relative abundance of all species. The table shows the percent frequency of occurrence of each species in collections made with each type of gear and its contribution to the total catch as percent of the total number of fish captured by each gear in each lake. The data are known to be biased in at least three ways: (1) most of the sampling was done from 15 July to 1 September, and marked seasonal changes in distribution are known to occur for many species; (2) each type of gear has its peculiar abilities to catch the various species; and (3) the distribution of fishing effort varied between areas in regard to type of gear, amount of effort, and season. Because of these biases, detailed discussion of the distribution of all species is not warranted and the abundance in relation to juvenile sockeye salmon will be treated in detail only for those species consistently and abundantly captured in the pelagic areas in tow nets — threesprine and ninespine sticklebacks and pond smelt.

Five species of fish were clearly predominant in the collections—sockeye salmon, threespine and ninespine sticklebacks, pygmy whitefish, and pond smelt (Table 3). The most widely distributed and, in general, the most abundant species was the sockeye salmon. Juvenile sockeye salmon were taken with all appropriate gear and in all major lakes of the system. The distribution of threespine and ninespine sticklebacks approximated that of the sockeye salmon and in a few areas the sticklebacks were more abundant than juvenile salmon (e.g., West End and Northwest Basin). The other two species that occurred abundantly in some collections, pygmy whitefish and pond smelt, were each abundant in some basins, but were never abundant together. The pond smelt was abundant only in tow net catches in Coville Lake and the pygmy whitefish only in trawl and seine catches in Brooks Lake and parts of South Bay.

None of the many other species were ever abundant in the collections. Some, such as the coho salmon (most gear) and the Arctic lamprey (tow nets and fyke nets), were collected in many locations, whereas others, such as the burbot and least cisco, were collected in only a few locations. Local concentrations of some predators coincide in time and place with migrations of juvenile sockeye salmon, for instance the lake trout and Arctic char at the outlet of Coville Lake and Arctic char and northern pike in parts of Grosvenor River. Intensive study of each species is needed to determine its abundance and role in the ecology of the system.

ABUNDANCE OF JUVENILE SOCKEYE SALMON

The tow netting to determine abundance of juvenile sockeye salmon was largely exploratory in 1961 when some areas and depths were sampled frequently and others not at all. From 1962 to 1964, however, the sampling was done systematically by season, area, and depth.

Although it has never been firmly established, the assumption that changes in the abundance of juvenile sockeye salmon in tow net catches reflect actual changes in their abundance has proved to be a workable hypothesis. The work of Pella (1968), who used a recording echo sounder in conjunction with tow netting, showed that tow netting is at least a good index of relative abundance of sockeye salmon in the area being sampled. The validity of tow net sampling for measuring the abundance of juvenile sockeye salmon was further substantiated in the present study: catches declined in the lake from which fish were migrating (Coville Lake) and increased in the lake to which they migrated (Iliuk Arm).

Assessment of the abundance of fish in the pelagic areas of the lakes is based on tow net data from sampling mainly at night. Night sampling with tow nets proved to be successful in western Alaska (Burgner et al., 1969), although workers in British Columbia found it best to sample with tow nets only during the transitional period from dusk to darkness (Johnson, 1956; Ruggles, 1966). Echograms and the results of concurrent tow netting by Pella (1968) in a lake in western Alaska demonstrate that juvenile sockeye salmon remain dispersed at night near the surface in pelagic areas of lakes. I found no consistent differences in the rate of catch of juvenile sockeye salmon in tow nets during different parts of the night in the Naknek system. Some of the tow net data from Iliuk Arm were collected in daylight because the water was so opaque that sampling was apparently as effective in daylight as in darkness.

The average catch per tow for four tows—two surface and two deep—was used as the standard unit of measure of abundance. The relative abundance in the two depths frequently varied between lakes within a year and between years within a lake. When unequal numbers of tows were made at the two depths, the averages for the two depths were averaged to give equal significance to each depth. The only exception to the use of this standard was for sampling in area N-1, which was too shallow for deep tows.

In 1964 to compare the fishing capabilities of the two

Table 3.--Percent frequency of occurrence (f_x) and percent total number (N) of fish captured in various types of collecting gear in lakes of the Naknek River system, 1962.

Species	Coville Lake												Grosvenor Lake					
	Tow net		Beach seine		Otter trawl		Gill net		Trap net		Fyke net[1]		Tow net		Beach seine		Otter trawl	
	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N
Arctic lamprey (*Lampetra japonica*)	2.7	Tr.	--	--	--	--	--	--	--	--	2.4	Tr.	--	--	--	--	--	--
Humpback whitefish (*Coregonus pidschian*)	--	--	9.4	0.3	--	--	16.0	8.2	7.7	0.1	1.2	Tr.	--	--	--	--	--	--
Least cisco (*C. sardinella*)	8.1	0.2	--	--	--	--	--	--	7.7	0.1	--	--	--	--	--	--	--	--
Pink salmon (*Oncorhynchus gorbuscha*)	--	--	3.1	Tr.	--	--	--	--	--	--	--	--	--	--	2.9	0.2	--	--
Chum salmon (*O. keta*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Coho salmon (*O. kisutch*)	--	--	6.3	0.3	--	--	--	--	--	--	1.2	Tr.	--	--	2.9	0.7	--	--
Juvenile sockeye salmon (*O. nerka*)	91.9	42.4	59.4	28.3	13.3	0.5	4.0	1.2	46.2	23.4	86.6	86.6	77.4	97.9	47.1	22.1	28.6	3.5
Adult sockeye salmon	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.9	2.6	--	--
Chinook salmon (*O. tshawytscha*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Pygmy whitefish (*Prosopium coulteri*)	2.7	Tr.	28.1	2.6	--	--	4.0	2.4	--	--	4.9	0.2	5.7	0.5	17.6	13.7	--	--
Round whitefish (*P. cylindraceum*)	--	--	12.5	1.1	19.9	0.5	--	--	7.7	0.2	--	--	--	--	14.7	13.2	19.0	1.5
Whitefish sp.	--	--	31.3	4.3	--	--	12.0	4.7	--	--	4.9	0.1	--	--	14.7	3.3	14.3	12.7
Rainbow (steelhead) trout (*Salmo gairdneri*)	--	--	6.3	0.1	--	--	--	--	--	--	--	--	--	--	2.9	0.7	--	--
Arctic char (*Salvelinus alpinus*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.9	0.4	--	--
Dolly Varden (*S. malma*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Char sp.	2.7	Tr.	--	--	--	--	20.0	7.1	--	--	1.2	Tr.	1.9	0.2	8.8	2.0	--	--
Lake trout (*S. namaycush*)	--	--	3.1	0.1	--	--	28.0	14.1	--	--	--	--	--	--	2.9	0.4	--	--
Arctic grayling (*Thymallus arcticus*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	-	--	--	--
Pond smelt (*Hypomesus pretiosus*)	56.7	24.6	9.4	0.5	19.9	0.2	8.0	8.2	46.2	48.6	29.3	5.4	1.9	0.3	5.9	7.9	19.0	5.0
Alaska blackfish (*Dallia pectoralis*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Northern pike (*Esox lucius*)	--	--	--	--	6.7	0.1	8.0	2.4	--	--	--	--	--	--	--	--	--	--
Longnose sucker (*Catostomus catostomus*)	--	--	6.3	0.1	13.3	0.1	28.0	21.2	15.4	0.6	4.9	Tr.	--	--	8.8	1.1	--	--
Burbot (*Lota lota*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Threespine stickleback (*Gasterosteus aculeatus*)	27.0	11.3	62.5	17.6	60.0	75.2	4.0	7.1	--	--	40.2	6.0	1.9	0.3	8.8	8.4	19.0	13.3
Ninespine stickleback (*Pungitius pungitius*)	51.3	11.1	9.4	0.5	40.0	4.6	8.0	4.7	--	--	4.9	0.1	1.9	0.2	2.9	0.2	4.8	0.2
Stickleback sp.	13.5	10.4	43.8	34.2	53.3	9.1	--	--	92.3	26.6	15.9	1.1	3.8	0.7	8.8	11.0	23.8	39.8
Coastrange sculpin (*Cottus aleuticus*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Slimy sculpin (*C. cognatus*)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sculpin sp.	--	--	78.1	9.5	73.3	9.9	--	--	23.1	0.4	23.2	0.5	--	--	58.8	11.9	90.5	24.0
Total catch		4,476		2,194		1,731		85		975		12,415		611		453		480
Total effort		37		32		15		25		13		82		53		34		21
Sampling days		11		21		3		25		13		20		14		19		3

[1]Fished in Coville River.

Table 5.--Percent frequency of occurrence (f_x) and percent total number (N) of fish captured in various types of collecting gear in lakes of the Naknek River system, 1962.--Continued

Species	Grosvenor Lake--Cont. Gill net[2] f_x	N	Trap net f_x	N	Fyke net[3] f_x	N	Iliuk Arm Tow net f_x	N	Beach seine f_x	N	South Bay Tow net f_x	N	Beach seine f_x	N	Gill net f_x	N	West End Tow net f_x	N
Arctic lamprey (Lampetra japonica)	--	--	--	--	18.9	0.4	5.6	0.1	--	--	8.2	0.2	--	--	--	--	--	--
Humpback whitefish (Coregonus pidschian)	--	--	--	--	--	--	--	--	8.3	0.4	--	--	--	--	--	--	--	--
Least cisco (C. sardinella)	--	--	--	--	--	--	6.9	0.1	25.0	15.6	9.8	0.3	15.4	1.5	25.0	6.2	--	--
Pink salmon (Oncorhynchus gorbuscha)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Chum salmon (O. keta)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Coho salmon (O. kisutch)	--	--	--	--	33.3	1.5	--	--	--	--	--	--	5.1	0.1	--	--	--	--
Juvenile sockeye salmon (O. nerka)	--	--	50.0	88.9	93.3	84.8	97.2	93.4	50.0	11.3	95.1	91.8	17.9	0.4	25.0	6.2	92.5	4.1
Adult sockeye salmon	--	--	--	--	--	--	--	--	41.7	31.5	--	--	10.3	0.6	--	--	--	--
Chinook salmon (O. tshawytscha)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Pygmy whitefish (Prosopium coulteri)	--	--	--	--	11.1	0.3	5.6	0.1	66.7	8.8	9.8	0.2	69.2	78.8	25.0	12.5	--	--
Round whitefish (P. cylindraceum)	--	--	25.0	1.1	--	--	--	--	16.7	2.1	--	--	30.8	1.5	--	--	--	--
Whitefish sp.	--	--	--	--	1.1	Tr.	--	--	--	--	--	--	2.6	0.3	--	--	--	--
Rainbow (steelhead) trout (Salmo gairdneri)	--	--	--	--	--	--	--	--	--	--	--	--	15.4	0.4	--	--	--	--
Arctic char (Salvelinus alpinus)	--	--	--	--	--	--	--	--	8.3	0.4	--	--	--	--	--	--	--	--
Dolly Varden (S. malma)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Char sp.	--	--	--	--	6.7	0.3	--	--	--	--	--	--	--	--	--	--	--	--
Lake trout (S. namaycush)	--	--	--	--	--	--	--	--	8.3	0.4	--	--	--	--	75.0	56.2	--	--
Arctic grayling (Thymallus arcticus)	--	--	--	--	--	--	--	--	--	--	--	--	2.6	Tr.	--	--	--	--
Pond smelt (Hypomesus pretiosus)	--	--	--	--	--	--	19.4	0.4	50.0	11.3	11.5	0.2	5.1	0.1	25.0	6.2	25.0	0.2
Alaska blackfish (Dallia pectoralis)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Northern pike (Esox lucius)	100.0	100.0	--	--	--	--	--	--	16.7	1.3	--	--	--	--	--	--	--	--
Longnose sucker (Catostomus catostomus)	--	--	--	--	6.7	0.1	--	--	25.0	1.7	--	--	2.6	0.1	--	--	--	--
Burbot (Lota lota)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	50.0	12.5	--	--
Threespine stickleback (Gasterosteus aculeatus)	--	--	--	--	48.9	3.8	63.9	5.6	8.3	0.4	57.4	4.0	23.1	4.9	--	--	97.5	38.5
Ninespine stickleback (Pungitius pungitius)	--	--	--	--	58.9	5.9	6.9	0.3	--	--	19.7	3.3	12.8	0.2	--	--	95.0	7.5
Stickleback sp.	--	--	50.0	10.0	7.8	1.2	--	--	--	--	--	--	--	--	--	--	15.0	49.6
Coastrange sculpin (Cottus aleuticus)	--	--	--	--	--	--	--	--	--	--	--	--	10.3	0.8	--	--	--	--
Slimy sculpin (C. cognatus)	--	--	--	--	--	--	--	--	--	--	--	--	5.1	0.2	--	--	--	--
Sculpin sp.	--	--	--	--	46.7	1.7	--	--	83.3	14.7	--	--	66.7	10.1	--	--	--	--
Total catch		17		90		5,840		4,370		238		3,770		2,749		16		11,028
Total effort		4		4		90		72		12		61		39		4		40
Sampling days		1		4		21		18		6		16		6		4		10

[2]Set in the upper end of Grosvenor River.
[3]Fished in the upper end of Grosvenor River.

Table 3.--Percent frequency of occurrence (f_x) and percent total number (N) of fish captured in various types of collecting gear in lakes of the Naknek River system, 1962.--Continued

Species	North Arm								Northwest Basin				Brooks Lake					
	Tow net		Beach seine		Gill net		Lake trap		Tow net		Beach seine		Tow net		Beach seine		Otter trawl	
	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N	f_x	N
Arctic lamprey																		
(Lampetra japonica)	4.0	0.1	--	--	--	--	--	--	6.2	0.1	--	--	9.9	2.5	--	--	--	--
Humpback whitefish																		
(Coregonus pidschian)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Least cisco (C. sardinella)	--	--	--	--	--	--	36.2	22.2	--	--	--	--	--	--	--	--	--	--
Pink salmon																		
(Oncorhynchus gorbuscha)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Chum salmon (O. keta)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	40.7	9.5	--	--
Coho salmon (O. kisutch)	--	--	--	--	--	--	14.5	0.6	--	--	--	--	--	--	11.1	0.8	--	--
Juvenile sockeye salmon																		
(O. nerka)	37.4	24.6	20.8	1.6	--	--	13.0	1.0	37.5	3.5	60.0	0.7	41.9	90.4	11.1	2.5	22.0	11.4
Adult sockeye salmon	--	--	--	--	--	--	--	--	--	--	--	--	--	--	7.4	0.2	--	--
Chinook salmon																		
(O. tshawytscha)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	22.2	6.7	--	--
Pygmy whitefish																		
(Prosopium coulteri)	4.0	0.1	--	--	75.0	78.6	4.3	0.1	--	--	--	--	6.6	2.4	85.2	21.0	39.0	31.0
Round whitefish																		
(P. cylindraceum)	--	--	41.7	1.5	--	--	--	--	--	--	--	--	--	--	14.8	1.3	--	--
Whitefish sp.	--	--	37.5	1.6	--	--	12.5	0.7	6.2	0.1	--	--	1.2	0.3	3.7	0.3	0.7	0.7
Rainbow (steelhead) trout																		
(Salmo gairdneri)	--	--	8.3	0.1	--	--	5.8	01	--	--	--	--	--	--	--	--	--	--
Arctic char																		
(Salvelinus alpinus)	--	--	25.0	0.4	50.0	4.8	8.7	0.4	--	--	--	--	--	--	--	--	--	--
Dolly Varden (S. malma)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Char sp.	--	--	20.8	0.5	--	--	4.3	0.2	--	--	--	--	--	--	14.8	0.5	3.4	Tr.
Lake trout (S. namaycush)	--	--	--	--	50.0	14.3	--	--	--	--	--	--	--	--	--	--	--	--
Arctic grayling																		
(Thymallus arcticus)	--	--	4.2	Tr.	--	--	--	--	--	--	--	--	--	--	3.7	0.5	--	--
Pond smelt																		
(Hypomesus pretiosus)	--	--	--	--	--	--	5.8	0.2	43.8	2.4	--	--	--	--	--	--	--	--
Alaska blackfish																		
(Dallia pectoralis)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	27.1	2.2
Northern pike (Esox lucius)	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Longnose sucker																		
(Catostomus catostomus)	--	--	4.2	0.1	--	--	17.4	1.1	--	--	--	--	--	--	--	--	--	--
Burbot (Lota lota)	--	--	--	--	--	--	1.4	Tr.	--	--	--	--	--	--	--	--	--	--
Threespine stickleback																		
(Gasterosteus aculeatus)	38.3	74.0	75.0	89.0	--	--	92.8	71.4	93.8	92.9	100.0	92.3	3.0	0.7	40.7	3.1	30.5	20.9
Ninespine stickleback																		
(Pungitius pungitius)	16.0	1.0	37.5	1.3	--	--	12.5	1.1	12.5	0.6	100.0	4.3	4.2	1.3	40.7	2.5	67.8	15.8
Stickleback sp.	4.0	0.1	--	--	--	--	3.1	0.4	--	--	--	--	--	--	--	--	15.3	1.3
Coastrange sculpin																		
(Cottus aleuticus)	--	--	--	--	--	--	--	--	--	--	20.0	0.1	--	--	--	--	--	--
Slimy sculpin (C. cognatus)	--	--	--	--	25.0	2.4	--	--	--	--	40.0	0.6	7.8	2.4	85.2	31.2	62.7	16.7
Sculpin sp.	--	--	66.7	3.9	--	--	12.5	0.4	--	--	60.0	1.8	--	--	11.1	19.8	19.8	Tr.
Total catch	736		4,175		42		2,890		773		1,578		708		1,179		7,606	
Total effort	94		24		4		69		16		5		67		27		59	
Sampling days	25		11		4		22		4		1		16		4		14	

shapes and sizes of the tow nets used—a 3-m-diameter round net and a 2.7-m-square net—I made 22 paired tows using the two nets alternately. The sampling consisted of 44 standard tows at the surface on four dates in three sampling units (two in Coville Lake and one in Iliuk Arm). The catch of age 0 sockeye salmon for each tow and the figures used to test the hypothesis of no difference in the rate of catch of the two nets with the Wilcoxon matched-pairs signed-ranks test (Siegel, 1956) are presented in Table 4. The derived $T = 53$ with $N = 19$ is greater than the theoretical $T = 46$ at the 5% level of significance, so the hypothesis of no difference in the effectiveness of the two nets is accepted. The results of sampling with the two types of nets are combined in my subsequent analyses.

Most of the 1961 tows were made only at the surface and their comparability to the data collected at both depths in later years was uncertain. A split-plot analysis of variance (Snedecor, 1956) was made to determine if the average catches of juvenile sockeye salmon in surface tows and deep tows were significantly different. This analysis was restricted to Coville Lake, Iliuk Arm, and South Bay, 1962 to 1964, because of lack of sufficient data from other areas. The model is

$$X_{ijk} = \mu + B_i + M_j + \epsilon_{ij} + T \quad + (MT)_{jk} + \sigma_{ijk},$$

where X_{ijk} = average catch at the kth depth in the jth time period in the ith area,
B_i = block effect, i.e., area,
M_j = fixed main treatment effect, i.e., time,
ϵ_{ij} = whole plot error, i.e., area-time interaction,
T_k = fixed subplot treatment, i.e., depth,
$(MT)_{jk}$ = time-depth interaction, and
σ_{ijk} = subplot error, i.e., area-depth plus area-time depth interactions.

The split-plot analysis involved only surface and deep paired tows (the subplot treatment), three time

Table 4.--Numbers of age 0 sockeye salmon taken in 22 paired tows in 3-m-diameter round and 2.7-m-square nets in two sampling units in Coville Lake and one in Iliuk Arm, 1964, and calculations used in Wilcoxon matched-pairs signed-ranks test (Siegel, 1956).

Sampling unit, date and sample number	Age 0 sockeye salmon in-- Round net	Square net	Difference	Rank	Rank of sign of least frequency
Coville Lake C-4					
August 8					
1	43	503	-460	19	--
2	13	12	1	1.5	1.5
3	14	10	4	3.5	3.5
4	4	41	-37	13	--
5	12	12	0	--	--
6	8	8	0	--	--
Coville Lake C-4					
August 18					
7	1	2	-1	1.5	--
8	3	3	0	--	--
9	7	21	-14	9	--
10	9	18	-9	8	--
11	9	14	-5	5	--
12	8	4	4	3.5	3.5
Coville Lake C-5					
August 21					
13	14	49	-35	12	--
14	27	46	-19	10.5	--
15	56	37	19	10.5	10.5
16	49	117	-68	15	--
17	118	49	69	16	16
18	17	23	-6	6	--
Iliuk Arm N-13					
September 1					
19	288	97	191	18	18
20	83	148	-65	14	--
21	19	97	-78	17	--
22	60	68	-8	7	--
Total (N = 19)	862	1,379	0	--	53.0

Table 5.--Subplot portion of a split-plot analysis of variance of catch of juvenile sockeye salmon (age 0 and 1 combined) in tow nets in three lake basins of the Naknek system, 1962-64. Depth of tow (shallow and deep) and depth-time interaction are tested.

Basin and year	Source	df	MS	F
Coville Lake				
1962	Depth	1	3,879.54	2.15(NS)
	Depth-time	2	4,353.78	2.41(NS)
	Error	3	1,804.51	
1963	Depth	1	55,472.78	3.93*
	Depth-time	2	43,788.31	3.10*
	Error	9	14,127.66	
1964	Depth	1	57,483.14	2.32(NS)
	Depth-time	2	38,489.71	1.55(NS)
	Error	12	24,830.54	
Iliuk Arm				
1962[1]	Depth	1	649.74	<1(NS)
	Depth-time	1	991.26	1.175(NS)
	Error	4	844.23	
1963	Depth	1	718.84	<1(NS)
	Depth-time	2	564.23	<1(NS)
	Error	6	2,686.76	
South Bay				
1962[2]	Depth	1	63.43	<1(NS)
	Depth-time	2	4,830.58	3.41(NS)
	Error	3	1,415.72	
1963	Depth	1	2,007.46	1.081(NS)
	Depth-time	2	7,833.65	4.22*
	Error	6	1,857.66	

[1]No 10- to 20-ft tows made in midperiod in 1962.
[2]No samples from area N-6 in late time period.
*Indicates 10% level of significance.

periods each season (pre-26 July, 27 July to 10 August, after 10 August—the main treatment effect), and the various number of areas within each lake (the block effect). Because of unequal numbers of observations per cell, the analysis was done with untransformed data consisting of one observation per cell—the mean for the area-time period-depth. In only two instances did a significant difference appear in the subplot treatments involving depth of tow (Table 5), i.e., there were no consistent significant differences in catches of juvenile sockeye salmon in surface versus deep tows. Because of the indicated lack of difference between surface and deep tows in the lakes with the largest catches and the most sampling, I have assumed that the surface catches in 1961 reasonably represent the abundance in the surface to 20-ft depth. Pella (1968) did not find a significant difference in abundance of juvenile salmon with depth in Lake Aleknagik.

A two-way analysis of variance among areas and times within lakes of average catches of juvenile sockeye salmon in tow nets was made for those lakes with the most useful data—Coville Lake, Iliuk Arm, and South Bay (Table 6). These lakes had the most samples and usually had the largest catches and the greatest changes in abundance. Only averaged paired tows (one shallow and one deep for the same night and area) were used in the analysis. The analysis was done with the same untransformed data as in the split-plot analysis. However, the error terms used for the *F* tests were obtained by using the individual catches in each area-time cell (resulting in more degrees of freedom than in the split-plot analysis) as suggested by Scheffé (1959).

Statistically significant effects of areas, time, and area-time interaction on the abundance of juvenile sockeye salmon occurred in less than half the tests (17 of 39). Although the effects of areas and times were frequently not statistically significant, the differences observed were usually consistent from year to year and agreed with the observed changes (such as inter-lake migrations) and with the observations that numbers of age 0 fish increase during the first part of each season and decrease later each season. I have, therefore, presented the quantitative results of the tow net sampling in general summaries consisting of bar and line graphs.

