BIOLOGICAL STUDIES AND ESTIMATES OF OPTIMUM ESCAPEMENTS OF SOCKEYE SALMON IN THE MAJOR RIVER SYSTEMS IN SOUTHWESTERN ALASKA

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ABSTRACT

An intensive research program was conducted in 1961 and 1962 by the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, and the Fisheries Research Institute, University of Washington, with the cooperation of the Alaska Department of Fish and Game. Many sockeye salmon river systems were studied concurrently with essentially the same techniques so that systems covering the entire range of production levels could be compared. The general objective of this research was to determine the optimum escapement of sockeye salmon for each of the major systems. This was accomplished through integration of the results of several related studies: (1) summarization and analysis of historical and current data on runs of adult sockeye salmon, (2) delineation and description of spawning areas and estimation of their capacities, (3) delineation and description of the nursery areas and estimation of their capacities.

The major systems studied were the Wood, Kvichak, Naknek, and Ugashik systems, which enter Bristol Bay; the Chignik system, on the south side of the Alaska Peninsula; and the Karluk system, on Kodiak Island. Adult sockeye salmon in the commercial catches and escapements, and sockeye salmon smolts, were counted and sampled. Spawning grounds were surveyed to determine their size and quality and the distribution and abundance of spawners. Bathymetric maps were prepared for some of the nursery lakes. Intensive limnological studies, including a major effort to measure primary productivity, were made on many nursery lakes. Several types of gear sampled juvenile sockeye salmon and associated species in the lakes. Interim optimum or target escapements required for highest production on a sustained-yield basis have been established for each major system.

The major task that the manager of a salmon fishery must undertake each year is to set a target escapement of fish to the spawning grounds for each salmon run (stock) under his management. He must have such a goal as a basis for numerous decisions that control the actual time, place, and method of fishing.

A correct decision is extremely valuable. The number of sockeye salmon *(Oncorhynchus nerka)* returning to a single river in Alaska may exceed 20 million in a single year, and each fish caught may be worth as much as $3 after being canned. Sometimes the number of adults returning to a system is much larger than the needed escapement; sometimes it is not large enough. Great year-to-year variability in the size of the run to a given system is common.

The manager must divide the return between catch and escapement, and he must do so in a way that ensures maximum sustainable yield. He must know the optimum escapement and then he must set a target escapement, having in mind the optimum and any modifications that may be indicated by the expected characteristics of the returning run and the expected conditions within the spawning and nursery areas. He will tend to set an escapement slightly higher than the optimum because his control of the fishery is not precise, and he is aware that the cost of slight underfishing is probably less than the cost of slight overfishing. In this way he attempts to make full use of the spawning and nursery areas.

The optimum escapement is usually considered to be the number of adults that will yield the greatest surplus of expected return over needed escapement. The optimum escapement is determined from the historical relation between

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Published April 1969

recruitment, which usually is measured as the number of adults returning, and the parent escapement. A simplified example of this relation, developed partly from inference and partly from observation, is a curve that starts at zero and rises to the left of the replacement line (the 45° line representing replacement reproduction at various levels of escapement), so that over a considerable range of escapements the expected return is greater than the parent escapement (fig. 1). The distance between the curve and the replacement line represents surplus production. The curve, however, either levels off or declines because the capacities of the spawning area, the nursery area, or the ocean feeding ground have been exceeded; and an increased number of spawners will not increase the expected return.

In practice, a satisfactory curve is difficult to obtain. First, observations over many years that include values for the entire range of escapement sizes are needed for each run. These observations are not available for most runs in southwestern Alaska. Attempts to estimate the escapement on the basis of the catch per unit of effort of the fishery (International North Pacific Fisheries Commission, 1962) yielded uncertain results because the relation between the catch per unit of effort and the level of the escapement varied with changing gear, changing management practices, and changing effects of competition between units of gear.

Data on the catches of sockeye salmon from runs to Bristol Bay since 1955 present a special problem. The Japanese fishing fleet has intercepted parts of these runs at sea, and its catches in some years have nearly equaled those of United States fishermen in Bristol Bay. The total Japanese catch of Bristol Bay sockeye salmon is not known with reasonable accuracy, and we have no breakdown of their catch by river system.

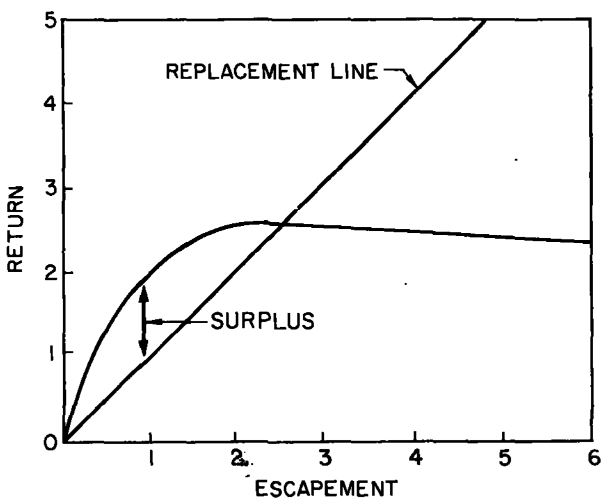

Figure 1.—Theoretical return-escapement relation of sockeye salmon.

Even when accurate catch and escapement data have been available, the relation between return and escapement has not been clearly defined—partly because of the cyclic nature of many sockeye salmon runs and partly because survival rates are greatly influenced by environmental conditions which differ from year to year. Obviously, it is desirable to measure abundance before the adults enter the fishery, particularly after completion of any critical part of the life cycle or residence in an environment that may limit production. The mortality of sockeye salmon in fresh water, from potential egg deposition to seaward-migrating smolt, is high and extremely variable; considerable evidence indicates that the fresh water rather than the marine environment usually places upper limits on the numbers of returning adults.

Thus, an important question is: What factors in the fresh-water environment are limiting the size of the sockeye salmon population in each system? First, the adult salmon must have access to spawning areas, and in some systems lack of access may be the limiting factor. Next, the spawning area must have gravel and water suitable for spawning and incubation of the eggs and for sheltering the fry until they emerge. Then, the young fish must find food and shelter for 1 or 2 years in the lake while they grow from a length of about 2.5 cm. to 7 to 13 cm.—smolt size. Finally, the smolts must be able to migrate successfully to sea.

In the sockeye salmon systems of southwestern Alaska, neither the adult's access to the spawning area nor the smolt's path of migration to the sea is restricted. It seems most logical, therefore, to seek limiting factors either during the salmon's life on the spawning grounds as adult, egg, larva, or fry or during its life in the lake as a growing juvenile. Our studies were planned on this assumption, and our task has been to determine approximately the number of spawners that can be expected to produce enough young to fully use the environment.

This report summarizes the data we now recognize as bearing on the question of cptimum escapement. In it we recommend (where possible) optimum escapement for each of the sockeye salmon river systems in southwestern Alaska and discuss the factors that affect those levels. The recommendations are the best that we can prepare at this time. They are not the last word—that must await a more detailed understanding of the life of young sockeye salmon.

Commercial fishing for sockeye salmon in southwestern Alaska started in 1884, and the annual catch rose rapidly to more than 10 million fish by 1900 and was rarely less than this until after 1940.[2] Between 1913 and 1938 the annual production in the Bristol Bay area alone exceeded 20 million fish 10 times. The record of 24,700,000 was in 1938. More than half of the catch usually came from the Naknek-Kvichak district, where the fishery produced a record catch of almost 21 million fish in 1938.

During many of the years that the Federal Government managed the sockeye salmon fisheries of southwestern Alaska, desired escapements in the major river systems were established by law. The White Act of June 26, 1924, declared the intent of Congress to limit the catch to 50 percent of the returning salmon—that is, one fish in the escapement for each one in the catch. As our knowledge of the life history of sockeye salmon increased, it became apparent that in some years the stocks were so small that the entire returns were not adequate to use fully the spawning grounds or nursery areas; in other years the returns were so large that escapements of 50 percent were obviously excessive. This provision of the act was repealed on September 4, 1957.[3]

In autumn 1960 it became evident that a major research program was needed to supply additional biological information to be used in the management of the sockeye salmon and pink salmon *(O. gorbuscha)* of Alaska.

This need for information was emphasized by the escapement of more than 3 million adult sockeye salmon to the rivers of the Nushagak fishing district and more than 2 million to the Naknek River in 1959, and an escapement of almost 15 million to the Kvichak River in 1960. These possibly excessive escapements again raised many questions about optimum escapements. In spring 1961, the Secretary of the U.S. Department of the Interior submitted a revised budget in which he requested an increase of $1½ million for an intensified salmon research program in Alaska.

The study of sockeye salmon was undertaken by the BCF (Bureau of Commercial Fisheries Auke Bay Biological Laboratory). About half the funds and research were contracted to the FRI (Fisheries Research Institute, University of Washington). The two agencies together planned several projects on the major sockeye salmon systems.[4] Both organizations had historically worked in specific sockeye salmon river systems; they concentrated their efforts in these areas during this study. The FRI worked on the systems tributary to Nushagak Bay (the Igushik, Snake, Wood, and Nuyakuk systems) on the mainland, the Kvichak system at the head of the Alaska Peninsula, and the Chignik system on the Gulf of Alaska side of the Peninsula. The BCF worked on the Alagnak, Naknek, Egegik, and Ugashik systems of the Alaska Peninsula and the Karluk system on Kodiak Island (fig. 2). By mutual agreement, one agency or the other analyzed historic records of catch and escapement for individual systems.

The intensified program began in April 1961, and field work continued through the summer of 1962. Most of the techniques used by the two organizations were standardized. Field research guides and standardized data sheets were prepared.

The satisfactory execution of this large program required the effort of many biologists. The research responsibilities within the BCF and FRI were as follows.

For the BCF—George Y. Harry, Jr., and Charles J. DiCostanzo, assisted by Wilbur L. Hartman, were responsible for general planning and supervision. DiCostanzo directly supervised the compilation and analysis of the data on the historical and current catch and escapement of adults and on the records of counts of smolts. Hartman supervised the limnological research

[2] Extensive statistics on the catch and pack are available in Rich and Ball (1928), Simpson (1960), and in annual publications such as the Pacific Fisherman Yearbook and the Statistical Yearbook of the International North Pacific Fisheries Commission.

[3] Public Law 85–296.

[4] Each lake or group of connected lakes and its outlet to the ocean is termed a "system" and designated in this report by the name of the outlet or trunk river. For example, Amanka and Ualik Lakes are connected to the ocean through the Igushik River, and the system is, therefore, called the Igushik.

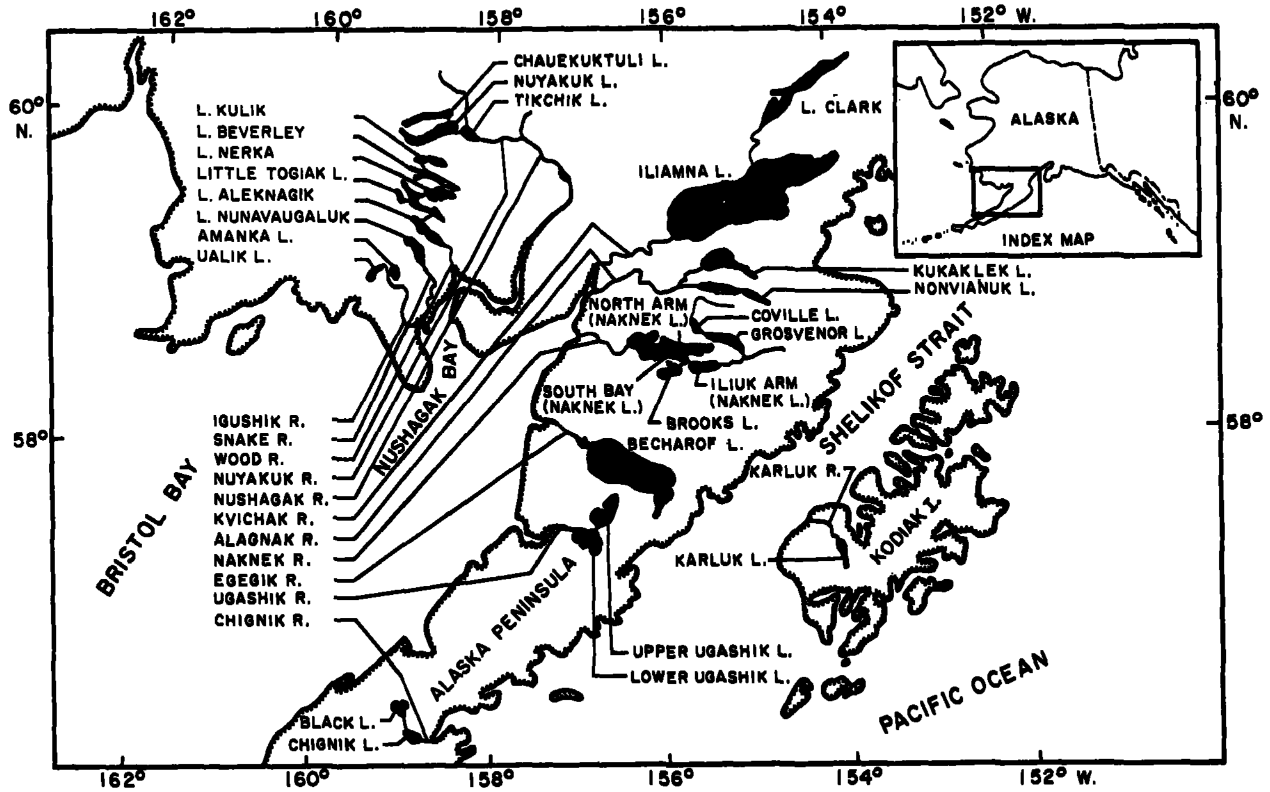

FIGURE 2.—Southwestern Alaska, showing major sockeye salmon river systems.

and assisted in studies of spawning ground capacities. John B. Owen helped compile and analyze historical and current records of catch and escapement. Herbert W. Jaenicke was responsible for counting smolts. Robert J. Ellis, William R. Heard, and Benson Drucker supervised studies of young fish. Ellis also assisted in studies of the spawning ground capacities. Richard Straty was responsible for studies of the timing of the migration of spawning fish in the Naknek system.

For the FRI—William F. Royce, Robert L. Burgner, and Ole A. Mathisen were responsible for general planning and supervision. Burgner and Ted S. Y. Koo supervised studies on the systems tributary to Nushagak Bay. Donald Rogers assisted in studies of the rearing areas in the systems tributary to Nushagak Bay. Mathisen, assisted by Orra E. Kerns, supervised studies on the Kvichak system. Royce supervised the studies of David Narver on the Chignik system.

Biologists who performed the research in each area compiled and analyzed the data on the historical and current catch and escapement in that area.

The Alaska Department of Fish and Game provided samples of scales and data for recent years on catch and escapement, length frequency of adults in escapements for many of the rivers, distribution of escapement for the Nushagak fishing district for 1960-62, and lengths, ages, and numbers of smolts for some rivers.

The broad aim of the intensified study of sockeye salmon was to determine the optimum escapement for each of the major systems in southwestern Alaska. In planning the investigation, we recognized that in the short time available little progress toward attaining our goal could be made by a detailed study of a single lake or river system. General principles applicable to each lake or system could be developed more rapidly by comparing the major sockeye salmon systems with respect to their salmon production and the factors in the spawning grounds or lakes that might limit this production. The bases for comparison were as follows: (1) type, quality, amount, and capacity of spawning areas; (2) type, quality, amount, and capacity of nursery areas; and (3) history and characteristics of sockeye salmon runs. Not all aspects of the three categories are discussed for all of the systems because for some systems the data are too few.

PHYSICAL DESCRIPTION OF THE LAKES

A substantial portion of this study was devoted to obtaining physical data on the lakes of sockeye salmon systems in southwestern Alaska. All of these lakes were either formed or modified by glaciation during the Pleistocene (Mertie, 1938; Keller and Reiser, 1959). Except for the Alagnak system, the lakes lie at elevations less than 100 m. above sea level (table 1). In some systems tidal influence extends to or almost to the outlet of the lowest lake.

On the basis of geological and biological aspects, the systems studied fall into two general groups—"Mainland" and "Peninsula." The Mainland Systems drain into Bristol Bay along the west and north shores and include the Igushik, Snake, Wood, Nuyakuk, and Kvichak. Several of the Peninsula Systems enter Bristol Bay from the northeast and east—the Alagnak, Naknek, Egegik, and Ugashik. Two other systems that we place in the peninsula category enter the Pacific Ocean—the Chignik on the east coast of the Alaska Peninsula and the Karluk on the northwest shore of Kodiak Island.

TABLE 1.—*Morphometry and altitudes of major sockeye salmon lakes of southwestern Alaska*

System and lake	Lake area	Depth		Volume	Development of shoreline[1]	Altitude
		Maximum	Mean			
MAINLAND SYSTEMS	*Km.*²	*M.*	*M.*	*Km.*³		*M.*
Igushik system						
Amanka Lake	35	65	23	0.80	3.94	9
Ualik Lake	39	72	28	1.10	1.78	15
Total	74					
Snake system						
Lake Nunavaugaluk	89	162	57	5.10	1.94	14
Total	89					
Wood system						
Lake Aleknagik	83	110	43	3.57	4.22	10
Lake Nerka	201	164	39	7.84	5.70	21
Lake Beverley	90	188	55	4.95	3.46	30
Lake Kulik	45	160	77	3.47	2.80	43
Little Togiak Lake	6	77	30	.18	3.50	28
Total	425			20.01		
Nuyakuk (Tikchik) system						
Tikchik Lake	58	45	15	.80	2.44	95
Nuyakuk Lake	144	283	113	16.27	2.92	95
Lake Chauekuktuli	82	268	111	8.94	2.83	98
Total	279			26.01		
MAINLAND SYSTEMS—Continued	*Km.*²	*M.*	*M.*	*Km.*³		*M.*
Kvichak system						
Iliamna Lake	2,622	301	44	115.81	2.75	15
Lake Clark	267	262	103	27.84	3.60	67
Total	2,889			142.65		
PENINSULA SYSTEMS						
Alagnak (Branch) system						
Kukaklek Lake	176				2.18	246
Nonvianuk Lake	121				1.95	192
Total	297					
Naknek system						
Coville Lake	33	53	19	.64	1.86	33
Grosvenor Lake	73	107	50	3.68	2.54	31
Naknek Lake						
North Arm	182	167	63	11.52	2.07	10
Iliuk Arm	94	173	96	9.00	1.71	10
South Bay	32	71	27	.86	1.41	10
West End	302	80	13	3.77	1.82	10
Brooks Lake	75	79	45	3.39	1.70	19
Total	790			32.86		
Egegik system						
Becharof Lake	1,132				2.26	15
Total	1,132					
Ugashik system						
Upper Ugashik Lake	208				1.72	3
Lower Ugashik Lake	177				1.70	3
Total	385					
Chignik system						
Chignik Lake	22	64	26	.60	2.40	5
Black Lake	39	6	3	.10	1.56	15
Total	61			.70		
Karluk system						
Karluk Lake	40	126	49	1.92	2.01	106
Total	40			1.92		

[1] Ratio of the length of the shoreline to the length of the circumference of a circle of area equal to that of the lake.

The geology of each general area is believed to be at least partly responsible for differences in water quality. Drainage areas of the Mainland Systems consist primarily of sedimentary rocks, which occasionally include local deposits of limestone. Minor bodies of igneous rocks and other products of volcanism also occur. In contrast, the drainage areas of the Peninsula Systems, although containing sedimentary rocks, have proportionally much more igneous material (Keller and Reiser, 1959). The Alaska Peninsula is an area of current and historical volcanism, and drainages of the Peninsula Systems (including the Karluk) contain many deposits of volcanic ash.

The differences in seasonal changes of water level and turbidity in the lakes are also partly due to differences in geology. Water levels are lowest in the winter in all the systems. Because lakes of systems tributary to Nushagak Bay and those of the Chignik and Karluk systems receive most of their water from snowmelt and rainfall, water levels are highest during spring thaw and autumn rainy periods. In contrast, lakes of the other Peninsula Systems and of the Kvichak system are low in the spring and tend to rise during the summer because of melting ice fields and glaciers. Turbidity often varies widely among the lakes within a system because of the localized source of rock flour carried by glacial meltwater. Turbidity is highest during the summer, especially in lakes that receive glacial melt.

The sockeye salmon lakes in southwestern Alaska differ considerably in the length of their ice-free periods, and presumably the growing season also differs. In general, the lakes of the Mainland Systems that are farther from the influence of the oceanic climate have shorter ice-free periods than lakes nearer the coast. For instance, the lakes of the Nuyakuk system are farthest from the coast and are the last to become ice-free in the spring. The upper lakes of the Wood system do not usually become ice-free until after June 1, whereas Lake Aleknagik, the lowest lake in the Wood system, is usually free of ice during late May. In the Kvichak system, Iliamna Lake, because of its large size and greater exposure to ocean storms, loses its ice cover earlier and forms it later than Lake Clark. Breakup generally occurs by mid-May in Iliamna Lake, which occasionally has areas free of ice during mild weather in the winter.

Lakes of the Peninsula Systems, which are more influenced by the oceanic climate and generally more exposed to wind action, may be ice-free over long periods during the winter. The ice in the Naknek system generally breaks up in early May. Iliuk Arm seldom freezes over completely, and the other Naknek lakes frequently develop areas of open water during mild winters. Lakes of the Egegik and Ugashik systems, which are farther down the peninsula, freeze later (if at all) than the Naknek lakes, and the ice (if any) breaks up earlier. In the Chignik system the shallower lake, Black Lake, is free of ice sooner in the spring than Chignik Lake. Both lakes are generally open by early May and frequently develop areas of open water in the winter. The Karluk system is strongly influenced by the oceanic climate; the ice in Karluk Lake frequently begins to break up in April. The lake occasionally remains ice-free during mild winters.

The two lakes in the Igushik system, Amanka and Ualik, have similar areas, maximum and mean depths, and volumes but have different shoreline developments. Lake Amanka has two distinct basins, which are separated by a sill, but Ualik Lake has a single basin. The Kathlene River flows from Ualik Lake into Amanka Lake and enters the latter in its outlet basin.

Lake Nunavaugaluk, the single lake in the Snake system, is relatively deep and has only one basin and a relatively low shoreline development.

The four main lakes of the Wood system (excluding Little Togiak) are similar in average depth and shoreline development (if Lake Nerka is considered to be two separate lakes joined at their west ends). The deep end of each lake is to the west among the mountains, and the shallower east end extends into lowlands. All of the lakes have altitudes of less than 50 m. (table 1).

The lakes of the Nuyakuk system contrast in size and form. Tikchik Lake is relatively shallow. Lakes Chauekuktuli and Nuyakuk are larger and extremely deep—each has a mean depth of about 112 m. and a cryptodepression that exceeds 170 m.

The two major lakes of the Kvichak system are sharply dissimilar in size and other morphometric characters. Iliamna Lake is the largest body of fresh water in Alaska. Its east end lies among the mountains and has a deeply scoured basin with an irregular shoreline, and because of the many islands and bays, it has a high shoreline development value. The western two-thirds of the lake is relatively shallow and uniform in depth and has few islands and a low shoreline development. Lake Clark, much the smaller of the two major lakes of the system, empties into Iliamna Lake through the Newhalen River. It lies in a long deeply glaciated valley and has a moderately high shoreline development, similar to the average of Iliamna Lake.

The Naknek system contains seven major interconnected lakes or basins all formed by glacial action. In general, the basins are elongate, deep, and steep sided. Within these basins, however, are representatives of most of the major physical and biological types of sockeye salmon lakes in southwestern Alaska. One exception is the lack of a basin as shallow and eutrophic as Black Lake of the Chignik system.

Three lakes of the Naknek system—Coville, Grosvenor, and Naknek—form a chain that drains through Naknek River into Bristol Bay. Coville Lake has the shallowest basin—mean depth, 19 m. It receives a great part of its water from snowmelt and runoff via 80-km.-long American Creek. Coville Lake acts as a settling basin for downstream Grosvenor Lake. Iliuk Arm of Naknek Lake receives drainage from Grosvenor Lake and from glacier fields via the Savonoski River, and from areas of volcanic ash and pumice in the Valley of Ten Thousand Smokes via the Ukak River. The heavy load of rock flour and volcanic materials from these drainages has a profound effect on the water quality and transparency of Iliuk Arm, and to a lesser extent on other areas of Naknek Lake. The South Bay basin of Naknek Lake receives water from Iliuk Arm and North Arm directly, and from Brooks Lake via 1.6-km.-long Brooks River. Brooks Lake receives snowmelt and runoff drainage from low mountains and extensive lowland wet tundra; the water is extremely clear. The North Arm basin of Naknek Lake has a restricted connection to South Bay because of a moraine that forms islands and shallow water along their common border. Drainage into North Arm is snowmelt and runoff, predominantly from areas of wet tundra. The west end of Naknek Lake leading to the outlet is less than 15 m. deep. The comparatively small and shallow northwest basin is separated from North Arm by a moraine and connected to the west end of Naknek Lake across a wide shoal.

Little is known about the morphometry of the remaining lakes in the Bristol Bay area. For lakes of the Alagnak, Egegik, and Ugashik systems we have only the information available from U.S. Geological Survey topographic maps.

The morphometry of the two major lakes of the Chignik system, Chignik and Black, is contrasting. Maximum and mean depths are only 6 and 3 m. for Black Lake, but they are 64 and 26 m. for Chignik Lake. Black Lake flows into Chignik Lake through Black River. Meltwater from an ice field on Mt. Veniaminoff enters Black River and, subsequently, Chignik Lake.

The Karluk system drains via Karluk River into Shelikof Strait on the northwest side of Kodiak Island. The system contains two small lakes and one large lake. The small lakes, Thumb and O'Malley, drain into separate basins of the large lake, Karluk. Karluk Lake is about 20 km. long, has a mean depth of 49 m., and appears to be of glacial origin. Drainage is snowmelt and runoff from a watershed composed predominantly of sedimentary rock.

LIMNOLOGY OF THE LAKES

The limnological studies were designed to help explain why the various lakes and systems produce salmon at different rates. In addition to morphometry of the lakes, we measured factors that other investigators have related to the biological productivity of lakes—chemical and thermal characteristics of the water. We measured biological productivity in terms of primary productivity and the standing crop of phytoplankton. The several measures of water chemistry and biological productivity are examined in relation to production of salmon.

WATER CHEMISTRY

The euphotic zones of the major sockeye salmon nursery lakes were sampled between May 1961 and November 1962 to determine their chemical characteristics. The number of determinations varies among characteristics and lakes, but sampling was concentrated in the more important systems (table 2). Standard methods of collection and analysis were used. In general, lakes of the Peninsula Systems contained higher concentrations of dissolved minerals than those of the Mainland Systems (table 3).

Total Dissolved Solids, Alkalinity, and pH

We have ranked the lakes according to total dissolved solids, total alkalinity, and pH (table 4). As would be expected, the rankings of the lakes by the three measurements tend to be similar, i.e., the more alkaline lakes tended to have higher total dissolved solids and generally higher pH values. Lakes of the Naknek, Chignik, Nuyakuk, and Karluk systems rank highest in total dissolved solids, and those of the Igushik and Snake systems rank lowest. Usually the values for the three characteristics were similar in all of the lakes of a system. The concentrations of total dissolved solids in other deep-water lakes in the Northern Hemisphere (reported by Hutchinson, 1957) are generally higher than the values in sockeye salmon lakes of southwestern Alaska.

Several investigators have used total dissolved solids to predict lake productivity (cf. Larkin and Northcote, 1958; Rawson, 1942, 1961). A comparison of this characteristic with measures of lake productivity is made later.

TABLE 2.—*Months and depths of sampling and numbers of determinations of temperature and various chemical characteristics of sockeye salmon nursery lakes of southwestern Alaska, 1961-62*

System and lake	Month of sampling	Depth sampled	Determinations made: O_2	Temperature	Alkalinity	pH	Total dissolved solids	Mineral analysis
MAINLAND SYSTEMS		*M.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Igushik system								
Amanka Lake	Aug.	0-25	2	24	-----		2	2
Ualik Lake	Aug.	0-25	2	36	4	4	2	2
Snake system								
Lake Nunavaugaluk	Aug.	0-45	0	16	4	4	2	2
Wood system								
Lake Aleknagik	June-Oct.	0-45	34	192	52	52	10	10
Lake Nerka	June-Oct.	0-45	172	1,915	175	175	14	14
Lake Beverley	June-Oct.	0-45	21	194	26	26	8	8
Lake Kulik	June-Oct.	0-45	25	221	26	26	8	8
Little Togiak Lake	June-Oct.	0-45	34	225	30	30	7	7
Nuyakuk (Tikchik) system								
Tikchik Lake	Aug.	0-30	1	30	4	4	2	2
Nuyakuk Lake	Aug.	0-30	-------	-------	-------	-------	2	2
Lake Chauekuktuli	Aug.	0-45	1	48	4	4	2	2
Kvichak system								
Iliamna Lake	June-Oct.	0-45	74	3,164	45	45	37	37
Lake Clark	June-Oct.	0-45	---	227	8	8	4	4
PENINSULA SYSTEMS		*M.*	*No.*	*No.*	*No.*	*No.*	*No.*	*No.*
Alagnak (Branch) system								
Kukaklek Lake	July-Aug.	20	8	17	7	8	4	8
Nonvianuk Lake	July-Aug.	25	9	20	9	9	4	8
Naknek system								
Coville Lake	June-Oct.	25	163	286	149	150	10	14
Grosvenor Lake	June-Oct.	45	198	553	178	178	10	15
Naknek Lake	June-May	35	260	742	254	255	14	19
Brooks Lake	June-May	35	249	675	248	249	15	20
Ugashik system								
Lower Ugashik Lake	Aug.	25	0	18	7	7	5	14
Chignik system								
Chignik Lake	June-Oct.	30	-------	-------	61	54	15	15
Black Lake	June-Oct.	4.5	-------	-------	43	41	11	12
Karluk system								
Karluk Lake	June-Oct.	45	214	557	227	222	15	15

TABLE 3.—*Chemical analyses of water from sockeye salmon nursery lakes of southwestern Alaska, 1961-62*

System and lake	Total dissolved solids	pH	Total alkalinity	Sodium	Potassium	Magnesium	Nitrate nitrogen	Silica	Iron	Manganese	Calcium	Boron	Copper	Strontium	Aluminum	Molybdenum
MAINLAND SYSTEMS	*P.p.m.*		*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
Igushik system																
Amanka Lake	21.5	7.80	10.84	0.55	<0.20	0.75	0.075	4.3	.010	.002	5.10	.007	.0003	.06	.005	.0015
Ualik Lake	17.5	7.13	10.50	.80	.35	.70	.020	2.1	.011	.001	3.95	.011	.0004	.08	.003	.0014
Snake system																
Lake Nunavaugaluk	18.0	7.16	10.42	.55	<.30	.65	.120	2.1	.010	.001	4.90	.007	.0003	.07	.003	<.0001
Wood system																
Lake Aleknagik	30.5	7.15	12.51	.63	.35	.95	.111	2.6	.006	.001	4.95	.008	.0003	.07	.004	.0004
Lake Nerka	20.7	7.14	11.99	.45	.37	.87	.167	2.2	.011	.001	4.68	.015	.0003	.06	.005	.0013
Lake Beverley	24.0	7.21	11.90	.80	<.33	.80	.160	2.8	.008	.001	4.23	.012	.0003	.07	.005	.0004
Lake Kulik	25.3	7.11	12.46	.68	.38	.68	.173	3.0	.009	.001	4.65	.005	.0003	.08	.004	.0015
Little Togiak Lake	35.0	7.29	18.69	.75	.50	1.33	.160	3.3	.006	.001	7.23	.013	.0002	.10	.004	.0006
Nuyakuk (Tikchik) system																
Tikchik Lake	42.0	7.34	22.45	.55	<.70	2.12	.090	5.4	.010	.001	7.70	.010	.0004	.09	.005	trace
Nuyakuk Lake	36.5	7.30	22.99	.40	Trace	1.55	.110	6.4	.007	trace	8.40	.017	.0004	.10	.005	<.0001
Lake Chauekuktuli	50.0	7.29	29.46	.40	Trace	2.60	.135	6.4	.005	trace	11.00	.009	.0004	.10	.003	.0003
Kvichak system																
Iliamna Lake	26.3	7.26	13.96	.83	.60	.83	.058	4.5	.011	<.003	5.11	.022	.0004	.06	.010	.0015
Lake Clark	32.0	7.28	19.59	.80	1.28	1.03	.113	8.6	.026	.001	6.75	.030	.0006	.09	.017	.0028

TABLE 3.—*Chemical analyses of water from sockeye salmon nursery lakes of southwestern Alaska, 1961-62—Continued*

System and lake	Total dissolved solids	pH	Total alkalinity	Sodium	Potassium	Magnesium	Nitrate nitrogen	Silica	Iron	Manganese	Calcium	Boron	Copper	Strontium	Aluminum	Molybdenum
PENINSULA SYSTEMS	*P.p.m.*		*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*	*P.p.m.*
Alagnak (Branch) system																
Kukaklek Lake	23.0	7.00	8.88	4.02	1.23	1.15	.018	1.1	--	--	3.29	--	--	--	--	--
Nonvianuk Lake	32.5	7.21	10.54	3.25	.90	1.12	.017	4.1	.040	.01	5.33	.003	--	--	--	--
Naknek system																
Coville Lake	51.6	7.13	25.28	3.18	.46	1.21	<.014	9.0	.052	.01	7.79	.003	--	--	--	--
Grosvenor Lake	53.5	7.24	25.42	2.98	.47	1.89	<.014	7.7	.040	.01	6.90	.003	--	--	--	--
Naknek Lake [1]	139.5	7.35	28.54	10.40	1.16	4.16	.087	9.3	.040	.01	18.16	.008	--	--	--	--
Iliuk Arm		7.27	28.61	--	--	--	--	--	--	--	--	--	--	--	--	--
Brooks Lake	74.8	7.31	26.78	4.30	.95	2.18	.012	10.5	.041	.01	8.88	.004	--	--	--	--
Ugashik system																
Lower Ugashik Lake	22.4	7.23	14.57	7.13	.80	1.28	.019	1.4	--	--	4.81	--	--	--	--	--
Chignik system																
Chignik Lake	55.9	7.65	21.31	2.35	1.31	3.04	.026	12.9	.024	.002	7.43	.027	.0006	.07	.007	.0011
Black Lake	69.7	7.44	21.53	4.07	1.43	3.04	.014	12.6	.016	.002	10.36	.042	.0009	.12	.010	.0001
Karluk system																
Karluk Lake	42.9	7.25	25.22	3.32	.26	1.47	.036	.4	.042	.01	6.61	--	--	--	--	--

[1] Excluding Iliuk Arm. Iliuk Arm is considered separately because of the large amount of suspended glacial material.

TABLE 4.—*Ranking of sockeye salmon nursery lakes of southwestern Alaska according to total dissolved solids, total alkalinity, and pH, 1961-62*

Lake	System	Total dissolved solids	Total alkalinity	pH
Naknek [1]	Naknek	1	2	3
Brooks	Naknek	2	3	5
Black	Chignik	3	9	2
Chignik	Chignik	4	10	1
Grosvenor	Naknek	5	4	13
Coville	Naknek	6	5	20
Chauekuktuli	Nuyakuk	7	1	8
Karluk	Karluk	8	6	12
Tikchik	Nuyakuk	9	8	4
Nuyakuk	Nuyakuk	10	7	6
Little Togiak	Wood	11	12	8
Nonvianuk	Alagnak	12	20	15
Clark	Kvichak	13	11	10
Aleknagik	Wood	14	15	18
Iliamna	Kvichak	15	14	11
Kulik	Wood	16	16	22
Beverley	Wood	17	18	15
Kukaklek	Alagnak	18	23	23
Lower Ugashik	Ugashik	19	13	14
Amanka	Igushik	20	19	7
Nerka	Wood	21	17	19
Nunavaugaluk	Snake	22	22	17
Ualik	Igushik	23	21	20

[1] Excluding North Arm and Iliuk Arm.

Equivalent Proportions of Sodium, Calcium, and Magnesium

Lakes of the Mainland Systems clearly differ from those of the Peninsula Systems in the proportion (based on number of equivalents per million)[5] of each of the three principal cations—sodium, calcium, and magnesium. To deter-

[5] Equivalents per million are determined by multiplying the parts per million by the reciprocals of combining weights of the appropriate ions. The combining weight of an ion equals the atomic weight of the ion divided by its ionic charge.

TABLE 5.—*Mean equivalent proportions of the three major cations—sodium, calcium, and magnesium—in water samples from sockeye salmon lakes of southwestern Alaska, June to September 1961-62*

System and lake	Sodium	Magnesium	Calcium
MAINLAND SYSTEMS	*Percent*	*Percent*	*Percent*
Igushik system			
Amanka Lake	7	18	75
Ualik Lake	12	20	68
Snake system			
Lake Nunavaugaluk	7	17	76
Wood system			
Lake Aleknagik	8	22	70
Lake Nerka	6	22	72
Lake Beverley	11	21	68
Lake Kulik	9	18	73
Little Togiak Lake	6	22	72
Nuyakuk (Tikchik) system			
Tikchik Lake	4	30	66
Nuyakuk Lake	3	23	74
Lake Chauekuktuli	2	27	71
Kvichak system			
Iliamna Lake	10	19	71
Lake Clark	8	19	73
PENINSULA SYSTEMS			
Alagnak (Branch) system			
Kukaklek Lake	40	22	38
Nonvianuk Lake	28	18	54
Naknek system			
Coville Lake	22	16	62
Grosvenor Lake	21	25	54
Naknek Lake	27	20	53
Brooks Lake	23	22	55
Ugashik system			
Lower Ugashik Lake	47	16	37
Chignik system			
Chignik Lake	14	35	51
Black Lake	19	26	55
Karluk system			
Karluk Lake	24	20	56

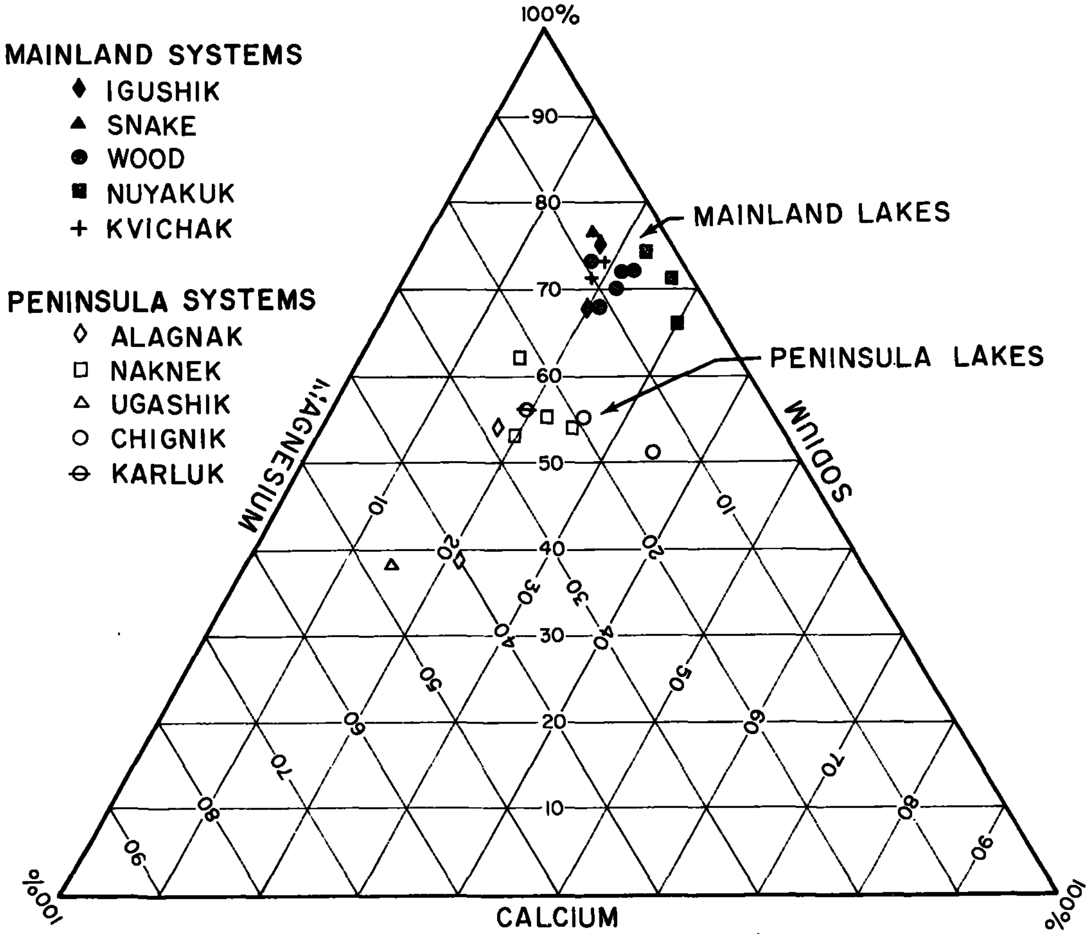

FIGURE 3.—Relative chemical proportions of the three major cations—sodium, calcium, and magnesium—in water samples from sockeye salmon lakes of southwestern Alaska. Each corner of a triangle is assigned a value of 100 percent for one of the cations. If a lake had equal equivalents of each cation, the value for that lake would be plotted in the center of the triangle. As the proportion of a cation increases toward 100 percent for that lake, the point is plotted closer and closer to the corresponding tip of the triangle.

mine these proportions, the concentrations of the three cations in equivalents per million were summed. Then the proportion of the total equivalents contributed by each cation was calculated (table 5). The data are presented graphically in figure 3.

The graphic analysis of the proportionate contribution of the three cations (fig. 3) reveals a similarity among the lakes of a system. Lakes of several systems—Wood, Nuyakuk, Naknek, and Chignik—show this grouping, which suggests that the sources of these elements (terrestrial and marine) influence all lakes within a system similarly. Figure 3 also shows that groups of lakes for systems on the mainland and on the peninsula do not overlap. Lakes of the Mainland Systems have proportionally more equivalents of calcium and less sodium than lakes of the Peninsula Systems. Our last comment on this analysis concerns lakes of the Nuyakuk system. In these waters the absolute concentrations of sodium were comparatively low (table 3), and the proportions of equivalents of sodium in relation to magnesium and calcium are also low (table 5).

Goldman (1960) found low concentrations of magnesium to be limiting to phytoplankton production in Brooks Lake during the summer of 1957. He concluded that magnesium at a low level, in comparison with other cations, was less available to the plankton because of the presence of relatively high quantities of sodium.

Other Nutrients and Trace Elements

We measured all of the dissolved chemicals our facilities permitted because more are either known or suspected to be important in the production of phytoplankton. In addition to those measurements previously discussed, we determined the concentrations of nitrogen, phosphorus, molybdenum, silica, iron, aluminum, boron, and copper.

Because nitrogen is essential for photosynthesis, it is commonly considered as a factor that may limit the production of phytoplankton. Although the ultimate source of nitrogen is the atmosphere, the combined nitrogen in lake water is derived primarily from inflowing waters (Hutchinson, 1957). Goldman (1960) found a nitrate-nitrogen deficiency in Brooks Lake in July and August 1957. In the lakes we studied concentrations of nitrate nitrogen were highest in the Mainland Systems and lowest in the Peninsula Systems (table 3). The lower values in the Peninsula Systems may be due in part to greater use of nitrate nitrogen in the higher production of phytoplankton.[6]

Some investigators have considered phosphorus as a possible limiting factor in the production of phytoplankton in sockeye salmon lakes (Krokhin, 1957; Nelson and Edmondson, 1955; Nelson, 1958; Goldman, 1960). Carcasses of adult salmon are considered an important source of replenishment of phosphorus to sockeye salmon lakes (Krokhin, 1957; Nelson and Edmondson, 1955). The limit of detectability of phosphate in our analysis of water samples was about 0.01 to 0.02 p.p.m. In general, concentrations of phosphorus were below these limits. Since a large part of the total phosphorus is bound in plankton, and phytoplankters are known to store more phosphorus than they need, the rate of phosphorus turnover largely controls the level in solution in water and, hence, determines its availability. Additional measurements and nutritional experiments are needed to establish whether availability of phosphorus is a factor that seriously limits production of phytoplankton in the lakes under study.

From limited nutritional experiments in 1962, Goldman (1964) concluded that low concentrations of molybdenum were limiting the phytoplankton growth in many lakes, including some sockeye salmon lakes of Bristol Bay. We measured molybdenum by colorimetric and spectrographic methods. Concentrations were low in all lakes. Comparison of spectrographic analyses of filtered water and phytoplankton from lakes of the Wood, Kvichak, and Chignik systems in 1964 indicates that molybdenum was generally detectable in water only. This finding indicates that phytoplankters were not concentrating the element. Experiments are needed to clarify the role of molybdenum in the production of phytoplankton.

Silica is necessary for the growth of diatoms and, "the main mechanism of loss of silica from lake waters is its utilization by diatoms. . . ." (Hutchinson, 1957). The peninsula lakes, except for Kukaklek and Lower Ugashik, had the highest concentrations of silica. Lakes of the Wood system had moderate levels; Karluk Lake, although highly productive, had considerably lower concentrations than the other lakes. It is likely that large amounts of silica are bound in the phytoplankton, especially in Karluk Lake, where Hilliard (1959) found that diatoms were the dominant phytoplankters throughout the year.

Some differences were found also between systems in concentrations of the other elements detected regularly in spectrographic analyses of water samples. Lakes in the Chignik system had the highest concentrations of iron, aluminum, boron, and copper; the Kvichak system followed. The concentrations of these elements were lower but fairly uniform in the lakes of the several systems tributary to Nushagak Bay. High concentrations of copper can inhibit growth of phytoplankton, but the concentrations found in this study were low.

Dissolved Oxygen

Concentrations of dissolved oxygen were near saturation whenever lakes were sampled, regardless of depth or season of year; winter samples through the ice were taken only in Naknek and Brooks Lakes.

THERMAL CHARACTERISTICS

Variation in both photosynthetic rates and water temperature during the summer is largely due to variation in solar radiation. Photosynthesis is at the base of primary productivity, and temperature greatly influences the rate of

[6] The low rates of productivity in the Ugashik and Alagnak systems are based on only one and two observations, respectively.

growth of fish; therefore, we measured solar radiation and water temperature in our limnology studies. Many data were collected, but only general comparisons were made among the systems.