Trends in Abundance for the Entire System

Some stocks of juvenile sockeye salmon in the Naknek system begin to migrate oceanward as soon as

Table 6.--Two-way analysis of variance of abundance of juvenile sockeye salmon in tow net catches in selected lakes of the Naknek system, 1961-64. The analysis involves effects of areas and time where one pair of surface and deep tows for each area and time was treated as one sample except for Coville Lake in 1961, when each tow was a sample.

Year	Source	df	MS	F
		Coville Lake		
1961 (age 0)	Area	1	6,088.739	1.985 (NS)
	Time	2	469.205	<1 (NS)
	Time-area	2	109.192	<1 (NS)
	Error	45	3,067.286	
1962 (age 0)	Area	1	173.344	<1 (NS)
	Time	2	41,369.197	6.954**
	Time-area	2	443.344	<1 (NS)
	Error	12	5,948.760	
1963 (age 0)	Area	3	44,960.561	1.007 (NS)
	Time	2	71,657.853	1.605 (NS)
	Time-area	6	19,975.607	<1 (NS)
	Error	13	44,637.880	
1964 (age 0)	Area	4	75,014.098	3.470*
	Time	2	51,733.660	2.393 (NS)
	Time-area	8	55,299.560	2.558**
	Error	35	21,615.91	
		Iliuk Arm		
1961 (age 0 and 1)	Area	2	96.310	<1 (NS)
	Time	2	435.171	<1 (NS)
	Time-area	4	670.576	1.245 (NS)
	Error	40	538.62	
(age 0)	Area	2	61.450	<1 (NS)
	Time	2	467.331	1.147 (NS)
	Time-area	4	505.180	1.240 (NS)
	Error	40	407.438	
1962 (age 0 and 1)	Area	2	3,311.066	35.375**
	Time	1	3,253.427	34.760**
	Time-area	2	6,139.228	65.691**
	Error	26	93.598	
1963 (age 0 and 1)	Area	2	7,316.271	7.266**
	Time	2	3,149.771	3.128*
	Time-area	4	7,256.416	7.207**
	Error	14	1,006.865	
(age 0)	Area	2	1,370.424	4.118**
	Time	2	299.361	<1 (NS)
	Time-area	4	1,221.070	3.670**
	Error	14	332.756	
		South Bay		
1961 (age 0 and 1)	Area	2	494.114	3.668*
	Time	1	187.391	1.391 (NS)
	Time-area	2	741.177	5.502**
	Error	42	134.715	
(age 0)	Area	2	223.296	10.401**
	Time	1	406.916	5.708**
	Time-area	2	243.122	6.219**
	Error	42		

Table 6.--Two-way analysis of variance of abundance of juvenile sockeye salmon in tow net catches in selected lakes of the Naknek system, 1961-64. The analysis involves effects of areas and time where one pair of surface and deep tows for each area and time was treated as one sample except for Coville Lake in 1961, when each tow was a sample.--Continued

Year	Source	df	MS	F
	South Bay--Cont.			
1962 (age 0 and I)	Area	1	5.445	<1 (NS)
	Time	2	5,066.558	1.952 (NS)
	Time-area	2	7,429.308	2.862*
	Error	15	2,595.589	
1963 (age 0 and I)	Area	2	2,386.507	<1 (NS)
	Time	2	7,099.841	2.724 (NS)
	Time-area	4	1,226.840	<1 (NS)
	Error	12	2,606.070	

*Indicates 10% level of significance.
**Indicates 5% level of significance.

they leave the spawning grounds, although they do not actually enter the ocean until the spring or early summer of their second or third year. As a result, the numbers of age 0 and age I sockeye salmon increase in the basins closer to the outlet river, while the number of juveniles in the system is declining gradually.

I, therefore, evaluate mortality of juvenile sockeye salmon in the Naknek system by examining the abundance data for the system as a whole. For 1962 I was able to calculate an average catch per tow by age class each day for the system from 10 July to 29 August. The sampling was done quite regularly and, in general, each sampling unit shown in Figure 1 was sampled once every 2 wk. By assigning the catch per tow found by averaging the most recent preceding and following sampling in each unit to those days on which no data were collected, the weighted (by the surface area of each sampling unit) rate of catch was calculated for each day for the entire Naknek system. The data were smoothed by a moving average of 3 (giving the middate a double weight) for age 0 and age I fish (Fig. 3). Three general time periods of abundance for age 0 fish appear in these data: (1) the early period, when catches were increasing—before 26 July; (2) the middle period, when catches were generally stable—from 26 July to about 10 August; and (3) the late period, when catches were decreasing rapidly—after 10 August. The rate of catch of age I fish decreased gradually during the season.

The mean catch per tow by lake and the contribution of each lake to the catch for the entire system for the early, middle, and late time periods were calculated for each year from 1961 to 1964 for age 0 and age I sockeye salmon. In 1961 and 1962 tow netting was done some place in the system on most nights from early July to early September, so that the averages for individual time periods may represent a period of as many as 20 days. In contrast, the data for the respective periods in 1963 and 1964 were collected within 2 days of 10 July, 1 August, and 29 August. Therefore, the figures for the early and late time periods are the results of shorter periods of mortality in 1963 and 1964 than in 1961 and 1962.

The weighted daily mean number of age 0 sockeye salmon caught per tow for the entire Naknek system in 1962 and the means for the early, middle, and late periods in 1963 and for the late period only in 1961 and 1964 are shown in Figure 4.

Only a general relation exists between the abundance of age 0 sockeye salmon in tow net catches in late August and the number of resulting smolts (Table 7). In 1961-63 the mean number of age 0 fish in the catches ranged from 8.8 to 13.2, and the number of resulting smolts (ages I and II) ranged from 11 to 16.7 million. Age 0 fish were about 1.5 times as abundant in 1964 as in the other years and produced an unusually large number of smolts—14.7 million age I (about 25%

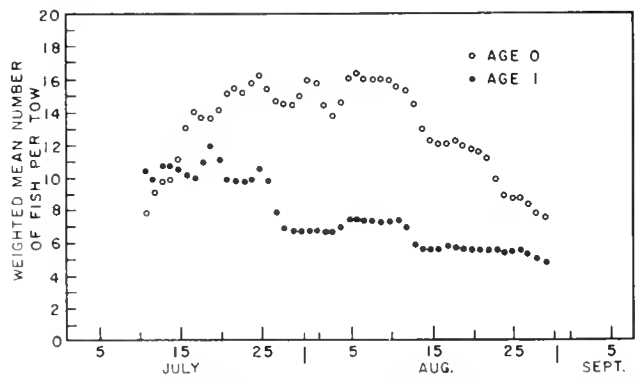

Figure 3.—Weighted daily mean number of age 0 and age I sockeye salmon per standard tow in Naknek River system (all lakes combined), 11 July to 29 August 1962. The mean catch for the system was weighted by the surface area of each sampling unit and the daily estimates were smoothed by a moving average of three— (A + 2B + C) ÷ 4.

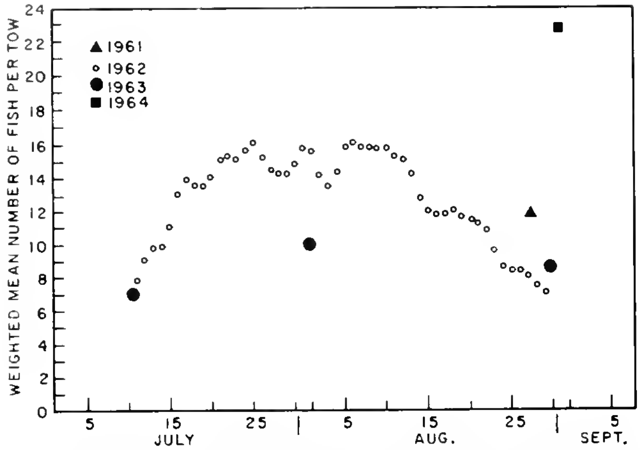

Figure 4.—Weighted daily mean number of age 0 sockeye salmon per standard tow in Naknek River system (all lakes combined) for 1962 and means for early, middle, and late periods for 1963 and for late period only in 1961 and 1964. (See Fig. 3 for explanation of weighting procedure.)

more than in the previous high year) and 20.8 million age I and age II combined.

The systemwide average catch per tow of age I sockeye salmon generally declined slowly from July through August each year and the abundance after 10 August ranged from 2.0 to 5.4 from 1961 to 1964 (Table 7). A decrease in abundance of age I fish was expected because of a continuing outmigration of smolts during the summer and natural mortalities. The range of abundance of age I fish after 10 August each year was similar to the range in abundance of age II smolts the next spring (age III smolts are rare in the Naknek system).

Comparative Abundance among Lakes

Although age 0 and age I sockeye salmon were commonly captured together, the abundance of each age class is considered separately because of differences in behavior and distribution among the lakes.

The general picture of the relative seasonal abundance of age 0 and age I sockeye salmon in tow net catches in each lake for 1961-63 are shown in Figures 5 and 6. Because it was not always feasible to maintain the sampling schedule, the data in Figures 5 and 6 are not complete for all years and all time periods. The great difference in the scale of the ordinates of Figures 5 and 6 should be noted: only general sampling periods are indicated in the graphs because I wish to consider only the seasonal trends in abundance.

The most marked changes in the abundance of age 0 fish (and changes involving the greatest numbers of fish) are the decreases in Coville Lake and concurrent increases in Iliuk Arm for each time period (Fig. 5); similar but much smaller increases for age 0 fish appear in Grosvenor Lake and South Bay. The decrease in abundance of age 0 fish in Coville Lake and the increase in the other lakes are due in part to an observed downsystem migration of age 0 fish. This summer outmigration is probably significant in Coville Lake, but the significance of these fish to the rest of the system is uncertain (discussed in more detail later). Part of the increase in numbers of age 0 fish downlake from Coville Lake was due to a continuing recruitment of fry from spawning grounds directly tributary to the lakes, as indicated by the occurrence of the small fish in samples taken in late July and most of August in all years.

The abundance of age 0 fish in each lake in July is

Table 7.--Mean number of age 0 and age I sockeye salmon taken in tow nets in the Naknek River system (all lakes combined) in August 1961-64 and resulting numbers of smolts produced. Age 0 fish in August can become age I or age II smolts, but age I fish in August can become only age II smolts (rarely age III).

Age of fish and year of sampling	Fish in parent escapement (thousands)	Mean number of fish per tow net catch	Smolts produced[1] (millions)		
			Age I	Age II	Total
Age 0					
1961	828.4	11.9	8.0	8.7	16.7
1962	351.1	13.2	6.0	5.0	11.0
1963	723.1	8.8	2.2	9.9	12.1
1964	905.4	23.0	14.7	6.1	20.8
Age I					
1961	2,231.8	1.9	--	8.5	--
1962	828.4	4.7	--	8.7	--
1963	351.1	3.2	--	5.0	--
1964	723.1	5.4	--	9.9	--

[1]Stewart, Donald M. (editor). 1969. 1967 Bristol Bay red salmon smolt studies. Alaska Dep. Fish Game, Inform. Leafl. 134.

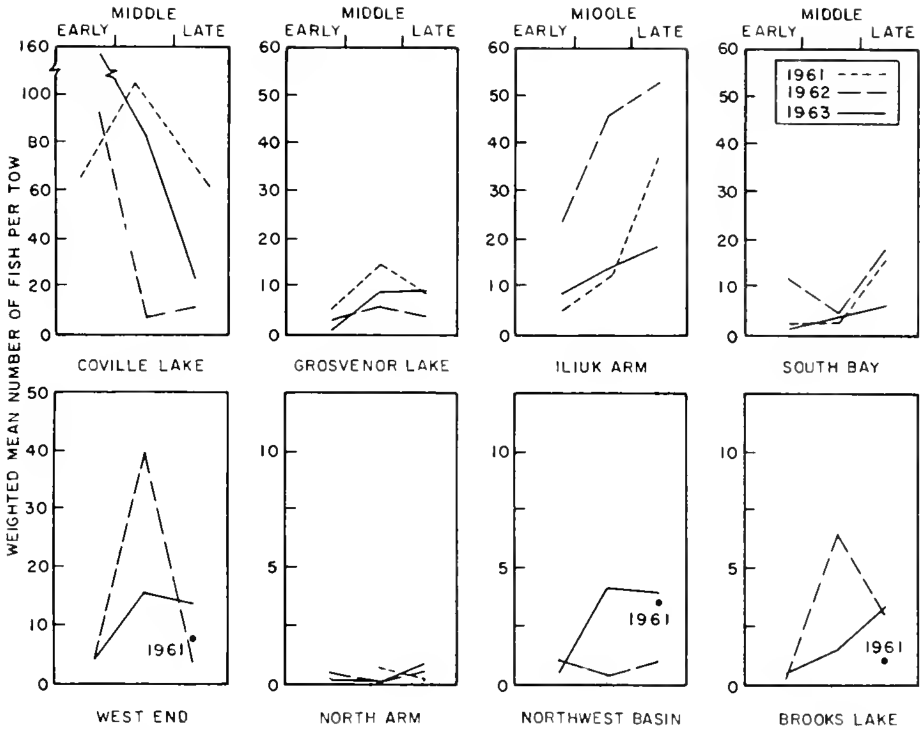

Figure 5.—Weighted mean number of age 0 sockeye salmon per standard tow by early, middle, and late time periods in each lake of the Naknek River system 1961-63.

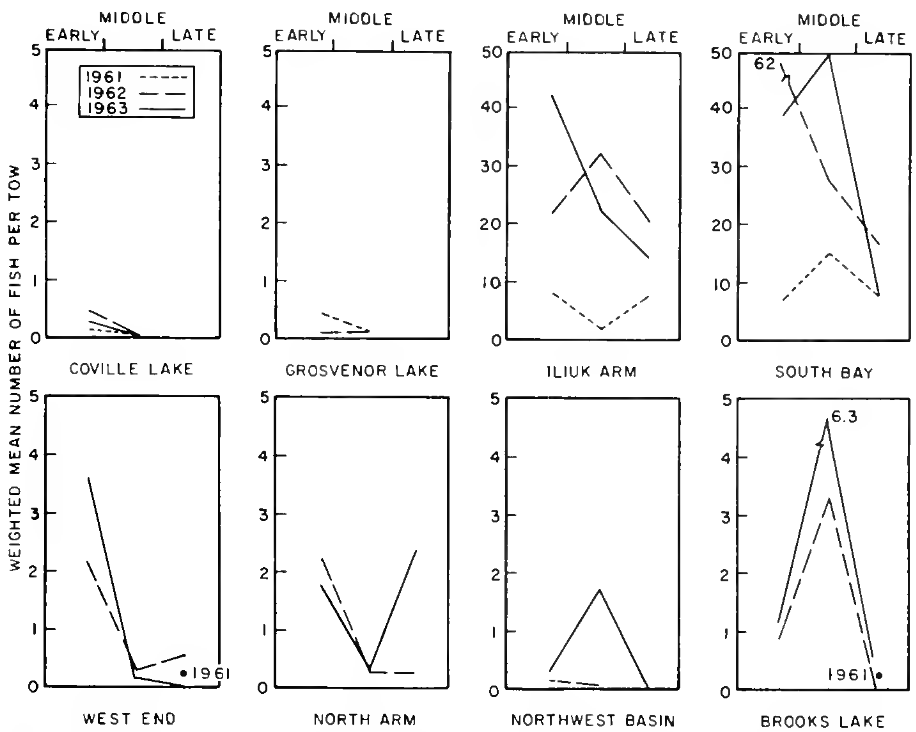

Figure 6.—Weighted mean number of age 1 sockeye salmon per standard tow by early, middle, and late time periods in each lake of the Naknek River system 1961-63.

related only in a general way to the abundance of potential spawning grounds per unit lake area (Table 8). The largest catches of age 0 fish came from the lake with the greatest amount of probable spawning grounds per unit of lake area—Coville Lake yielded about 96 fish per tow and has 3.32 ha of spawning area per square kilometer of lake. The lowest densities of age 0 fish were generally in basins that had the lowest ratios of spawning grounds to lake area—Northwest Basin has 0.02 ha of spawning ground per square kilometer of lake and North Arm has 0.04. The exception to this is Brooks Lake which has an intermediate abundance of spawning area (0.24 ha), but a low abundance of young sockeye salmon. The other lakes had variable catches of age 0 sockeye salmon, seemingly independent of the abundance of their spawning grounds.

The lakes fall into three groups in terms of abundance of age 1 sockeye salmon (Fig. 6): (1) lakes that never have many age 1 fish and usually none after July—Coville and Grosvenor Lakes and Northwest Basin; (2) lakes that usually have a few age 1 fish all summer—Brooks Lake, North Arm, and West End; and (3) lakes that have many age 1 fish through the summer—Iliuk Arm and South Bay. The last two basins constitute only about 25% of the system's surface area, but contain about 90% of the age 1 sockeye salmon in the July to September period. The decline in abundance of age 1 fish in Iliuk Arm and South Bay each summer is concurrent with the downsystem migration of age 1 fish into these lakes from Grosvenor Lake and the continued outmigration of smolts from the system via the Naknek River.[2]

Abundance in Each Lake of the System

The preceding section described in general terms the abundance of juvenile sockeye salmon in the pelagic areas of the system as a whole. This section will discuss the abundance of juvenile sockeye salmon in the lakes and connecting rivers in detail and some of the factors affecting it. To facilitate comparisons among the lakes, Figure 7 shows the number of age 0 fish for the early, middle, and late time periods by sampling unit in each lake of the Naknek system for 1961-63. The 1964 data are not shown in Figure 7 because they are complete only for Coville Lake.

Coville Lake.—Studies of juvenile sockeye salmon in the Naknek system were gradually concentrated in Coville Lake because it seemed to have special features which would facilitate understanding the dynamics of the population. These features are: (1) an abundant population of fast-growing juvenile sockeye salmon and associated species; (2) a single major spawning stock of sockeye salmon; and (3) a narrow lake basin with the major source of sockeye salmon fry at the end opposite the outlet. This combination of characteristics simplified sampling and offered a better opportunity for detecting gradients in biological conditions.

[2]The main smolt migration is complete and sampling was usually ended by late July, but the migration was sampled intermittently in August 1956 and 1958 and to 7 September 1962. The smolt migration extended through August, but involved relatively few fish. (H. W. Jaenicke, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, AK 99821, pers. comm.)

Table 8.--Relative abundance of spawning grounds and average catch per unit of effort of age 0 sockeye salmon in early July 1961-63 in lakes of the Naknek River system.

Lake or basin	Area of potential spawning grounds per unit lake area (ha/km^2)	Age 0 sockeye salmon per tow
Coville Lake	3.32	96
West End	0.68	3
Grosvenor Lake	0.40	3
Iliuk Arm	0.37	13
Brooks Lake	0.24	1
South Bay	0.07	5
North Arm	0.04	1
Northwest Basin	0.02	2

The mean rate of catch of age 0 sockeye salmon in tow nets in sampling units of Coville Lake is shown in Figure 7 for the standard time periods for 1961-63 and in Figure 8 for several time periods for 1961-64. In 1961 the abundance differed markedly from the other years in that an early-season (about mid-July) high was not observed. Although it may be that sampling in 1961 began after the early-season maximum of abundance, the pattern of recruitment of fry from American Creek, the major source of fry to the lake, and mortality in the lake may have been quite different in 1961 than in 1962-64, as indicated by the greater abundance of age 0 fish at the end of the summer in 1961 (Fig. 7). The catches of age 0 sockeye salmon in the lake declined markedly through the summer in 1962, 1963, and 1964 and were similar at the end of August each year. The analysis of variance showed significant differences in abundance due to time only in 1963 (Table 6).

Because the major source of juvenile sockeye salmon in Coville Lake is at the end opposite the outlet, a gradient in abundance and possibly in size of juveniles might be expected. To increase the chance of detecting such a gradient, the downlake sampling area—unit C-2 in 1961 and 1962 (Fig. 1)—was divided into three units in 1963 and into four in 1964 (Fig. 2). In Figure 8, C-1 is the sampling unit closest to American Creek in all 4 yr and C-2, C-2L, and C-5 are the units closest to the outlet of the lake in 1961-62, 1963, and 1964 respectively.

Neither abundance nor size of age 0 sockeye salmon in Coville Lake showed a gradient from the source to

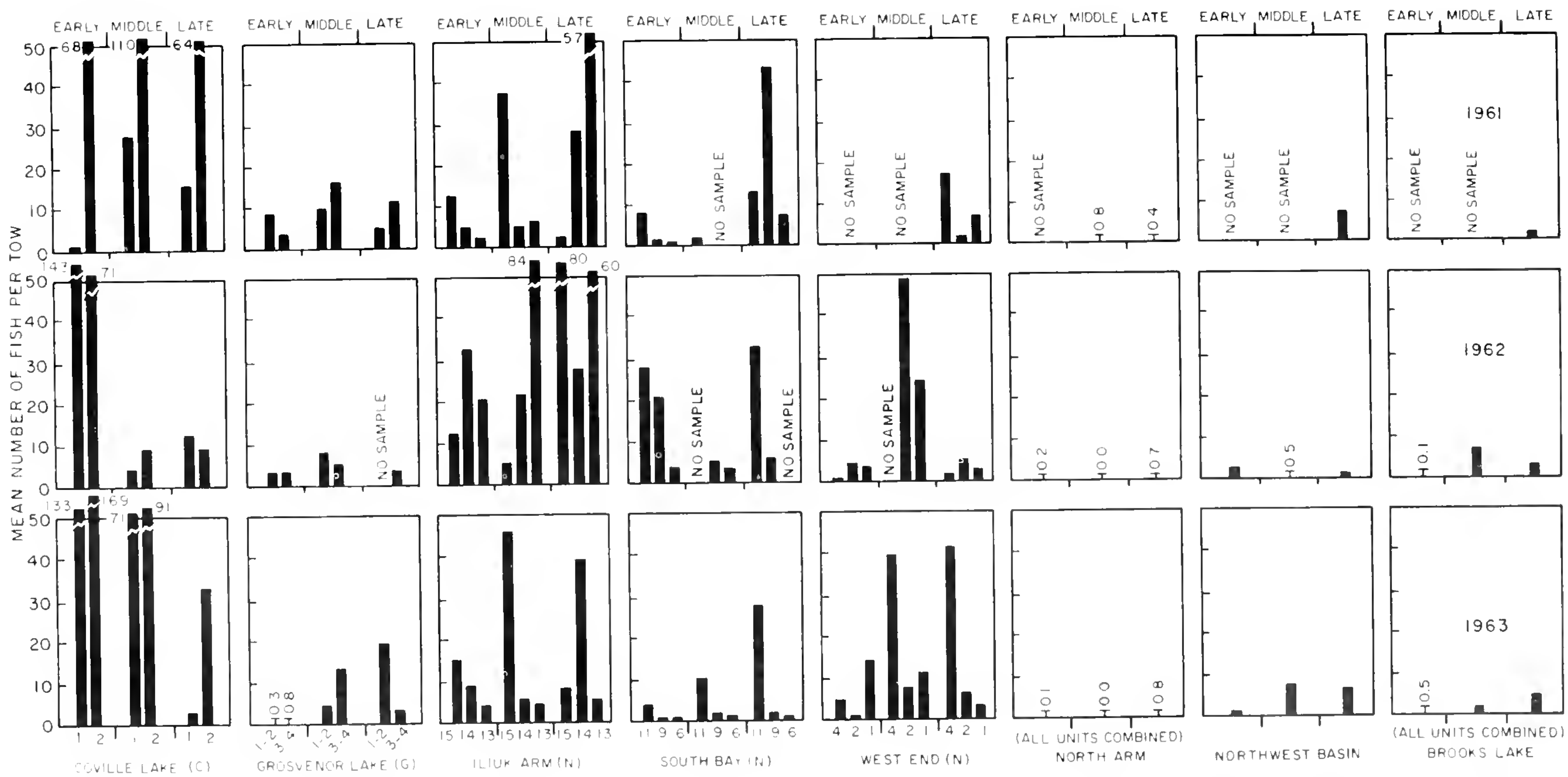

Figure 7.—Mean number of age 0 sockeye salmon per standard tow by early, middle, and late periods in sampling units of each lake of the Naknek River system 1961-63. The catches in Coville Lake units C-2U, C-2M, and C-2L for 1963 are combined in this figure and are designated simply "2." Letters in parentheses beside each lake name are prefix letters used in Figure 1 to designate units from that lake.