Thermal stratification and development of thermoclines are most pronounced in lakes protected from the mixing action of strong and persistent winds. During our study, thermoclines usually were well developed in the upper lakes of the Wood system, which are generally protected from strong winds; they were less well defined in the lower, more exposed lakes. The larger, broadly exposed lakes, such as Iliamna and those of the Naknek system, were generally without thermoclines. Thermoclines were common in the smaller lakes, such as Chignik and Karluk, but were easily destroyed by the strong persistent winds which result from the lakes' exposure to the ocean climate.

PRIMARY PRODUCTIVITY AND STANDING CROP OF PHYTOPLANKTON

The measure of primary productivity used in this study was the rate of carbon fixation by phytoplankton per 4-hour midday incubation period throughout the water column, calculated on the basis of a square meter of the surface and a cubic meter in the euphotic zone. The rate of carbon fixation was determined by the in situ light- and dark-bottle C^{14} technique (method I of Steemann Nielsen, 1952). The measure of the standing crop of phytoplankton was the concentration of chlorophyll *a*. In general, rates of carbon fixation were lower in 1961 than in 1962, but the values for 1962 rather than the averages for 1961-62 are used here to compare lakes because productivity measurements were available for more lakes in 1962. These data along with concurrent measures of the transparency of the water (Secchi disk extinction values) are given in table 6.

The results of our measures of basic productivity are discussed by system.

Mainland Systems

Among lakes of the Mainland Systems, those of the Nuyakuk rank highest in concentrations of total dissolved solids and alkalinity; yet in the single series of observations in two lakes of the system (Tikchik and Chauekuktuli), phytoplankton production and standing crop were low. The average Secchi disk reading of more than 15 m. in Lake Chauekuktuli was the highest in any of the systems—a further indicator of low phytoplankton density; and the rate of carbon fixation per cubic meter had the lowest average for any of the lakes. Deficiencies of trace elements may limit productivity.

The single series of observations of photosynthetic rates in Ualik Lake of the Igushik system and Lake Nunavaugaluk of the Snake system indicated that they were intermediate in the ranking among all systems tested and were similar to those of the Wood system. The standing crops of phytoplankton, however, were lower.

The lakes of the Wood system had carbon fixation rates, chlorophyll *a* concentrations, and Secchi disk readings intermediate in the range of values for all systems. The photosynthetic rate and chlorophyll *a* concentration in Little Togiak Lake were slightly higher than in the other lakes. The differences among lakes in the Wood system were rather small.

Rates of carbon fixation were only slightly lower in lakes of the Kvichak system than in lakes of the Wood system. The photosynthetic rate per cubic meter in the euphotic zone and the chlorophyll *a* concentrations were as high in Lake Clark as in Iliamna Lake, but the total carbon fixed in the water column was less in Lake Clark because of the restricted depth of the euphotic zone (caused by rock flour). The Secchi disk extinction value was only 3.8 m. in Lake Clark, in contrast to 9.8 m. in Iliamna Lake and 8.7 to 12.6 m. in lakes of the Wood system.

Peninsula Systems

Among lakes of the Peninsula Systems, those of the Alagnak system ranked near the bottom in basic productivity and also had low standing crops of phytoplankton.

Lakes within the Naknek system had a wide range in productivity. Shallow Coville Lake is very productive and ranks next to lakes of the Chignik and Karluk systems in primary productivity and standing crop of phytoplankton, whereas deep and clear Brooks Lake is among the least productive systems. The Secchi disk readings in each lake were correspondingly low and high.

In the Ugashik system the primary productivity and standing crop of phytoplankton in Lower Ugashik Lake (the only lake examined) were about as low as in the Alagnak system.

Lakes of the Chignik system had by far the

TABLE 6.—*Primary productivity, chlorophyll a concentration, and water transparency for sockeye salmon nursery lakes of southwestern Alaska, 1962*

System and lake	Primary productivity: Determinations	Primary productivity: Mean carbon fixation per 4-hour period per square meter lake surface area	Primary productivity: Mean carbon fixation per 4-hour period per cubic meter in euphotic zone	Chlorophyll a: Determinations	Chlorophyll a: Mean concentrations	Water transparency: Samples	Water transparency: Mean Secchi disk reading
MAINLAND SYSTEMS	*Number*	*Mg.*	*Mg.*	*Number*	*Mg./l.*	*Number*	*M.*
Igushik system							
Amanka Lake	----	----	----	1	0.7	2	8.5
Ualik Lake	9	73	2.5	2	.8	3	9.7
Snake system							
Lake Nunavaugaluk	10	66	1.4	1	.6	1	13.0
Wood system							
Lake Aleknagik	240	65	2.0	8	1.3	25	8.7
Lake Nerka	659	58	1.7	22	.9	63	12.6
Lake Beverley	118	71	1.7	8	1.0	11	12.0
Lake Kulik	108	66	1.6	7	.8	11	11.5
Little Togiak Lake	133	73	1.9	6	1.4	14	10.4
Nuyakuk (Tikchik) system							
Tikchik Lake	10	52	1.6	3	.6	3	10.7
Nuyakuk Lake	----	----	----	2	.2	2	10.0
Lake Chauekuktuli	10	54	1.0	3	.5	3	15.3
Kvichak system							
Iliamna Lake	455	54	1.5	165	.8	24	9.8
Lake Clark	41	13	1.6	4	1.1	4	3.8
PENINSULA SYSTEMS							
Alagnak (Branch) system							
Kukaklek Lake	18	22	1.1	4	.6	3	10.2
Nonvianuk Lake	20	24	1.2	4	.5	4	13.2
Naknek system							
Coville Lake	411	99	5.9	80	1.0	72	5.4
Grosvenor Lake	553	61	2.9	85	.7	84	8.4
Naknek Lake [1]	810	59	3.4	86	.9	135	4.4
Iliuk Arm	----	----	----	----	----	----	.9
Brooks Lake	832	47	1.7	73	.5	154	10.8
Ugashik system							
Lower Ugashik Lake	20	41	1.2	4	.8	3	8.5
Chignik system							
Chignik Lake	311	242	13.5	41	15.3	41	1.9
Black Lake	137	121	33.4	26	5.4	28	1.6
Karluk system							
Karluk Lake	606	131	5.9	73	2.1	105	8.6

[1] Excluding Iliuk Arm. Iliuk Arm is considered separately because of the large amount of suspended glacial material.

highest photosynthetic activity and the greatest standing crop of phytoplankton of all lakes studied. Chignik Lake had a high average value for carbon fixed in the water column, but the rate per cubic meter in the euphotic zone was much higher in shallow Black Lake where a high rate of carbon fixation extended to the bottom. Although the low transparency in these two lakes was primarily due to heavy phytoplankton blooms, in Chignik Lake it was partially due to suspended rock flour.

In Karluk Lake, the rate of carbon fixation per cubic meter in the euphotic zone was high but considerably below the rate in the Chignik system. Because of the greater depth of the euphotic zone at Karluk Lake, however, the rate of carbon fixation per square meter of surface was greater than in Black Lake. The Secchi disk readings were 8.6 and 1.6 m., respectively, for Karluk and Black Lakes. The standing crop of phytoplankton in the Karluk system was second only to that of the Chignik system.

PRODUCTIVITY MEASUREMENTS AND SALMON PRODUCTION

Studies of the size of escapements and the growth of progeny indicate that in some systems at least (Wood, Kvichak, and Chignik), the growth of young salmon is slower when population densities are high (see later sections of this paper). This slow growth suggests that the abundance of food in the nursery lake limits production. A primary aim of the limnological studies was to determine if those lakes that usually support high population densities of salmon are basically the more productive. In other words, do they have higher concentrations of dissolved plant nutrients, higher standing crops of phytoplankton, and higher rates of photosynthetic activity?

The only measure of salmon production available for all the systems is the average escapement for recent years. To use this measure we must assume that the average catch-to-escapement ratio is about the same for all systems. Although this ratio can vary somewhat, the escapement levels provide a useful index of salmon production.

The systems are ranked in table 7 according to: (1) the average sockeye salmon escapement per square kilometer of lake surface for 1955-62, (2) primary productivity as indicated by the rate of carbon fixation by photosynthesis per square meter of lake surface and per cubic meter in the euphotic zone, (3) the standing crop of phytoplankton as indicated by the concentration of chlorophyll *a*, and (4) the concentration of total dissolved solids.

The four systems with the higher rates of primary productivity (considering both rate per square meter and rate per cubic meter) produced more adult salmon per square kilometer of lake (Karluk, Chignik, Igushik, and Wood). Among the other systems the correlation between rates of primary productivity and salmon production is not marked. The number of observations was too small in several of the systems to give reliable averages for primary productivity and chlorophyll *a* values; hence, the true rankings of the lake systems may diverge from those given here.

The primary productivity and escapement per unit lake area for the Naknek system are unusual. Although this system does not rank high (no. 6) in rate of carbon fixation in the water column under a square meter of lake area, it does rank high (no. 3) in rate of carbon fixation per cubic meter in the euphotic zone. Furthermore, the escapement per unit lake area is a misleading statistic for this system because two basins, North Arm and Brooks Lake, make up about 32 percent of the area of the system but usually receive only about 5 percent of the escapement. These two basins also have the lowest

TABLE 7.—*Ranking of sockeye salmon nursery lakes of southwestern Alaska according to average escapement density (1955-62), primary productivity, standing crop of phytoplankton, and total dissolved solids (1961-62)*

System	Escapement per square kilometer		Primary productivity (rate of carbon fixation): Per square meter lake surface area	Primary productivity (rate of carbon fixation): Per cubic meter in euphotic zone	Standing crop of phytoplankton (chlorophyll *a* per liter)	Total dissolved solids in p.p.m.
	Rank	*Number*	*Rank*	*Rank*	*Rank*	*Rank*
Karluk	1	8,350	2	2	2	3
Chignik	2	8,070	1	1	1	2
Igushik	3	4,360	[1] 3	[1] 4	[1] 7	[1] 10
Wood	4	2,340	4	5	3	6
Alagnak	5	1,441	10	10	9	5
Ugashik	6	1,338	9	9	6	8
Kvichak	7	1,330	7	7	4	7
Naknek	8	1,122	6	3	5	1
Snake	9	290	[1] 5	[1] 8	[1] 8	[1] 9
Nuyakuk	10	280	[1] 8	[1] 6	[1] 10	[1] 4

[1] Only a few determinations were made; see tables 2 and 6.

rates of primary productivity in the system. If North Arm and Brooks Lake were not considered, the Naknek system would rank about no. 5 in terms of escapement and no. 4 or 5 in terms of primary productivity.

Measurements of the standing crops of phytoplankton (chlorophyll *a* concentrations) and concentrations of total dissolved solids are not clearly related to rate of production of salmon. We cannot expect the standing crop of phytoplankton to be as sensitive a comparative measure of productivity as rates of carbon fixation because of the problems of unknown rates of turnover or utilization of phytoplankton by the zooplankton. Similarly, our measures of total dissolved solids do not give a good estimate of the potential of a system to produce salmon because the phytoplankters need a proper balance of nutrients.

CAPACITY OF SPAWNING GROUNDS

Our purpose in studying the capacity of the spawning grounds was to determine whether the space available is sufficient to produce enough salmon fry to use the nursery areas fully. In considering the amount of spawning ground as a limiting factor, we first present information on the size of past escapements and their characteristics. Next we will estimate potential spawning populations by using estimates of the space available for spawning, estimates of the space requirements of a spawning female, and data on past spawning populations. Finally, we consider the question—is the capacity of the spawning grounds to produce young sockeye salmon less than or greater than the capacity of the lakes to rear them?

MEASURES OF ESCAPEMENT

Statistics on the escapements of sockeye salmon to the major river systems of southwestern Alaska are incomplete before 1955. Between 1900 and 1933, escapement counts were obtained at weirs in a few rivers. Since the late 1930's, rough estimates of escapements have been made by ground and aerial surveys. Weirs were reinstalled in the Chignik and Ugashik Rivers in 1949, in the Naknek River in 1950, and in the Egegik River in 1952. Intensive ground and aerial surveys of spawning grounds in the Wood system were started in 1946. On the Wood River in 1953, FRI first used observation towers to obtain sample counts for estimating escapements of migrating adult salmon. This technique has supplanted weirs in most areas and was extended to the Kvichak River in 1955; the Egegik in 1956; the Naknek, Ugashik, and Alagnak in 1957; the Igushik in 1958; the Nuyakuk in 1959; and the Snake in 1960 (fig. 2). Since 1921, weirs have been used in Karluk River except in 1958 and 1959 when counting towers were used. A weir is still used in the Chignik River.

Size of Escapements

Estimates of the size of escapements to the several river systems in 1955-62 (table 8) provide an index of the relative production of each system. Escapements may vary widely within a system and may be cyclic in some. For instance, in the Kvichak system (which is the only system with clearly defined cycles of abundance of sockeye salmon) the escapement in 1960 was almost 60 times that in 1955. In each of the next three largest systems—Wood, Naknek, and Egegik—the greatest escapements were only six to eight times the smallest. The escapements to Chignik and Karluk Rivers have not varied as much—in the Karluk system the largest was about four times the smallest, and in the Chignik system it was only twice the smallest.

Distribution of Spawners within Systems

Sockeye salmon use four major types of spawning grounds: streams tributary to lakes, rivers between lakes, outlet rivers (trunk streams), and lake beaches. The relative importance of each type varies among systems and from year to year within systems.

TABLE 8.—*Estimates of sockeye salmon escapements to major river systems of southwestern Alaska, 1955-62*

[Thousands of fish]

Year	Igushik	Snake	Wood	Nuyakuk	Kvichak	Alagnak	Naknek	Egegik	Ugashik	Chignik	Karluk
1955	[1] 500	[1] 30	1,383	[1] 16	251	[1] 172	273	269	77	447	386
1956	[1] 400	[1] 4	773	[1] 30	9,443	[1] 784	1,773	1,104	425	748	138
1957	[1] 130	[1] 3	289	[1] 67	2,843	127	635	391	215	509	221
1958	108	[1] 9	960	[1] 196	535	95	278	246	279	325	274
1959	644	[1] 140	2,209	49	680	825	2,232	1,072	219	411	444
1960	495	17	1,016	146	14,630	1,241	828	1,799	2,304	608	349
1961	294	5	461	80	3,706	90	351	702	349	407	297
1962	16	2	874	38	2,581	91	722	1,027	255	483	561
Average	323	26	996	78	4,334	428	886	826	515	492	334

[1] Aerial survey estimates by FRI.

Variation may be considerable in the age composition of sockeye salmon that use the different types of spawning grounds within a given system. The most striking difference is in the number of years the salmon have spent in the ocean. Although most adult sockeye salmon are 2- or 3-ocean fish (i.e., remain in the ocean 2 or 3 years before they return to spawn), the proportion varies among groups of fish occupying specific spawning areas from year to year. Three-ocean fish are larger than 2-ocean and are more susceptible to capture by the gill nets in Bristol Bay.

Natural fluctuations in the relative abundance of various components of a stock, combined with selective effects of the fishery, often lead to poor distribution of the escapement among the spawning grounds. The total escapement may be adequate for a system, but if the distribution of the escapement does not conform to the relative spawning capacities of various grounds, some grounds will be underutilized and others will be overutilized. Various races and age groups of sockeye salmon bound for the many spawning grounds of a system may pass through the fishery at different times. Therefore, the fishery that operates at different intensities through each season could harvest components at different rates—for example, through a combination of net selectivity and closed fishing times. This section examines the evidence bearing on these problems in the sockeye salmon systems of southwestern Alaska.

Igushik system.—The type of spawning grounds used varies greatly from lake to lake

TABLE 9.—*Distribution of spawning sockeye salmon among three types of spawning areas in lakes of the Wood system, 1955-62*

Lake and year	Fish spawning in— Tributary creeks	Lake beaches	Rivers between lakes
	Percent	*Percent*	*Percent*
Aleknagik			
1955	55	0	45
1956	54	2	44
1957	38	2	60
1958	51	5	44
1959	29	5	66
1960	37	5	58
1961	10	2	88
1962	47	6	47
Average	40	3	57
Nerka			
1955	32	55	13
1956	11	43	46
1957	37	49	14
1958	17	74	9
1959	29	5	66
1960	37	49	14
1961	11	43	46
1962	32	55	13
Average	26	47	27
Beverley			
1955	0	95	5
1956	13	85	2
1957	29	70	1
1958	1	95	4
1959	1	95	4
1960	0	94	6
1961	14	76	8
1962	6	85	9
Average	8	87	5
Kulik			
1955	0	53	47
1956	0	49	51
1957	0	16	84
1958	0	90	10
1959	0	61	39
1960	0	63	37
1961	0	51	49
1962	0	88	12
Average	0	59	41

in the Igushik system. Most sockeye salmon spawn on the beaches at Lake Ualik and in the streams at Lake Amanka.

Wood system.—The distribution of adult sockeye salmon among the three types of spawning grounds in the Wood system differs markedly from lake to lake, but each lake has a characteristic distribution (table 9). For example, tributary creeks and the rivers between lakes receive the greatest part of the spawners in Lake Aleknagik (over 90 percent from 1955 to 1962), whereas in Lake Beverley almost 90 percent of the spawners use the lake beaches. The spawners in Lake Nerka are usually distributed about equally among the three types of spawning grounds. The year-to-year changes in distribution of the spawners in the system as a whole are largely the result of changes in the relative escapement to each lake.

Most sockeye salmon entering the Nushagak fishing district are bound for lakes of the Wood system. Tagging results in 1961 indicated that spawners bound for the different lakes of the Wood system may have passed through the fishery at different times. Overlap was considerable, however, and the same pattern of entry may not occur every year. Time of passage to the two major river spawning grounds, Agulowak and Agulukpak Rivers, was average for the system.

Although the percentages of 2-ocean and 3-ocean sockeye salmon in the run vary annually with year class strength and other undetermined factors, consistent differences in age composition tend to prevail among spawning groups. For instance, in 1960-62, samples of spawning sockeye salmon from Agulowak and Agulukpak Rivers consistently had a higher proportion of 3-ocean fish than samples from other areas of the system (table 10).

TABLE 10.—*Proportions of 3-ocean sockeye salmon in escapements from areas of the Wood system, 1960-62*

Year and sex	Agulowak River	Agulukpak River	Average for remaining areas
	Percent	*Percent*	*Percent*
1960			
Male	80	49	16
Female	84	66	18
1961			
Male	99	92	60
Female	100	96	69
1962			
Male	42	40	8
Female	76	64	7
Average	80	68	30

Nuyakuk system.—The type of spawning grounds used also varies greatly among the lakes of the Nuyakuk system. Sockeye salmon in Lake Chauekuktuli spawn almost exclusively on beaches; in Tikchik Lake they spawn only in rivers and creeks. The escapement to the Nuyakuk system has a consistently higher proportion of 3-ocean fish than that to the Wood system.[7]

Kvichak system.—Sockeye salmon of the Kvichak system spawn in streams tributary to lakes, rivers between lakes, beaches of Iliamna Lake, and spring-fed ponds, which are usually located at the heads of small tributaries. They

[7] Burgner, R. L. 1965. Age composition of Nushagak sockeye runs by river system. Univ. Wash., Fish. Res. Inst., Circ. 234, 14 pp.

spawn also in the tributaries to, and on beaches of, small lakes. Some of the fry from these small lakes migrate to nursery areas in Iliamna Lake or Lake Clark.

The distribution of the escapements to large streams, lake beaches, and all other spawning grounds of the Kvichak system in 1959-62 is shown in table 11. When the escapement was extremely large in 1960, the beaches of Iliamna Lake received a larger proportion of the total escapement and the large streams received a smaller proportion than in years when the escapements were smaller. The importance of the other spawning grounds remained nearly constant from 1959 to 1962.

TABLE 11.—*Distribution of sockeye salmon escapements in spawning grounds of the Kvichak system, 1959-62*

Year	Fish in escapement	Fish spawning in— Large streams	Beaches of Iliamna Lake	All others
	Millions	*Percent*	*Percent*	*Percent*
1959	0.7	57.8	25.4	16.8
1960	14.6	26.9	50.0	23.1
1961	3.7	55.0	33.8	11.2
1962	2.6	64.7	19.7	15.6

Escapements to large streams have varied by a factor of 10, whereas those to the system varied by 20 and those to the lake beaches by about 50. Thus, the cyclic nature of the production of sockeye salmon in the Kvichak system could be reinforced or perhaps caused by the cyclic nature of the production from the beaches alone.

We found marked contrasts in age characteristics — both ocean and fresh-water — among spawning groups in the Kvichak system in 1962. Stream spawning groups (except those of the Copper River) had a significantly lower proportion of 3-ocean fish than beach spawning groups.[8] Differences also existed in the average fresh-water age of various spawning groups in the Kvichak system in 1956-58 (Koo and Smith, 1960).

Smith (1964) found little or no difference in the time the various spawning groups entered the Kvichak system in 1957, 1958, and 1959. Adult sockeye salmon were tagged as they entered Iliamna Lake, and the tagged fish were recovered on the spawning grounds. The migration into the lake lasted about 4 weeks. Fish tagged in any one of these weeks were recovered in about the same proportion in large and small streams, on lake beaches, and in spring-fed ponds, regardless of whether spawning in these places occurred early or late in the season.

Naknek system. — The principal spawning grounds of the Naknek system are: (1) Brooks and Grosvenor Rivers (rivers between lakes); (2) American and Hardscrabble Creeks (tributary streams); (3) Naknek River (outlet or trunk river); and (4) beaches of Grosvenor Lake. Some sockeye salmon also spawn on beaches in Iliuk Arm and South Bay of Naknek Lake. The proportions of sockeye salmon that spawn on the several major spawning grounds change markedly from year to year. In some years a single major ground may receive more than 60 percent of the escapement to the system and in other years the same ground may receive less than 10 percent.

Each of the major groups of spawning sockeye salmon in the Naknek system in 1962 was characterized by different proportions of combinations of fresh-water and ocean ages (Straty, 1966). Most major spawning grounds contained a smaller proportion of adults that migrated seaward as age II smolts than did the total escapement to the Naknek River. This anomaly suggests the existence of spawning groups as yet undetected.

Tagging in the Naknek River in 1961 and 1962 demonstrated that all major spawning areas within the system received fish from all parts of the run about in proportion to the sizes of the spawning groups (Straty, 1966). Some slight indication appeared, however, that Brooks Lake and Brooks River received more of the earlier fish than the other areas.

Chignik system. — Sockeye salmon in runs to the Chignik system are predominantly 3-ocean fish. The greatest contrast in age composition in this system is in the time the young live in fresh water: most of the smolts migrate at age I from Black Lake and at age II from Chignik Lake.

Tagging and studies of scales have established that adults returning to Chignik and Black Lakes pass through the fishery at different times (Narver, 1963). The early run (in June) has primarily sockeye salmon bound for Black Lake,

[8] Kim, Wan Soo, and Robert L. Demory. 1963. Kvichak salmon studies, 1962 spawning ground studies. Univ. Wash., Fish. Res. Inst., Circ. 195, 26 pp.

and the late run (in July and August) has primarily fish bound for Chignik Lake.

Karluk system. — The distribution of sockeye salmon on the spawning grounds in the Karluk system has been well documented from data collected on weekly surveys carried out on foot each summer in 1947-62. Salmon that enter the system during May, June, and July tend to occupy all tributaries; those entering during August and September tend to occupy only the large tributaries at the south end of the lake, the lake beaches, and the outlet river.[9]

Sockeye salmon in Karluk Lake have a marked temporal as well as spatial segregation by age group (Rounsefell, 1958; also see footnote 9). In general, salmon that spend the longest time in the ocean (3 years or more) return early in the spawning season and those that spend the least time at sea return late. Since late spawners tend to occupy the large terminal streams, lake beaches, and the upper end of Karluk River, these areas usually receive a disproportionately large number of smaller 2-ocean fish.

The Chignik and Karluk systems contrast sharply with the systems tributary to Bristol Bay in having temporal segregation of spawning units in the trunk river. The absence of marked segregation in Bristol Bay systems may be the result of the short duration of these runs. In general, the Bristol Bay runs last about 4 weeks, and more than 50 percent of each run enters the fishing areas and trunk streams during a few days in early July. In the Chignik and Karluk systems the escapements enter the trunk stream over a 2- to 4-month period.

POTENTIAL SPAWNING POPULATION

The physical capacity of the rivers or beaches to contain adult sockeye salmon imposes a limit on the number of fish that could spawn in each system. It was obvious, however, that a large portion of most of the rivers and beaches was in fact unsuitable for spawning and that the amount of space required for a pair of salmon to spawn varied among different types of spawning grounds. Therefore, to estimate the capacity of each river or beach in terms of numbers of females we determined the area of potential spawning ground and divided this figure by the estimated area required per female.

[9] Owen, John B., Charles Y. Conkle, and Robert F. Raleigh. 1962. Factors possibly affecting production of sockeye salmon in Karluk River, Alaska. Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska. [Manuscript. 57 pp.]

Estimates of Area of Potential Spawning Grounds

The amount of potential spawning ground for streams and for lake beaches was measured to determine if the area of suitable spawning grounds might limit salmon production in any of the river systems. The data obtained are first approximations because complete and accurate surveys of all spawning grounds could not be completed in 2 years. Estimates of suitable potential spawning area were made for the Wood, Kvichak, Naknek, and Karluk systems (table 12).

During the 2-year study period, catalogs of spawning grounds, which contain descriptions of the physical characteristics and estimates of the area of the potential or utilized spawning grounds and estimates of annual escapements

TABLE 12.—*Estimates of surface area of potential sockeye salmon spawning grounds in streams and lake beaches of Wood, Kvichak, Naknek, and Karluk systems*

System and lake	Streams	Lake beaches	Total
	Hectares	*Hectares*	*Hectares*
Wood system			
Lake Aleknagik	134.6	[1] 86.2	220.8
Lake Nerka	40.9	[1] 1,437.0	1,477.9
Lake Beverley	47.0	[1] 862.6	909.6
Lake Kulik	11.7	[1] 337.9	349.6
Little Togiak Lake	7.2	[1] 108.9	116.1
Total	241.4	2,832.6	3,074.0
Kvichak system			
Iliamna Lake	649.6	[2] 33.0	682.6
Gibraltar Lake	23.0	28.8	51.9
Lake Clark	167.1	49.7	216.8
Total	839.7	111.5	951.3
Naknek system			
Coville Lake	111.0	[3]	
Grosvenor Lake	29.6	[3]	
Naknek Lake [4]	188.3	[3]	
North Arm	7.5	[3]	
Brooks Lake	18.0	[3]	
Total	354.4	[3]	
Karluk system			
Karluk Lake	33.7	[5] 1.2	34.9

[1] Estimates based on gravel types only.
[2] Minimum estimate based on incomplete information.
[3] No estimate made.
[4] Excludes North Arm; North Arm is considered separately because it constitutes a rearing area for juvenile salmon discrete from the rest of Naknek Lake.
[5] Only the beach spawning areas of Thumb and O'Malley Lakes are included here.

by stream, were completed for the Kvichak system (Demory, Orrell, and Heinle, 1964) and the Wood system (Marriott, 1964). A catalog for the Naknek system is being prepared.

The amount of potential spawning grounds for streams was estimated as follows: (1) The stream was divided into sections from the mouth to the upper limit of possible spawning, i.e., to the source or to obstructions to the passage of fish, e.g., falls and beaver dams. (2) The total area of each section was determined. (3) The percentage of each section not usable for spawning was estimated on the basis of bottom composition, gradient, and water velocity. Bottom types defined as not usable included silt, bedrock, and large rock. Pools and torrential water were considered unsuitable for spawning. (4) The amount of potential spawning grounds in each section was estimated by subtracting the area unsuitable for spawning from the total area. Spring-fed ponds were treated as streams.

Wood system.—The estimates of the amount of potential spawning grounds in streams of the Wood system (table 12) apply only to streams in which spawning had been observed.

Size of the gravel and depth of the water were used in the lakes of the Wood system as criteria in estimating the area of beach suitable for spawning. The area of lake surface from the shore to 10-m. depth contours (over bottom judged by field observations to be suitable for spawning) was measured on bathymetric maps. Because other factors, such as upwelling ground water, also appear to be important in beach spawning, the estimates based only on size of the gravel and depth of the water exceed the amount of potential beach spawning grounds.

Kvichak system.—The estimates of the amount of spawning grounds in the Kvichak system are minimal. For stream spawning, estimates were made only for streams in which spawning had been seen. For beach spawning in Iliamna Lake, estimates were made only for beaches on which a small escapement of sockeye salmon had spawned (1961). Beaches in the following areas were not examined: Flat Island, Southeast Beaches, Tommy Beach, Lonesome Bay, and Finger Beach.

Observations in Iliamna Lake during the spawning of a large escapement (1960) indicated that beach spawning was much more extensive than was formerly thought, particularly around islands, where it extended to depths of 30 m.

Naknek system. — Estimates of the amount of potential sockeye salmon spawning grounds are available for all streams in the Naknek system, even those in which spawning has never been seen. The reliability of the estimates varies from stream to stream, and the estimates will be modified as more information is obtained.

Sockeye salmon spawn on beaches in Grosvenor Lake and in a lesser amount in other lakes in the Naknek system, but the extent of these spawning grounds has not been estimated.

Karluk system. — Data on the amount of spawning grounds in the Karluk system are from Owen et al. (footnote 9) and are for grounds on which sockeye salmon are known to spawn.

Estimates of Space Requirements of Spawning Females

A spawning female sockeye salmon requires a certain minimum area of gravel bed in which to deposit her eggs. Eggs are buried in about five pockets in an area of disturbed gravel known as the redd. During construction of the redd and spawning and postspawning activities, both the female and male defend a certain territory surrounding the redd.

Wood and Kvichak systems. — Estimates of the minimal space requirements for spawning females in the Wood and Kvichak systems were based on the egg-carrying capacity of the gravel independent of observed spawning density.

Three principal sources of loss of eggs were considered: (1) increased retention of the eggs by the female because of increased density of spawners, (2) dislodgment of eggs from the redds because of repeated excavations of the same gravel by subsequent females (superimposition), and (3) increased egg mortality because of crowding of eggs in the gravel. Data from the Wood and Kvichak systems indicate that as spawning density increases, superimposition of redds limits survival of the eggs. We estimated egg loss from superimposition to be less than 10 percent with a spawning density of one female per 2 $m.^2$ This density is low enough to avoid significant egg loss by increased retention or crowding of eggs in the gravel. Calculation of the capacity of streams in the Wood and Kvichak systems to support spawning sockeye salmon is based, therefore, on a density of one female per 2 $m.^2$

Naknek and Karluk systems. — General observations had indicated that the space requirements for spawning female sockeye salmon vary with differences in quality of the gravel and size and stage of the stream and that the space used by a spawning female is elastic — large when escapements are low and small when they are high. We estimated, therefore, the space requirement for a spawning female from maximum observed densities of spawners in measured sections of streams in the Naknek system. Average densities for entire streams were used in the Karluk system.

Our studies confirmed the earlier general observations that space requirements vary among different kinds of streams. For example, in the large and relatively deep rivers between lakes and the terminal rivers in the Naknek system, the space requirements are between 4 and 9 $m.^2$ per female. In the smaller streams the requirements are much less — 2 to 3 $m.^2$ In the open-water beach areas the requirements are probably similar to or perhaps larger than those in the large rivers. In the shallow torrential lateral streams in the Karluk system, space requirements were often substantially less than 2 $m.^2$ (table 13), but 2 $m.^2$ would appear typical for the system as a whole on the basis of stream survey data from many areas (Richard Gard, personal communication).

Our calculations of the potential capacity of the streams in the Naknek and Karluk systems to support spawning sockeye salmon are based on the estimate of maximum density for each type of stream.

TABLE 13.—*Estimated numbers of potential redd sites in various types of spawning grounds of the Naknek and Karluk systems*

System and type of spawning ground	Area of potential spawning ground	Area required per female	Redd sites
	Hectares	*M.* ^{2}	*Number*
Naknek system			
Terminal streams	124.9	4.1	302,000
Small lateral streams	12.3	2.6	47,000
Large lateral streams	62.7	7.6	83,000
Rivers between lakes	7.2	[1] 8.8	8,000
Outlet river	147.3	8.0	184,000
Lake beaches			[2]
Total	354.4	....	624,000
Karluk system			
Terminal streams	1.67	2	8,000
Lateral streams	6.71	2	34,000
Lake beaches	1.25	2	6,000
Outlet river	25.28	2	126,000
Total	34.91	....	174,000

[1] Does not take into consideration successive waves of spawners.

[2] An estimate of 20,000 redd sites is based on number of fish seen using the beaches of Grosvenor Lake. Other beach spawning areas exist.

TABLE 14.—*Estimated maximum populations of adult sockeye salmon in streams and lake beaches of Wood system in any year between 1946 and 1962*

Lake	Fish in—		
	Streams	Lake beaches	Total
	Number	*Number*	*Number*
Aleknagik	622,000	15,000	637,000
Nerka	929,000	392,000	1,321,000
Beverley	98,000	487,000	585,000
Kulik	94,000	144,000	238,000
Little Togiak	16,000	47,000	63,000
Total	1,759,000	1,085,000	2,844,000

Estimates of Potential Spawning Capacity by System

The potential capacity for the streams in each system to support spawning adults was based on the amount of potential spawning grounds and the space required per spawning female. The potential spawning capacities of the beach areas were estimated from escapement surveys and various other data.

Wood system. — The potential spawning area of rivers and streams (including connected ponds) of the Wood system was estimated to be 241.4 hectares (table 12), and the area required per spawning female was estimated to be 2 $m.^2$ By dividing the spawning area by the area required per female and assuming a 1:1 sex ratio, we calculate that the maximum spawning population in streams in the Wood system is 2,414,000 sockeye salmon.

The maximum numbers of sockeye salmon observed on each spawning ground in 1946-62 were summed by lake for stream spawning and for beach spawning. Since only about 43 percent of the fish that enter the system (estimated by counts from towers) are seen during spawning surveys, the summed maxima have been increased to produce the estimate of the maximum populations for streams and for lake beaches (table 14).

Maximum populations and the estimated potential capacity of the spawning grounds in streams are thought to be in reasonable agreement, because use of the spawning grounds is highly variable and some of the larger streams have very small populations. Because the maximum number of spawners estimated on beaches is less than the maximum estimated in streams (table 14), the spawning ground potential of the beaches is probably not in excess of that of the streams.

The largest escapement of sockeye salmon to the Wood system since counting from towers began in 1953 was 2,209,000 in 1959 (table 8). Although some spawning grounds were overcrowded in 1959, as evidenced by a large mortality of eggs, most were greatly underutilized. Escapements in 1955-62 varied between 289,000 and 2,209,000 sockeye salmon. Thus, the potential capacity of the spawning grounds in the Wood system greatly exceeds the normal escapements.

Kvichak system. — The area of potential spawning grounds in rivers, streams, and ponds in the Kvichak system was estimated to be 839.7 hectares (table 12), and the space required per spawning female was estimated to be 2 m.^{2} A capacity of 4,199,500 spawning females is calculated from these data; on the basis of 1:1 sex ratio, the potential capacity of the nonlake spawning grounds in the Kvichak system is about 8,399,000 spawners.

We do not have enough data to make a direct estimate of the area of the potential beach spawning grounds in the Kvichak system, but we can estimate it indirectly. The area used by 3,706,000 spawners in 1961 on 16 of 21 recognized spawning beaches was 111.5 hectares (table 12). The area used by the 14,630,000 spawners of 1960 would have been 435 hectares if we assume a constant relation between numbers of spawners and area used (the ratio of spawners in 1961 and 1960 was 1:3.9). Because only 75 percent of the beaches known to be used have been surveyed, the estimate of 435 hectares is further expanded by 4/3, to give 579.9 hectares of beach actually used in 1960. Because only beach areas used for spawning have been considered and the average use of potential spawning grounds in the streams has been 48 percent, the amount of potential beach spawning grounds was calculated by assuming the same rate. This computation gives an estimate of 1,208 hectares of potential beach spawning grounds with a capacity of 12,080,000 spawners.

On the basis of the above information, we postulate a potential spawning population of about 20,500,000 sockeye salmon for the Kvichak system. This figure is greater than the maximum observed escapement through 1962. Escapements since 1955 have varied between 251,000 and 14,630,000 (table 8).[10]

Naknek system. — The amount of potential spawning ground in the Naknek system, the space required per female, and the capacity of the spawning ground were calculated for each of several types of streams. We made estimates of the total potential of the beach spawning grounds.

The total number of potential redd sites — calculated from estimates of the amount of spawning ground available and the size of redd sites—is 624,000 for the streams of the Naknek system (table 13). An estimate of 20,000 redd sites for the beach spawning grounds of Grosvenor Lake is based on past spawning ground surveys. Other beach spawning grounds exist, but their capacity is unknown.

Since estimates of the size of redd sites were based on observations of spawning density on single days, the effect of spawning in waves or surges must be considered. Three waves of fish commonly enter the Brooks River (Hartman, Merrell, and Painter, 1964), which is the major interconnecting stream that produces sockeye salmon. The number of redd sites in the interconnecting streams has been expanded, therefore, by a factor of 3 to produce a more realistic estimate of the capacity of these areas to receive spawning salmon.

If all of these factors are considered and a 1:1 sex ratio is assumed, the estimated spawning capacity of the Naknek system is about 670,000 females, or 1,340,000 fish of both sexes. Escapements in recent years varied between 273,000 and 2,232,000 salmon (table 8). Escapements exceeded 1,260,000 twice in the 14 years from 1949 to 1962.

Karluk system. — Estimates of the size of a redd site for several tributaries in the Karluk system are about 2 m.^{2}, and because estimates are not available for other areas, 2 m.^{2} is used for all. The estimated number of redd sites for streams and lake beaches is 174,000 (table 13), and (assuming a 1:1 sex ratio) the capacity is

[10] The escapement in 1965 was 24.3 million. Some of the spawning grounds had few adult fish; others were so densely occupied that superimposition of redds and retention of eggs caused a great loss of eggs. On most spawning grounds, however, density appeared to be optimal and confirmed the figure given above.

348,000 adults. This estimate is only approximate — the situation in the Karluk system is complicated by the occurrence of successive waves of spawners in most streams and incomplete information on the amount of potential spawning ground, especially on lake beaches. Escapements to Karluk neared or exceeded 1 million fish for many years during the early 1900's.

SPAWNING AREA AS THE LIMITING FACTOR IN PRODUCTION

An excessive density of spawners may cause increased retention of eggs, loss of eggs because of dislodgment from gravel during spawning, and increased mortality of eggs because of crowding of eggs in the gravel. We do not know the relation between these variables and density of spawners.

With the possible exception of the Karluk system, the tentative data on potential spawning areas indicate that the major lake systems could accommodate spawning populations considerably in excess of average present-day escapements. Full use of potential spawning grounds would, however, require a distribution of spawners strictly in proportion to the capacity of each ground. Such a distribution has never been observed.

CAPACITY OF REARING AREAS

Young sockeye salmon usually emerge from the spawning gravels in the spring to begin their stay in the rearing areas of the lakes. Here they remain 1 or 2 years (occasionally 3, as at Karluk) before they migrate seaward in May, June, and July as smolts. The abundance and growth of juvenile sockeye salmon and the age and size of smolts produced in each system were determined and were examined in relation to several physical and biological factors of the rearing areas: (1) number of spawning sockeye salmon per unit of rearing area; (2) relative numbers of other fish species in each system, both possible competitors and predators; (3) movement of presmolt sockeye salmon within and between lakes of a system; (4) basic biological productivity of the waters; and (5) innate characteristics of the various stocks of sockeye salmon.

Because long-term observations were not available for most individual systems, the carrying capacity of each system was judged by means of comparisons among the several systems of the biological and physical characteristics of the rearing areas.

RELATION BETWEEN NUMBERS OF SPAWNERS AND SIZE OF REARING AREAS

In the systems of southwestern Alaska the capacity of the rearing areas to support sockeye salmon is, in general, reflected in the number of adults returning to each system. The most extensive data on the comparative numbers of fish in the returns are found in the escapement records; the escapement is also generally a good indicator of the magnitude of the total return. Because the size of the lakes and systems considered varies widely, the escapements and other measures of productivity are frequently expressed as numbers per square kilometer of lake area. Table 15 gives the average number of adults in the escapements in 1955-62, the area of the lakes, and the numbers of spawners per square kilometer of lake for the major systems in southwestern Alaska.

The systems fall into four general levels of escapement per unit area (table 15): (1) escapements that averaged about 8,000 spawners per square kilometer (Karluk and Chignik); (2) escapements of about 2,300 to 4,400 spawners per square kilometer (Igushik and Wood); (3) escapements between 1,100 and 1,500 spawners per square kilometer (Kvichak, Alagnak, Naknek, and Ugashik); and (4) escapements less than 800 spawners per square kilometer (Egegik, Snake, and Nuyakuk).

For some systems data are available for examining variation in productivity between lakes (in terms of numbers of adults in the escapements to individual lakes) and between years within lakes.

TABLE 15.—*Average sockeye salmon escapements, area of lakes, and spawners per square kilometer of lake by system in southwestern Alaska, 1955-62*

System	Fish in escapement	Lake area	Spawners per square kilometer
	Thousands	*Km.²*	*Number*
Igushik	323	74	4,360
Snake	26	89	290
Wood	996	425	2,340
Nuyakuk (Tikchik)	78	279	280
Kvichak	4,334	2,889	1,500
Alagnak (Branch)	428	297	1,441
Naknek	886	790	1,122
Egegik	826	1,132	730
Ugashik	515	385	1,335
Chignik	492	61	8,070
Karluk	334	40	8,350

Igushik System

In the Igushik system, in 1955-62 the number of spawners per square kilometer of lake in Ualik Lake was only slightly larger than in Amanka Lake if we assign the adults spawning in the interconnecting river and its branch (Ongoke River) to Amanka Lake.

Snake System

Nunavaugaluk Lake is the only lake in the Snake system that produces significant numbers of salmon.

Wood System

The average numbers of spawners per square kilometer in each of the four main lakes of the Wood system in 1955-62 were: Aleknagik, 2,090; Nerka, 2,430; Beverley, 2,490; and Kulik, 2,040. Little Togiak Lake, tributary to Lake Nerka, had a slightly higher density of spawners than the main lakes.

Nuyakuk System

The low average number of spawners per unit lake area in the Nuyakuk system (table 15) is largely due to the low densities in Nuyakuk Lake, the largest lake in the system, where the figure was only 50 spawners per square kilometer from 1959 through 1962.

Kvichak System

The Kvichak is the only major sockeye salmon system in Bristol Bay that has a pronounced cyclic variation in number of adults in the escapement. The effects of this cycle overshadow problems of distribution of the spawners within each year. Over the years 1955-63, the number of spawners per square kilometer of lake varied from 84 — among the lowest numbers observed in Bristol Bay — to 4,890 (table 16). Peak years modify the reproductive potential in subsequent off years. This problem is discussed later.

TABLE 16.—*Numbers of sockeye salmon in escapements and spawners per square kilometer of lake, Kvichak system, 1955-63*

Year	Fish in escapement	Spawners per square kilometer
	Thousands	*Number*
1955	251	84
1956	9,443	3,156
1957	2,843	950
1958	535	179
1959	680	227
1960	14,630	4,890
1961	3,706	1,239
1962	2,581	863
1963	339	113

Naknek System

Many nursery areas of the Naknek system receive juvenile sockeye salmon from upsystem areas; that is, from other than adjacent beaches and tributary streams. Coville Lake represents about 3 percent of the rearing area of the Naknek system but has received as much as 65 percent of the escapement in a given year. This lake is at the upper end of the system, and many of the juvenile sockeye salmon that originate in its tributaries spend some growing time in downsystem lakes. North Arm basin and Brooks Lake make up about 35 percent of the area of the system but receive less than 10 percent of the escapement, and they do not receive fry produced in other areas. The distribution of escapement and subsequently the distribution of the juveniles are considered later.

Chignik System

Chignik Lake had the greatest average concentration of spawners in the Chignik system — about 14,000 per square kilometer of lake in 1956-62. The average for Black Lake during the same period was slightly more than 4,600, about the same as for the Igushik lakes.

Karluk System

Recently emerged fry behave in such a way in the Karluk system that the total escapement is assignable to Karluk Lake for consideration of rearing areas. The progeny of spawners that use the outlet (Karluk River) move upstream into the lake, and progeny of spawners from areas above O'Malley and Thumb Lakes move down into Karluk Lake early in their first summer of life.

SPECIES OF FISH IN THE LAKES

Knowledge of the abundance of species of fish associated with juvenile sockeye salmon in the lakes is essential to understand the factors that may affect the survival and growth of sockeye salmon. Differences in behavior and the distribution of the habitat of the many species required the use of several types of collecting gear: tow nets, beach seines, trap nets, gill nets, and bottom and midwater trawls.

Although as many as 25 species of fish were found in a system, the abundance of most was low. Species of salmon other than sockeye were not sufficiently abundant to compete seriously for rearing area. Juvenile sockeye salmon and one other species of fish constituted 75 to 95 percent of the catches.

Of the species that may be competitors with juvenile sockeye salmon, the threespine stickleback *(Gasterosteus aculeatus)* is most important in the Igushik, Snake, Wood, Kvichak, Nuyakuk, Chignik, and Karluk systems and part of the Naknek system. In other parts of the Naknek system the ninespine stickleback *(Pungitius pungitius)*, pond smelt *(Hypomesus olidus)*, or pygmy whitefish *(Prosopium coulteri)* seem to be of greatest significance. Species of fish in most systems that have varying degrees of importance as predators on juvenile sockeye salmon include Arctic char *(Salvelinus alpinus)*, lake trout *(S. namaycush)*, northern pike *(Esox lucius)*, juvenile coho salmon *(O. kisutch)*, and Dolly Varden *(S. malma)*.

The data on the species in the other systems of southwestern Alaska are too few to permit generalizations.