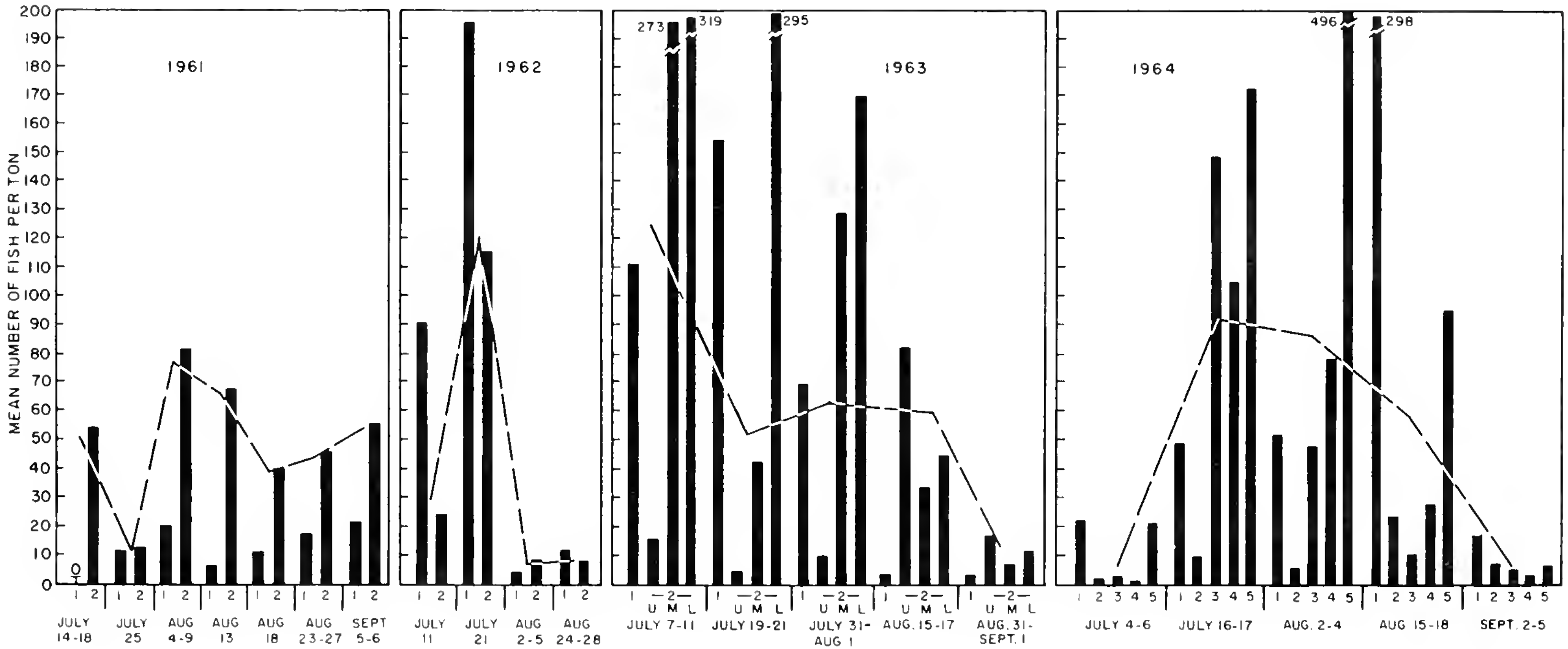

Figure 8.—Mean number of age 0 sockeye salmon per standard tow in sampling units in Coville Lake for several time periods, 1961-64. The designation for each unit should be prefixed by the letter C as shown in Figures 1 and 2. See Figure 2 for explanation of changes in numbers of sampling units in 1963 and 1964. Dotted line is weighted average for the entire lake each year.

Table 9.--Mean fork length ($\bar{X}$) and standard deviation (SD) of age 0 sockeye salmon taken in tow nets in sampling units of Coville Lake and in fyke nets in Coville River by time periods, July 11 to September 1, 1963.

Sampling	July 7-11		July 19-21		July 31-Aug. 1		Aug. 15-17		Aug. 31-Sept. 1	
unit	$\bar{X}$ length	SD	$\bar{X}$ length	SD	$\bar{X}$ length	SD	$\bar{X}$ length	SD	$\bar{X}$ length	SD
C-1	34.8	±3.8	41.6	±5.2	51.0	±5.6	--	--	57.0	±9.1
C-2U	47.0	±3.0	--	--	54.0	±6.3	53.6	±5.3	57.8	±6.5
C-2M	44.2	±3.4	47.4	±4.8	51.3	±6.1	57.1	±5.3	62.0	±3.4
C-2L	41.2	±3.9	45.2	±4.3	53.4	±4.8	51.1	±6.9	57.4	±8.3
Coville River	--	--	49.8	±4.6	51.7	±5.3	56.6	±5.1	61.5	±5.4

the outlet. In 1963 and 1964 the second sampling units downlake (C-2U and C-2 respectively) yielded fewer fish per tow than did the adjacent units uplake (C-1) or downlake (C-2M and C-3) in July and the first part of August. In mid- and late-August the rate of catch of juveniles was greatly reduced in C-1 and it appears that in 1963 many of the fish that had been in C-1 had moved downlake into C-2U. Analysis of variance showed significant differences in abundance among areas of Coville Lake only in 1964 (the year when five areas were sampled). In early July of both years the average length of fish was smaller close to the upper end of the lake, but later, fish with the smallest average lengths were from the area closest to the outlet. No clines or gradients among the areas appear in the length data (Tables 9 and 10).

The migration of age 0 sockeye salmon from Coville Lake to Grosvenor Lake began in mid-July, but did not involve many fish until about the first of August. In 1963 and 1964 juvenile salmon captured in fyke nets in Coville River as they were leaving the lake were generally larger than the average size of those remaining in the lake (Tables 9 and 10). In 1964, when the lake was sampled in most detail, the smallest average size was found in the area adjacent to the outlet (Table 10). It appears that fish leaving the lake were the larger members of the "normal" length frequency which resulted in a smaller average size for those remaining in the area adjacent to the outlet.

Grosvenor Lake.—The seasonal change in abundance of age 0 sockeye salmon in tow net catches from Grosvenor Lake was generally similar to that of the system as a whole (Fig. 3) in 1961, 1962, and 1963; i.e., the abundance increased during July and decreased in the latter part of August (Figs. 5 and 7). The only exception was the unusually large (for Grosvenor Lake) average catch for one series of tows made in areas G-1 and G-2 in the sampling in the late period in 1963 (Fig. 7). There was no marked concentration of young salmon early in the summer in the pelagic areas near the major spawning grounds (sampling units G-3 and G-4—Fig. 1).

The decline in abundance of juveniles in Grosvenor Lake in August occurred during the time of an immigration of fish from Coville Lake via Coville River and an emigration from Grosvenor Lake via Grosvenor River. Several large catches of juveniles were made with tow nets very close to the outlet of Grosvenor Lake indicating that migrants accumulated here; these data are not included in Figure 7 because this area was not part of a regular sampling area.

Sockeye salmon in the 27- to 39-mm size groups were recruited to Grosvenor Lake in middle and late

Table 10.--Mean fork length ($\bar{X}$) and standard deviation (SD) of age 0 sockeye salmon taken in tow nets in sampling units of Coville Lake and in fyke nets in Coville River by time periods, July 4 to September 5, 1964.

Sampling	July 4-6		July 16-17		Aug. 2-4		Aug. 15-18		Sept. 2-5	
unit	$\bar{X}$ length	SD	$\bar{X}$ length	SD	$\bar{X}$ length	SD	$\bar{X}$ length	SD	$\bar{X}$ length	SD
C-1	34.2	±2.8	46.3	±2.9	50.3	±4.0	57.1	±4.9	59.3	±4.7
C-2	--	--	46.2	±2.7	52.6	±6.3	57.6	±6.0	59.4	±5.0
C-3	--	--	43.6	±2.4	51.3	±4.2	57.5	±4.7	58.0	±7.2
C-4	--	--	42.6	±3.7	50.2	±4.4	57.1	±3.9	--	--
C-5	36.4	±3.4	42.5	±3.2	48.4	±4.2	49.7	±4.8	54.8	±5.4
Coville River	--	--	--	--	54.9	±3.4	60.7	±3.3	61.1	±5.2

August 1961 and 1963, but relatively few fish in these size groups were collected during this time in 1962 (see section on length frequencies). These small and presumably late-emerging fish must originate within the Grosvenor Lake basin because they have never appeared in samples from Coville Lake or Coville River. They may be progeny of adults that spawn in the shallow beach areas—the development of these fish could be slower than normal because of low temperature and oxygen levels accompanying severe winter conditions, as has been reported for progeny of beach spawners at Lake Kitoi (Smoker, 1957).

Iliuk Arm.—Iliuk Arm has only one known intrabasin spawning ground of significant size, Margot Creek, but it has enough extrabasin spawning ground (including one tributary to the Savonoski River above Grosvenor River) to yield a spawning-area-to-lake-area ratio intermediate for the Naknek system—0.37 ha per square kilometer (Table 2). In addition to the known grounds, it is suspected that spawning occurs in beach areas within Iliuk Arm and in streams tributary to the Savonoski River. A variable recruitment to Iliuk Arm from Hardscrabble Creek in Grosvenor Lake is known to occur, but the potential spawning ground of Hardscrabble Creek is not assigned to Iliuk Arm. The greatest number of recently emerged fry and interlake migrants probably enter Iliuk Arm through Savonoski River in sampling unit N-15 (Fig. 1).

The abundance of age 0 sockeye salmon increased in Iliuk Arm in the summers of 1961, 1962, and 1963 (Fig. 5), but the relative abundance in the three sampling areas varied from year to year (Fig. 7). This variation may be due to year-to-year changes in the relative number of recruits from different sources. The trends in abundance in each of the sampling areas during the summer in 1961 and 1963 are similar—mortality or migration from the basin exceeded recruitment in August in N-15 and N-14 and resulted in a shift in the center of abundance to the downlake end of the basin by the end of August (Fig. 7). This did not happen in 1962 when a relatively intensive summer migration of age 0 sockeye salmon down Grosvenor River was observed. A similar migration occurred in Grosvenor River during the summers of 1961 and 1963, but was not well sampled. The analysis of variance showed significant differences in abundance of juvenile salmon (age 0 and 1 combined) among sampling areas, times, and in time-area interaction for 1962 and 1963 (Table 6). The differences between areas and the time-area interaction were also significant in 1963, but time alone was not when only age 0 are considered.

In 1964 Iliuk Arm was sampled only at the end of August, and at this time (as in 1963), age 0 sockeye salmon were least abundant in the uplake unit, N-15, and most abundant in the midlake unit, N-14. The weighted average catch per tow for the entire basin at this time was the greatest observed in Iliuk Arm from 1961 to 1964.

South Bay.—South Bay receives sockeye salmon fry from both outside and inside its basin. The only significant source within the basin is Brooks River in unit N-11, although some fry may result from beach spawning along the south shore of N-6. Because downsystem migrants are recruited from Iliuk Arm, the major recruitment from outside the basin is also into N-11.

There was generally a gradient in abundance of age 0 fish in South Bay—the largest catches were made in N-11 and the smallest in N-6 (Fig. 7). The greatest abundance of age 0 sockeye salmon recorded for South Bay between 1961 and 1964 was at the end of August 1964; at that time (as in 1963) the catches were largest in N-11 and smallest in N-6. Analysis of variance for age 0 indicated significant differences in abundance among sampling areas, times, and time-area interactions in 1961 and only in time-area interactions in 1962 (Table 6). During the 4 yr of this study, South Bay always had its greatest number of age 0 fish at the end of summer.

West End.—The West End basin is the shallow outlet end of Naknek Lake and is mostly less than 10 m deep. It contains a few small spawning streams and the extensive but essentially unknown spawning areas of the upper end of Naknek River, i.e., between the rapids and the lake. It is assumed that sockeye salmon that hatch in the Naknek River move upstream into West End shortly after they emerge. The evidence for this is all negative—very few zero freshwater-age-type adults return to the system,[3] and the Naknek River and adjacent lagoons are probably not extensive enough to rear enough smolts to produce the large number of adults that spawn in the river in some years. However, sampling with tow nets in the early period in unit N-1 never yielded many age 0 sockeye salmon (Fig. 7).

The abundance of age 0 sockeye salmon in the West End in 1962 and 1963 (Fig. 5) was low in the early period, high in the middle period, and low in the late period. In 1964 this basin was sampled only on 3 September. Comparison of length frequencies of age 0 fish (discussed later) and their seasonal abundance in Iliuk Arm and South Bay with similar data from West End (Fig. 7) indicates that the movement of interlake migrants during the summer does not continue on into West End. This is also shown by the marked reduction in abundance of age 0 fish through South Bay from sampling units N-11 to N-9 to the unit adjacent to the West End, N-6. Although it seems that the movement of age 0 fish downlake does not extend through South Bay by early September, the situation in Coville Lake thoughout July 1963 should be recalled, i.e., areas of greater abundance occurred both uplake and downlake from an area of low abundance (Fig. 8) comparable to

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

N-11 (high abundance), N-9 and N-6 (low abundance), and N-4 (high abundance).

The source of the relatively larger number of age 0 fish in N-4 in 1963 (Fig. 7) may have been the beach spawning areas along the south shore of N-6 (the base of the north slope of Dumpling Mountain). But again the situation may be comparable to the situation in Coville Lake where juveniles were relatively scarce over the deep water of the central basin but were abundant over the shallower water at both ends. The age 0 fish may have passed through or around the deep water of N-9 and N-6 without being sampled. The data for 1962 and 1963 in Figure 7 indicate this may have happened. If it did, this movement involved more of the larger fish, for the average lengths of the age 0 fish were generally greater in the West End.

North Arm.—The North Arm basin is the largest in the system in surface area (over water deeper than 5 m) and volume, but has next to the lowest ratio of potential spawning area to lake area (Table 2). In addition to having little intrabasin spawning grounds, recruitment of juvenile sockeye salmon to North Arm from other basins is limited by the drainage pattern —the flow of water into North Arm is surface runoff via several small streams and the flow out is through narrow channels and over shoals. The two factors —little intrabasin spawning and little recruitment from other lakes—resulted in the lowest abundance of juvenile sockeye salmon observed in the Naknek system (Fig. 7).

Northwest Basin.—The Northwest Basin appears to be as much an entity as North Arm. The Northwest Basin is small and comparatively deep and has only a shallow connection to the rest of the Naknek system via the West End. This basin has several small lateral spawning streams along its north shore, but the ratio of spawning area to lake area is the lowest in the system (Table 2). The general abundance of age 0 sockeye salmon is also quite low—only North Arm and Brooks Lake produced lower rates of catch.

The type of spawning ground in Northwest Basin —small lateral streams—is generally more intensively utilized by sockeye salmon than the larger intermediate-sized streams such as Bay of Islands Creek in North Arm and Headwater Creek in Brooks Lake (Burgner et al., 1969). The greater intensity of use of the spawning grounds in the Northwest Basin could account for the greater abundance of age 0 sockeye salmon there (Fig. 7) than in North Arm or Brooks Lake, in spite of their larger ratios of spawning area to lake area.

Brooks Lake.—Brooks Lake is similar to North Arm and Northwest Basin in terms of abundance of juvenile sockeye salmon (relatively low—Fig. 7), in lacking recruitment from other basins, and in not having a recruitment of fry in midsummer (based on shape of the 1962 catch curve [Fig. 5] and length frequency data). In late summer and early fall it is usual for few to several thousand age 0 sockeye salmon to migrate from Brooks Lake to South Bay.[4]

ABUNDANCE OF ASSOCIATED SPECIES

In general, the catches of fish other than sockeye salmon in tow nets were not consistent within or between years either for species or basin. The effects of such factors as spawning migrations and recruitment of age 0 fish cannot be analyzed because there are not enough data on age composition or length frequency. Hence, only general comments can be made on the abundance of associated species.

The three species most commonly associated with sockeye salmon in tow nets were pond smelt, threespine sticklebacks, and ninespine sticklebacks. In the sections that follow, the catch-per-tow data for these three species were summarized by semimonthly periods for 1961-63 for areas and lakes. The lake averages were derived by the procedure used with the salmon data. Although most sampling was in the surface to 3-m zone in 1961, the data for that year are treated here as equivalent to those of 1962-64 because, as with juvenile sockeye salmon, the split-plot analysis of variance tests did not indicate consistent differences between average catches at the two depths (Table 11).

Pygmy whitefish and least cisco were captured with some type of gear in most basins of the system (Table 3), but because neither species consistently occurred in significant numbers in the tow net samples, they will not be discussed in this section.

Pond Smelt

Pond smelt occur in all basins of the Naknek system[5] and have been taken by all suitable gear, but they occurred in large numbers only in samples collected with tow nets in Coville Lake. In Coville Lake, tow net catches of pond smelt fluctuated greatly and erratically during the season (Fig. 9)—much more than the catches of juvenile salmon, which were characterized by a relatively steady seasonal decline (Fig. 5). Age 0 pond smelt, which first occurred in late August, were never the most numerous age group in the catches.

The comparatively large catches of pond smelt in Coville Lake in 1963 may reflect good survival of the 1962 year class. Generally favorable growing conditions for fish in 1962 were indicated by the greater growth of juvenile sockeye salmon that year. Significant differences in abundance were indicated in the split-plot analysis of variance for depth in 1962 and 1963 and for interaction of depth-time in 1963 (Table

[4]From Brooks Lake Field Station Reports, 1961-65, on file National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, AK 99821.

[5]Pond smelt have not been reported from Brooks Lake, but have been seen in a tributary to Brooks Lake and in Brooks River near the outlet of Brooks Lake (Heard, Wallace, and Hartman, 1969).

Table 11.--Split-plot analysis of variance of abundance in tow net catches of pond smelt (Coville Lake), threespine stickleback (Coville Lake and West End) and ninespine stickleback (Coville Lake and West End), 1962-64. Analysis involves only paired surface and deep tows and considers variation due to sampling areas, time (July 1-15, July 16-31, August 1-15, August 16-31), and depth (surface versus deep) of tow.

Species and year	Source	df	MS	F
	Coville Lake			
Pond smelt				
1962	Main plot			
	Area	1	5,160.7	2.84 (NS)
	Time	3	864.88	<1 (NS)
	Error	3	1,819.94	
	Subplot			
	Depth	1	9,469.72	4.95*
	Depth-time	3	1,733.01	<1 (NS)
	Error	4	1,911.32	
1963	Main plot			
	Area	1	55,508.54	<1 (NS)
	Time	3	7,181.71	<1 (NS)
	Error	3	87,479.80	
	Subplot			
	Depth	1	56,921.61	6.18*
	Depth-time	3	70,008.62	7.63**
	Error	4	9,207.64	
1964	Main plot			
	Area	4	1,578.45	<1 (NS)
	Time	3	1,845.53	<1 (NS)
	Error	12	1,974.71	
	Subplot			
	Depth	1	792.90	<1 (NS)
	Depth-time	3	1,535.92	1.07 (NS)
	Error	16	1,439.89	
Threespine stickleback				
1962	Main plot			
	Area	1	19,320.31	<1 (NS)
	Time	3	21,865.52	<1 (NS)
	Error	3	26,681.30	
	Subplot			
	Depth	1	30,989.20	1.39 (NS)
	Depth-time	3	21,231.25	<1 (NS)
	Error	4	23,664.14	
1963	Main plot			
	Area	1	152.52	<1 (NS)
	Time	3	425.19	<1 (NS)
	Error	3	683.69	
	Subplot			
	Depth	1	971.26	1.79 (NS)
	Depth-time	3	410.51	<1 (NS)
	Error	4	543.64	
1964	Main plot			
	Area	4	127.11	1.06 (NS)
	Time	3	259.55	2.16 (NS)
	Error	12	120.10	
	Subplot			
	Depth	1	9.43	<1 (NS)
	Depth-time	3	2.93	<1 (NS)
	Error	16	43.03	

Table 11.--Split-plot analysis of variance of abundance in tow net catches of pond smelt (Coville Lake), threespine stickleback (Coville Lake and West End) and ninespine stickleback (Coville Lake and West End), 1962-64. Analysis involves only paired surface and deep tows and considers variation due to sampling areas, time (July 1-15, July 16-31, August 1-15, August 16-31), and depth (surface versus deep) of tow.--Continued

Species and year	Source	df	MS	F
	Coville Lake--Cont.			
Ninespine stickleback				
1962	Main plot			
	Area	1	114.08	3.68 (NS)
	Time	2	2,209.52	71.22**
	Error	2	31.02	
	Subplot			
	Depth	1	1,430.08	21.23**
	Depth-time	2	31.02	<1 (NS)
	Error	3	67.37	
1963	Main plot			
	Area	1	1.05	<1 (NS)
	Time	3	924.80	4.04 (NS)
	Error	3	229.05	
	Subplot			
	Depth	1	81.45	<1 (NS)
	Depth-time	3	224.87	<1 (NS)
	Error	4	288.01	
1964	Main plot			
	Area	4	12.96	2.84*
	Time	3	23.75	5.20**
	Error	12	4.56	
	Subplot			
	Depth	1	2.85	3.43*
	Depth-time	3	0.50	<1 (NS)
	Error	16	0.83	
	West End (N4-N2 only)			
Threespine stickleback				
1963	Main plot			
	Area	1	568,327.69	<1 (NS)
	Time	2	686,189.58	<1 (NS)
	Error	2	881,226.75	
	Subplot			
	Depth	1	611,782.52	<1 (NS)
	Depth-time	2	760,305.58	1.06 (NS)
	Error	3	716,034.73	
Ninespine stickleback				
1963	Main plot			
	Area	1	1,064.08	2.14 (NS)
	Time	2	681.02	1.37 (NS)
	Error	2	497.90	
	Subplot			
	Depth	1	18.75	<1 (NS)
	Depth-time	2	422.69	10.5**
	Error	3	42.04	

*Indicates 10% level of significance.
**Indicates 5% level of significance.

11). The significant results in 1963 were due to a few very large catches in the middle and late time periods in surface tows only. No consistent differences are apparent.

Threespine Sticklebacks

Threespine sticklebacks were captured with tow nets and all other suitable gear in all basins of the Naknek system (Table 3). In general, the areas that yielded only few juvenile sockeye salmon—North Arm, Grosvenor Lake, and Brooks Lake—also yielded only few threespine sticklebacks.

The outstanding feature of the abundance of threespine sticklebacks in the tow net catches is the variation from one sampling period to the next. The abundance of threespine sticklebacks during each summer from 1961 to 1963 in the West End (a region of great abundance) by sampling area (Fig. 10) illustrates this point. No significant differences in abundance with time, depth, or area appeared in the split-plot analysis of variance of data collected in 1962-64 in Coville Lake, the lake for which most data are available (Table 11). Catches of threespine sticklebacks resemble those of the pond smelt (Fig. 9) in that the abundance in tow nets fluctuated independently in adjacent sampling areas.

The catches of threespine sticklebacks increased during the summer in some lakes and were fairly uniform through the summer in others. Only a few threespine sticklebacks were captured with tow nets in the first half of July in Coville Lake, Iliuk Arm, and South Bay, but in August they were taken in moderate numbers in these basins. A similar increase in catches during the summer occurred in the lakes where they were never taken abundantly, i.e., Grosvenor Lake, North Arm, and Brooks Lake. In the areas of relatively great abundance, Northwest Basin and West End, this species was about as numerous in catches the first half of July as in late August. At Karluk Lake on Kodiak Island, in 1961 and 1962, threespine sticklebacks were abundant in the littoral areas and virtually absent in the pelagic areas in early July, but by summer they were mostly in the pelagic areas.[6] A similar shift to pelagic areas was found in Lake Nerka of the Wood River system (Burgner, 1962).

Age 0 threespine sticklebacks were rare in tow net catches until late August and even then they were so small that they could pass easily through the smallest mesh of the net unless their spines were erect.

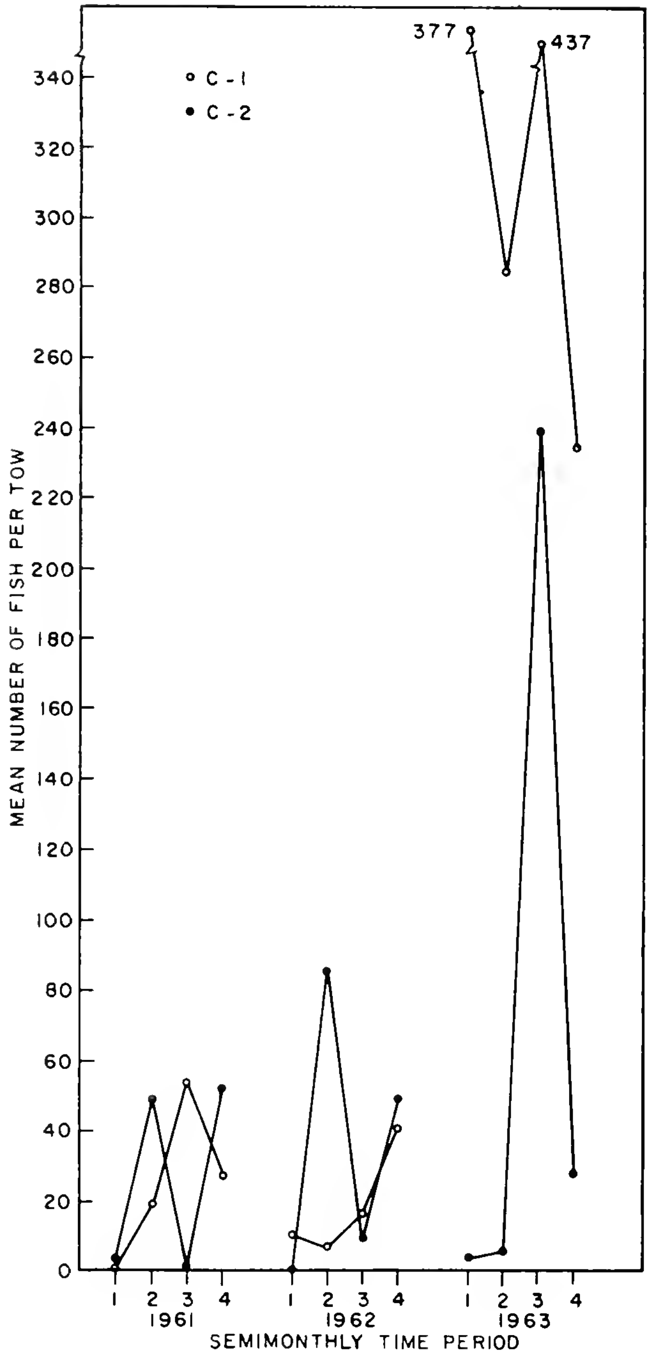

Figure 9.—Mean number of pond smelt per standard tow in Coville Lake (units C-1 and C-2) by semimonthly time periods, 1961-63. Time periods are: 1—July 1-15; 2—July 16-31; 3—August 1-15; 4—August 16-31.

Ninespine Sticklebacks

Ninespine sticklebacks and threespine sticklebacks commonly occurred in the same catches and, in general, the observations on threespine sticklebacks apply to ninespine sticklebacks. The average abundance of ninespine sticklebacks in the tow nets was markedly lower in July than in August both in Coville Lake, where moderate numbers were captured, and in Iliuk Arm, South Bay, and Northwest Basin, where only a few were captured. Four of the five significant differences in abundance shown in the split-plot analysis for

[6] B. Drucker, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, AK 99821, pers. comm.

Coville Lake (Table 11) involve both time and depth, which may reflect the offshore movement of adults after the early summer spawning and recruitment of yearlings to catchable size. The seasonal change in abundance was not as evident in West End, where this species occurred in greatest numbers. No consistent year-to-year trends in abundance were observed.

The abundance of ninespine sticklebacks in tow net catches exceeded that of threespine sticklebacks only in area C-1 of Coville Lake—this is the uplake end adjacent to large areas of submerged aquatic plants, mostly *Potamogeton* spp. The catches of the two species were about equal in the rest of Coville Lake, but in the other lakes ninespine sticklebacks were generally much less abundant than threespine sticklebacks.

INTERLAKE MIGRATION OF PRESMOLT SOCKEYE SALMON

Although juvenile sockeye salmon normally transform to smolts and migrate to salt water at age I or older, some oceanward migration of presmolts (age 0 fish) has been reported[7] (Narver, 1968). Outmigrations of presmolt sockeye salmon amounting to as much as 21% of the subsequent smolt production for the brood year had occurred in Brooks River in 1958 and 1960 and again in 1961. In the summer of 1961 a similar migration of age 0 fish from Coville Lake to Grosvenor Lake via Coville River was sampled intermittently. From these data, I estimated that several million age 0 fish had left Coville Lake.

The results of the sampling at Coville Lake in 1961 prompted further studies to answer the following questions: (1) Do significant numbers of age 0 sockeye salmon usually migrate from Coville Lake? (2) Do significant numbers of juvenile sockeye salmon overwinter in Coville Lake and migrate as age I smolts in May and June? (3) Do the age 0 sockeye salmon leaving Coville Lake during the summer remain in Grosvenor Lake until they become smolts, or do they continue downsystem to Naknek Lake their first summer? (4) What is the cause of the presmolt migration? (5) Do the behavior patterns of these fish resemble those of smolts or fry, or are they unique to summer migrants? Information pertaining to these questions was gathered by the routine sampling of the Naknek system and by special studies in Coville and Grosvenor Rivers in 1962, 1963, and 1964, in addition to the sampling in Coville River in 1961.

Large and small fyke nets were both used to sample migrating fish in the rivers. Although current velocities were not measured, the small nets (1 m) were fished in waters of about 0.3 meters per second (mps). The large nets (1.2 × 1.2 m or 1.2 × 1.5 m) were generally fished only in currents greater than 0.3 mps. Newly emerged fry could pass through the wings and body of the large nets, but would be retained in the cod end and by all parts of the small nets. The small nets were usually fished from stakes driven into the streambed and the large nets were fished from a cable strung across the river. The cod end of the large fyke net was often connected to a floating box (Craddock, 1961) that held the fish so that they could be released alive and uninjured.

In Coville River the estimate of the outmigration of juvenile salmon is based on sampling with fyke nets fished near the mouth where the river is about 24 to 46 m wide and 0.3 to 2 m deep; the current velocity is

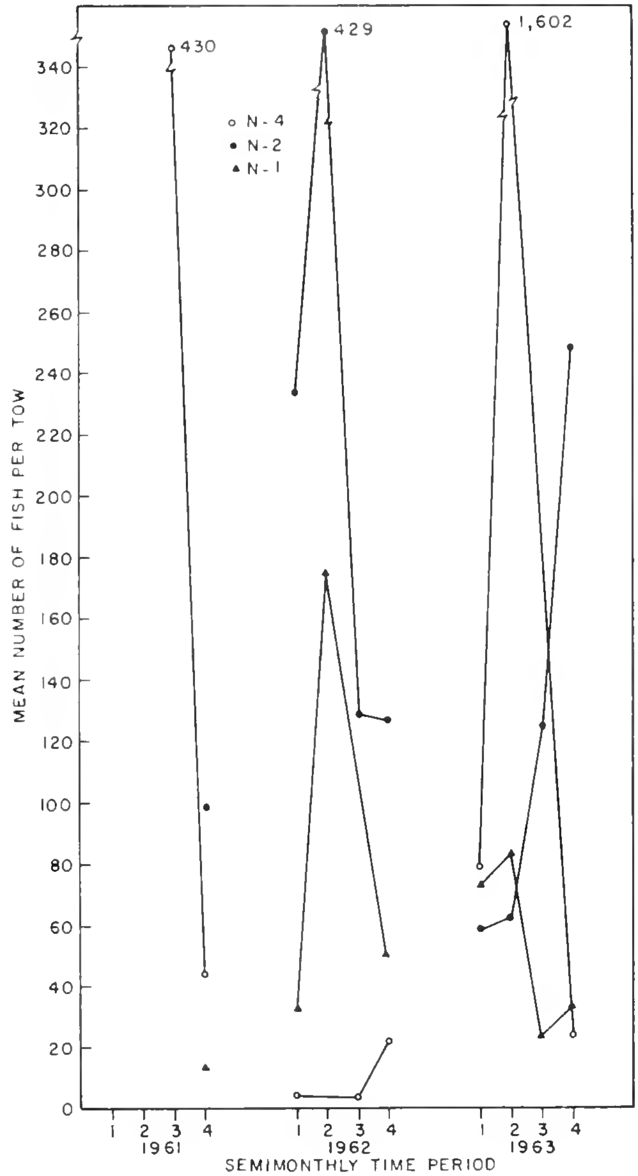

Figure 10.—Mean number of threespine sticklebacks per standard tow in West End (units N-4, N-2, and N-1) by semimonthly time periods, 1961-63. Time periods are: 1—July 1-15; 2—July 16-31; 3—August 1-15; 4—August 16-31.

[7]Wilbur L. Hartman, William R. Heard, and Charles W. Strickland. 1962. Red salmon studies at Brooks Lake Biological Field Station, 1961. On file, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, AK 99821, 53 p.

about 0.3 to 1.2 mps. The width of the stream was divided into four equal segments and the middle 1.2 m of each segment was sampled with a 1.2-m-wide fyke net. Two sampling schemes were used: (1) regularly, the site that passed the most water (and caught the most fish) was fished as an index; and (2) at intervals, based on observed changes in the character of the migration, nets were fished at the four sites following a modified Latin-square design (Cochran and Cox, 1957) so that the number of fish migrating in the entire stream during the period could be estimated. In the Latin-square scheme catches were classified according to site, time of day, and days—factors considered to have the greatest influence on variability of the individual catches. Estimates of the numbers of fish that migrated through the sites were obtained by fitting a multiplicative model[8] to the observed catches, estimating numbers migrating through unsampled site-time of day-day strata from parameter estimates of the model, and then summing over all strata (sampled and unsampled), and finally expanding this total to account for the proportion of the river sampled by the nets.

The estimated outmigration of juvenile sockeye salmon during the Latin-square and the number caught in the index site during the same period (the index site was fished continuously) were used to estimate the portion of the total migrants captured at the index site. This figure, the index catch expansion factor, is used to estimate the number migrating when only the index net was fished.

The estimate of the numbers of juvenile salmon migrating out of Coville Lake during the period sampled each year is based on a combination of the Latin-square estimates and the index catches. For periods when migration estimates from Latin-square sampling were made, the daily migration was estimated by dividing the expanded Latin-square estimate by the number of days involved; when only index sampling was done, the daily migration was estimated by expanding the catch in the index net by the index catch expansion factor. The index catch expansion factor was used up to the halfway date toward the next Latin-square period and then the factor for the next period was used. When no sampling was done for a day or days, the average of the preceding and the following estimates was used. The estimated total migration for the season is the sum of the estimates for each day.

In Grosvenor River juvenile salmon were sampled with fyke nets at two general locations. Recently emerged fry were sampled with the 1-m fyke nets in the shallow water along shore near the outlet of the lake. Older fish were sampled with the 1.2-m nets which were attached to a cable at a point about 2 miles below Grosvenor Lake, just above the island in Grosvenor River. The river was about 78 m wide and 0.6 to 2 m deep where the cable crossed and the water velocity was from 0.6 to 1.2 mps where the fyke net was fished.

For purposes of analysis, I have summarized the data by 10-day intervals; 1 August was arbitrarily selected as the starting date.

Migration from Coville Lake to Grosvenor Lake

1961.—In 1961 the sampling of juvenile sockeye salmon migrating down Coville River was exploratory and intended mainly to determine the timing and the age classes involved. The sampling was done in two periods—early (18 May to 11 June) and late (27 July to 10 September). During the early period the small (1-m-square) fyke nets and seines were used and both age 0 and age 1 fish were caught. During the late period the fishing was mainly with the 1-m-square fyke net and mostly age 0 fish were caught.

Because so many age 0 fish appeared to be involved in the summer migration, I have made an order of magnitude approximation of the number that migrated from Coville Lake to Grosvenor Lake from 27 July to 10 September. Knowledge gained in subsequent years makes the following assumptions reasonable: (1) the fyke nets caught 4% of the juvenile sockeye salmon migrating down Coville River during the periods fished (based on portion of river sampled); (2) the rate of catch during the time fished each day was typical of the whole day; and (3) the catch per day can be averaged for 10-day periods. Using these assumptions, I estimated that in 1961 about 5.6 million age 0 sockeye salmon migrated from Coville Lake to Grosvenor Lake between 22 July and 10 September (Table 12).

1962.—In 1962 the migration of sockeye salmon down Coville River was sampled from 29 May to 15 September and more systematically than in 1961. A cable was installed across the river near Grosvenor Lake where the river was about 24 m wide. The four 6-m sites were established on the cable and the large fyke nets were fished in the middle of each site. Nets

Table 12.--Estimated number of age 0 sockeye salmon migrating from Coville Lake to Grosvenor Lake by 10-day periods between July 22 and September 10, 1961.

Period	Fish migrating each period
July 22-31	871,000
August 1-10	1,058,000
August 11-20	3,459,000
August 21-30	96,000
August 31-September 10	71,000
Total	5,555,000

[8]The model was developed by Jerome J. Pella of the National Marine Fisheries Service, Auke Bay Fisheries Laboratory, and a full description and analysis of the model and its application will be published soon.

were fished on Latin-square schedules as follows: four 1.5-h periods (2100 to 0300) each sampling day from 31 May to 2 August and sixteen 1.5-h periods each sampling day from 16 to 23 August. Seven Latin-square sampling schemes were completed, three of 4 days length and four of 1 day. The estimated outmigration for each of the Latin-square schemes was: (1) from 2100, 31 May to 2100, 5 June (sampled every other day), 43,700 age I and older; (2) 2100, 8 June to 2100, 15 June (sampled every other day), 3,210 age I and older; (3) from 2100, 26 July to 2100, 2 August (sampled every other day), 160,703 age 0; (4) 2100, 16 August to 2100, 17 August, 151,240 age 0; (5) 2100, 18 August to 2100, 19 August, 50,075 age 0; (6) 2100, 20 August to 2100, 21 August, 13,120 age 0; and (7) 2100, 22 August to 2100, 23 August, 28,940 age 0. The numbers of each age of sockeye salmon migrating from Coville Lake to Grosvenor Lake from 21 May to 15 September 1962 (based on the sampling with fyke nets) were about 2,237,000 age 0 and 60,500 age I (Table 13).

1963.—In 1963 the outmigration of sockeye salmon from Coville Lake was sampled from 20 June to 17 September. Fyke nets were fished in Coville River from a cable as in 1962, but the location was about 15 m downstream where the river is 30 m wide and the depth more uniform. Nets were fished on Latin-square schedules 5 to 12 August and 13 to 17 September with four sites and four 6-h fishing periods each day. The estimated outmigration for each of the Latin-square schemes was: (1) from 2100, 5 August to 2100, 12 August (sampling every other day), 120,100 age 0 and (2) 2100, 13 September to 2100, 17 September, 28,275 age 0. The estimates of the juvenile sockeye salmon migrating by 10-day periods from 20 June to 17 September are 918,000 age 0 and 8,300 age I (Table 14). The relatively few age 0 fish that migrated before 12 July were probably not interlake migrants, but were progeny of females that spawned in Coville River.

Table 13.--Estimated numbers of age 0 and age I sockeye salmon migrating from Coville Lake to Grosvenor Lake (by 10-day periods), May 29 to September 15, 1962, based on results of fishing with 4-ft fyke nets in Coville River.

Period	Age 0 fish	Age 1 fish
May 29-June 1	[1]0	18,344
June 2-11	[1]0	36,875
June 12-21	[1]0	2,389
June 22-July 1	[1]0	240
July 2-11	0	899
July 12-21	4,109	1,383
July 22-31	184,468	268
August 1-10	92,699	104
August 11-20	414,702	0
August 21-30	774,079	0
August 31-September 9	516,036	0
September 10-15	250,819	0
Total	2,236,912	60,502

[1]Several thousand age 0 fish were captured in 1-m fyke nets fished intermittently along shore. These fish are assumed to have originated from spawning in Coville River.

Table 14.--Estimated numbers of age 0 and age 1 sockeye salmon migrating from Coville Lake to Grosvenor Lake (by 10-day periods), June 20 to September 17, 1963, based on results of fishing with 4-ft fyke nets in Coville River.

Period	Age 0 fish	Age 1 fish
June 20-21	762	289
June 22-July 1	2,539	2,537
July 2-11	3,598	516
July 12-21	40,756	3,189
July 22-31	148,318	1,650
August 1-10	393,619	83
August 11-20	132,672	0
August 21-30	55,330	0
August 31-September 9	69,688	0
September 10-17	70,448	0
Total	917,730	8,264

1964.—The migration of juvenile sockeye salmon from Coville Lake was sampled with the same techniques and at the same cable site in 1964 as in 1963. Sampling was done intermittently from 11 July to 8 September. The index net was fished on 31 days and two Latin-square schedules were completed—one from 31 July to 4 August and the other from 20 to 25 August. The estimated outmigration for each of the Latin-square schemes was: (1) from 1800, 31 July to 1800, 4 August, 122,569 age 0 and (2) from 1800, 20 August to 1800, 25 August (22-23 August not fished), 715,719 age 0. The estimates of the juvenile sockeye salmon that migrated in 10-day periods from 11 July to 7 September 1964 are about 3,036,000 age 0 and 3,900 age I (Table 15).

Migration from Grosvenor Lake to Iliuk Arm

The numbers of presmolt sockeye salmon migrating from Grosvenor Lake to Iliuk Arm, the next basin downstream, was estimated from the results of fyke netting in Grosvenor River. The nets were fished intermittently on 29 days between 30 May and 17 September 1962 and on 4 days between 10 August and 10 September 1963. On the basis of the seasonal variation in the rate of catch of age 0 fish in Coville and Grosvenor Rivers, I assumed that the summer interlake migration of this age group began about 15 July. Some age I fish were usually found in the fyke net catches in Grosvenor River and I assumed that these fish had

Table 15.--Estimated numbers of age 0 and age I sockeye salmon migrating from Coville Lake to Grosvenor Lake (by 10-day periods), July 11 to September 7, 1964, based on results of fishing with 4-ft fyke nets in Coville River.

Period	Age 0 fish	Age I fish
July 11	302	86
July 12-21	2,723	1,883
July 22-31	189,595	1,351
August 1-10	183,921	292
August 11-20	1,288,903	116
August 21-30	1,139,396	218
August 31-September 7	231,135	0
Total	3,035,975	3,946

originated in Grosvenor Lake or had spent at least one winter there because age I fish were virtually absent from the Coville River summer migrations.

My estimate of the number of age 0 sockeye salmon that migrated from Grosvenor Lake to Iliuk Arm from 15 July to 17 September 1962 is 3.9 million (Table 16). This estimate is made by expanding the daily estimates by a factor of 20. The factor of 20, though subjective, is believed to be conservative and was selected after considering the width of the channel at the fishing site (about 76 m), other physical conditions (such as water depth and current velocity), and the behavior of these migrating fish in relation to the fyke nets at Grosvenor and Coville Rivers.

Significance of the Summer Outmigrations from Coville Lake

The significance of the summer outmigrations of age 0 sockeye salmon from Coville Lake can now be considered. The best estimates of the number of age 0 sockeye salmon in Coville Lake about 1 September and estimates of the number that migrated from the lake during the summer each year from 1961 to 1964 are shown in Table 17. The number that migrated in 1961, 1962, and 1964 greatly exceeded the number that remained in the lake and in 1963, the number that migrated was equal to the number that remained in the lake. Furthermore, in none of the years did the migration appear to be over when the sampling was ended. Although none of these data are precise, the summer outmigration of age 0 fish from Coville Lake appears to be significant to that lake.

Table 16.--Estimated numbers of age 0 sockeye salmon migrating from Grosvenor Lake to Iliuk Arm (by 10-day periods), July 15 to September 17, 1962, based on fyke net catches in Grosvenor River.

Period	Age 0 fish
July 15-21	860
July 22-31	67,400
August 1-10	126,180
August 11-20	842,960
August 21-30	941,280
August 31-September 9	499,500
September 10-17	1,390,940
Total	3,870,900

The question of whether significant numbers of age 0 sockeye salmon remain in Coville Lake through the winter to migrate as age I smolts cannot be answered directly. Because ice frequently persists in Coville and Grosvenor Lakes until early June, it is difficult to reach Coville River and sample the spring migration. In 1961 and 1962 the migration apparently started while ice covered the lakes and was well underway when sampling began because the rate of migration of age I fish (assumed to be smolts) generally declined from the first sampling. It is possible that the migration of age 0 fish usually continues into the fall and only relatively few fish remain to migrate as age I. Ruggles (1966) reported such an overwinter shift in distribution (seaward) of presmolts between basins of Owikeno Lake, British Columbia.

Table 17.--Number of age 0 sockeye salmon in Coville Lake at the end of summer (September 1) and number that migrated from the lake during the summer, 1961-64.

Year	Age 0 sockeye salmon[1] in Coville Lake on Sept. 1	Number migrating during summer
	----------Millions----------	
1961	3.8	5.5
1962	0.6	2.2
1963	0.9	0.9
1964	0.4	3.0

[1]Product of average catch per standard tow and number of standard tow volumes to a depth of 10 m; there are about 61,000 such standard tow volumes in Coville Lake.

Evidence on the immediate fate of age 0 sockeye salmon that leave Coville Lake indicates that these fish continue downsystem through Grosvenor Lake and into Iliuk Arm the same summer. This evidence, which is circumstantial and pertains to numbers and size of the fish, comes from fyke netting in Coville and Grosvenor Rivers and tow netting in Grosvenor Lake and Iliuk Arm. The data indicate that age 0 sockeye salmon migrating from Coville Lake during the summer continue downsystem into Iliuk Arm within a few weeks.

The immediate fate of age 0 sockeye salmon that migrated from Coville Lake to Grosvenor Lake can be inferred from the number that enter and the number that leave Grosvenor Lake and from the trends in abundance of the populations in Grosvenor Lake and Iliuk Arm. Order of magnitude estimates of the number of age 0 fish at these points—Coville River, Grosvenor Lake, Grosvenor River, and Iliuk Arm—in July and August 1961-63 are summarized in Table 18. The estimate for Grosvenor River in 1963 is based on the relation of the catches in August and September of 1962 (Table 16) and 1963 and the estimated total migration of 1962. There is no evidence that the number of age 0 fish in Grosvenor Lake increased in August, even in 1961 when the migration from Coville Lake was largest. The number of age 0 fish in Iliuk Arm increased during the summer each year, however, and the increase was greatest in the year of migration of greatest numbers of fish to Grosvenor Lake from Coville Lake—1961. Observations of even the general magnitude of the migration out of Grosvenor Lake into Grosvenor River are available only for 1962 and 1963 (fyke nets were fished in Grosvenor River 30 days in 1962 and 14 days in 1963). These observations indicate that more age 0 fish left Grosvenor Lake in 1962—the year when more entered from Coville Lake. All indications are that most of the age 0 fish entering Grosvenor Lake from Coville Lake in July and August continue downsystem into Iliuk Arm the same summer.

The sizes (length frequencies) of the age 0 sockeye salmon that left Coville Lake and entered Grosvenor Lake are similar to those for age 0 fish taken by tow nets in Coville Lake and those leaving Grosvenor Lake. All three differ, however, from the samples collected with tow nets in Grosvenor Lake (see length frequency graphs in later section of this paper). The fish migrating from Coville Lake were either not present in the parts of the lake sampled by tow nets in Grosvenor Lake, or the number present in these areas at the time of sampling (the "instantaneous" number) was too small to be significant in the catches. The latter is likely because visual observations, beach seining, and trap netting along the shores of Grosvenor Lake all indicated very few age 0 sockeye salmon in the littoral areas—the area not sampled by tow nets.