MIGRATION OF PRESMOLT SOCKEYE SALMON

To study the relation between density of parent spawners (numbers per unit lake area), growth and abundance of progeny, and capacity of the rearing areas, we had to know how long the young sockeye salmon remain in the lake that they first enter as fry. Fyke nets were fished, therefore, in some interconnecting rivers during the summer to detect possible migrations from various lakes. Changes in length frequencies of juveniles and their abundance in tow net catches supplied indirect information on their movements.

Wood System

Catches of fyke nets fished in the connecting rivers of the Wood system indicated no appreciable migration of young sockeye salmon during the summer between Little Togiak Lake and Lake Nerka in 1961 or between Lake Nerka and Lake Aleknagik in 1962.[11] Two other kinds of observations in the Wood system support the conclusion that these fish do not migrate during the summer: (1) the abundance of young-of-the-year in tow net catches after mid-August is generally proportional to the number of parent spawners for each lake (the density of spawners varies widely between lakes within years); and (2) the growth of young-of-the-year is often reduced in lakes that had high densities of spawners the previous fall. We, therefore, assumed that in the main lakes of the Wood system, juvenile sockeye salmon remain within their lake of origin at least during their first growing season.

Kvichak System

Most of the sockeye salmon in the escapement to the Kvichak system spawn in tributaries or on beaches in Iliamna Lake. The only possible significant presmolt interlake migration would be from Lake Clark to Iliamna Lake, and we have no indication that this movement occurs. We investigated this problem directly only at the time of normal smolt migrations in 1959, 1962, and 1963 when we found that the juveniles leaving Lake Clark are mostly age II.[12] Because no age III smolts have been captured at the outlet of Iliamna Lake and no adults with three freshwater annuli have been captured in the system, we assume that the age II juveniles migrating in June from Lake Clark are smolts that pass directly to the outlet of Iliamna Lake. As indicated elsewhere in this paper, the abundance of spawners within Iliamna Lake is greatest in the east end. This concentration produces a greater abundance of fry in that area. Entire age groups move in the lake toward the outlet in the west end, however; this movement is comparable to interlake migrations in other systems.

Naknek System

Interlake migrations of presmolt (age 0 and age I) sockeye salmon are known in the Naknek system.[13] In one movement fish left an area of high density of juveniles to enter areas of low densities (Coville Lake to downlake areas), and in another the migration was from a low- to a high-density area (Brooks Lake to Naknek

[11] Burgner, R. L., and J. M. Green. 1963. Study of interlake migration of red salmon fry, Agulowak River. Univ. Wash., Fish. Res. Inst., Circ. 182, 13 pp.

[12] Orrell, R. F. 1963. Abundance and age of Lake Clark red salmon smolts, 1962. Univ. Wash. Fish. Res. Inst., Circ. 186, 13 pp.

[13] Ellis, Robert J. 1963. The abundance and distribution of juvenile red salmon and associated species in lakes of the Naknek River system and Karluk Lake. Bur. Commer. Fish. Biol. Lab., Auke Bay, Alaska. [Manuscript, 80 pp.]

Lake). The interlake and interbasin migrations of presmolt fish in the Naknek system caused large numbers of fish to accumulate in downsystem lake areas, which have comparatively limited spawning grounds. Fyke net catches from Coville, Grosvenor, and Brooks Rivers and tow net catches from the lakes indicate that Naknek Lake, except for the relatively isolated North Arm basin, serves as a rearing area for fish originating in other lakes.

Chignik System

Interlake migration of age 0 sockeye salmon from Black Lake to Chignik Lake was detected by fishing fyke nets in Black River in 1961 and 1962. Scales of age 0 and age I salmon from Chignik Lake indicate that some Black Lake progeny use Chignik Lake as a rearing area, but scales from spawning populations in Black Lake indicate that most fry remain in Black Lake to age I and then migrate directly to the ocean (Narver, 1963). Extensive sampling of Chignik Lagoon with tow nets and seines in 1962 and 1963 revealed that some of the progeny of spawners of Chignik Lake migrate into Chignik Lagoon soon after they emerge from the gravel and use the lagoon as a rearing area.

Karluk System

Interlake movements of presmolt sockeye salmon have not been investigated in the Karluk system. Because Karluk Lake is the only rearing area of significant size, these movements could not be important.

ABUNDANCE AND GROWTH OF FISH IN PELAGIC AREAS

The capacity of a system to produce juvenile sockeye salmon is measured ultimately in the number of smolts produced. We have discussed our studies of the capacities of the spawning grounds. To locate and define factors that affect production of smolts in the rearing areas, we investigated the relation of the abundance of adult sockeye salmon to the abundance and growth of juveniles and associated species in the lakes.

Sockeye Salmon

The abundance of juvenile sockeye salmon in the lakes was measured with the pelagic tow net developed by Johnson (1956) and improved by Burgner (1958; footnote 9). In this study the standard unit of gear was a conical tow net 10 feet (3.1 m.) in diameter and 25 feet (8.3 m.) long. This net was pulled behind a pair of boats at night and fished with the center of the opening at two depths — 1.6 and 5 m. Modifications of the standard tow net were (1) a square opening of 9 feet (2.7 m.) and a length of about 25 feet (8.3 m.), used in the Wood and Kvichak systems; and (2) a square opening of 6 feet (1.8 m.) and a length of about 19 feet (5.8 m.), used in the Chignik system. The rate of catch is expressed in terms of the standard round opening 3.1-m. net pulled 1,500 feet (457 m.) in about 6 minutes.

Because we expected the abundance and growth of juvenile sockeye salmon and associated fishes would vary within lakes, we divided each lake into several sampling areas. The areas were not generally of uniform size, even within a lake. When we wish to discuss the average abundance or size of fish in a lake we must consider the relative contribution of each sampling area to the total population. We do this by a process of weighting in which we consider the portion of the total lake area in each sampling area and the relative abundance and size of the fish in the sampling area.[14] This process is repeated to compile an average for a system of more than one lake.

The mean catches of age 0 and age I and older sockeye salmon in tow nets (surface and deep tows combined) in the Wood, Kvichak, Naknek, Chignik, and Karluk systems, August 16 to September 15, are given in tables 17 and 18. Differences in abundance between systems within years were large (for example, 1961) as were

[14] The following formulas yield the weighted average catch per tow and the weighted average length of fish.

$$C_W = \sum_{i=1}^{n} \left(\frac{a_i}{A}\right) c_i$$

$$L_W = \frac{\sum_{i=1}^{n} (c_i a_i)\, l_i}{\sum_{i=1}^{n} (c_i a_i)}$$

where C_W = weighted catch per tow for entire lake
c_i = average catch per tow for sampling area i
A = surface area of entire lake
a_i = surface area of sampling area i
L_W = weighted average length of fish in the lake
l_i = average length of fish in sampling area i

TABLE 17.—*Weighted mean catches of age 0 sockeye salmon per standard tow (surface and deep tows combined), August 16 to September 15, by lake and year, in lakes of the Wood, Kvichak, Naknek, Chignik, and Karluk systems, 1958-62*

System and lake	Surface area	Fish per tow 1958	1959	1960	1961	1962
	*Km.*²	*Number*	*Number*	*Number*	*Number*	*Number*
Wood system						
Lake Aleknagik	83	31.5	25.5	183.2	215.6	92.2
Lake Nerka	201	26.7	12.2	80.4	98.0	31.0
Lake Beverley	90	3.7	61.3	56.4	94.2	2.8
Lake Kulik	45	4.3	63.1	274.4	92.2	27.0
Little Togiak Lake	6	60.0	240.5	153.5	223.7	39.6
Kvichak system						
Iliamna Lake	2,622	-----	-----	-----	-----	5.0
Lake Clark	267	-----	-----	-----	-----	6.3
Naknek system (all lakes combined)	790	-----	-----	-----	9.5	11.6
Chignik system						
Chignik Lake	22	-----	-----	-----	-----	28.9
					[1] 180.0	[1] 36.0
Black Lake	39	-----	-----	-----	-----	35.7
					[1] 290.0	[1] 56.0
Karluk system						
Karluk Lake	40	-----	-----	-----	10.5	4.3

[1] Surface tows only.

TABLE 18.—*Weighted mean catches of age I and older sockeye salmon per standard tow (surface and deep tows combined), August 16 to September 15, by lake and year, in lakes of the Wood, Kvichak, Naknek, Chignik, and Karluk systems, 1958-62*

System and lake	Surface area	Fish per tow 1958	1959	1960	1961	1962
	*Km.*²	*Number*	*Number*	*Number*	*Number*	*Number*
Wood system						
Lake Aleknagik	83	1.9	0.4	0.3	17.2	3.8
Lake Nerka	201	1.2	.2	1.3	7.0	2.6
Lake Beverley	90	.2	.2	11.2	7.1	2.1
Lake Kulik	45	.8	.4	4.3	31.4	6.9
Little Togiak Lake	6	2.3	2.5	3.1	25.4	18.7
Kvichak system						
Iliamna Lake	2,622	-----	-----	-----	-----	20.2
Lake Clark	267	-----	-----	-----	-----	.0
Naknek system (all lakes combined)	790	-----	-----	-----	2.0	5.5
Chignik system						
Chignik Lake	22	-----	-----	-----	-----	118.2
					[1]86.4	[1]125.9
Black Lake	39	-----	-----	-----	.0	.0
						[1].0
Karluk system						
Karluk Lake	40	-----	-----	-----	.9	1.2

[1] Surface tows only.

differences within systems between years (1961 and 1962 for all lakes of the Wood system). Some of these differences are examined in the following analyses for individual systems.

Wood system.—Preliminary use of the tow net to sample young sockeye salmon was started in lakes of the Wood system in 1957, and full-scale sampling began there in 1958. The relation between numbers of parent spawners per unit lake area and the production of age 0 sockeye salmon as measured by the geometric mean catch per standard tow (mid-August to mid-September) in each of the five Wood system lakes is presented for 1958-62 in figure 4. The relation between catch per tow of age 0 sockeye salmon and density of parent spawners seems to differ among lakes; hence, the data must be examined separately for each lake. A curve describing the relation between abundance of juveniles in the lake and density of parent spawners might be expected to start at zero, reach a maximum, and level off or decline as a result of increased mortality due to overcrowding of adults or eggs and larvae in the spawning areas or of young in the rearing areas. The relatively low catch of juveniles per tow in Little Togiak Lake and Lake

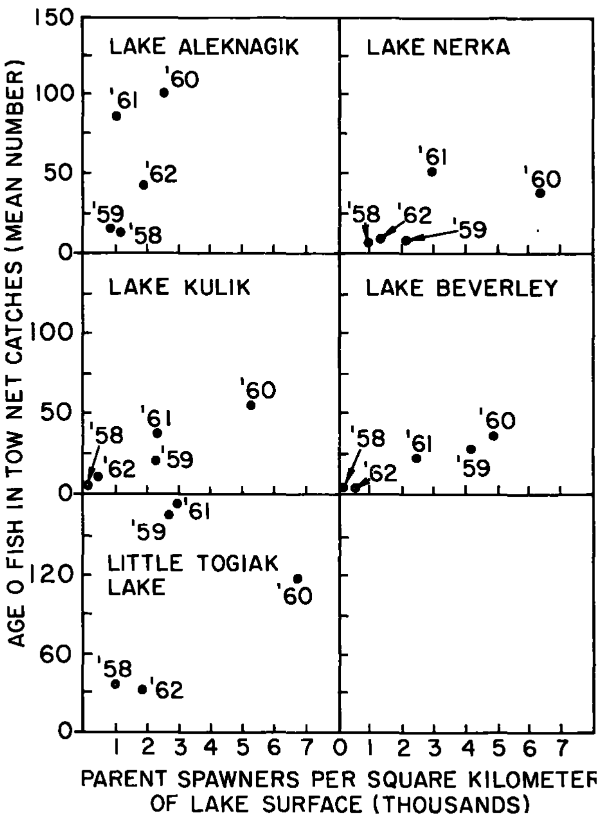

FIGURE 4.—Relation between abundance of age 0 sockeye salmon and numbers of parent spawners per unit lake area in each of the major lakes of the Wood system, 1958-62. The abundance of age 0 fish is the geometric mean of the abundance in tow net catches (mid-August to mid-September) weighted by depth and sampling area. The figure beside each point indicates the year of sampling.

Nerka at parent population densities approaching 7,000 spawners per square kilometer of nursery area (fig. 4) suggests decreased spawning efficiency or increased mortality of young at high population densities. There is some evidence of both.

The variation in the relations of abundance of juveniles to number of parent spawners per unit lake area in lakes of the Wood system is probably due to a combination of several factors: (1) errors in estimating numbers of spawners, (2) changes in survival from egg to juveniles available to the tow nets, and (3) random error in tow net sampling. Catches with the tow net indicate the same general abundance of juvenile salmon as do echo soundings recorded at the time of towing.

Evidence that the capacity of the nursery area may control the growth of fish in the Wood system is provided by data on growth of age 0 sockeye salmon in each of the four main Wood system lakes in 1958-62. The mean length of age 0 juveniles on September 1 is plotted against numbers of parent spawners per unit lake area for each lake (fig. 5). The inverse relation indicates that

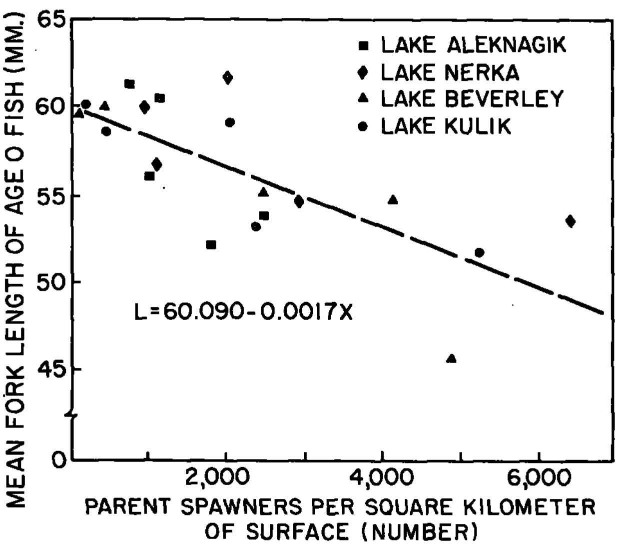

FIGURE 5.—Relation between mean fork length of age 0 sockeye salmon captured in tow nets, 1958-62, and abundance of parent spawners in lakes of the Wood system. The weighted mean fork length of the age 0 fish in each sample was adjusted to September 1 by applying a mean growth of 0.33 mm. per day, computed from growth data. The fish were measured after at least 24 hours in 10 percent Formalin.[15]

the progeny of large spawning populations grow slowly. Although the trend of the relation is obvious, the true shape of the line is probably obscured by five factors: (1) minor differences in growth potential (factors such as food availability and temperature) between lakes, (2) competition with variable numbers of yearling sockeye salmon from the previous year, (3) variability in the abundance of competitor species, (4) annual differences in climate that could affect the time of emergence, the length of growing season, and food supply, and (5) inaccuracies in estimates of numbers of spawners.

Differences are frequently observed in size of juvenile sockeye salmon between various parts of nursery lakes. These differences may be due to many factors including (1) real differences in growth rates, (2) differences in length of time the young have been in the lake, (3) differences in size of fry at hatching, and (4) differential rates of dispersion of faster and slower growing individuals. We have, therefore, used the term "apparent growth rate" in discussions of differences in size of juvenile sockeye salmon.

The apparent growth of young sockeye salmon in each of the three single-basin lakes in the Wood system is greatest in the east third and least in the west third of each lake (table 19). This relation holds for years of high and low population densities. Although the difference in apparent growth suggests basic differences in the growth potential of lake areas, progeny are smaller in the end of the lake that is closer to the major spawning grounds; and the differences in size within each lake may be the combined result of the longer lake residence of the early emerging fry and a more rapid dispersion of the larger fish.

TABLE 19.—*Mean fork lengths*[1] *of age 0 sockeye salmon on September 1*[2] *in three single-basin lakes of the Wood system, 1958-62*

Year	Lake Aleknagik			Lake Beverley			Lake Kulik		
	West third	Middle third	East third	West third	Middle third	East third	West third	Middle third	East third
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
1958	59.0	59.0	63.4	59.0	60.0	----	58.8	59.8	60.0
1959	57.5	62.7	60.8	50.5	57.3	61.2	61.5	60.6	58.8
1960	53.3	53.7	54.3	42.0	44.5	46.4	50.3	51.7	52.3
1961	52.2	57.5	57.5	51.1	52.2	59.2	51.7	52.8	55.1
1962	47.8	54.2	55.2	58.6	58.9	67.3	57.6	59.5	60.1
Mean	54.0	57.4	58.2	52.2	54.6	59.8	56.0	56.9	57.3

[1] After at least 24 hours in 10 percent Formalin.

[2] Lengths were adjusted to September 1 by applying a mean growth of 0.33 mm. per day computed from growth data.

[15] Trade names referred to in this publication do not imply endorsement of commercial products.

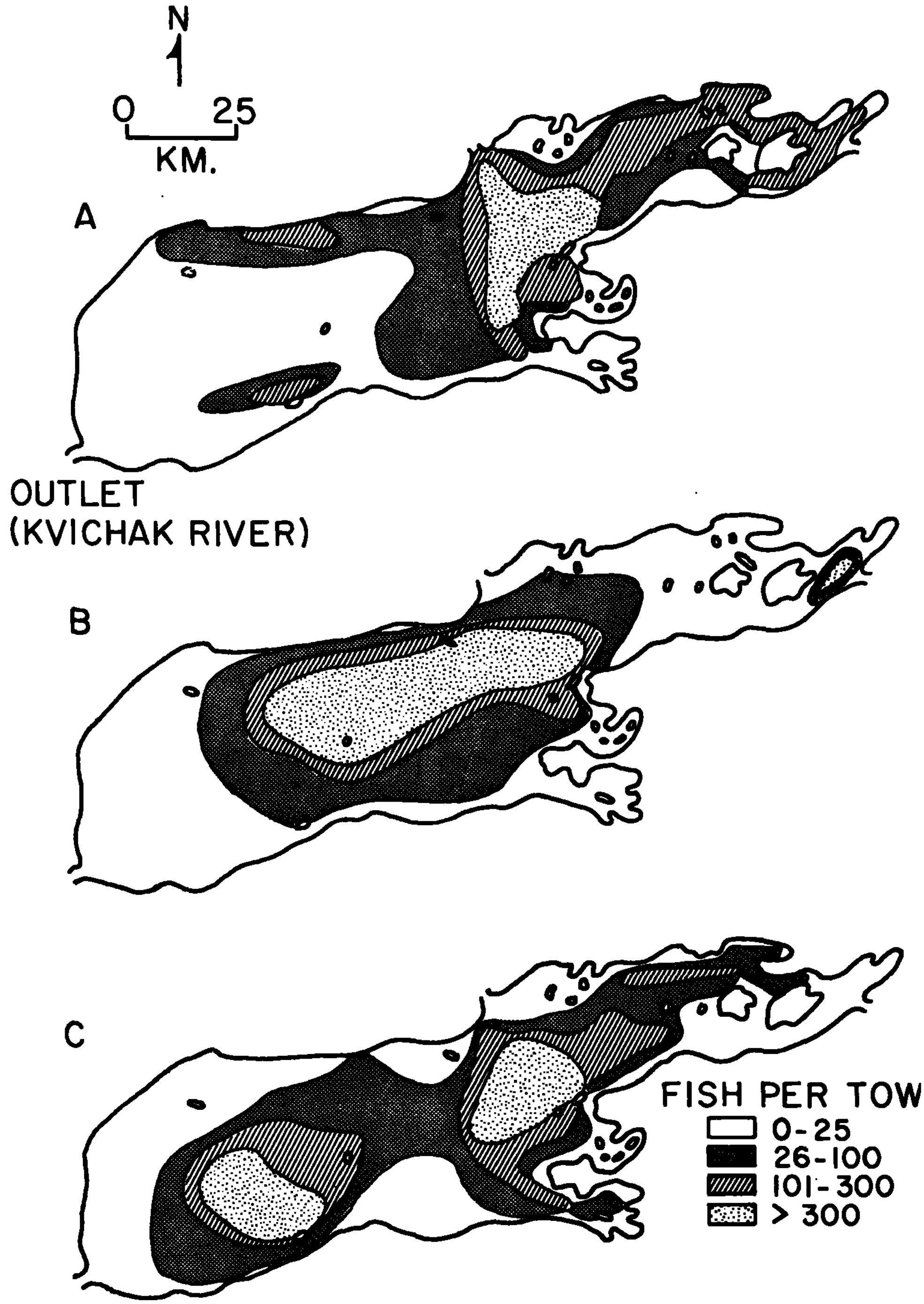

FIGURE 6.—Spatial distribution of juvenile sockeye salmon as indicated by the average catch per tow in Iliamna Lake, 1962. Catches in A (upper) are of age 0 fish caught between August 1 and September 15; in B (middle) are of age I fish caught between June 15 and July 31; and in C (lower) are of age I fish caught between August 1 and September 15.

Kvichak system.—Our most complete measure of the distribution and abundance of juvenile sockeye salmon in the Kvichak system is from tow net samples from Iliamna Lake in 1962 (fig. 6). The contour lines of density in the figure were determined by interpolation of the data on rate of catch between stations sampled and are not precise, but they illustrate the general distribution of the two age classes. The distribution and abundance changed during the summer and was different for age 0 and age I sockeye (fig. 6).

Most of the age 0 fish were in the eastern two-thirds of the lake from August 1 to September 15 —fig. 6A (the major spawning areas are in the eastern half of the lake).

Comparison of the distribution and abundance of age I sockeye salmon in early and late summer indicates a westerly movement, away from the principal spawning areas (fig. 6B and 6C). Age I juveniles had two centers of maximum concentration near the end of August—one in the west third and one in the middle third of the lake. These progeny of the 1960 escapement, therefore, occupied an area of the lake during their second summer (1962) that is probably not heavily used when most of the juveniles migrate to sea as age I smolts in early summer.

We found gradients in proportion of young-of-the-year and yearling sockeye salmon in the tow net catches in 1962 and in the average length of each age group from the outlet of the system to distant points in the system in catches made with an Isaacs-Kidd midwater trawl in 1961 and tow nets in 1962 (table 20). Yearling sockeye salmon were essentially absent from catches in 1961, but in 1962 they made up about 90 percent of the catches in the third of the lake closest to the outlet, about 85 percent in the middle third, and 45 percent in the most distant third. None were taken in Lake Clark. The average lengths of both age classes were greater nearer the outlet and less at the more distant points both years.

A strong gradient was found at the end of August 1962 in the mean length of age I sockeye salmon from three areas of Iliamna Lake. The average lengths in the east, middle, and west thirds of the lake were 81.5, 88.1, and 99.6 mm., respectively. Since spawning is most limited in the west end of the lake, the gradient is thought to be due to the more rapid or earlier migration of the larger and possibly older fish. By the following spring (1963) the westward movement of these fish (now age II smolts) must have been completed because most of them migrated in the first few days after the ice in the lake broke up.

TABLE 20.—*Age class composition and mean fork length of juvenile sockeye salmon on September 1 in various areas of the Kvichak system, 1961-62. The fish were captured with an Isaacs-Kidd midwater trawl in 1961 and in a 6-foot-square opening tow net in 1962. Original measurements were made of live fish and these data converted to preserved fish equivalents*

Area	1961				1962			
	Young-of-the-year		Yearlings		Young-of-the-year		Yearlings	
	Frequency	Average length	Frequency	Average length	Frequency	Average length	Frequency	Average length
	Percent	*Mm.*	*Percent*	*Mm.*	*Percent*	*Mm.*	*Percent*	*Mm.*
Iliamna Lake								
Igiugig					0	----	100	98.6
Shoulderblade					0	----	100	96.3
Grassy					81	56.6	19	90.5
Middle Talarik					24	56.1	76	91.5
Chekok					0	----	100	93.1
Dennis					20	57.8	80	80.2
Upper Talarik	100	59.7	0	----	18	54.7	82	85.3
Ten-Mile Island					15	50.6	85	77.9
Middle Island					8	53.6	92	81.9
Gibraltar					26	52.7	74	88.4
Kakhonak Bay					3	----	97	89.1
Intricate Bay					22	53.6	78	83.8
Tommy Point	100	54.3	0	----	25	50.7	75	79.2
Iliamna	100	53.9	0	----	56	50.2	44	79.5
Triangle Island	100	52.4	0	----	30	52.9	70	77.0
Knutson Bay	100	46.2	0	----	66	52.5	34	76.7
Pedro Bay	100	51.7	0	----	78	48.8	22	76.7
Pile Bay	100	50.2	0	----	75	48.4	25	74.6
Lake Clark								
Lower lake					100	51.3	0	----
Middle lake					100	46.3	0	----

Naknek system.—The interlake migration of sockeye salmon in the Naknek system during their first summer influences the relation between the abundance of young salmon in each lake at the end of the summer and the number of adults in the parent escapement to each lake. Data collected with tow nets in 1962 have been used to estimate a systemwide average catch per tow by day, weighted by area of each lake, for July 11 to August 29. Sampling was not daily. Missing data for an area were derived by averaging the figures of the most recent preceding and the first following sampling in that area. These weighted figures were combined for all areas each date to find the hypothetical catch per tow for the entire system and were smoothed by a moving average of three. The data (fig. 7) show a gradual increase in abundance of age 0 fish while recruitment from the spawning grounds exceeds mortality, a general leveling of the curve from July 20 to August 10, and a decline in rate of catch per tow after August 10. The curve

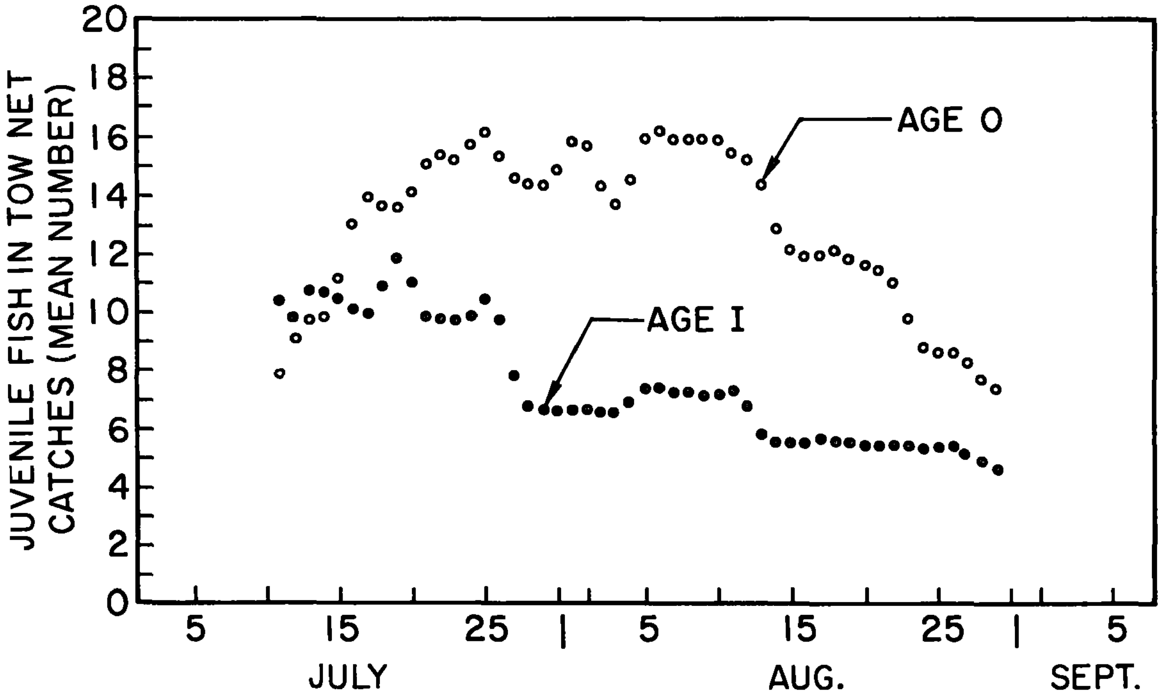

FIGURE 7.—Weighted daily mean catch of juvenile sockeye salmon per tow in Naknek system, all lakes combined, 1962. The mean catch for the system has been weighted by the size of each sampling area, and the daily estimates have been smoothed by a moving average of three—$(A + 2B + C) \div 4$.

would be somewhat higher if data from North Arm, which is not involved in the interlake movement, were omitted. The weighted mean catch of age I juveniles for the system was greatest in the earliest tows, July 11 to 20, and declined gradually during the summer.

Within lakes of the Naknek system we found a wide range in numbers of adult spawners per unit area of lake and also in the abundance of their progeny. Coville Lake had an escapement of about 6,600 adults per square kilometer in 1961; Brooks Lake had 267; and North Arm had 55. In July 1962 (before the presmolt interlake migrations) the average number of age 0 sockeye salmon in tow net catches was 150 in Coville Lake, 2 in Brooks Lake, and 0.5 in North Arm. The abundance of spawning adults (table 15) and of age 0 juveniles in these three lakes nearly cover the range found in southwestern Alaska.

Studies of juvenile salmon in the Naknek system have run too few years to determine the relation between the abundance of age 0 sockeye salmon and the size of the parent population. The escapement to the Naknek system in 1960 was 828,000 spawners, and the average catch of age 0 sockeye per tow in 1961 (in late August) was about 9.5. The escapement in 1961 was about 350,000, and the average catch per tow in 1962 was about 11.6.

The age composition and mean fork lengths of juvenile sockeye salmon on September 1 are presented for the Naknek and Karluk systems in table 21 by lake or sampling area. The average lengths of age 0 sockeye salmon in the Naknek system were greater in 1962 than in 1961, although the numbers of age 0 and age I fish in the system were essentially the same, as indicated by tow net catches in 1961 and 1962 and the smolt emigration in 1962 and 1963. The average catches per tow were 9.5 and 11.6 age 0 fish on August 20, and the smolt migrations were 8 million age I and 8 million age II in 1962 and 6 million age I and 8 million age II in 1963.

The year-to-year variation in basic productivity of the lakes of the Naknek system may cause marked differences in growth of juvenile sockeye salmon independent of their abundance. As was shown earlier in this report, basic productivity was comparatively low in 1961 and high in 1962. The resulting apparent growth of juvenile sockeye salmon reflected these differences.

The variation among mean lengths of age 0 sockeye salmon in the several basins of the Nak-

TABLE 21.—*Age composition and calculated[1] mean fork lengths[2] on September 1 of age 0 and age I sockeye salmon captured in tow nets in lakes of the Naknek and Karluk systems, weighted by surface area and catch per tow, 1961-62*

System, lake, and year	Age 0 fish: Frequency	Age 0 fish: Mean fork length	Age I fish: Frequency	Age I fish: Mean fork length
	Percent	Mm.	Percent	Mm.
Naknek system				
Coville Lake				
1961	100.0	54	0	----
1962	100.0	60	0	----
Grosvenor Lake				
1961	100.0	46	0	----
1962	100.0	52	0	----
Naknek Lake				
North Arm				
1961	----	----	----	----
1962	62.5	56	37.5	98
Iliuk Arm				
1961	84.1	57	15.9	78
1962	69.2	61	30.8	91
South Bay				
1961	64.3	47	35.7	86
1962	26.0	63	74.0	85
West End				
1961	75.1	65	24.9	89
1962	91.8	69	8.2	---
Brooks Lake				
1961	96.3	51	3.7	----
1962	97.1	60	2.9	----
Karluk system				
Karluk Lake				
1961	88.7	40	11.3	83
1962	81.9	49	18.1	76

[1] Curves describing the average length were calculated for each lake each summer; only those data involving 10 or more fish were used.

[2] After at least 48 hours, preservation in 10 percent Formalin.

TABLE 22.—*Calculated mean fork length of age 0 sockeye salmon from the upper end of Naknek system to outlet on September 1, 1962*

Sampling area	Fork length
	Mm.
Coville Lake	
Upper half	56
Lower half	60
Coville River	61
Grosvenor Lake	52
Grosvenor River	63
Naknek Lake	
Iliuk Arm	
Upper third	57
Middle third	63
Lower third	61
South Bay	
Upper third	61
Middle third	66
Lower third	--
West End [1]	69

[1] Does not include samples from the small basin in the northwest corner of Naknek Lake.

nek system (table 22) seems to reflect the results of a combination of at least three factors: (1) movement of the large fish first in the interlake migrations, (2) midseason recruitment of recently emerged fry (especially evident in Grosvenor Lake), and (3) differences in productivity of waters. The average size of juveniles taken in tow nets in Coville Lake increased from the upper to the lower end and increased again in juveniles taken in fyke nets as they migrated from Coville Lake to Grosvenor Lake. The juveniles captured in fyke nets in Grosvenor River were larger than those taken in tow nets in the lake. In the next basin downsystem, Iliuk Arm, smaller fish were more abundant at the inlet (upper third) even though the larger juveniles that migrated from Grosvenor Lake enter this end. The average size was the same in the upper third of South Bay and the adjacent area of Iliuk Arm but increased toward the outlet of the lake.

Chignik system.—The number of parent spawners per unit lake area in the Chignik system was greater in 1960 than in 1961, and, correspondingly, age 0 progeny were more abundant in 1961 than in 1962. The mean lengths of the age 0 progeny on September 1 were less in the year of greater abundance (table 23). The relations are similar to those in the Wood system. In the Chignik lakes, however, the apparent growth of progeny at similar densities of spawners and progeny is better than in the lakes of the Wood system; this difference may be due to a combination of richer nursery areas and fewer competitors in the Chignik lakes.

Karluk system.—The escapement of sockeye salmon in Karluk Lake was greater in 1960 than in 1961, and, correspondingly, age 0 progeny were more abundant in 1961 than in 1962. In 1960 about 349,000 adults entered the system and the average catch per tow of age 0 fish in 1961 was 8.9 from August 16 to September 15. The escapement in 1961 was about 297,000, and the average catch per tow in 1962 was 4.3.

The average length of age 0 sockeye salmon in Karluk Lake was greater in 1962 than in 1961 (table 21). The juveniles were larger in the year of lesser abundance (1962), so it might be assumed that the size of age 0 fish is density-dependent. But because of the long period of recruitment of recently emerged fry into the lake —caused by the extended spawning period (4-5 months)—the mean size of young-of-the-year at the end of the summer is based on fish that may differ in age by many weeks. Differences in the abundance of early- and late-spawning stocks might result, therefore, in apparent but non-

TABLE 23.—*Parent escapement of sockeye salmon, as numbers per square kilometer of lake, average catch of age 0 progeny per standard tow, and average length of age 0 progeny in Black and Chignik Lakes, 1960-61*

Lake and year of spawning	Parent spawners per square kilometer	Age 0 progeny: Average catch per tow	Age 0 progeny: Average fork length
	Number	*Number*	*Mm.*
Black Lake			
1960	6,128	180	58.9
1961	3,359	36	69.0
Chignik Lake			
1960	16,773	90	46.9
1961	12,545	56	47.2

existent differences in growth rates between seasons.

For Karluk Lake, both the average catches of juvenile sockeye salmon in tow nets (tables 17 and 18) and the average lengths for each age group (adjusted to September 1) were among the lowest recorded in this study (tables 19, 20, 21).

Associated Species

Several species of fish are captured frequently with juvenile sockeye salmon in the tow nets. The species and abundance vary from system to system. The most common in order of general abundance are threespine stickleback, ninespine stickleback, pond smelt, and pygmy whitefish.

The threespine stickleback is the most abundant species associated with young sockeye salmon in the Wood, Kvichak, Naknek, Chignik, and Karluk systems (table 24). Both species tend to concentrate near shore in the spring and spread toward the pelagic area of the lake as the season advances. Similarities in the food habits of these two species have been well established (Rogers, 1961).

Wood system.—The average abundance of threespine sticklebacks in tow net catches in the Wood system varied in 1958-62 (table 24) almost as much as, but seemingly independently of, that of juvenile sockeye salmon. In some years the biomass of the sticklebacks, as indicated by abundance in tow net catches, has approached or exceeded that of the juvenile salmon.

The average rate of growth of threespine sticklebacks varies from year to year and usually in the same direction as that of the juvenile sockeye salmon (fig. 8). The slowest growth of threespine sticklebacks (and of juvenile sockeye) generally is in years of greatest abundance

TABLE 24.—*Weighted mean catch of sticklebacks per standard tow (surface and deep tows combined), August 16 to September 15 in lakes of the Wood, Kvichak, and Chignik systems, 1958-62*

Species, system, and lake	Fish per tow: 1958	1959	1960	1961	1962
	Number	*Number*	*Number*	*Number*	*Number*
Threespine sticklebacks					
Wood system					
Lake Aleknagik	81.4	310.2	85.2	62.4	188.0
Lake Nerka	51.5	53.4	26.4	24.0	30.2
Lake Beverley	133.0	51.2	53.7	22.0	3.0
Lake Kulik	285.6	21.9	14.8	13.2	14.1
Little Togiak Lake	113.4	106.3	25.2	51.0	65.6
Kvichak system					
Iliamna Lake					27.8
Lake Clark					.0
Chignik system					
Chignik Lake					3.8
				[1] 4.1	[1] 5.0
Black Lake					170.3
				[1] 196.4	[1] 162.4
Ninespine sticklebacks					
Chignik system					
Chignik Lake					7.2
				[1] 6.6	[1] 7.0
Black Lake					32.2
				[1] 7.2	[1] 28.9

[1] Surface tows only.

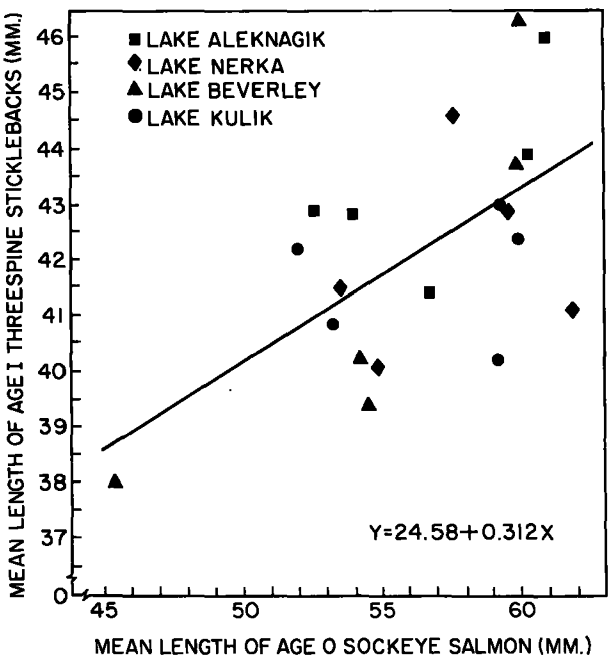

FIGURE 8.—Relation between mean length of age I threespine sticklebacks and mean length of age 0 sockeye salmon taken in tow nets each year, 1958-62, in each of four lakes of the Wood system. The mean lengths of both species have been weighted and adjusted to September 1.

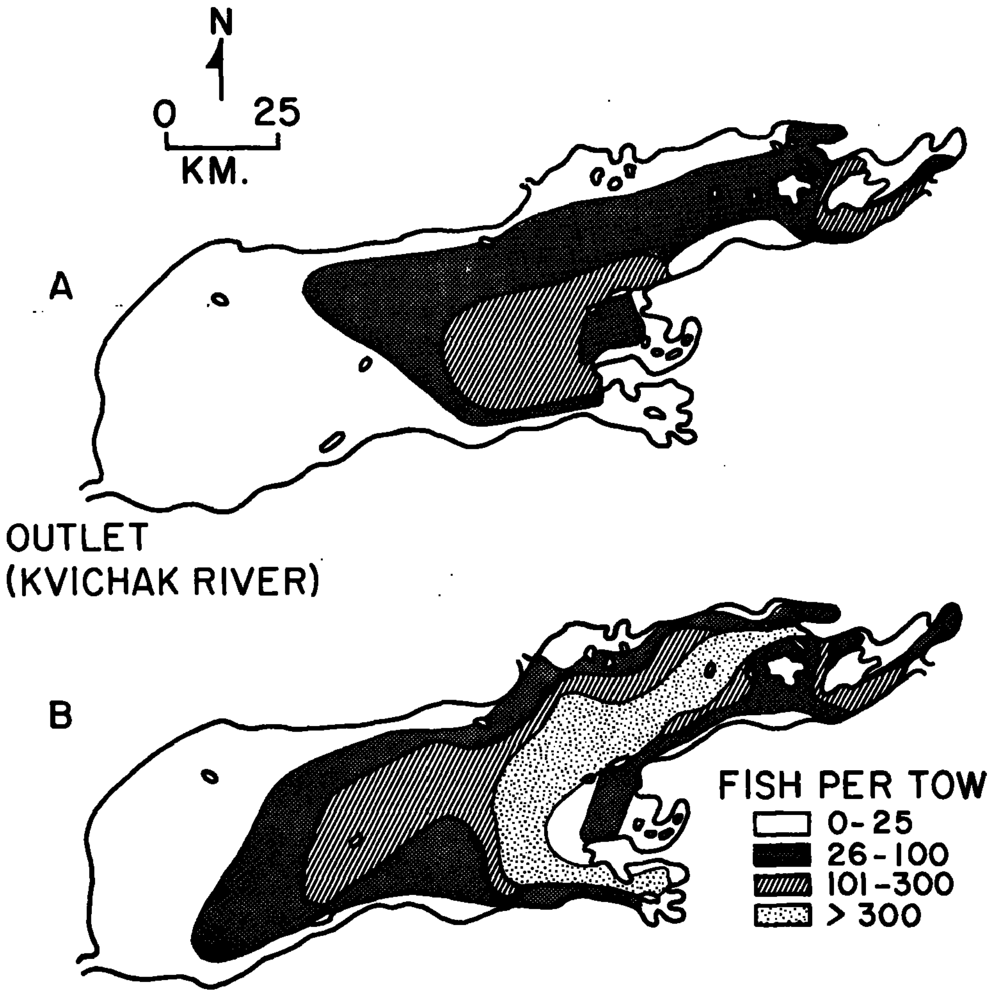

FIGURE 9.—Abundance and distribution of threespine sticklebacks in Iliamna Lake, 1962, as indicated by average catches in tow nets. Catches in A (upper) made June 15 to July 31; in B (lower) August 1 to September 15.

of juvenile salmon. The smaller size of threespine sticklebacks and the juvenile sockeye salmon in the western ends of the lakes of the Wood system suggests that the same factors influence the growth of both species.

Kvichak system.—The abundance and distribution of threespine sticklebacks in Iliamna Lake in tow net catches in 1962 before and after August 1 are shown in figure 9. The abundance contours of figure 9 are intended only to indicate the general situation in the pelagic areas.

Threespine sticklebacks were most abundant in the pelagic areas before August 1 in the upper bays of Iliamna Lake and in an area west of but adjacent to the Kakhonak-Intricate Bay complex (fig. 9A). After August 1, threespine sticklebacks were abundant over a much larger area (fig. 9B). The increased abundance in a larger area must be caused by a seasonal movement of sticklebacks from the littoral zone. Comparisons of the seasonal distribution of threespine sticklebacks and of age 0 and age I sockeye salmon suggest that competition could be greater between sticklebacks and age 0 salmon than between sticklebacks and age I salmon.

No threespine sticklebacks were caught in the limited tow net sampling in Lake Clark in 1962 or 1963.

Naknek system.—The species and abundance of fish caught in the Naknek system in tow nets with juvenile sockeye salmon varied among the lakes (table 25). Threespine sticklebacks were caught in tow nets in all of the lakes and were more abundant than all of the other species,

TABLE 25.—*Weighted mean catch per standard tow (surface and deep tows combined) of species associated with juvenile sockeye salmon, August 16-31, in lakes of the Naknek and Karluk systems, 1961-62*

Species, system, and lake	Fish per tow	
	1961	1962
	Number	*Number*
Threespine sticklebacks		
Naknek system		
Coville Lake	8.0	85.5
Grosvenor Lake	.2	.0
Naknek Lake		
North Arm	.1	3.6
Iliuk Arm	3.4	6.1
South Bay	9.3	12.0
West End	647.8	54.8
Brooks Lake	[1].0	.1
Karluk system		
Karluk Lake	63.9	115.1
Ninespine sticklebacks		
Naknek system		
Coville Lake	8.8	34.4
Grosvenor Lake	.1	.0
Naknek Lake		
North Arm	.0	.2
Iliuk Arm	.2	.8
South Bay	.9	15.0
West End	65.0	29.3
Brooks Lake	.1	.2
Karluk system		
Karluk Lake	.0	.0
Pond smelt		
Naknek system		
Coville Lake	91.0	49.5
Grosvenor Lake	.2	.0
Naknek Lake		
North Arm	.0	.1
Iliuk Arm	.0	.4
South Bay	.1	.1
West End	.1	.6
Brooks Lake	.0	.0
Karluk system		
Karluk Lake	.0	.0
Pygmy whitefish		
Naknek system		
Coville Lake	.0	.2
Grosvenor Lake	.0	.0
Naknek Lake		
North Arm	.0	.1
Iliuk Arm	.0	.1
South Bay	.5	.0
West End	.0	.0
Brooks Lake	.3	.2
Karluk system		
Karluk Lake	.0	.0

[1] Less than 0.05.

except pond smelt in Coville Lake. Although ninespine sticklebacks were distributed the same as threespine sticklebacks, they were generally less abundant. Pond smelt were taken in tow nets in all basins of the Naknek system except Brooks Lake but were abundant only in Coville Lake. Pygmy whitefish, which are basically benthic, were rarely taken in the tow net catches but were highly abundant in trawl catches from Brooks Lake. Areas of the Naknek system that yielded the largest catches of juvenile sockeye salmon or the fastest growing juveniles or both also yielded the largest catches of associated species.

Chignik system.—In the Chignik system, threespine sticklebacks were about 30 times as abundant in tow net catches in Black Lake as in Chignik Lake (table 24). The sticklebacks may be unable to compete successfully with the large populations of young sockeye salmon that often occur in Chignik Lake. Ninespine sticklebacks were slightly more abundant than threespine sticklebacks in Chignik Lake but were less abundant in Black Lake (table 24). Pond smelt were not as abundant as sticklebacks but occurred frequently in tow net catches in both lakes. Other species were seldom taken.

Karluk system.—The threespine stickleback was the only species other than juvenile sockeye salmon captured in tow nets at Karluk Lake (table 25), and sticklebacks were much more abundant than juvenile salmon in all sampling with all gear.