Diel Timing of Migrations

Although juvenile sockeye salmon usually migrate downriver only during dusk or darkness (Hartman, Heard, and Drucker, 1967), the interlake migrants did not always follow this pattern. A restriction of downstream migration to the dark period of each day was clearly the case for presmolts in Grosvenor River and just as clearly not the case for similar fish in Coville River. Results of sampling in Coville River in 1961 and 1962 and in Grosvenor River in 1962 show the diel timing of this migration (Table 19). In Coville River no consistent differences in intensity of movement occurred—age 0 sockeye salmon migrated in great numbers in both daylight and darkness. In Grosvenor River, however, relatively few migrants were captured during daylight, but large catches were made during darkness.

Differences in the abundance and size of juveniles in tow net catches near the outlets of Coville and Grosvenor Lakes probably resulted from the differences in their diel migratory behavior. Unusually large catches of age 0 sockeye salmon were made with tow nets near the outlet of Grosvenor Lake on 3 nights during the period when large catches of migrants were made with fyke nets in Grosvenor River. The rate of catch in tow nets decreased progressively as fishing was done farther from the outlet of the lake. The length frequency distributions of fish from these large catches were similar to those in samples of fish from Grosvenor River and unlike those from Grosvenor Lake. Although juvenile sockeye salmon were abundant in the sampling area near the outlet end of Coville Lake, tow netting in the immediate vicinity of the outlet did not produce unusually large catches. It appears that migrants accumulated at the outlet end of Coville

Table 18.--General magnitude of age 0 sockeye salmon in interlake migrations and of lake populations in July and August 1961-63, Covile River-Iliuk Arm area.

Year	Fish migrating down Coville River into Grosvenor Lake in July and August	Fish in Grosvenor Lake[1] on--		Fish migrating from Grosvenor Lake in July and August	Fish in Iliuk Arm[1] on--	
		Aug. 1	Sept. 1		Aug. 1	Sept. 1
	Millions					
1961	5.0	2	2	--	3	11
1962	1.5	1	1	2	12	14
1963	0.9	2	2	<2	4	5

[1]Product of average catch per standard tow and number of standard tow volumes to a depth of 10 m. There are about 270,000 such standard tow volumes in Iliuk Arm and 200,000 in Grosvenor Lake.

Table 19.--Rate of catch in fyke nets and mean size of age 0 sockeye salmon migrating down Coville and Grosvenor Rivers during dark and light periods[1] between July and September 1961-62.

Area and period	Mean fork length (mm)	Dark: Hours fished	Dark: Mean number of fish per hour	Partly dark and partly light: Hours fished	Partly dark and partly light: Mean number of fish per hour	Light: Hours fished	Light: Mean number of fish per hour
Coville River[2]							
July 27-31, 1961	49.1	1.0	27.0	7.0	1.7	5.0	240.0
Aug. 1-15, 1961	52.1	0.0	--	1.5	333.3	17.8	73.4
Aug. 16-31, 1961	56.5	0.0	--	22.0	6.6	7.7	103.9
Sept. 1-8, 1961	56.2	0.8	242.7	39.8	7.8	0.0	--
July 3-13, 1962	--	18.0	0.0	3.0	0.0	0.0	--
July 16-31, 1962	50.3	43.0	34.0	21.0	322.5	49.0	83.9
Aug. 1-16, 1962	56.2	24.0	60.6	13.0	19.5	45.0	37.9
Aug. 17-31, 1962	58.6	76.5	112.6	85.5	157.5	90.5	308.6
Sept. 13-15, 1962	63.1	25.0	54.6	39.0	37.0	27.0	274.6
Grosvenor River[3]							
July 6-8, 1962	--	7.0	0.7	0.0	--	0.0	--
July 15-26, 1962	42.2	13.0	0.7	17.0	2.7	4.0	0.0
Aug. 9-12, 1962	57.2	6.0	88.7	29.0	65.4	22.0	0.0
Aug. 18-31, 1962	60.8	38.0	592.6	22.5	129.0	21.0	0.5
Sept. 1-9, 1962	62.3	19.5	271.6	35.8	61.8	28.5	[4]53.6
Sept. 15-17, 1962	65.9	22.8	102.2	0.0	--	12.5	11.2

[1]Average sunrise and sunset times were determined for each semimonthly period from pyrheliograph records from Coville Lake outlet. Dark = sunset to sunrise when pyrheliograph reading was 0. Light = sunrise to sunset.

[2]In 1961, a 1-m-square fyke net was fished from steel posts driven into stream bottom. In 1962, a 1.2-m-square fyke net was fished from a cable strung across the stream; the wings were spread to 1.3 m.

[3]A 1.2-m-square fyke net was fished from a cable strung across the stream; the wings were spread to 1.8 m.

[4]One fishing period of 4 hours duration produced an exceptional catch of 1,500 juvenile sockeye salmon.

Lake, but were not concentrated near the river as at Grosvenor Lake. The accumulation of fish near the outlet of Grosvenor Lake probably resulted from their reluctance to migrate down the river during daylight.

Juvenile sockeye salmon have been studied in several multibasin systems similar to the Naknek system and oceanward interlake migrations of significant numbers of age 0 sockeye salmon during the summer are apparently rare. The several basins of the Babine River system have markedly dissimilar densities of fry early in the summer as the result of the unequal distribution of spawning adults (much as in the Naknek system). Unlike the fry of the Naknek system, the fry of the Babine system do not disperse over the lakes during summer (Johnson, 1958). (The greatest number of spawners per unit lake area is in the most upsystem lake of the Naknek system, but in the lower end of the Babine system.) In the Wood River system there is a minor migration of fry from small lakes to a larger lake (Burgner, 1962). In the Chignik River system there is little downsystem movement of age 0 fry between lakes, but here (similar to the Babine system) the downsystem lake usually has the greater density of spawners. There is a migration of fry from the lower lake (Chignik Lake) to the lagoon-like estuary (Burgner et al., 1969). A recent study of growth patterns on scales of adult sockeye salmon from the Chignik system indicates that age 0 fish did migrate to a downsystem lake in 1956[9] (Narver, 1968).

A migration unusual because of its direction has been reported for Owikeno Lake, British Columbia. Ruggles (1966) found a movement of age 0 sockeye salmon from one lake basin to another away from the direction of the outlet to the ocean. The time of the migration and relative density of fish in the two basins before and after the migration were not reported. During the winter another migration occurred, but this time it was oceanward.

[9]At 1700 on 30 July 1962 the speed of movement was estimated for 10 schools of age 0 sockeye salmon moving downstream at the outlet of Coville Lake. The current speed, gaged by observing a floating wood chip, was about 0.2 feet per second (fps). The speed of the schools averaged about 1.9 fps, indicating a swimming speed downstream of about 1.7 fps.

Behavior of Schools of Age 0 Fish at Outlet of Coville Lake

Although the behavior of the juvenile sockeye salmon in the interlake migrations in the Naknek system were not studied in detail, incidental observations of the fish involved are presented here because the phenomenon of large-scale interlake migrations of these presmolt fish is unique.

Interlake migrants first appeared in the shoal waters (less than 3 m) at the outlet of Coville Lake (i.e., the origin of Coville River). Here the basin of the lake becomes so narrow and shallow that the current is readily visible. In mid-June 1962, groups of several hundred age 0 fish were frequently seen moving downstream about the same speed as the current and apparently feeding at or near the surface—the fish were breaking the surface so frequently that the movement of the groups could be followed by an observer on shore. These groups were not concentrated along the shore or over the deepest water, but were seen at one time or another over the entire outlet area. Individual fish were most often facing downstream. When the water depth decreased to about 1 m and the current velocity had noticeably increased (and possibly when the fry first made visual contact with the bottom—i.e., they first "realized" they were moving downstream), the fry abruptly changed their orientation.

The visual cue as to direction or perhaps simply the existence of movement seemed to halt the downstream migration. All the fish of a group would suddenly turn, face upstream, and move laterally across the current until they were in water about 15 to 20 cm deep. They then moved upstream in a narrow band until they reached slower water and disappeared into deeper water—that is, they appeared to return to the lake. From mid-June to mid-July, during daylight, schools of age 0 sockeye salmon were frequently seen feeding in shallow (1 to 2 m) water along the lake shores and islands over most of Coville Lake.

About mid-July the behavior of the age 0 sockeye salmon at the outlet of Coville Lake had noticeably changed and the schools now appeared to be actively migrating. They were still close to the surface, but moved faster than the current (see footnote 10) and no longer changed orientation when the water became shoaled to about 1 m deep or moved toward shore when the currently velocity increased. The orientation of individuals and ultimately the entire school was suddenly reversed (Hartman, Heard, and Drucker, 1967) as the school passed over the edge of the shoal water into deeper water of the stream proper. This orientation was soon reversed and the fish again moved actively downstream into Grosvenor Lake and deeper water.

On one occasion after the summer outmigration of age 0 sockeye salmon was in progress, a reversal of the migration was noted. At 0900 on 19 August 1962 fish were seen moving upstream near the outlet of Coville Lake. The characteristics of the movement, i.e., speed, school compactness, size, etc., were the same as for the downstream movement. In the afternoon of the same day the migration had resumed its normal (for that time of the summer) direction. This was the only reversal of the direction of migration observed here, but reversed migration has been commonly observed in smolts in the Babine system (Groot, 1965).

EARLY REARING AREAS OF SOCKEYE SALMON FRY FROM GROSVENOR RIVER AND HARDSCRABBLE CREEK

Some stocks of sockeye salmon spawn in rivers that connect lakes or connect a lake to the ocean; their progeny may migrate either upstream (Andrew and Geen, 1960) or downstream (most commonly) to reach freshwater pelagic rearing areas. A choice of migration direction is possible in three major connecting rivers in the Naknek system—Brooks, Naknek, and Grosvenor (Fig. 1). Fry from Brooks River move downstream into South Bay (Merrell, 1964); we assume fry from Naknek River move upstream into Naknek Lake rather than going directly to the ocean because adults of freshwater-age 0 are rare in the escapement. The immediate destination of fry migrating from Grosvenor River was unknown until 1962.

In the spring of 1962 I studied the fry originating in Grosvenor River and Hardscrabble Creek to determine the basin to which they first migrated. Hardscrabble Creek was studied because it is close to Grosvenor River and the work in the two streams could be done from a single camp. Moreover, I felt that information on the timing and other characteristics of the outmigration from Hardscrabble Creek might corroborate the work in Grosvenor River. Ultimately the two streams were found to be closely related. This work was exploratory and the results are qualitative. Descriptions of the upstream migration of fry in other areas indicated the upstream migration is obvious—for example, Johnson (1956) described these fry as ". . . a massed living band moving upstream. . ."; McCart (1967) stated ". . . (upstream) migrants moved in tightly knit schools at the surface, close to shore, often in water only a few centimeters deep."

In Grosvenor River small fyke nets were fished along each side (east and west shores) of the river (usually with one wing extended to shore) near Grosvenor Lake where the river first becomes less than 50 m wide. Initially, nets were fished to sample both the upstream and downstream migrations, but most sampling was done to catch downstream migrants. In Hardscrabble Creek a fyke net was fished in fast water about 0.6 m deep on the first gravelly riffle above Grosvenor Lake (about 200 m from the lake at low lake water level). One fyke net set was made in the Savonoski River to learn if fry were produced in that system above its confluence with Grosvenor River.

Visual observations were made during daylight and darkness while walking along Grosvenor Lake from Hardscrabble Creek to Grosvenor River and along Grosvenor River on the shore or in shallow water. Hand-held lights were used at night.

Most of the sockeye salmon fry captured in the fyke nets (Table 20) or seen migrating were moving downstream on the east shore of Grosvenor River at night. A few fry were seen moving upstream near shore from Grosvenor River to Grosvenor Lake from May to June; the only other indication of an upstream movement from Grosvenor River was the capture of a few fry in fyke nets open downstream (Table 20). Fyke nets fished in shallow water near the lower end of Grosvenor River on 11, 16, 17, and 19 May indicated that recently emerged fry were moving downstream, but the origin of these fry is uncertain. Presumably they were a mixture of fry originating in Grosvenor River and Hardscrabble Creek.

Migrating fry were also sampled intermittently with fyke nets in Hardscrabble Creek between 11 May and 25 June. During this time the water level and velocity changed so that the rate of catch of fry in Hardscrabble Creek is the result of straining greatly different proportions of the total flow and, presumably, of the nightly migration. Therefore, only one general conclusion can be made about the migration—some sockeye salmon fry were moving downstream in Hardscrabble Creek between 11 May and 25 June.

Visual observations along the edge of Hardscrabble Creek at night below the fyke net collecting site showed that the fry usually swam downstream. Some fry stayed in shallow water in the delta of the stream and could be seen along the lake shore and on into Grosvenor River. It appeared that at least some fry from Hardscrabble Creek never entered the pelagic area of Grosvenor Lake but stayed in water from Hardscrabble Creek well downstream in Grosvenor River. Hardscrabble Creek water was not mixed with water from Grosvenor Lake until about 180 m below the lake. The two waters were initially quite distinct—the water of Hardscrabble Creek was murky from erosion products and glacial melt and the water of Grosvenor Lake was clear. Further evidence that at least some fry moved directly from Hardscrabble Creek to Grosvenor River was found by comparing fry from Hardscrabble Creek and from the head of Grosvenor River. Samples collected on the same or adjacent nights in the two areas were nearly identical in regard to length frequencies and the proportion of fry containing visible yolk. If the fry leaving Grosvenor Lake had been in the lake very long, they would have absorbed more yolk and increased in length.

I concluded that Iliuk Arm is the basin of first residence of practically all sockeye salmon fry originating in Grosvenor River and of an unknown portion of those originating in Hardscrabble Creek. Iliuk Arm also receives some fry from streams tributary to the Savonoski River above Grosvenor River.

SIZE, LENGTH FREQUENCY, AND GROWTH

Intimately associated with the abundance of animals are the growth and size of individuals. In the present study, the sizes of individual fish in the catches were measured so that the effects of biological and physical factors on size could be determined and groups of fish could be identified. Although both length and weight were measured, only the length

Table 20.--Numbers of recently emerged sockeye salmon fry captured in fyke nets set on the east and west shores of Grosvenor River near Grosvenor Lake in May and June 1962 to determine whether fry were migrating upstream or downstream.

Date	Downstream migrants				Upstream migrants			
	East shore		West shore		East shore		West shore	
	Hours fished	Fry caught per hour	Hours fished	Fry caught per hour	Hours fished	Fry caught per hour	Hours fished	Fry caught per hour
May 17	3.3	12.1	1.7	8.2	--	--	--	--
May 18	1.0	31.0	1.0	20.0	--	--	--	--
May 19	--	--	--	--	5.5	0.4	--	--
May 20	0.5	44.0	--	--	0.5	0.0	--	--
May 21	2.5	190.0	--	--	2.0	2.0	--	--
May 22	4.8	105.0	--	--	2.8	1.1	--	--
May 23	1.7	95.3	1.7	2.2	--	--	--	--
May 24	4.2	94.2	4.2	158.3	--	--	--	--
May 25	7.5	12.7	--	--	--	--	--	--
June 10	3.3	194.5	--	--	--	--	--	--
June 11	21.0	36.8	--	--	--	--	--	--
June 16	7.5	40.1	--	--	--	--	--	--
June 17	1.8	70.6	--	--	--	--	--	--
June 19	2.8	70.7	--	--	--	--	--	--
June 25	11.4	1.6	--	--	--	--	--	--

measurements proved to be useful in final analysis.

The most extensive data on size of juvenile sockeye salmon came from collections made with tow nets. These data, in the form of average lengths and length frequencies, have been used to relate changes in average size with time (apparent growth) to abundance of sockeye salmon and other species and in some instances to investigate the effects of migrations.

Average lengths of juvenile sockeye salmon in catches were used to calculate "growth" curve equations which describe the average size by age class each day. After trying several mathematical models and visually examining the fit of the curves to the actual data, I selected a second-degree polynomial (Snedecor, 1956), in which length is related to time in days since 30 May (i.e. 1 June = day 1; 1 July = day 31; and 1 September = day 93). The equations describing the average length have been used to: (1) calculate the average size on other than dates of sampling by extrapolation or interpolation; (2) make estimates of size from combined data for sampling areas within a basin; and (3) plot graphs (apparent-growth curves) describing the changes in length during a season.

Juvenile Sockeye Salmon

Curves depicting the average lengths of juvenile sockeye salmon in the summers from 1961 to 1963 for all basins and 1961 to 1964 for Coville Lake are presented in this section as each lake is discussed. Because of known differences between the average size of migrating and nonmigrating fish, probable size-related differences in mortality, and known variations in time of recruitment of fry from the spawning grounds, the curves represent only "apparent growth."

A comparison of the average size of the fish from different areas supplies part of the knowledge needed to understand differences in apparent growth, but for a more complete understanding knowledge of the length frequency composition of the population is also needed. Graphs of the percent frequency of juvenile sockeye salmon by 3-mm size groups by time periods have been prepared for 1961 to 1964. The length frequencies of fish sampled will be discussed and related to their average lengths for each lake.

The mean fork length of age 0 and age I sockeye salmon on 20 August and 1 September 1961-64 by sampling area and lake are summarized in Table 21 for each basin. The sizes used are those estimated from the calculated growth curves rather than the empirical data even when collections were made on 20 August or 1 September. The dates 20 August and 1 September were selected for comparison for different reasons—20 August is late enough in the season to indicate growth conditions for the summer and early enough to avoid most sampling problems caused by the early fall storms; 1 September is the date used in much of the

Table 21.--Mean fork lengths of age 0 and age I sockeye salmon in each lake of the Naknek River system and in Coville and Grosvenor Rivers on August 20 and September 1, 1961-64. (Weighted by abundance and average size in each sampling area.)

Age of fish and sampling area	Mean fork length (mm) on--							
	August 20				September 1			
	1961	1962	1963	1964	1961	1962	1963	1964
Age 0								
Coville Lake	51.1	55.8	56.3	56.9	54.2	59.6	57.8	58.2
Coville River	--	58.0	58.6	59.2	--	60.6	62.7	61.1
Grosvenor Lake	46.5	51.0	45.8	46.3	46.3	51.7	51.0	47.3
Grosvenor River	--	60.1	62.0	--	--	62.8	64.9	--
Iliuk Arm	46.9	51.0	53.2	--	57.4	61.3	58.3	47.4
South Bay	42.8	54.8	50.7	--	46.8	63.4	55.3	52.3
West End	59.8	62.9	56.2	--	64.7	69.0	60.8	57.7
North Arm	--	--	--	--	--	--	56.0	--
Northwest Basin	53.7	--	--	--	--	--	53.7	--
Brooks Lake	45.7	55.3	49.7	--	51.3	60.2	53.7	--
Age I								
Coville Lake	--	--	--	--	--	--	--	--
Coville River	--	--	--	--	--	--	--	--
Grosvenor Lake	--	--	--	--	--	--	--	--
Grosvenor River	--	--	--	--	--	--	--	--
Iliuk Arm	84.3	83.4	79.9	--	78.4	91.0	86.0	77.9
South Bay	84.5	83.8	81.9	--	86.5	85.0	84.9	85.2
West End	--	--	--	--	89.3	--	--	89.4
North Arm	--	--	--	--	--	--	94.0	--
Northwest Basin	--	--	--	--	--	--	--	--
Brooks Lake	--	--	--	--	--	--	--	--

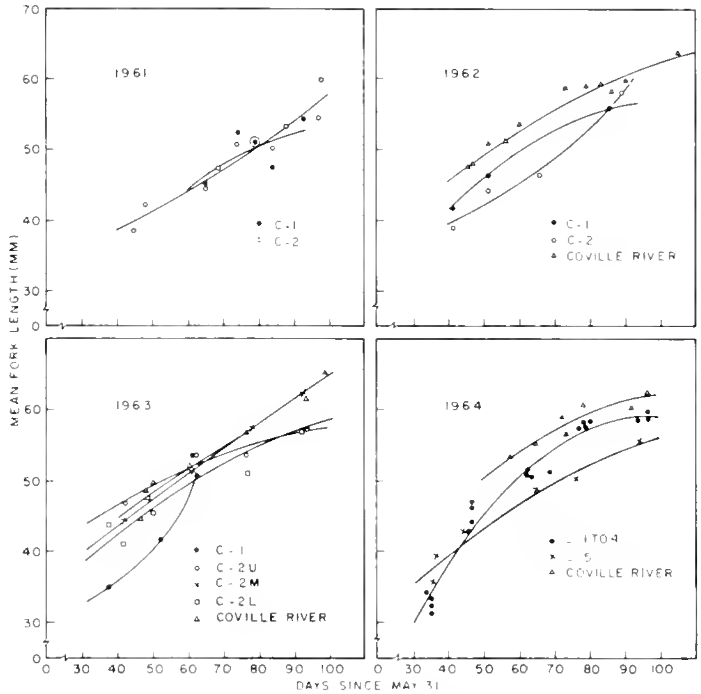

Figure 11.—Curves of apparent growth of age 0 sockeye salmon captured in tow nets in sampling units of Coville Lake and in fyke nets in Coville River 1961-64.

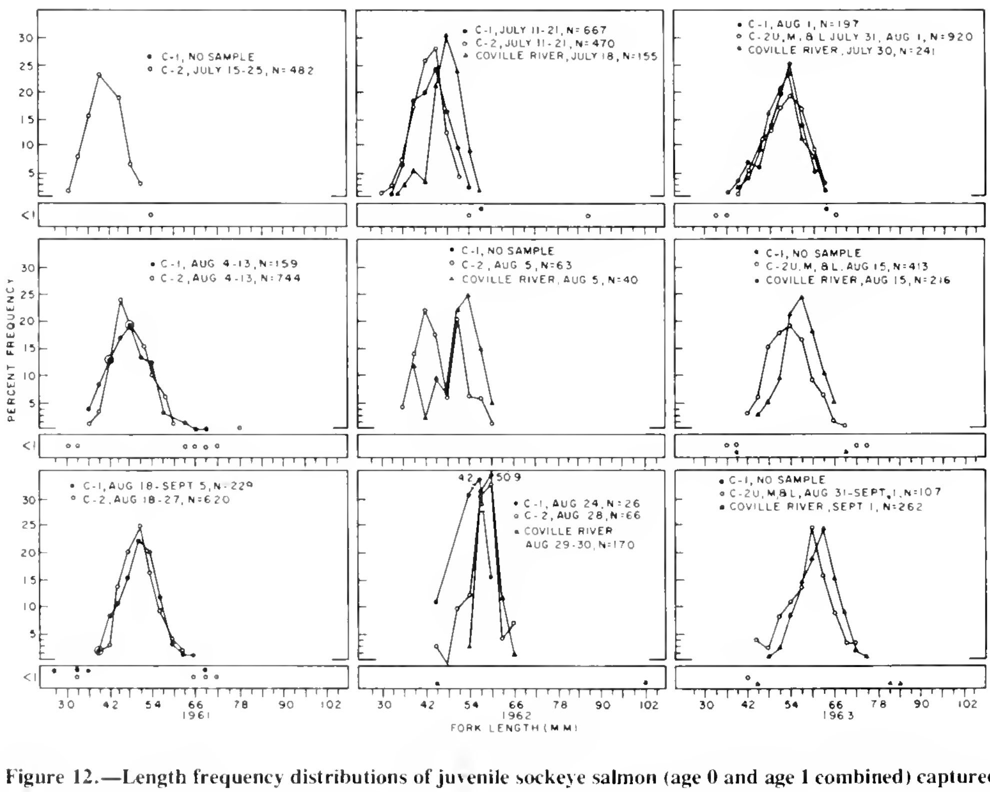

Figure 12.—Length frequency distributions of juvenile sockeye salmon (age 0 and age 1 combined) captured in tow nets in sampling units of Coville Lake and in fyke nets in Coville River for several time periods between July and September 1961-63. (See Figs. 1 and 2 for designations of sampling units.)

existing literature on size of juvenile sockeye salmon. When sampling was not done on or after 1 September or the apparent growth was negative or otherwise anomalous, the length on 1 September was estimated as follows: for age 0 fish, the increase in length in Coville Lake and for age I fish, the increase in length in Iliuk Arm between the last date of sampling in the lake in question and 1 September was added to the calculated size on the last date of acceptable sampling in the lake in question.