PREDATION ON JUVENILE SOCKEYE SALMON

Predation on juvenile sockeye salmon in fresh water occurs during their emergence, migration from the spawning areas, and residence in and migration from the nursery lakes. Predation by birds and fish is often very obvious and dramatic in southwestern Alaska.

A few studies and many general observations have been made of the relative intensity of predation by various animals in several systems. Most of the predators to be mentioned are present in all the sockeye salmon systems in southwestern Alaska.

In the Mainland Systems the Arctic char is the most significant predator on sockeye salmon, but many others do occur.

In the Igushik, Snake, Wood, and Kvichak systems the Arctic char is the fish that eats the most sockeye salmon juveniles—as migrating fry, as residents in the lakes, and as migrating smolts. In the Nuyakuk system, lake trout are more abundant than Arctic char and consume more young sockeye salmon. Other fish predators observed to eat young sockeye salmon in these lake systems are juvenile coho salmon, northern pike, grayling, and rainbow trout. During the smolt migrations, Arctic Terns (*Sterna paradisaea*) and Bonaparte's Gulls (*Larus philadelphia*) prey on sockeye salmon in the rivers connecting lakes and in the trunk river.

Several species prey on juvenile sockeye salmon at different stages in the Naknek system. Dolly Varden are abundant and in several areas feed actively on sockeye salmon fry during their emergence and migration. Juvenile coho salmon, present throughout the system, have been observed feeding on sockeye salmon fry in Brooks Lake. Presmolt sockeye salmon migrate out of Coville Lake in late summer day and night; at that time predation by lake trout, Arctic Terns, and Bonaparte's Gulls is very obvious.

Dolly Varden and rainbow trout prey on migrating smolts in the Naknek River. Other possible fish predators in the Naknek system are Arctic char, northern pike, Arctic grayling *(Thymallus arcticus)*, and sculpins (*Cottus* spp.).

Dolly Varden and juvenile coho salmon both prey on juvenile sockeye salmon in the Chignik system (Roos, 1960), but the predation by coho salmon seems to be the more significant (Roos, 1959).

The Karluk system has large numbers of Dolly Varden and Arctic char (DeLacy and Morton, 1943), which may be serious predators of juvenile sockeye salmon.

The effectiveness of predators in keeping competitors of sockeye salmon in check is unknown but may be important. In the Wood system, for example, threespine sticklebacks are an important item in the diet of Arctic char.

The destruction of a constant number of juvenile sockeye salmon by predators each year would help sustain and perhaps reinforce the cyclic nature of some runs to the Bristol Bay systems. A constant annual demand would have a greater effect in years of low abundance of juvenile sockeye salmon. Such an effect is suggested for the sockeye salmon of Shuswap Lake of the Fraser system (Ward and Larkin, 1964).

REPRODUCTIVE RELATIONS OF POPULATIONS IN FRESH AND SALT WATER

The relations between numbers of smolts produced and numbers of adults in the parent escapements (described by the reproductive curve) are highly variable, even within a system, because they are determined by the interaction of many physical and biological factors. In this section we consider the relations between numbers of adults in the parent escapement and their progeny in terms of numbers, size, and age of smolts migrating to sea, and numbers of adults returning from the sea (catch and escapement).

RELATION BETWEEN NUMBERS OF SMOLTS AND NUMBERS OF ADULTS IN PARENT ESCAPEMENT

The major purpose of studies of the numbers of smolts produced by various numbers of spawners is to define the relation and interpret it to make estimates of optimum escapement (in terms of numbers of smolts) either directly or with the aid of ancillary information.

Smolt migrations were sampled with fyke nets in the trunk rivers. The abundance is expressed in index points for the Wood and Kvichak Rivers and in numbers of fish for the Naknek, Ugashik, and Karluk Rivers. The methods of counting the escapement of adults were described earlier in this report.

The index method of estimating production of smolts requires the use of standard fishing gear, site, and effort. The numbers of smolts captured are then given value in relation to the catches of a base year which has an arbitrary value of 100 index points. This method is used in the Kvichak system (Kerns, 1961) and the Wood system (Burgner, 1962). It yields data comparable between years within a system but not between systems.

The estimates of numbers of smolts produced by a system were based on a regular system of sampling. Many fishing sites were set up across the width of the river, and fyke nets were fished for a fixed period of time once a day in each site in random order. The sequence of fishing sites and times of day was a modified Latin-square design (Cochran and Cox, 1957). Catches were classified according to site, time of day, and date —factors considered to have the greatest influence on variability of the individual catches. Estimates of the total numbers of smolts in the annual migrations were obtained by expanding the mean catch per standard fishing period according to the number of potential fishing sites in the width of the river and the number of fishing periods in the season. We used this method to estimate the numbers of smolts migrating in the Naknek and Ugashik systems.

The age composition of the smolts in each migration was estimated from length-frequency measurements or scale samples taken during the season and weighted by magnitude of fyke net

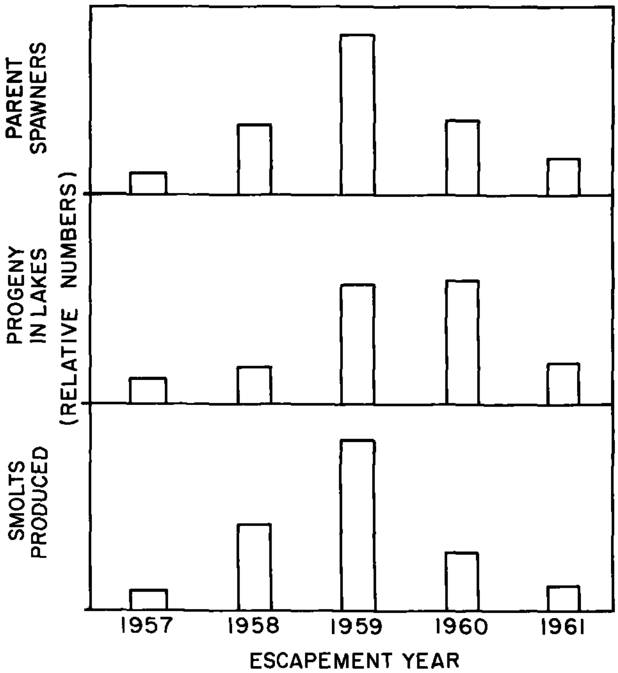

FIGURE 10.—Comparison of relative size of sockeye salmon escapement, abundance of progeny in lakes (based on tow net catches), and smolts in Wood River (based on fyke net catches), Wood system, parent escapement years of 1957-61.

catches for the day (or days) on which the samples were taken. Smolts were measured in the fresh state soon after capture.

Wood System

The Wood system showed two general levels of production of smolts (index points) per 1,000 adults in the escapement, the high level (1951 to 1954) was 0.50 to 1.87 index points (base of 1.00), and the low level (all other years from 1949 to 1961) was 0.10 to 0.27 (table 26). The cause of the considerable difference between the two levels is not known—it might be due to unusually good conditions for survival in the lakes or to a consistent error in indexing smolt abundance from 1951 to 1954.

The index estimates of smolt abundance in the Wood system for later years, 1957-61, can be checked against estimates of abundance at two other stages of fresh-water residence—the relative size of escapements and the abundance of progeny in the lakes (based on tow net samples in late August). The three estimates of abundance had the same general changes from 1957 through 1961 (fig. 10).

TABLE 26.—*Number of sockeye salmon in escapements and abundance, age composition, and mean length of smolts produced, by year of spawning, Wood system, 1949-61*

[Size of escapements for years 1949-52 based on stream surveys only]

Year of spawning	Adults in escapement	Smolts produced	Smolts produced per 1,000 spawners	Age composition of smolts		Mean length [1] of smolts	
				Age I	Age II	Age I	Age II
	Thousands	*Index points*	*Index points*	*Percent*	*Percent*	*Mm.*	*Mm.*
1949	101	10	0.10	----	----	[2] 91	----
1950	452	115	.25	87	13	[2] 87	[2] 103
1951	458	299	.65	94	6	[2] 86	107
1952	227	425	1.87	99	1	87	102
1953	516	290	.56	75	25	85	95
1954	571	286	.50	89	11	82	93
1955	1,383	215	.16	62	38	77	102
1956	773	154	.20	97	3	82	105
1957	289	59	.20	97	3	88	114
1958 [3]	960	255	.27	86	14	88	102
1959 [4]	2,209	508	.23	95	5	82	98
1960 [4]	1,016	167	.16	92	8	80	102
1961 [4]	461	82	.18	92	8	83	104

[1] Fork length of live anesthetized fish.

[2] Based on several samples taken during the main migration season but not weighted by catch.

[3] Age composition and mean length approximated in 1958 because of difficulty in determining age of smolts.

[4] Smolt data furnished by Alaska Department of Fish and Game for 1961-63.

The relation between numbers of smolts produced and numbers of adults in the parent escapement in the Wood system (fig. 11) is nearly linear in years when production per spawner was low (years other than 1951-54). Since the cause of the high rate of smolt production from 1951-54 is unknown, all points on figure 11 must be given equal weight, and, therefore, optimum escapement in terms of smolt production cannot be determined from these data.

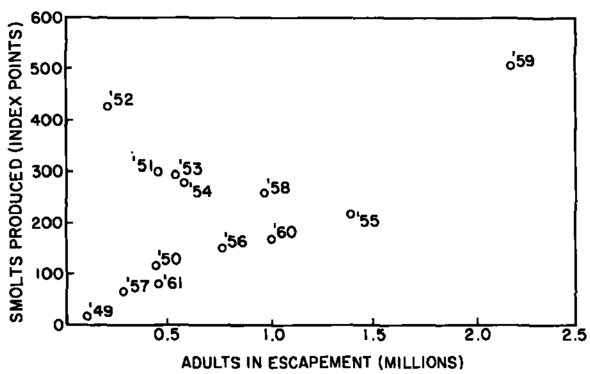

FIGURE 11.—Relation between smolt production (indexed by catches made in fyke nets in Wood River) and number of sockeye salmon in parent escapement, 1949-61, Wood system. The figure beside each point is the year of the parent escapement.

TABLE 27.—*Number of sockeye salmon in escapements and abundance, age composition, and mean length of smolts produced, by year of spawning, Kvichak system, 1952-60* [1]

[Size of escapements for 1952-54 based on stream surveys]

Year of spawning	Fish in escapement	Smolts produced	Smolts produced per 1 million spawners	Age composition of smolts: Age I	Age composition of smolts: Age II	Mean length [2] of smolts: Age I	Mean length [2] of smolts: Age II
	Thousands	*Index points* [3]	*Index points* [3]	*Percent*	*Percent*	*Mm.*	*Mm.*
1952	5,970	----	----	----	----	----	109
1953	321	1.95	6.1	28	72	89	116
1954	241	1.15	4.8	78	22	92	120
1955	251	2.65	10.6	23	77	96	114
1956	9,443	181.32	19.2	54	46	84	99
1957	2,843	19.14	6.7	13	87	80	108
1958	535	2.15	4.0	86	14	91	118
1959	680	2.96	4.4	27	73	93	110
1960	14,630	[4] 157.38	10.8	22	78	82	98

[1] Abundance and length data for age II smolts from the 1958 escapement and age I smolts from the 1959 escapement supplied by Alaska Department of Fish and Game.

[2] Fork length of live anesthetized fish.

[3] Based on 24-hour catches.

[4] Marriott (1965).

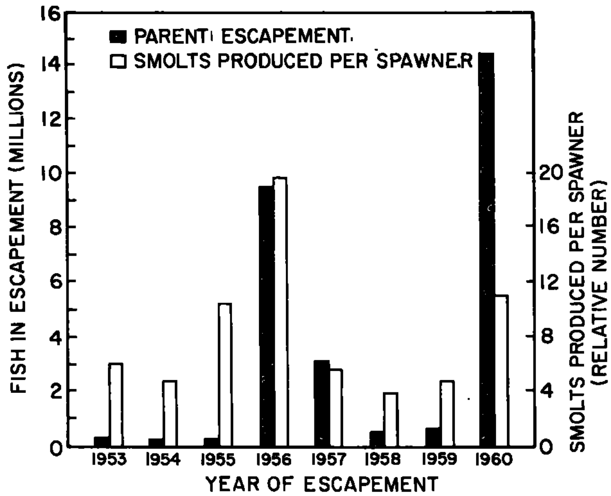

FIGURE 12.—Number of sockeye salmon in parent escapement and relative numbers of smolts produced per spawner, by year of escapement, in the Kvichak system, 1953-60.

Kvichak System

Data on smolts produced (index points) and the numbers of adults in the parent escapement in the Kvichak system are presented in table 27 for 1953-60.

The production of smolts per spawner in the Kvichak system does not follow the classic reproduction curves described by Schaefer (1954), Beverton and Holt (1957), and Ricker (1958). Reproduction curves are based on the assumption that the return per spawner is inversely related to the numbers of spawners, but in the Kvichak system the maximum production of smolts per spawner was produced by the relatively large escapement of 9.4 million in 1956 (table 27, fig. 12). The escapement of 14.6 million adults in 1960 apparently produced smolts at a lower rate per spawner[16] than that of 1956 but still greater than in most years of low escapement.

We assume that two reproduction curves are applicable in the Kvichak system—one for large escapements or "peak" years (over 5 million fish) and one for small escapements or "low" years (5 million fish or fewer). Two derived points are available for calculating the relation between smolt production and large escapements, namely the most recent peak years of the cycle, 1956 and 1960. Axiomatically, the reproduction curve includes the origin. A compound exponential curve of a type suggested by Ricker (1958) fitted to these three points necessarily produces a flat dome. These data indicate that the optimum escapement is less than the 1956 escapement, i.e., less than 9.4 million spawners (footnote 16).

We conclude that our estimate of the number of smolts produced by the 1960 escapement was too low, and, consequently, our estimate of the optimum escapement for peak years is also too low and will be raised as more data become available.

Naknek System

Estimates were made of the number of smolts produced in the Naknek system from each escapement in 1954-61 (table 28). Within these years the escapements ranged from 0.28 to 2.23 million.

The number of smolts produced increased as the escapement increased, up to an escapement of about 1 million (fig. 13). Beyond this point the number of smolts tended to level off (at about 14 million smolts) or decline.

[16] The extraordinarily large return of sockeye salmon to the Kvichak system in 1965 from the 1963 smolt run was unexpected. The smolt production from the 1960 escapement must have been greater than that indicated by the fyke net catches (shown as index points in table 27 and figure 12) because the return was disproportionately large, and ocean survival was not unusually high for sockeye salmon from other systems during this period. Intermittently occurring ice floes in the Kvichak River between May 15 and June 1, 1963, made it difficult to fish the fyke nets properly (footnote 4, table 27).

TABLE 28.—*Number of sockeye salmon in each escapement and number of smolts produced, by year of spawning, Naknek system, 1954-61*

Year of spawning	Fish in escapement	Smolts			
		Age I	Age II	Age III	Total
	Thousands	*Millions*	*Millions*	*Millions*	*Millions*
1954	804	5.06	1.28	----	6.34
1955	279	1.76	.36	----	2.12
1956	1,773	9.70	2.43	0.02	12.15
1957	635	10.03	3.12	----	13.15
1958	278	3.55	1.25	Trace	4.80
1959	2,232	4.37	8.46	.13	12.96
1960	828	8.00	8.72	Trace	16.72
1961	351	6.05	4.97	----	11.02

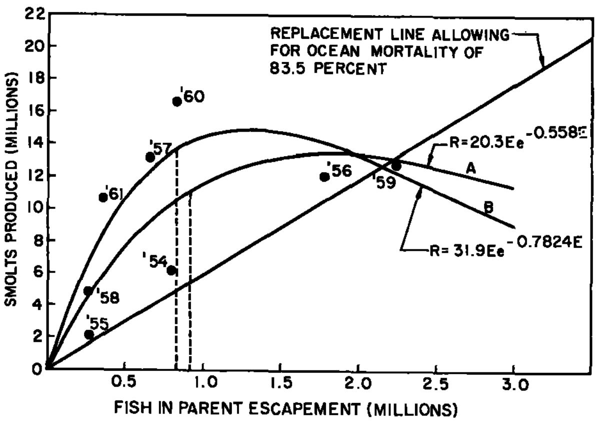

FIGURE 13.—Relations between numbers of smolts produced and number of sockeye salmon in parent escapement in the Naknek system for the escapements in 1954-61. The number beside each point indicates the escapement year. The dashed line indicates the optimum escapement for each curve. R=number of smolts in millions, and E=number in escapement in millions. Curve A fitted to all points; curve B fitted to 1956-61 points (see text).

Ricker-type reproduction curves have been fitted to the smolt-escapement data from the Naknek systems for the escapements of 1954-61 (fig. 13). Curve A was fitted to all points and curve B to the escapements of 1956-61. Smolt production from the 1954 and 1955 escapements may have been underestimated by a substantial amount (because of problems in establishing the procedures for sampling smolts). Curve B is assumed, therefore, to describe the smolt-escapement relation better.

For the Naknek system, estimates of total ocean mortality for sockeye salmon from 3 years of smolt migration ranged from 77.6 to 95.2 percent and averaged 83.5 percent. No attempt was made to correct these estimates for the take of salmon by the high seas fishery.

The replacement line in figure 13 is straight—it is based on the assumption that the average total mortality (83.5 percent) applies to all levels of smolt migrations; i.e., ocean mortality is largely independent of numbers of smolts. If ocean mortality tended to increase with increasing numbers of smolts in the seaward migrations, the replacement line would not be straight but would curve upward. Conversely, if ocean mortality tended to decrease with increasing numbers of smolts, the slope of the replacement line would decrease toward the right. Not enough information is available to determine the nature of ocean mortality, and the safest assumption seems to be that its effects are mostly independent of numbers of smolts entering the ocean.

As indicated in figure 13, maximum yield to the inshore fishery may be realized with escapements ranging from 600,000 to 1 million spawners. If the high-seas catches of Naknek River sockeye salmon were taken into account (i.e., if they were included among the survivors), the total ocean mortality would be lower, the slope of the replacement line correspondingly less, and the apparent optimum escapement range somewhat higher. Thus, we encounter a paradox. If reproduction curves of the kind shown were used to maximize the inshore catch, the total catch (inshore plus high seas) would be less than is biologically possible.

Additional observations are required to define more precisely the form of the smolt-escapement relation and ocean mortality rate.

Ugashik System

Estimates of the numbers of smolts produced in the Ugashik system are available each escapement year, 1956-60 (table 29). These estimates have been used to construct a figure showing the smolt-escapement relation for the system (fig. 14). Escapements of fewer than one-half million fish in 4 of the 5 years caused a crowding of points at the lower end of the scale; interpretation of the form of the smolt-escapement relation is, accordingly, difficult. Smolt production appears nevertheless to increase as the size of the escapement increases. The greatest number of smolts (31.6 million) was produced by the greatest number of adults—2.3 million spawners in 1960. Because we lack observations on escapements of intermediate size, the best that can be determined is that target escapements for the

TABLE 29.—*Number of sockeye salmon in each escapement and number of smolts produced, by year of spawning, Ugashik system, 1956-60*

Year of spawning	Fish in escapement	Smolts			
		Age I	Age II	Age III	Total
	Thousands	*Millions*	*Millions*	*Millions*	*Millions*
1956	425	11.43	0.37	0.06	11.86
1957	215	2.52	2.16	Trace	4.68
1958	280	3.28	3.03	----	6.31
1959	219	.78	3.22	Trace	4.00
1960	2,294	13.47	18.12	[1]	31.59

[1] Age III smolts will migrate seaward in the spring of 1964.

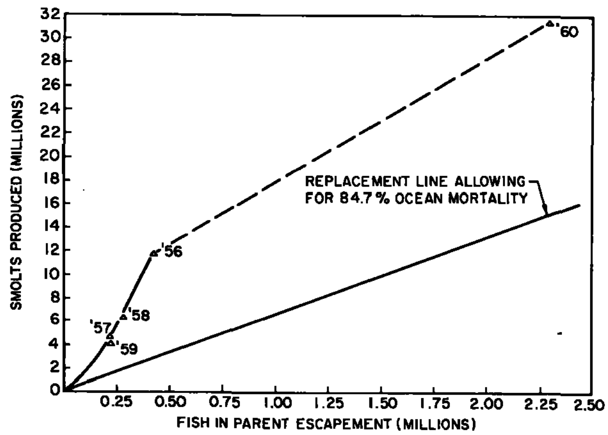

FIGURE 14.—Relation between numbers of smolts produced and number of sockeye salmon in parent escapement in the Ugashik system for the escapements of 1956-60. The number beside each point indicates the escapement year. A broken line is used to connect the values for 1956 and 1960 because the escapements were so different that the probable shape of the curve between them is not apparent.

Ugashik system should probably be greater than one-half million.

Karluk System

Estimates have been made of the numbers of sockeye salmon smolts produced by the Karluk River system for 3 years (1961-63). About 1.5 million smolts were produced each year, although parent escapements varied from 210,000 to 435,000. Within this range of escapements, the relation between numbers of smolts produced and numbers of parents is not definable.

RELATION BETWEEN LENGTH OF SMOLTS AND NUMBERS OF ADULTS IN PARENT ESCAPEMENT

Small smolts would be expected to have greater ocean mortality than large smolts. Indeed, Ricker's (1962) compilation and analysis of return-per-smolt data from six sockeye salmon systems outside Bristol Bay confirmed this general relation. Burgner (1962) determined that a group of age I smolts that migrated from Wood River in 1955 at an average length of about 72 mm. suffered about twice the ocean mortality of a group of age I smolts 90 mm. long that migrated in the same year. This influence of size on survival agrees well with the data shown in Ricker's figure 1 (1962). We, therefore, consider the relation of length of smolts to numbers of adults in the parent escapement and discuss the effects of size of smolts on their survival in the ocean.

Wood System

The relation between the mean length of age I smolts and numbers of adults in the parent escapements in the Wood system is presented in figure 15, where a regression line has been fitted. The equation for the regression of length of age I smolts on number of spawners in the parent escapement is

$$L_I = 87.86 - 4.4X$$

where L_I is the average fork length in millimeters of age I smolts, and X is the parent escapement in millions of spawners. The correlation is significant at the 98-percent level. Thus, the mean length of age I smolts (the dominant age group) is inversely related to the number of parent spawners.

On the basis of this equation, age I smolts from an escapement of 2 million spawners would be expected to have an average length of about 79 mm. and those from 500,000 spawners, about 86 mm.

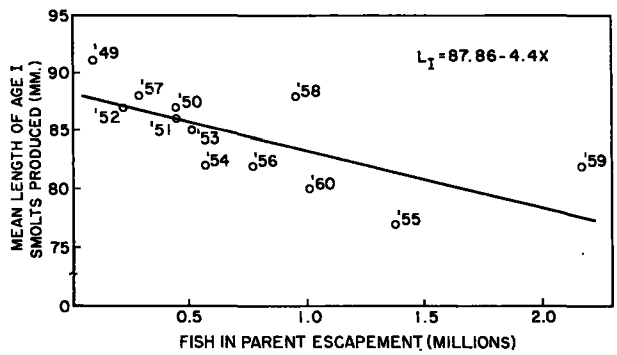

FIGURE 15.—Relation between growth of progeny (as indicated by mean length of age I smolts) and number of adults in the parent escapement, 1949-60, Wood system. The number beside each point indicates the escapement year.