Coville Lake and Coville River.—Curves depicting the apparent growth of age 0 sockeye salmon collected in tow nets in Coville Lake and in fyke nets in Coville River are presented by area for 1961-64 in Figure 11. In general, average lengths increased rapidly from early July to mid-August (days 31 to 80) and somewhat slower thereafter. The decrease in rate is most apparent in 1963 and 1964 when more areas were sampled at shorter intervals. The average size of the emigrants in Coville River was clearly greater than that of the juveniles taken in tow nets in the area adjacent to the river—C-2L in 1963 and C-5 in 1964. There was little difference among the other four areas (C-1 to C-4) in 1964.

The length frequency distributions of the juvenile sockeye salmon from Coville Lake and Coville River in 1961-64 are presented in Figures 12 and 13. The frequencies are generally unimodal and the observed differences in average length (Table 21) are due to the greater abundance of larger sizes rather than to differences in ranges in lengths in the samples.

The greater average lengths of age 0 sockeye salmon in the lakes of the Naknek system on 1 September 1962 (Table 21) than in the other years was true for fish from Coville Lake, but not for those from Coville River. No explanation is offered for the lack of a larger average size for fish in Coville River.

Age I and older fish were rare in catches from tow nets in Coville Lake and fyke nets in Coville River during the summer. These older fish appear in the length frequencies in sufficient numbers to cause a bimodal curve in the samples from tow net catches only in early July 1964 (Fig. 13).

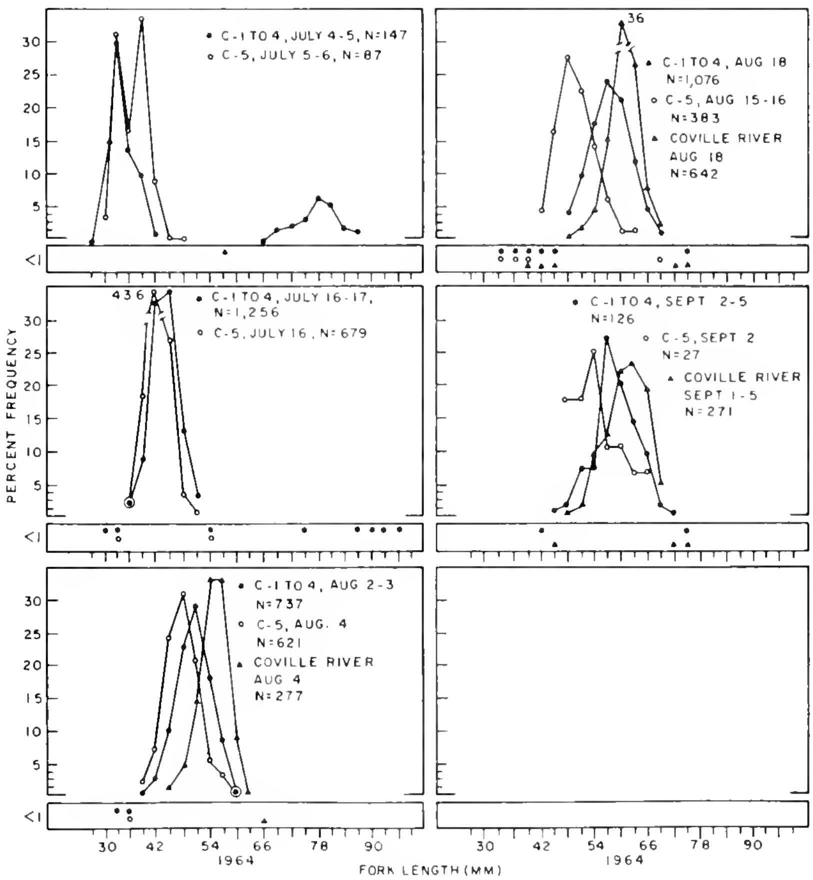

Figure 13.—Length frequency distributions of juvenile sockeye salmon (age 0 and age I combined) captured in tow nets in sampling units of Coville Lake and in fyke nets in Coville River for several time periods between July and September 1964. (See Figs. 1 and 2 for designations of sampling units.)

Grosvenor Lake and Grosvenor River.—The apparent growth of age 0 sockeye salmon each summer in 1961-63 in Grosvenor Lake and Grosvenor River is shown in Figure 14. Grosvenor Lake was divided into four areas for tow net sampling, but only in 1961 were enough samples obtained to describe the growth for each area. For 1962 and 1963 data for the four areas were combined to calculate a single growth curve. Collections were made in Grosvenor River only in 1962 and 1963.

The apparent growth of juvenile sockeye salmon from Grosvenor Lake is unique in two regards—the average length of fish in particular sampling areas frequently decreased during the summer, and the fish here were generally the smallest in the system on any date. The size of the outmigrating fish captured in fyke nets in Grosvenor River increased during the summer and these fish were generally the largest in the system on any date.

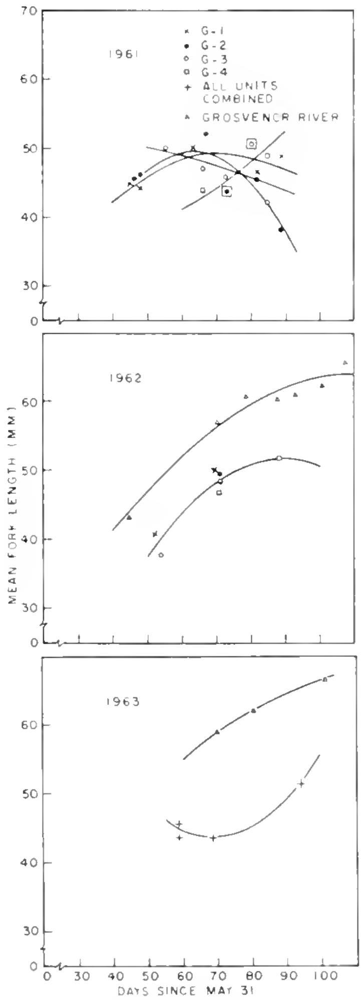

Figure 14.—Curves of apparent growth of age 0 sockeye salmon captured in tow nets in sampling units of Grosvenor Lake and in fyke nets in Grosvenor River 1961-63.

The decrease in average length of age 0 sockeye salmon in Grosvenor Lake in August was at least partly due to a late recruitment of fry that had recently emerged from the spawning gravels. This late recruitment appeared each year from 1961 to 1963 and caused the marked bimodality of length frequency curves—these late recruits are represented in the peak on the left in the 30- to 45-mm size range in Figure 15. The spawning grounds and circumstances that produce these fry in Grosvenor Lake are unknown, but a similar late recruitment has been observed for sockeye salmon in Karluk Lake where spawning occurs over a period of 4 to 5 mo (Burgner et al., 1969).

Age I and older sockeye salmon were rarely taken in tow nets in Grosvenor Lake and were relatively scarce in fyke nets in Grosvenor River.

Iliuk Arm.—Because there were no consistent differences in size of age 0 or of age I fish among the three sampling units of Iliuk Arm in 1961-63 (for 1962, growth curves for each unit are shown for comparison), the data from all the units were combined in calculating the growth curves (Fig. 16). The apparent growth of age 0 fish showed little or no evidence of slowing by 1 September and the average size of the age 0 fish in Iliuk Arm (Table 21) was generally intermediate among the lakes of the system. This good apparent growth was not expected in Iliuk Arm because glacial flour makes the water quite opaque which would result in little light penetration and thus low photosynthetic activity. Both of these apparent anomalies in growth (no slowing by September and good apparent growth) are probably caused by the recruitment of the larger fish from the upsystem areas during the summer.

The calculated growth curves for age I sockeye salmon in Iliuk Arm for 1961-63 in the three units combined (Fig. 17) resemble those of age 0 fish in that they do not show a decrease during the summer. There was no trend in length of age I fish from one end of the basin to the other (N-15, N-14, N-13).

The length frequency diagrams for samples of juvenile sockeye salmon from Iliuk Arm for 1961-63 also indicate a general uniformity among the three sampling units (Fig. 18). The length frequencies are generally bimodal, reflecting the presence of the two age classes—age 0 and age I.

South Bay.—The seasonal changes in apparent growth and length frequencies of young sockeye salmon from South Bay are similar to those from Iliuk Arm. The data were too few to permit analysis of growth by sampling unit, but do permit considerations of apparent growth for the entire basin (all units combined). As in Iliuk Arm the apparent growth of age 0 fish had slowed little if at all by 1 September (Fig. 19).

The apparent growth curves for age I sockeye salmon in South Bay for all units combined for 1961-63 (Fig. 20) do not have the same shape as those for Iliuk

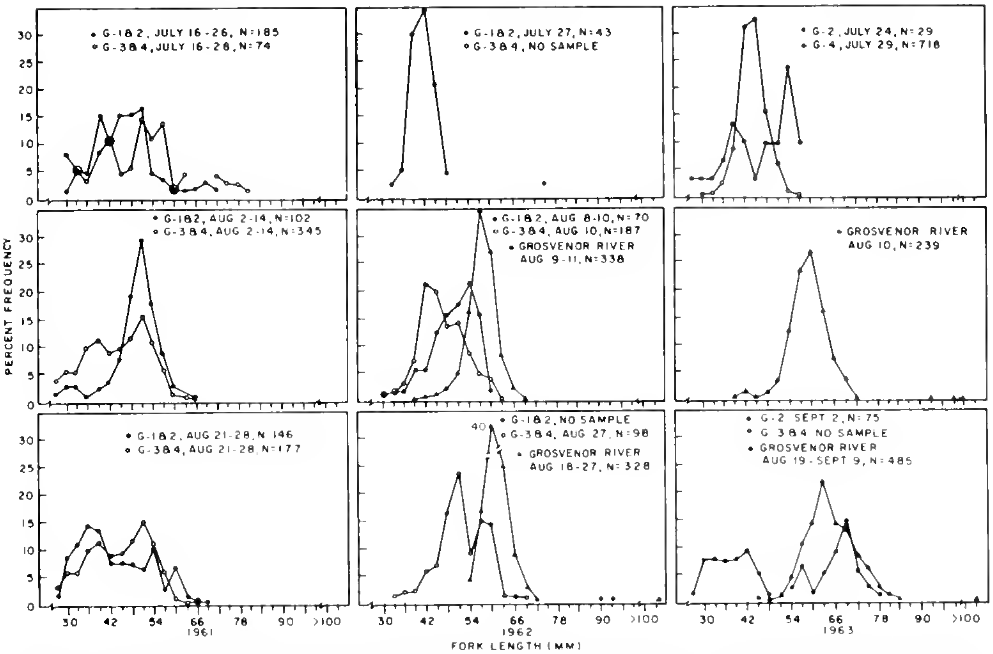

Figure 15.—Length frequency distributions of juvenile sockeye salmon (age 0 and age I combined) captured in tow nets in sampling units of Grosvenor Lake and in fyke nets in Grosvenor River for several time periods between July and September 1961-63.

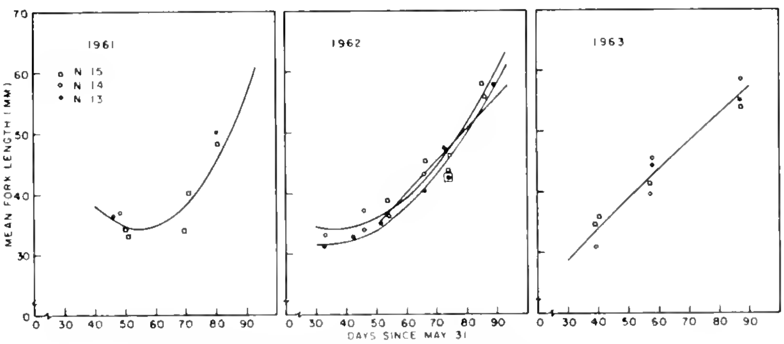

Figure 16.—Curves of apparent growth of age 0 sockeye salmon captured in tow nets in sampling units of Iliuk Arm, 1961-63.

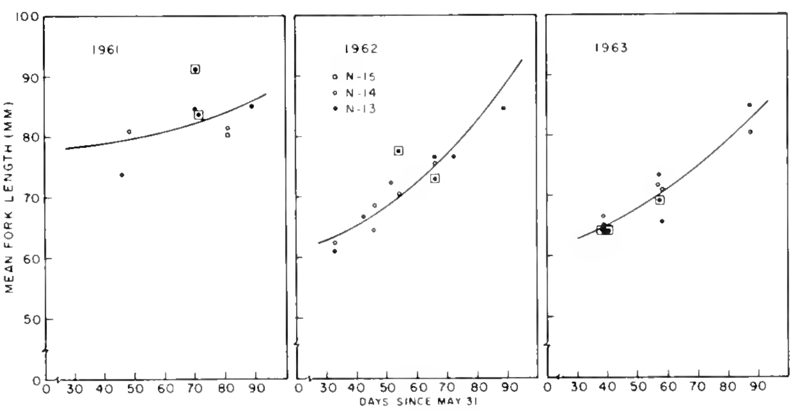

Figure 17.—Curves of apparent growth of age I sockeye salmon captured in tow nets in sampling units of Iliuk Arm, 1961-63.

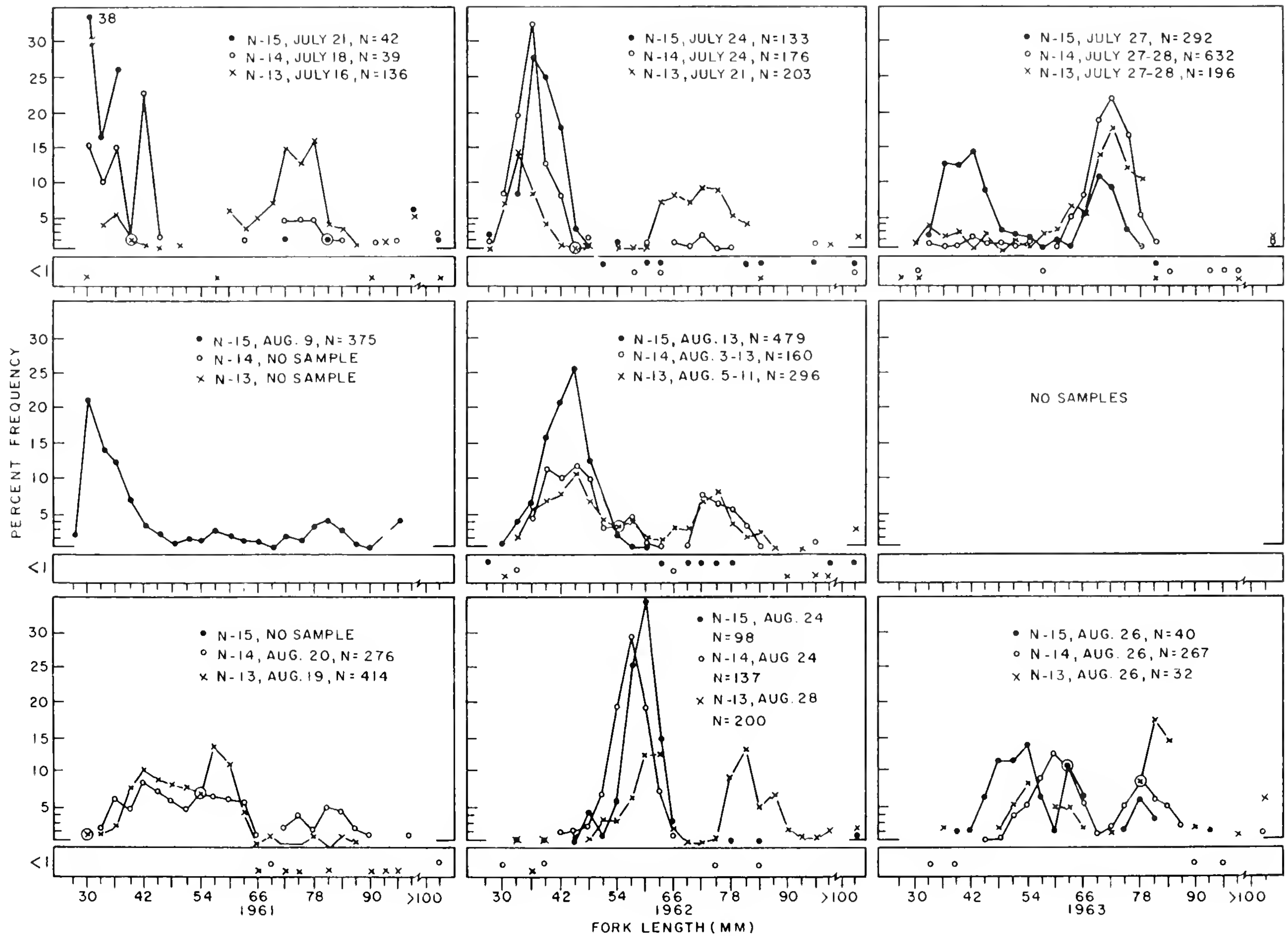

Figure 18.—Length frequency distributions of juvenile sockeye salmon (age 0 and age I combined) captured in tow nets in sampling units of Iliuk Arm for several time periods in July and August 1961-63.

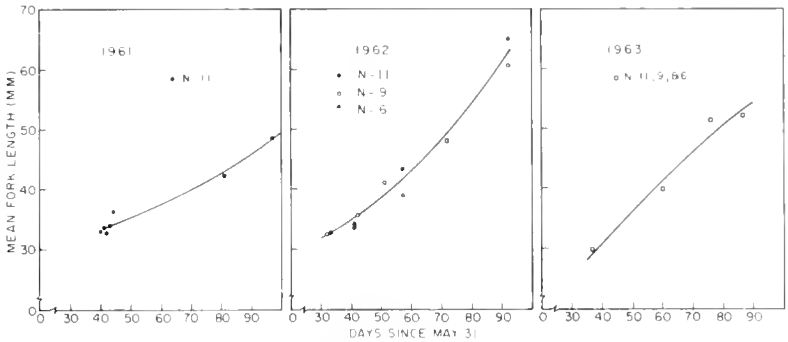

Figure 19.—Curves of apparent growth of age 0 sockeye salmon captured in tow nets in sampling units of South Bay 1961-63.

Arm—a decrease in growth rate and average length appears in the South Bay data. The apparent negative growth of age I fish in South Bay may be due to the combining of data to produce a single curve. On the other hand, it may be due to the loss of larger fish to the summer migration of smolts in the Naknek River. If this summer migration of smolts did not involve fish from Iliuk Arm, the observed difference in growth curves of South Bay and Iliuk Arm would result.

The length frequency diagrams of juvenile sockeye salmon from South Bay (Fig. 21) resemble those from Iliuk Arm. In general, there is a bimodality indicating two age groups (age 0 and age I). In those periods when all three sampling units of South Bay were sampled, the curve for age I fish from unit 6 (the most downsystem area) was to the right of those of the other two units—larger age I fish were relatively more abundant in the downsystem portion of South Bay. Age I and older sockeye salmon in South Bay were similar in length to those in Iliuk Arm (Table 21).

West End.—Apparent growth curves for sockeye salmon in the West End are available only for age 0 fish and only in 1962 and 1963 (Fig. 22). The growth of age 0 fish from West End differed from that in Iliuk Arm and South Bay in that the growth in West End fish tended to decrease during the summer. The average lengths of age 0 fish were, however, usually greater in samples from West End than in those from other lakes of the system on the same date (Table 21). Although the samples were small, within West End the average lengths were generally greatest in N-4, the area adjacent to South Bay. The average lengths (in millimeters) of age 0 sockeye salmon in samples from N-4, N-2, and N-1 were as follows:

Date	N-4	N-2	N-1
20 August 1962	66.0	64.2	62.1
31 August 1963	62.3	58.6	57.8
3 September 1964	([10])	61.7	56.6

Age I and older sockeye salmon were too scarce in tow net catches from West End to permit construction of growth curves. The average length of this group was greater here than in Iliuk Arm or South Bay.

The length frequency graphs for samples of juvenile sockeye salmon from West End (Fig. 23) are unimodal because of relatively few age I fish in the tow net catches.

[10]No sample taken.

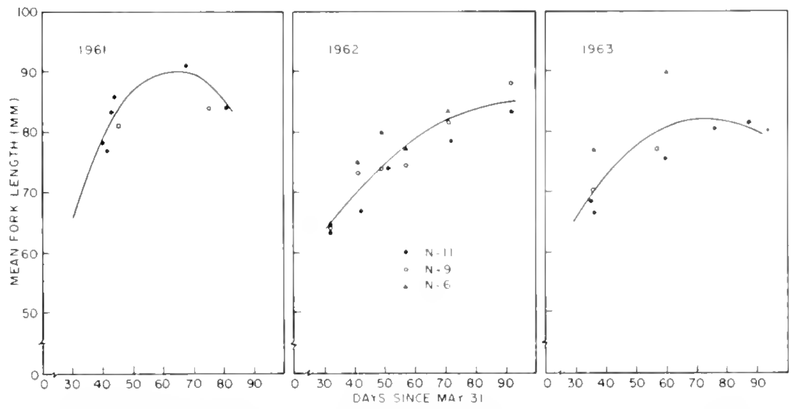

Figure 20.—Curves of apparent growth of age I sockeye salmon captured in tow nets in sampling units of South Bay 1961-63.

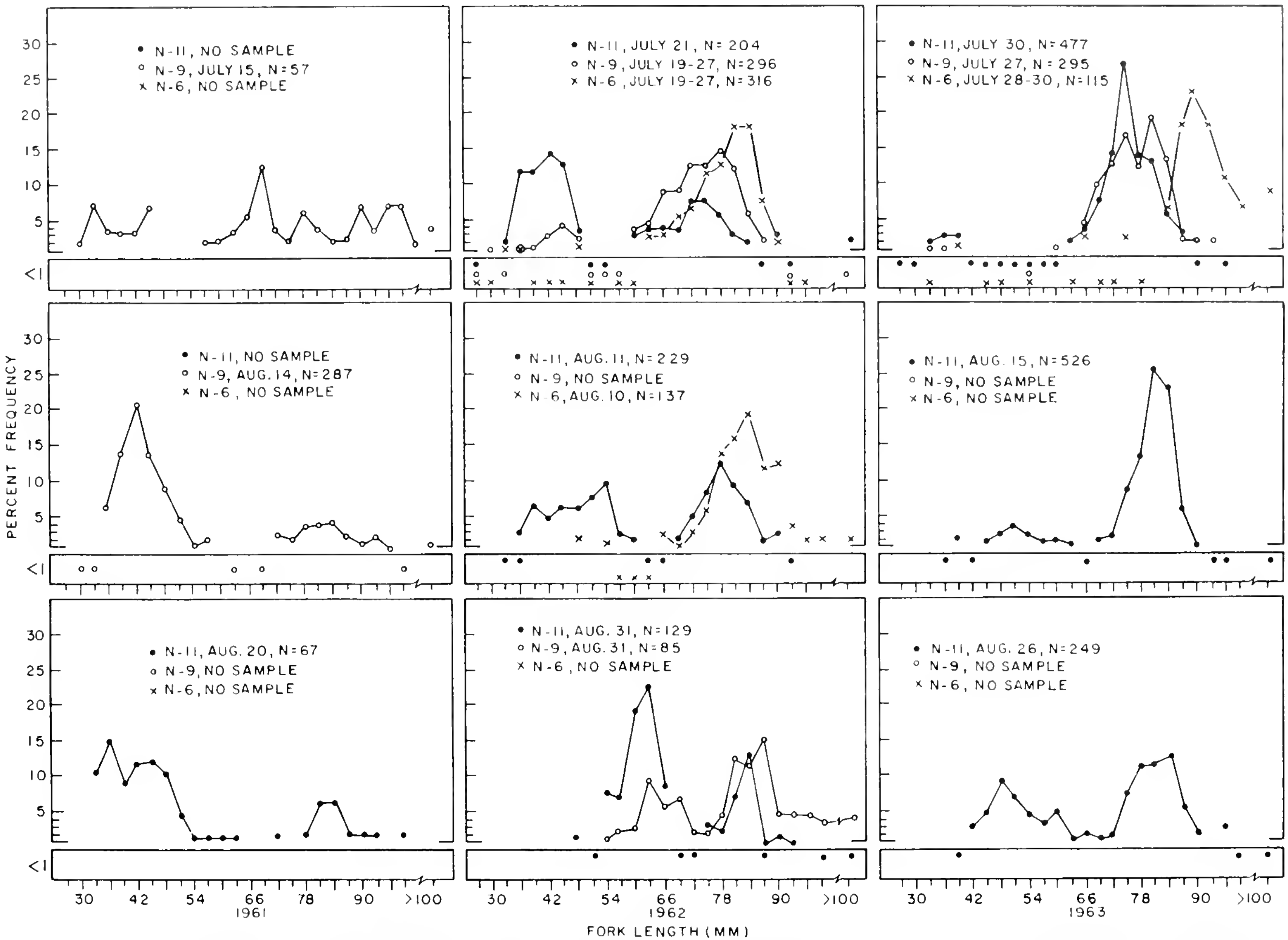

Figure 21.—Length frequency distributions of juvenile sockeye salmon (age 0 and age I combined) captured in tow nets in sampling units of South Bay for several time periods in July and August 1961-63.

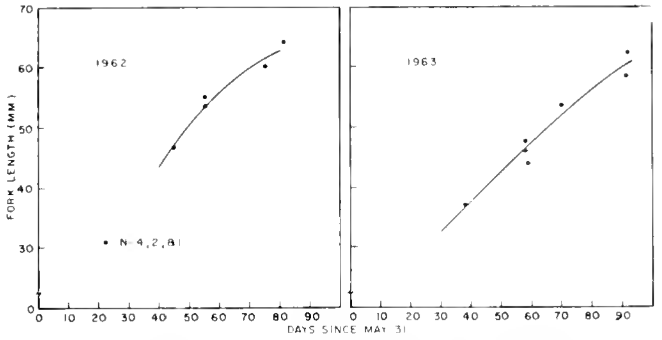

Figure 22.—Curves of apparent growth of age 0 sockeye salmon captured in tow nets in sampling units (combined) of West End 1962-63.

North Arm.—Although North Arm is the largest basin in the Naknek system (about one-quarter of the system's surface area), apparent growth curves and length frequency curves could not be constructed because so few fish were captured in tow nets. The only sample captured near 1 September that had more than 20 age 0 fish was obtained in 1963; the average length of these age 0 fish (Table 21) was close to the average for the system. Only one large sample of age I sockeye salmon was taken in tow nets in North Arm and this happened during a daytime test tow on 13 August 1963. The average length of 225 fish in this tow was 93 mm. The average length of 18 fish taken during regular tow netting in North Arm on 1 September 1963 was 94 mm. The average lengths of the age I fish in these two samples were several millimeters longer than the average lengths in similar samples elsewhere in the system.

Northwest Basin.—Northwest Basin is small and relatively insignificant in the production of sockeye salmon in the system and consequently was not sampled as intensively as the other basins. Too few data were obtained to permit construction of growth or length frequency curves. Average size data are available for two dates—20 August 1961 and 1 September 1963 (Table 21). The size of age 0 fish was about average for the system. Age I and older sockeye salmon occurred only occasionally in tow net catches in Northwest Basin and the general size of these fish was similar to those from Iliuk Arm and South Bay.

Brooks Lake.—Juvenile sockeye salmon were generally as scarce in tow net catches in Brooks Lake as in North Arm, but because more tow netting was done in Brooks Lake data were sufficient to permit construction of growth curves. The calculated curves describing the apparent growth of age 0 sockeye salmon in Brooks Lake (Fig. 24) were based on samples of one or more fish. Although the minimum sample size was small, all the points fall close to the calculated curves. These curves show the typical (for the Naknek system) declining rate of growth in late August. The average lengths of age 0 sockeye salmon on 20 August and 1 September were generally about average for the system (Table 21). Age I and older fish were seldom captured in Brooks Lake, but in general they were about the same size as comparable fish in Iliuk Arm and South Bay.

Causes of Differences in Size of Juvenile Sockeye Salmon on 1 September

Differences in the size of juvenile sockeye salmon within a year between areas and within areas between years have commonly been reported for other systems. These differences may be due to one or more factors, of which I will consider the following for the Naknek system: (1) real differences in rates of growth, (2) differences in time of recruitment of fry and resulting differences in number of growing days by a given date, (3) differences in rates of dispersion of large and small or fast- and slow-growing fish, and (4) differences in size of fry at time of emergence.

Real differences in rates of growth.—Differences in the rates of growth of juvenile sockeye salmon within a system are most likely due to differences in the availability of food and in water temperatures. A reduction in the average size of juvenile sockeye salmon has often been directly or indirectly attributed to large numbers of feeders, both sockeye salmon and other species such as sticklebacks. Some examples in systems of western Alaska are the Wood system (Burgner, 1964); the Kvichak system;[11] and the Chignik system (Narver and Dahlberg, 1964). Examples in other areas are: British Columbia, Babine Lake of the Skeena system (Johnson, 1958) and Cultus Lake of the Fraser system (Foerster, 1944), and the east coast of Kamchatka Peninsula, USSR, Lake Dalnee (Krogius, 1961).

For the seven largest lakes of the Naknek system (Northwest Basin is excluded because of too few samples), the mean surface water temperatures in the month of August, the mean number of age 0 and age I sockeye salmon per tow, and the mean fork lengths of the age 0 fish for the years 1961-63 are shown in Table 22; the mean number per tow of the three species of fish most commonly taken in tow nets with the juvenile sockeye salmon (pond smelt, threespine sticklebacks, and ninespine sticklebacks) are also shown in the table. Some of the differences in the size of the age 0 sockeye salmon are probably due to real differences in growth rate. The largest age 0 fish generally occurred in Coville Lake and West End (Table 22). These two basins also had the greatest average combined catches of sockeye salmon juveniles and associated species in tow nets and the highest surface

[11] Orra E. Kerns. 1966. Abundance and size of juvenile sockeye salmon and major competitor species in Iliamna Lake and Lake Clark, 1964 and 1965. Univ. Wash., Fish. Res. Inst. Circ. 66-15, 35 p.

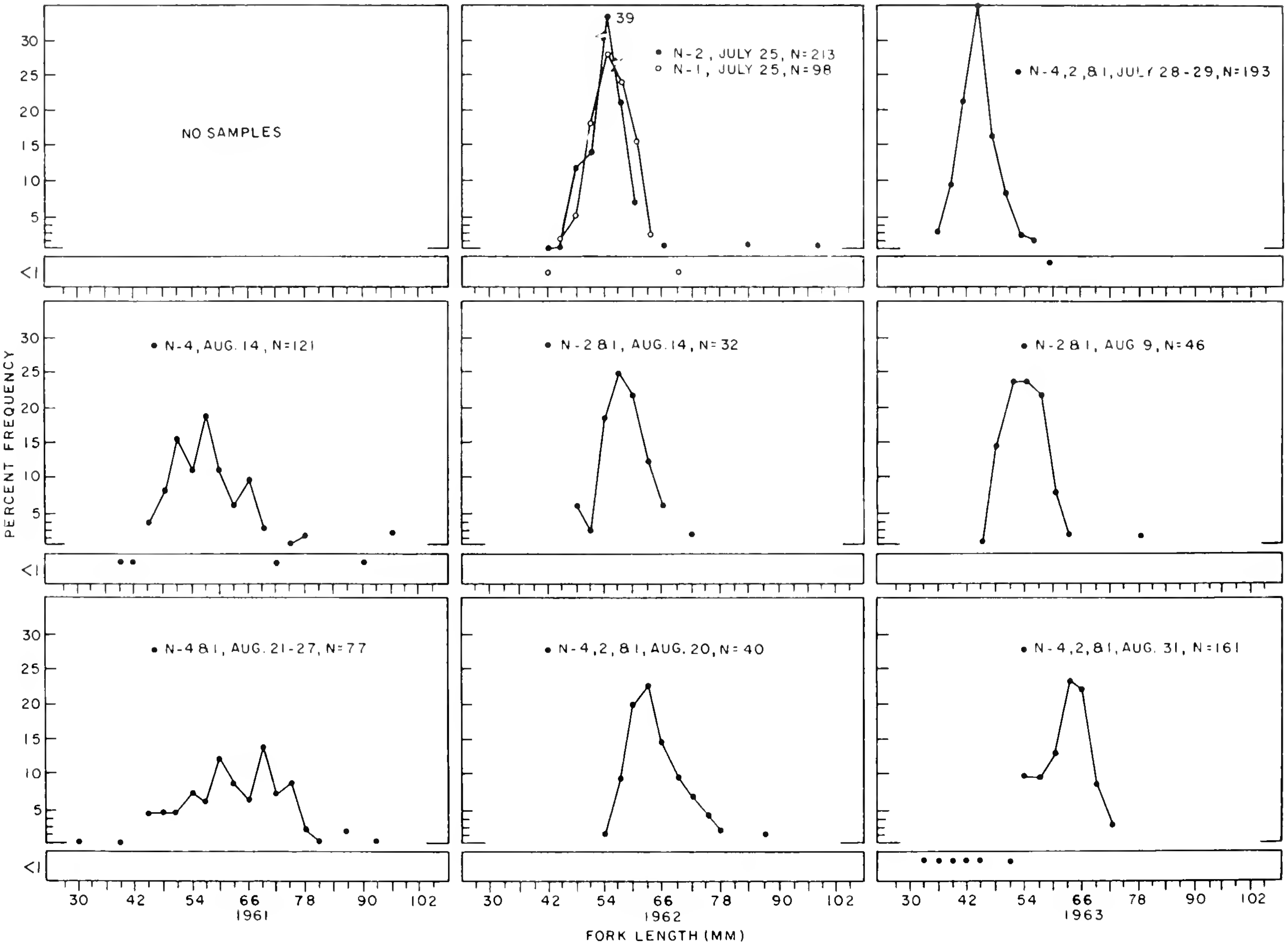

Figure 23.—Length frequency distributions of juvenile sockeye salmon (age 0 and age 1 combined) captured in tow nets in sampling units (combined) of West End for several time periods in July and August 1961-63.

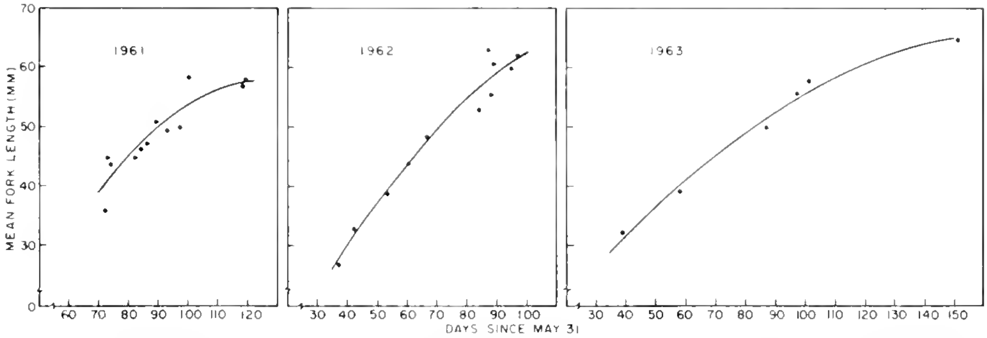

Figure 24.—Curves of apparent growth of age 0 sockeye salmon captured in tow nets in Brooks Lake 1961-63.

water temperatures during August. The lakes with the smallest combined catches of sockeye salmon and associated species, North Arm and Brooks Lake, were intermediate in size of age 0 sockeye salmon and in water temperatures. I conclude that the abundance of associated species such as pond smelt and sticklebacks is not restricting the growth of juvenile sockeye salmon. The growth of juvenile sockeye salmon seems to be more directly related to temperature, but the mechanism is not known.

Differences in time of recruitment of fry.—A greatly prolonged period of recruitment of fry from the spawning grounds has been reported for Karluk Lake on Kodiak Island (Burgner et al., 1969) and in 1 yr at Kitoi Lake on Afognak Island (Smoker, 1957). In the Naknek system a late recruitment of recently emerged sockeye salmon fry was apparent only in Grosvenor Lake and the length frequency graphs for this lake (Fig. 15) show two groups of age 0 fish in August 1962 and 1963. The location of the peak of the larger groups indicates a smaller average length than in the rest of the system, which is probably due in part to late emergence and lake entry. Grosvenor Lake is intermediate in the system in regard to summer water temperatures (Table 22) and in productivity (Burgner et al., 1969).

Differences in rates of dispersion of large and small or fast- and slow-growing fish.—Differences in the average size of age 0 sockeye salmon at various distances from the major spawning grounds have been reported in Lake Aleknagik of the Wood River system (Pella, 1968) and Iliamna Lake of the Kvichak system (see footnote 12). In these two lakes differences in lengths of juvenile sockeye salmon could be explained by the more rapid migration of larger and faster growing fish. Within the Naknek system the earlier migration of the larger fish is apparent in the differences between the size of the summer migrants in Coville River and the fish collected at the same time with tow nets in Coville

Table 22.--Mean surface water temperatures in August, mean number of age 0 and age 1 sockeye salmon and of pond smelt and threespine and ninespine sticklebacks, and mean fork lengths of age 0 sockeye salmon in seven lakes of the Naknek River system, 1961-63.

Lake or basin	Mean[1] surface water temperature (°C)	Mean number of fish per tow[2]						Mean[3] fork length of age 0 sockeye salmon (mm)
		Sockeye salmon		Pond smelt	Threespine sticklebacks	Ninespine sticklebacks	Four species combined	
		Age 0	Age 1					
Coville Lake	14.4	30	0	46	35	29	140	56
Grosvenor Lake	10.8	8	0	<0.5	<0.5	<0.5	8	48
Iliuk Arm	10.2	37	10	<0.5	6	1	54	52
South Bay	11.7	10	9	<0.5	19	5	43	53
West End	12.5	8	<0.5	<0.5	108	6	192	59
North Arm	11.8	1	1	<0.5	1	<0.5	3	52
Brooks Lake	11.9	3	<0.5	0	<0.5	<0.5	3	53

[1]Mean of all observations made in each lake during tow netting in August 1961-63.
[2]Mean for 1961-63, August 16 to September 1, for species other than sockeye salmon, and post-August 11 for sockeye salmon.
[3]Mean for 1962 and 1963 on August 20.

Lake. The migration of larger fish may also be the cause of the reversal between 20 August and 1 September of the relation between the average size of age 0 sockeye salmon in Iliuk Arm and the average size in Coville Lake (Table 21). The average size of age 0 fish was smaller in Iliuk Arm than in Coville Lake on 20 August (1961, 1962, 1963), but by 1 September the fish were larger in Iliuk Arm than in Coville Lake.

Differences in size of fry at time of emergence.—Differences in the average sizes of fry produced by different spawning groups within a system have been documented (Raleigh, 1967; Brannon, 1967). McCart (1967) considered the question of differences in size of fry and suggested that they could result from differences in the size of adults and of eggs. Although detailed study may reveal differences in the size of fry within the Naknek system, the similarities of shape and in location of peaks of length frequency graphs for late July during this study do not indicate differences in the size of fry at the time they leave the gravel.

Species Commonly Associated with Juvenile Sockeye Salmon

Data on size, length frequency, and growth of species commonly captured with juvenile sockeye salmon in tow nets are too few to permit description of growth. Therefore I discuss data on length frequency in some of the lakes for only three species—threespine sticklebacks, ninespine sticklebacks, and pond smelt.

Two to several age groups were present in the length frequency samples of each associated species, usually including age 0 fish. The variation in the rate of capture of age 0 fish with season and species and in year-class strength from year to year makes it difficult to compare the abundance either between species or within a species at different times.

Threespine sticklebacks.—The length frequencies of threespine sticklebacks from nine samples collected with tow nets from 1961 to 1964 are presented in Figure 25. Although these samples represent diverse areas and times, two important facts were evident. (1) Age 0 threespine sticklebacks did not appear in tow net catches in appreciable numbers until late August when they ranged to about 30 mm fork length. When sticklebacks hatch in early July they are about 5 mm long and they grow to about 7 mm in their first week.[12] I substantiated these laboratory observations by visual observations of small threespine sticklebacks close to shore near the outlet of Coville Lake during seining and diving in July 1963. (2) Although it is probable that only two age classes other than age 0 made up most of the population, the older classes usually could not be separated on the basis of length because of a broad overlap in length of fish assumed to be age I and older.

These two general observations also appear to be true for threespine sticklebacks in Karluk Lake and in Bare Lake on Kodiak Island (Greenbank and Nelson, 1959) and in lakes of the Wood system (Rogers, 1968). When comparing my data with those of Greenbank and Nelson it appears that they overlooked the real age 0 fish when they did appear in the length frequency graphs (only on 27 August 1954 for Bare Lake and probably from 17 August to 13 September according to length frequency histograms for fish from Karluk Lake). As a result, Greenbank and Nelson may be 1 yr off in assigning ages to fish represented by portions of these histograms. Kerns (1961), however, was able to separate age I threespine sticklebacks from age 0 and age II and older fish by length.

European workers also have difficulty in separating age groups of threespine and ninespine sticklebacks on the basis of size distribution because of the slow growth of the age I and older fish and a resulting overlap in size of the various year groups (Jones and Hynes, 1950).

The largest threespine stickleback I measured was 66 mm in fork length and came from West End. It appears that few threespine sticklebacks survive after spawning in their third or fourth summer.

Ninespine sticklebacks.—Length frequency data are available for only four samples of ninespine sticklebacks (Fig. 26). It appears probable that three age classes, 0, I, and II, are present in the length frequency tabulations, but their definition by length is not possible because of the broad overlap in length. Wallace (1969) could not separate the age classes of ninespine sticklebacks from the Naknek system, although he examined otoliths as well as length frequencies. A higher proportion of ninespine sticklebacks than threespine sticklebacks was in the 60 mm and greater size groups. The relatively fewer ninespine than threespine sticklebacks less than 36 mm may be due to differences in habitat preference or size of age 0 fish of the two species. The ninespine sticklebacks were more abundant than the threespine sticklebacks only in the shallower water of Coville Lake. The largest ninespine stickleback collected was 72 mm in fork length.

Pond smelt.—Length frequency data are presented for four samples of pond smelt from Coville Lake and one from West End in Figure 27. As with sticklebacks, age 0 pond smelt did not appear in the tow net catches until late August. The fork length of 73 pond smelt collected with a small-mesh dip net near the outlet of Coville Lake on 18 July 1962 ranged from 26 to 48 mm. These fish were probably all in their second summer. It appears that at least three age classes, 0, II, and II, are in the samples represented in Figure 27 and that there is broad overlap in length of the age I and older fish.

[12]Based on observations of progeny of a pair of threespine sticklebacks from Brooks Lake that spawned in an aquarium. (W. R. Heard, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, AK 99821, pers. comm.)

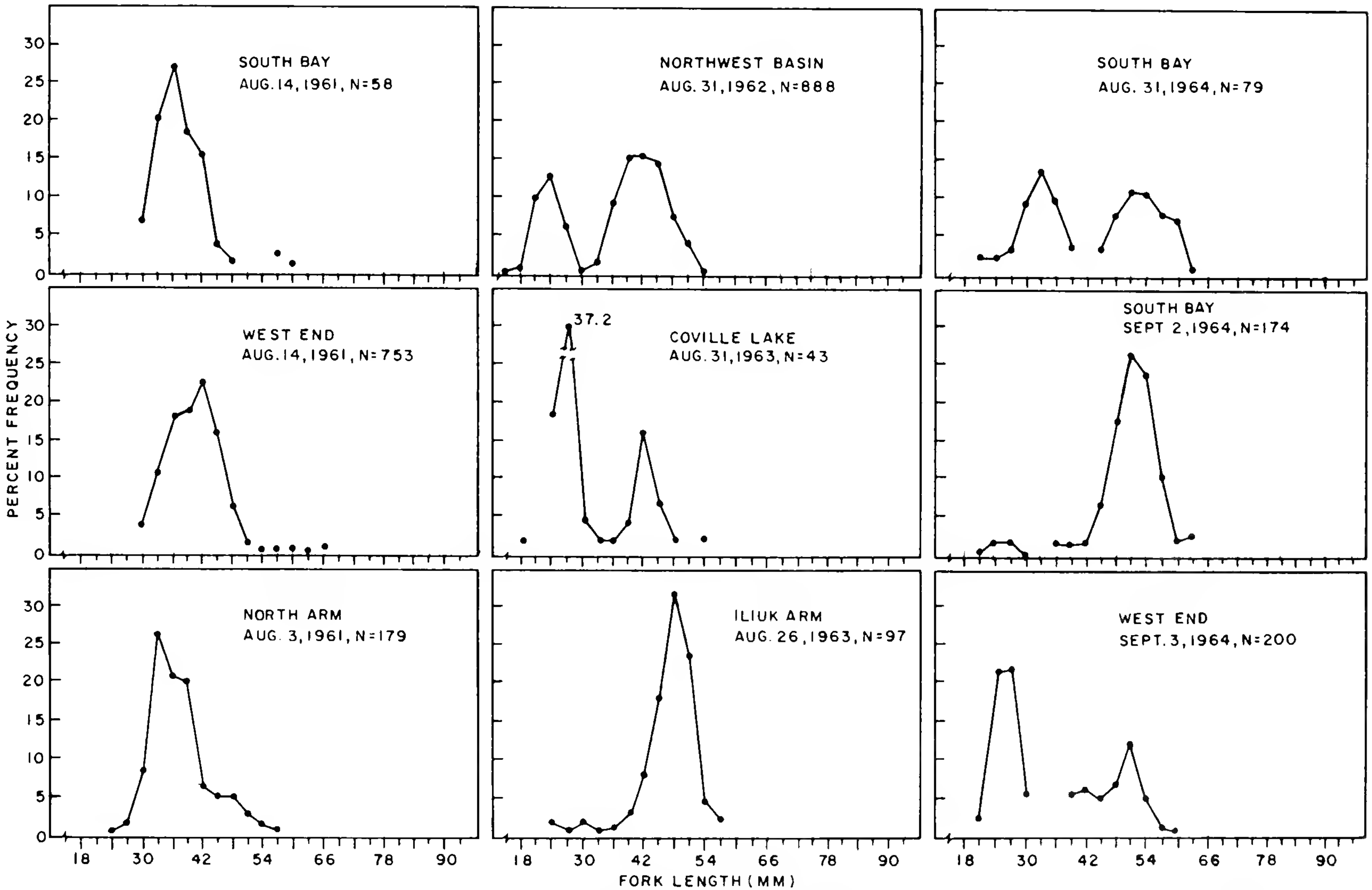

Figure 25.—Length frequency distributions of nine samples of threespine sticklebacks captured in tow nets in sampling units in lakes of the Naknek River system 1961-64.

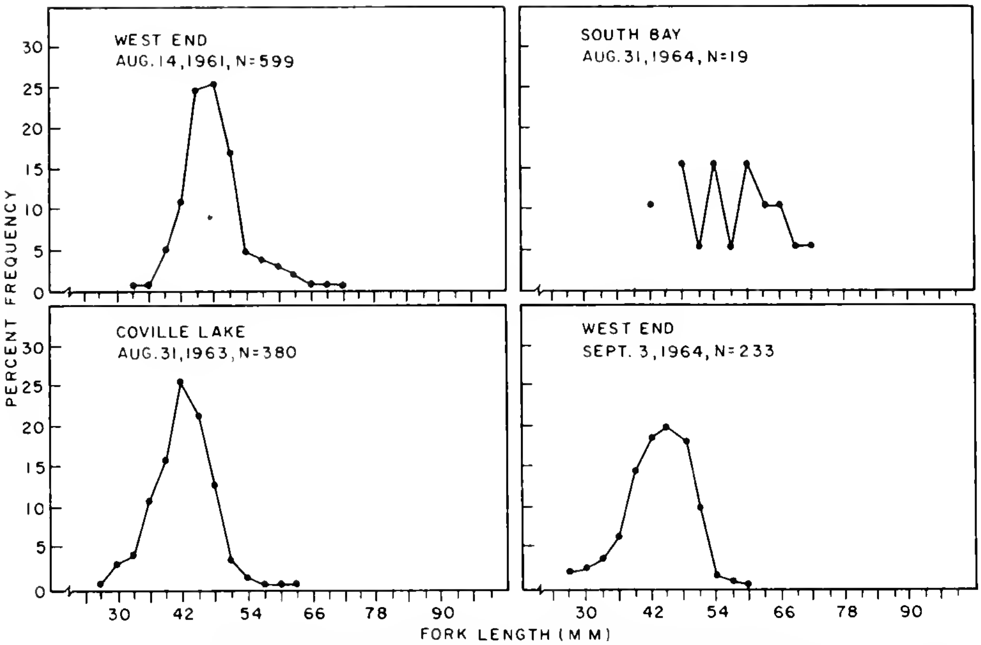

Figure 26.—Length frequency distributions of four samples of ninespine sticklebacks captured in tow nets of lakes of the Naknek River system, 1961, 1963, and 1964.

Wallace (1969) presented more data on this species in the Naknek system and concluded from analysis of otoliths that as many as six age classes are present in the lakes, but that broad overlap of lengths for each age prevents separation of age I and older fish by length.

Pygmy whitefish and least cisco.—Pygmy whitefish and least cisco were seldom captured in tow nets, but were frequently taken in gear that sampled near shore or close to the bottom. The life history of the pygmy whitefish in the Naknek system was described by Heard and Hartman (1966) who found populations of large and small types of pygmy whitefish in the system. The maximum ages and sizes reported by Heard and Hartman were age III and 84 mm for the small type and age V and 163 mm for the large type.

Information on the life history of the least cisco in the Naknek system was compiled by Wallace (1969). The range in ages and sizes he encountered were age 0 to VI and length 61 mm to 336 mm. The largest and oldest individuals came from Coville Lake.

PREDATION ON JUVENILE SOCKEYE SALMON

Predators have been considered to be both significant in determining the abundance of juvenile sockeye salmon (Foerster and Ricker, 1942; Rounsefell, 1958) and not significant (DeLacy and Morton, 1943; Roos, 1959). During the present study it became obvious that the Naknek system contained many potential sockeye salmon predators and, although no specific studies of predation were made, data and observations were collected incidentally. This information is included here to add to the overall knowledge of the biology of the system and to aid in the planning for future studies. In the apparent general order of importance, the fish that prey on sockeye salmon in the Naknek system are: lake trout, Arctic char, Dolly Varden, rainbow trout, northern pike, and juvenile coho salmon. The burbot and humpback whitefish are probable predators. Arctic terns, *Sterna paradisaea*, and Bonaparte's gulls, *Larus philadephia*, appear in large numbers and feed actively at the mouth of Coville River during the summer migration of age 0 sockeye salmon. Mergansers and other fish-eating ducks occur throughout the system.

Lake Trout

Many studies have shown that fish frequently constitute the major portion of the diet of lake trout. Van Oosten and Deason (1938) present a summary of earlier literature on food habits and present additional data. More recent studies were done by Miller and Kennedy (1948) and Rawson (1951). Lake trout are often found in deep cool water, but have been observed in shallow water when water temperatures permit (Rawson, 1951; Connecticut State Board of Fisheries and Game, 1942). Lake trout occur in most of the Naknek system (Table 3), but information on their food habits is available only for a group occurring in shallow water at or near the outlet of Coville River in Grosvenor Lake.

Lake trout feed voraciously near the mouth of

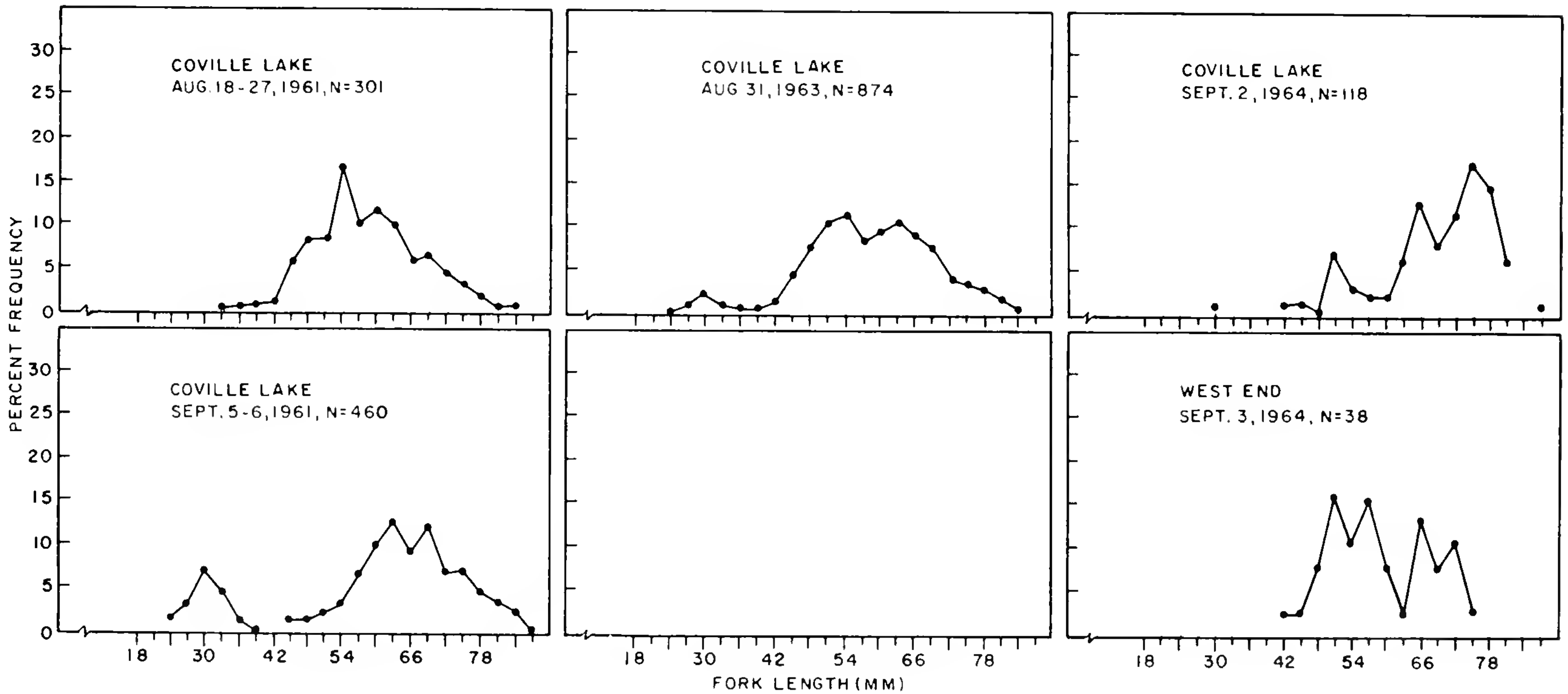

Figure 27.—Length frequency distributions of five samples of pond smelt captured in tow nets in lakes of the Naknek River system, 1961, 1963, and 1964.

Table 23.--Stomach contents of 18 lake trout[1] captured by angling in 1963 in Grosvenor Lake near the mouth of Coville River on July 3-5 (before presmolt sockeye salmon migration) and of 21 lake trout[2] captured on August 4-5 (during migration).

Dates of capture	Stomachs containing food	Stomachs with sockeye salmon	Sockeye salmon per stomach		Stomachs with other fish	Other fish per stomach	
			Mean	Range		Mean	Range
July 3-5	9	0	--	--	6	[3]0.1	0-2
August 4-5	21	21	41	4-167	21	[4]6.6	1-20

[1]Mideye fork length range 47.0-60.9.
[2]Mideye fork length range 46.2-58.9.
[3]Some of these were salmonlike but were too digested for positive identification.
[4]Most of these were too digested to be identified, but many were the size of sockeye salmon found in some stomachs.

Coville River during the summer migration of presmolt sockeye salmon from Coville Lake and are readily taken by angling in the vicinity both before and during this migration. In 1963, 39 lake trout were captured by angling—18 on 3-5 July before the presmolt migration and 21 on 4-5 August when many age 0 sockeye salmon were migrating from Coville Lake. The stomach contents were examined. None of the trout captured on 3-5 July contained sockeye salmon and half of the stomachs were empty (Table 23). In the trout collected on 4 and 5 August every stomach contained sockeye salmon.

Lake trout have been observed in this area all summer (June to September) and it is possible that they constitute a local resident population rather than being fish attracted from wide areas of the lake. On 12 August 1964 I fished with sport gear in Grosvenor Lake near each of the four smaller stream tributaries (omitting Hardscrabble Creek) and hooked lake trout readily in each area. Visual observation from a slowly moving boat along the shores of the south side of Grosvenor Lake (the tributaries are all on the north side) revealed many solitary lake trout.

Two lake trout (both about 47 cm long) were taken by angling in Grosvenor River near Grosvenor Lake on 20 May 1962. These fish contained age 0 sockeye salmon, ninespine sticklebacks, and sculpins.

I determined the length frequencies for 70 lake trout collected by angling in Grosvenor Lake at the mouth of Coville River and for 26 taken in gill nets (about 10-cm stretch mesh) in areas C-4 and C-5 of Coville Lake in 1963 (Table 24) and for 94 collected by angling in Grosvenor Lake near the mouth of Coville River in 1964 (Table 25). The gill nets fished in Coville Lake included small mesh sizes down to those which held ninespine sticklebacks and so could have captured smaller lake trout, which are notably absent in the length frequencies. Most of the fish fell in the 45- to 58-cm size range, but fish as short as 40 cm and as long as 69 cm were collected. The length frequency data indicate the presence of several year classes (because of the wide range in length and an expected slow growth) and the absence of the larger lake trout found in some northern lakes (for example, Great Slave Lake [Rawson, 1951]) and of the smaller sizes.

Humpback Whitefish

Humpback whitefish are widely distributed in the

Table 24.--Length frequencies of lake trout captured in Grosvenor Lake at the mouth of Coville River by angling, June 22 to August 5, and in units C-4 and C-5 of Coville Lake in gill nets,[1] June 22 to July 20, 1963. The mideye-fork lengths of fresh dead fish were measured with calipers to the nearest millimeter.

Length group (cm)	Fish captured	
	June 22-August 5 Grosvenor Lake	June 22-July 20 Coville Lake
40.1-42.0	--	1
42.1-44.0	1	0
44.1-46.0	1	3
46.1-48.0	12	0
48.1-50.0	14	3
50.1-52.0	14	2
52.1-54.0	13	3
54.1-56.0	10	6
56.1-58.0	2	3
58.1-60.0	1	0
60.1-62.0	2	2
62.1-64.0	--	0
64.1-66.0	--	2
66.1-68.0	--	0
68.1-70.0	--	1
Total	70	26

[1]One net was 10-cm stretch mesh and the other consisted of equal length sections of different sizes: 9.5 mm, 12.7 mm, 19.0 mm, 22.2 mm, and 25.4 mm. About half the trout were captured in the 10-cm net and the rest in the smaller sizes, but the exact sizes were not recorded.

Table 25.--Length frequencies of lake trout captured in Grosvenor Lake at the mouth of Coville River by angling, July 29 to September 6, 1964. The total lengths of the live fish were measured with a tape measure to the closest higher inch.

Length group		Fish captured
Inches	Centimeters	
14.1-15.0	35.8-38.1	--
15.1-16.0	39.2-40.6	--
16.1-17.0	40.9-43.2	2
17.1-18.0	43.4-45.7	2
18.1-19.0	46.0-48.3	8
19.1-20.0	48.5-50.8	20
20.1-21.0	51.1-53.3	20
21.1-22.0	53.6-55.9	26
22.1-23.0	56.1-58.4	10
23.1-24.0	58.7-61.0	3
24.1-25.0	61.2-63.5	3
25.1-26.0	63.8-66.0	0
Total		94

Naknek River system (Heard, Wallace, and Hartman, 1969), but data on length frequency and food are available only for fish collected with gill nets in Coville Lake. Studies of the food of fish in Great Slave Lake (Larkin, 1948) and Great Bear Lake (Kennedy, 1949) both indicated that the food of the closely related lake whitefish, *Coregonus clupeaformis*, in these northern lakes was mainly invertebrate animals and that fish occurred only rarely. Larkin (1948) found fish remains in only one sample (number of fish stomachs in sample not given) for Great Slave Lake and Kennedy (1949) reported that none of the fish in 86 samples from Great Bear Lake contained food (202 fish examined).

Briefly, the results of the examination of the stomachs of 38 humpback whitefish (mideye-fork length 12.1 to 55.5 cm) taken from Coville Lake 14 July to 12 September 1963 are as follows: 23 of the 38 stomachs held no food; 4 contained unidentifiable mass or "white paste"; 7 contained snails or mussels; and 4 contained evidence of fish (1 pond smelt, 1 whitefish, 1 sculpin, and 3 unidentifiable fish remains). It appears that fish were more important in the diet of humpback whitefish in Coville Lake than in the lake whitefish of Great Slave and Great Bear Lakes. The fork lengths of 165 humpback whitefish (Table 26) collected with gill nets in Coville Lake from 22 June to 12 September 1963 ranged from 121 to 560 mm and several modes were apparent. The presence of several modes in the length frequency indicates several year classes; a preliminary study of scale samples from these fish indicated that the ages ranged from 4 to 12 yr.

Arctic Char and Dolly Varden

Arctic char and Dolly Varden cannot be differentiated without detailed examination and may have been confused in many instances in the present study. Therefore, I will refer to both species as char unless the identification is certain.

Char occur throughout the system in lakes and frequently in the streams and probably eat juvenile sockeye salmon when they are available. Arctic char were taken with lake trout, but in fewer numbers, in the gill nets in Coville Lake and by angling in Coville and Grosvenor Rivers. The stomachs of a few Arctic char captured by angling in Grosvenor Lake near Coville

Table 26.--Length frequencies of humpback whitefish captured in gill nets in Coville Lake, June 22 to September 12, 1963. The fork lengths of fresh dead fish were measured to the nearest millimeter.

Length group (mm)	Fish captured
121-130	1
161-170	1
171-180	1
181-190	1
191-200	1
201-210	4
211-220	5
221-230	5
231-240	4
241-250	0
251-260	3
261-270	2
271-280	0
281-290	3
291-300	6
301-310	11
311-320	0
321-330	1
331-340	0
341-350	1
361-370	0
371-380	2
381-390	2
391-400	2
401-410	17
411-420	12
421-430	16
431-440	17
441-450	11
451-460	6
461-470	7
471-480	1
481-490	4
491-500	5
501-510	3
511-512	2
513-520	2
521-530	2
531-540	2
541-550	0
551-560	2
Total	165

River contained food similar to that of lake trout from the same area. A char (about 40 cm long) was seen feeding in upper Grosvenor River on 20 May 1962 and was captured by angling. This fish contained several sockeye salmon fry, two of which were still alive.

Other Species

Only general observations are available on the other pisciverous fish in the Naknek River system—rainbow trout, juvenile coho salmon, northern pike, and burbot.

Rainbow trout inhabit most of the larger streams in the system and were often taken by angling in the lakes near the mouths of these streams. Sportsmen fish for this species in American Creek and Coville, Brooks, and Naknek Rivers; fish above 60 cm are commonly caught in these locations. No food studies have been made here, but rainbow trout have been observed feeding on young sockeye salmon that were migrating from stream spawning grounds to the lakes and from lake to lake via connecting rivers either as presmolts or smolts.

Juvenile coho salmon were taken in appropriate gear in many streams and beach areas in the system, but were virtually absent from tow net samples. Because of their relatively small size (no juvenile coho salmon over 130 mm were taken), I would expect coho salmon to be most effective as predators on sockeye salmon during the first few weeks after the sockeye salmon leave the gravel—in streams and lake margins before the sockeye salmon become pelagic.

Northern pike are widely distributed in the Naknek system wherever suitable habitat is found. The lake areas where northern pike seem to be abundant are the shallow north end of Coville Lake and the shallow waters of Northwest Basin. Generally the habitat in which northern pike are abundant does not contain many juvenile sockeye salmon. Possible exceptions to this occur in Grosvenor River near Grosvenor Lake and in the upper Naknek River where lagoons containing northern pike are closely connected to river areas containing migrating sockeye salmon. Sockeye salmon have not been reported in stomachs of northern pike from this system.

Burbot have been captured in Iliuk Arm, South Bay, and North Arm (Heard, Wallace, and Hartman, 1969), but were never abundant. They were caught in gill nets and trap nets in South Bay, in trap nets in North Arm, and in seines in Iliuk Arm. In Lake Michigan, the stomachs of lake trout and burbot that were captured in gill nets contained the same kinds of fish, but the burbot contained only 74% fish by volume and the lake trout contained 98% (Van Oosten and Deason, 1938). Both species were predators on coregonids. No data are available on the diet of burbot in the Naknek system, but apparently so few are present that they would not be a significant predator even if sockeye salmon were important in their diet.

General Significance of Predation

Although many species of fish and birds are potential or known predators on juvenile sockeye salmon in the Naknek system, the role of predators in determining freshwater survival is unknown. The abundance of smolts from the escapement of 1961 shows that smolt production per adult may be high in spite of predation in the Naknek system. In 1961 a relatively small escapement of about 350,000 adult sockeye salmon entered the Naknek system, of which about 220,000 went to the most distant spawning grounds, American Creek. The production of smolts from the total escapement to the system in 1961 was about 32 smolts per adult (see footnote 3)—the highest rate recorded for the Naknek system between 1956 and 1963. The survival of these smolts to returning adults in 1966 and 1967 was about 15.5%,[13] very close to the long-term average of about 16.5% (Burgner et al., 1969). A different distribution or abundance of adult sockeye salmon or predators might result in a much different effect on survival in another year.

SUMMARY AND SIGNIFICANCE FOR RESOURCE DEVELOPMENT

Although most stocks of sockeye salmon have the same general life history, each stock is unique because it has its own combination of biological and physical environments. The principal objective of this study was to determine the distribution, abundance, and growth of juvenile sockeye salmon in the Naknek River system, Bristol Bay, Alaska. The work was done from 1961 through 1964.

The Naknek system contains eight interconnected and generally biologically discrete lakes or basins with different ratios of potential spawning grounds to rearing area for sockeye salmon and different densities of juvenile sockeye salmon and associated species of fish. The sockeye salmon was the most common and abundant fish in all basins, followed by threespine sticklebacks, ninespine sticklebacks, and pond smelt. Eighteen other species of potential competitor or predator fish were present.

Juvenile sockeye salmon in the pelagic areas had a characteristic pattern of abundance in tow net catches during the summer of 1961-64. For the entire system the abundance of age 0 fish increased from early summer to midsummer and then declined to late August. The abundance in late August varied by a factor of about 2.5 and, although data are available for only 4 years, the abundance appears to be independent of variations in the number of parents from 1960 to 1963.

In July the catches of age 0 sockeye salmon in each basin were about proportional to the abundance of contiguous spawning grounds, but by late August this relation no longer existed. This change was at least

[13] C.J. DiCostanzo, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, AK 99821, pers. comm.

partly due to migration of age 0 fish—generally from basins of greater abundance of fish to others of lesser abundance. The larger and faster growing fish probably were the first to migrate. Not all basins were involved in these migrations.

In the Naknek system smolt production has varied only about twofold with parent escapements of 350,000 to 2,000,000 (escapements of less than 300,000 have produced markedly fewer smolts). Several factors are suggested as contributing to this relatively uniform production of smolts. The maintenance of a minimum level of fry production is enhanced by the presence of several major spawning units or races in widely separated spawning grounds of different types. This combination helps ensure against a total loss of a year's production of eggs and alevins due to adverse physical conditions on the spawning grounds. Examples of the value of having different types of habitat are: scouring action of floods would not affect beach spawning areas; extreme freezing would not greatly reduce the flow in major rivers connecting lakes; and warm dry weather causing low lake levels and low flows in small streams would increase the flow of streams fed by snow and icefields. The possibility of full utilization of fry is greatly enhanced by the presence of several connected lakes and the migratory behavior of the juvenile sockeye salmon during their first summer.

No indications that the population of juvenile sockeye salmon was near its upper limit were apparent during this study. In other systems the first obvious effect of too high populations is a reduction in growth. Such a reduction was not evident in juveniles in the lakes of the Naknek system in 1961-64 and apparently did not occur in the period 1957-65, as evidenced by the size of age I smolts—age I smolts from the Naknek system are as large as, or larger than, those of other Bristol Bay systems (Burgner et al., 1969). Much of the variation in the average length of age I smolts (-8.5% to + 6.6% of the mean of 99.4 mm) in the Naknek system is thought to be due to variations in growing conditions in the spring just before the smolts leave (Burgner et al., 1969).

The data on abundance and growth of juvenile sockeye salmon and the distribution of the escapement and spawning grounds indicate the possibility that production of sockeye salmon in the Naknek system could be greatly increased. Two of the major basins, North Arm and Brooks Lake, which constitute about 35% of the system, are now producing relatively few juveniles. The low production of juvenile salmon in both basins appears to be the result of too few fry being produced by the spawning grounds, but the reason for the low production of fry differs in the two basins: North Arm has limited but heavily used spawning grounds, whereas Brooks Lake has apparently adequate but lightly used spawning grounds.

North Arm contains about 24% of the rearing area of the system but only about 2% of the spawning grounds (and usually receives about 2% of the escapement) and the basin does not receive juveniles from other areas. Even full use of all the present spawning grounds in North Arm would probably result in too few juveniles to use the rearing area fully.

Ninety-five percent of the area of potential spawning grounds and 90% of the escapement in North Arm are in Bay of Islands Creek and most of the rest is distributed among seven small streams. Bay of Islands Creek runs about 27 km from a high tundra lake down to North Arm. A falls impassable to salmon is located about 14 km upstream from North Arm. The probable difficulty in making the falls passable and the potential of the stream above the falls for production of sockeye salmon are unknown. It is possible that the present production of sockeye salmon in North Arm could be increased significantly by simply making all of Bay of Islands Creek accessible to spawners. The lake probably could support 10 to 20 times the present density of juvenile salmon. The increase in fry production required to produce the numbers of lake residents North Arm could support could be obtained from a combination of enhancement techniques used elsewhere.

The reason for the low production of juvenile sockeye salmon by Brooks Lake is not clear. The major spawning area, Headwater Creek, has an estimated spawning ground capacity of about 40,000 adult sockeye salmon, but the largest number recorded in the last 20 yr was about 11,000. An intensive study of the biology of the sockeye salmon of Headwater Creek could be expected to reveal the time, place, and cause of mortality in fresh water. With this information action could be taken to bring Brooks Lake into full production.

Three factors in the biology of juvenile sockeye salmon of the Naknek system are of special significance to the managers of the resource: (1) the abundance of smolts each spring has been fairly constant for the system as a whole and not closely related to the abundance of the parents, or from 1961-64, apparently even to the abundance of age 0 fish during early summer, (2) the apparent growth of juvenile sockeye salmon and potential competitor species was not related to the abundance of these fish in any lake of the Naknek system, and (3) two major lakes, constituting about 35% of the rearing waters, do not receive age 0 sockeye salmon from other basins and are supporting relatively few sockeye salmon.

These three factors and their causes and effects could form the basis for a program to increase the production of sockeye salmon by the Naknek River system.

The question of what escapement of adult sockeye salmon is needed to ensure full production of juveniles is of primary importance to fishery managers. From 1961 to 1964, as few as 350,000 adult spawners were apparently adequate in the Naknek system. However, the special circumstance involved, i.e., the majority of fish in this low escapement used one spawning area with probable special benefits, must be considered. It seems that to ensure full production with adequate insurance against catastrophes, every major spawning ground should be utilized every year. On the basis of the smolt-escapement data, Burgner et al. (1969) placed the desired escapement for the Naknek system at 600,000 to 1,000,000 fish. The present study indicates that escapements in this range probably fully utilize the present combination of spawning and rearing areas without danger of overburdening the food supply.

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