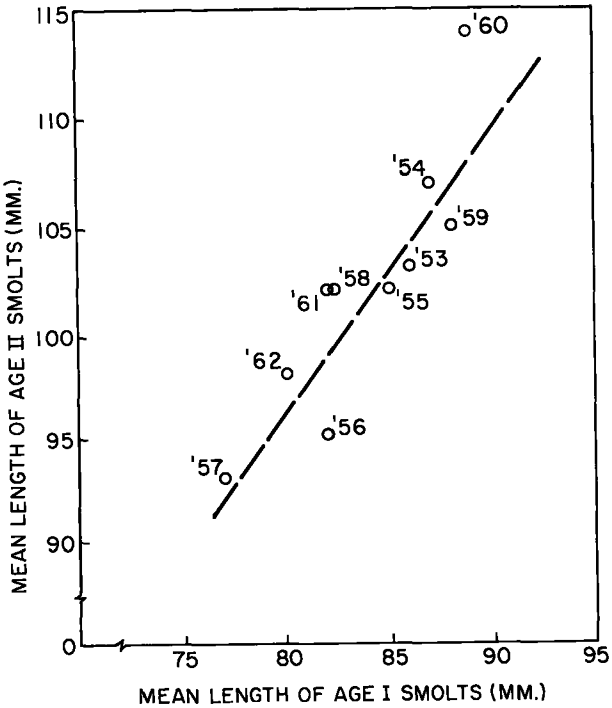

FIGURE 16.—Relation between mean lengths of age II and age I sockeye salmon smolts in the same year of seaward migration, 1953-61, Wood system. The number beside each point indicates the year of smolt migration.

The individual points in the relation between the length of smolts and numbers of adults in the escapement do not fit the regression closely, and, in addition, exact data on natural mortality in the ocean are lacking for the Wood system. Hence, the illustration from the Wood River smolt migration of 1955 given above can only suggest the effect of the size of smolts on ocean survival. It is probable, however, that ocean mortality related to size attained by age I sockeye salmon in fresh water is an important factor in the determination of the numbers of adults in the returns to the Wood system.

The average length of age II smolts was better correlated with the mean length of age I smolts of the following year class than with the number of fish in the parent escapement (fig. 16). This relation suggests the presence of competition for food between age classes of juvenile sockeye salmon.

A lack of significant competition for food among individuals of an age class after their first year in the lake is due to their comparatively small numbers—most sockeye salmon smolts of the Wood River are age I (table 26).

Kvichak System

The data on mean lengths of age I and age II smolts produced by each escapement to the Kvichak system in 1952-60 (table 27) were used to calculate a straight-line regression of smolt length on numbers of adults in the parent escapement for these years. The relation for age I smolts is

$$L_{I} = 90.64 - 0.7X$$

and for age II smolts

$$L_{II} = 115.51 - 1.4X$$

where L is the length of smolts in millimeters and X is the number of fish (millions) in the parent escapement (fig. 17). The correlation coefficient for age I smolts was $r = -0.73$ and for age II smolts, $r = -0.93$.

The slope of the regression line of smolt size on escapement for age II smolts of the Kvichak system is almost twice that of the age I; the growth retardation caused by competition for food among the progeny of each escapement seems to continue during their second year in fresh water. The contrast to the Wood system in this regard may be the result of the proportionately greater holdover of young to age II smolts in the Kvichak system.

The regression of length of age I smolts on numbers of adults in the parent escapement for the Wood system has a slope six times that derived for age I smolts in the Kvichak system.

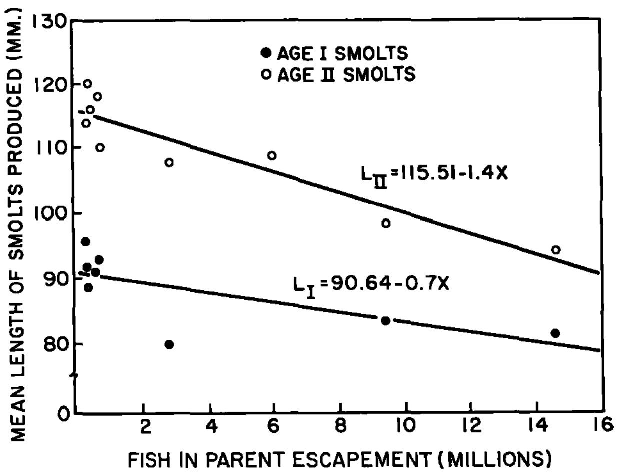

FIGURE 17.—Relation between mean lengths of age I and II sockeye salmon smolts by age class and numbers of adults in the parent escapements, Kvichak system.

This difference may be caused by the relative sizes of the rearing areas of the two systems, because the slopes of the regressions of smolt size on numbers of parent spawners per square kilometer of nursery area are similar for the two systems.

A regression of ocean survival on smolt size with a positive slope of about 0.25 can be calculated from data compiled by Ricker (1962). Thus, although it appears that in the Kvichak system an escapement of about 10 million spawners will produce the greatest number of smolts (age groups I and II combined),[17] the survival of these smolts after they leave the lake will be reduced because the average size of fish in each age group is less than the size of the fewer smolts produced by a smaller escapement. Clearly, the optimum escapement for peak years in the Kvichak system must be determined by maximizing the return as it is influenced by numbers and quality of smolts produced. The optimum escapement must be less, therefore, than that which produces the largest number of smolts.

Another factor also indicates a need for a lower escapement. The regression line in figure 17 has one aberrant point, namely, the length of age I smolts from the 1957 escapement (2,843,000) which followed the large escapement of 1956 (9,443,000). Although the escapement in 1957 was comparatively small, the mean length of age I smolts from the 1957 escapement was less than that of age I smolts from the large 1956 escapement. This discrepancy is interpreted to mean that as young-of-the-year, the age I smolts of the 1957 escapement competed for food with the abundant yearling fish from the 1956 escapement which migrated as age II smolts. Optimum escapement cannot be determined, therefore, by considering one year alone—possible effects of competition between progeny of successive escapements must be carefully considered.

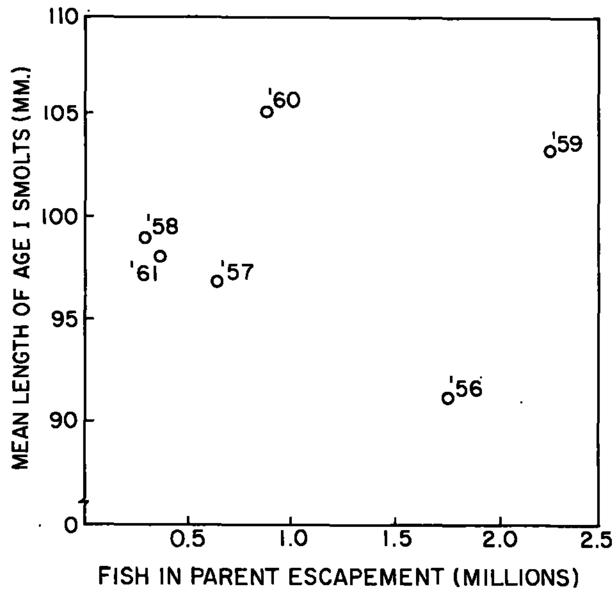

FIGURE 18.—Relation between mean lengths of age I sockeye salmon smolts and number of adults in parent escapements, Naknek system, 1956–61. The number beside each point indicates the parent escapement year.

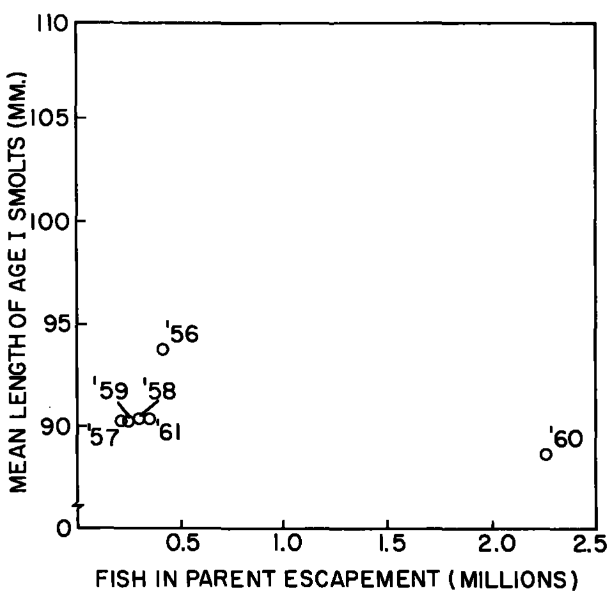

FIGURE 19.—Relation between mean lengths of age I sockeye salmon smolts and number of adults in parent escapements, Ugashik system, 1956-61. The number beside each point indicates the parent escapement year.

Naknek and Ugashik Systems

Little indication exists for the Naknek and Ugashik systems that the average size of age I smolts is correlated with the number of adults in the parent escapement (figs. 18 and 19). The age II smolts show a similar lack of correlation (data not shown). Scales from smolts indicate that the variations in size of age I fish at the time of seaward migration are caused to a great extent by variations in growing conditions in the lakes just before the smolts leave.

Mortality of sockeye salmon in the ocean is

[17] This estimate is based on data collected through 1963 (see footnote 16).

influenced by oceanic conditions, the high seas fishery, and the amount of time the salmon spend in the ocean—factors that may mask the effects of the size of smolts on mortality. Estimates of ocean mortality of Bristol Bay sockeye salmon are available for only the Naknek and Ugashik systems (table 30). Age I smolts in the seaward migration from the Naknek system in 1958 were smaller (91 mm.) than smolts of the same age in 1959 (97 mm.) and 1960 (99 mm.). Yet the 1958 group suffered the lowest total ocean mortality (from smolt to return—table 30). Age I smolts of the same year class also had the lowest total ocean mortality for the Ugashik system. The age I smolts in the 1958 Ugashik migration were larger, however, than those of 1959 and 1960. Any effect that smolt size in 1958 might have had on ocean mortality may have been masked by effects of environmental conditions especially conducive to good survival. Valid comparisons can be made only if groups of smolts of different sizes encounter conditions that are similar. Obviously, this situation is rare.

The data in table 30 afford an opportunity for comparison of ocean mortality for age I and age II smolts. Age II smolts without exception suffered a lower total mortality. How much of this difference can be attributed to their larger size rather than time of entry into the estuary cannot be determined, for age II smolts generally enter the sea at least 1 or 2 weeks before age I smolts.

RELATION BETWEEN FRESH-WATER AGE OF SMOLTS AND NUMBER OF ADULTS IN PARENT ESCAPEMENT

The tendency for slow-growing sockeye salmon juveniles to remain an additional year in fresh water before they migrate seaward has been documented (Foerster, 1937; Barnaby, 1944; Krogius and Krokhin, 1956; Koo, 1962). Data presented by Foerster (1944) suggest that in some studies, however, the tendency is reversed, and slow-growing sockeye salmon go to sea at age I. Also, an increase of a year or more in length of residence in fresh water accompanied an increase in growth rate that resulted from reduction of populations (Krogius, 1961). Little is known regarding the factors that cause juvenile sockeye salmon to migrate to sea.

Wood System

We might anticipate in this system a higher percentage of age II smolts from the larger spawning populations than from the smaller because of the inverse relation between number of parents and growth of progeny during their initial year of lake residence. This tendency is suggested by the data (fig. 20), but the progeny of the large escapement year, 1959, are an outstanding exception to the theory that slowly

TABLE 30.—*Ocean mortality of sockeye salmon by fresh-water age, Naknek and Ugashik systems*

System, year of seaward migration, and fresh-water age	Smolts in seaward migration	Average length	Average time in ocean	Total mortality
	Millions	*Mm.*	*Years*	*Percent*
Naknek system				
1958				
Age I	9.698	91	2.74	82.8
Age II	.362	114	2.25	28.7
Total	10.060	----	2.68	80.8
1959				
Age I	10.035	97	2.88	96.8
Age II	2.431	106	2.99	89.0
Total	12.466	----	2.93	95.2
1960				
Age I	3.553	99	2.64	92.2
Age II	3.118	109	2.56	67.2
Total	[1] 6.691	----	2.57	80.5
1961				
Age I	4.367	103	2.52	85.6
Age II	1.246	113	2.25	50.1
Total	5.613	----	2.39	77.6
Ugashik system				
1958				
Age I	11.438	93	2.17	69.7
Age II	.222	112	2.04	49.7
Total	11.660	----	2.17	69.3
1959				
Age I	2.520	90	2.78	95.4
Age II	.367	120	2.34	75.5
Total	2.887	----	2.59	92.8
1960				
Age I	3.286	90	2.61	95.6
Age II	2.163	108	2.21	81.4
Total	[1] 5.504	----	2.32	90.0
1961				
Age I	.776	90	2.70	93.5
Age II	3.026	112	2.14	85.3
Total	3.802	----	2.20	86.6

[1] The 1960 totals include age III smolts; none were recorded in other years.

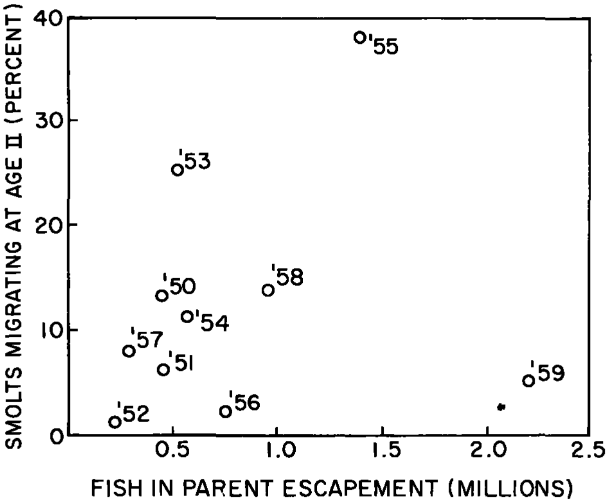

Figure 20.—Relation between proportion of total smolt production migrating at age II and number of sockeye salmon in parent escapement, Wood system, 1951-59. The number beside each point indicates the parent escapement year.

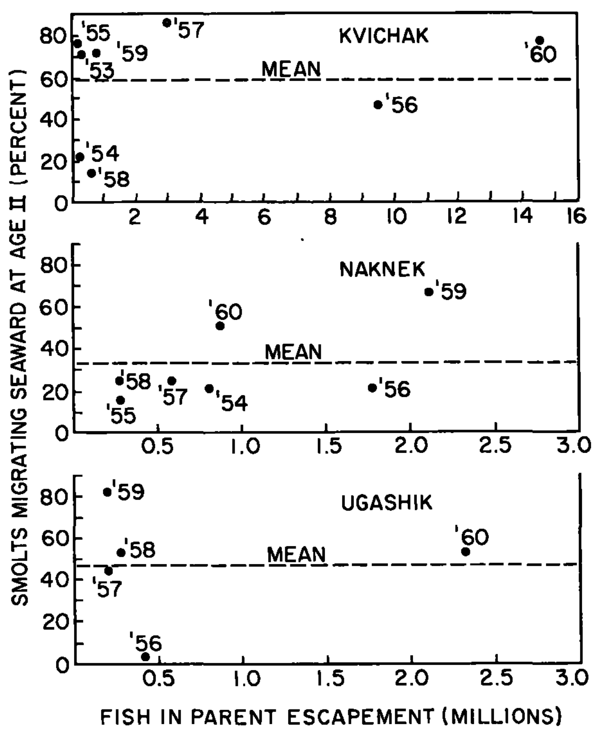

Figure 21.—Relation between proportion of progeny migrating as age II smolts and number of sockeye salmon in parent escapement, Kvichak system, 1953–60, Naknek system, 1954-60, and Ugashik system, 1958-60. Figure beside each point indicates year of parent escapement.

growing juveniles go to sea as age II smolts—these progeny grew slowly, but most went to sea at age I. The tow net indices of abundance of this year class as yearlings residing in the lake indicated a considerably higher percentage holdover than was indicated in the index sampling of smolts; some question exists, therefore, as to the accuracy of the index of abundance of age II smolts in the Wood River.

Kvichak System

The lowest recent escapements of sockeye salmon in the Kvichak system (1954 and 1958) produced mostly age I smolts, whereas the intermediate escapements (1953, 1955, 1957, 1959) produced mostly age II smolts. More of the progeny of the largest escapements (1952, 1956, 1960) tended to hold over to age II smolts as the escapement levels increased. The escapement of about 6 million fish in 1952 produced mostly age I smolts (or at least only fish of this age returned in large numbers). The only information we have on the smolt migration in the Kvichak River in 1954 (age I smolts from the 1952 escapement and age II from 1951) is that local residents in Levelock observed it to be "heavy." The 1956 escapement of 9.4 million produced 46 percent age II smolts, and the 1960 escapement of 14.6 million produced at least 78 percent age II smolts (fig. 21, table 27).

Naknek and Ugashik Systems

Data for the Naknek and Ugashik systems do not indicate that the percentage of sockeye salmon progeny migrating seaward as age II smolts is correlated with the number of fish in the parent escapement (fig. 21). The escapements in the Naknek system in 1954-58 ranged from 0.278 to 1.77 million, but the portion of age II smolts remained nearly constant between 16 and 25 percent.

The amount of growth added in the spring before the juveniles migrate as smolts is influenced by climate (Burgner, 1962). In years of favorable growing conditions early in the season, a higher percentage of yearlings may attain some size threshold for migration and leave as age I smolts. Thus, the influence of climate may tend to mask the relation between percentage holdover of progeny in the lakes and the number of parent spawners.

The major sockeye salmon systems on the east side of Bristol Bay tend to have concurrent fluctuations in the percentages of smolts migrating at age II, although the escapement levels vary somewhat independently. The proportions of age II smolts were at or below average for the escapement years 1954, 1956, and 1958 in the Naknek and Kvichak systems and for 1956 and 1958 in the Ugashik system (no data are available for Ugashik in 1954 and 1955). The percentages were above average in the three systems for the escapement years 1959 and 1960 (fig. 21). These concurrent fluctuations suggest the influence of general climatic factors.

RELATION BETWEEN RETURN AND ESCAPEMENT FOR THE NUSHAGAK FISHING DISTRICT

The relation between the numbers of adults returning (catch plus escapement) and the numbers in the parent escapement is of general interest, though frequently the intermediate statistic—numbers of smolts produced—is now available. The longest series of return-escapement data available is for the Nushagak fishing district (Igushik, Snake, Wood, and Nuyakuk Rivers combined) for the escapements of 1946-57 and the resulting returns (table 31).

TABLE 31.—*Number of sockeye salmon in parent escapements and resulting returns, Nushagak district, 1946-57*

Year of spawning	Fish in parent escapement	Fish in resulting return
	Thousands	*Thousands*
1946	4,719	1,207
1947	2,507	953
1948	2,091	1,484
1949	138	376
1950	573	1,751
1951	540	3,749
1952	434	1,574
1953	829	1,431
1954	692	3,122
1955	1,934	5,056
1956	1,212	2,129
1957	499	520

The return-escapement data from the Nushagak district were used to calculate the recruit-spawner relation (reproductive curves) of Schaefer (1954), Beverton and Holt (1957), and Ricker (1958). When the weighted sums of squared deviations of the observed data from each of the predicted curves were calculated, the deviations were least from the curve derived from Ricker's formula:

$$R = aEe^{-bE}$$

where R = number of sockeye salmon in the return, E = number in the parent escapement, and a and b are constants. For the Nushagak district return-escapement data, a = 3.951 and b = 0.6269. The calculated curve and original data for the Nushagak system are presented in figure 22. The estimated maximum yield is at the point where a line parallel to the replacement line is tangent to the curve—for the Nushagak district this point corresponds to an escapement of about 900,000 fish.

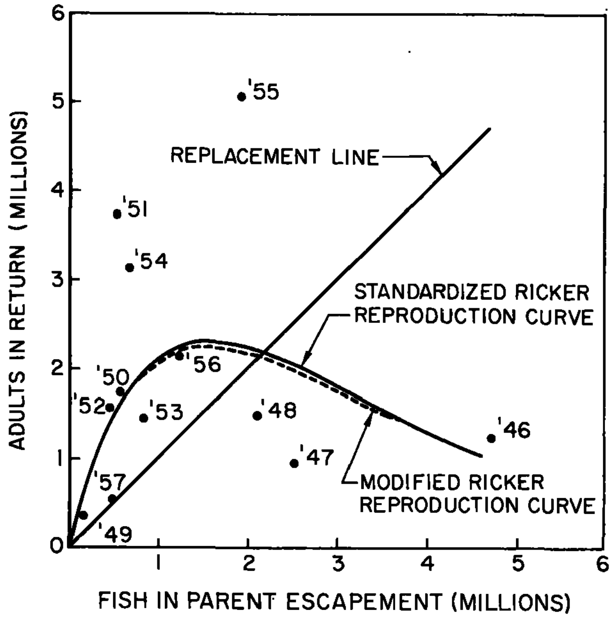

FIGURE 22.—Relation between number of sockeye salmon in return (catch plus escapement) and number in parent escapement, Nushagak fishing district, 1946-57. The number beside each point indicates the parent escapement year.

Addition of another parameter (n) to Ricker's formula as follows

$$R = aEe^{-bE^n}$$

gives greater flexibility in fitting the data. This modified version of Ricker's curve permits more exact fitting of a reproduction curve to observed data.

For the Nushagak data the relation was

$$R = 4.191Ee^{-0.699E^{0.936}}$$

The modification also gives an estimated optimum escapement of about 900,000. This curve is essentially the same as the standardized curve produced by the unmodified Ricker formula.

Ricker's formula can also be used to study the relation of return to potential egg deposition.

The numbers of 2- and 3-ocean female sockeye salmon in the escapements to the Nushagak district are known for 1946-57, and the potential egg deposition by each age group has been estimated (table 32). With potential egg deposition in billions as the independent variable (E), the formula which describes the relation between return and potential egg deposition is

$$R = 1.7456Ee^{-0.2699E}$$

The curves describing this relation permit the estimation of the optimum number of eggs on the spawning grounds. To convert number of eggs to number of spawners, an average fecundity of 4,000 eggs per female and a sex ratio of 1:1 are assumed. This calculation also yields an estimated optimum escapement of about 900,000 fish.

Since 1956 the high seas fishery has taken a substantial portion of the Bristol Bay sockeye salmon run each year. We approximated the high seas catch of fish from the Nushagak fishing district by prorating a portion of the estimated high seas catch of each ocean age group of Bristol Bay sockeye salmon according to the ratio of Nushagak district returns to the total Bristol Bay returns. The optimum escapement was then computed with these corrected returns; it was again found to be between 0.9 and 1.0 million fish.

TABLE 32.—*Number of 2-ocean and 3-ocean females in sockeye salmon escapements and estimated potential egg deposition, Nushagak district, 1946-57*

Year	Two-ocean females [1]		Three-ocean females [1]		Potential egg deposition
	Fish	Eggs	Fish	Eggs	
	Thousands	*Millions*	*Thousands*	*Millions*	*Millions*
1946	2,638	9,600	429	1,840	11,440
1947	850	3,093	704	3,020	6,113
1948	109	397	958	4,110	4,507
1949	32	116	50	215	331
1950	163	593	158	678	1,271
1951	110	400	187	802	1,202
1952	123	448	116	498	946
1953	126	459	338	1,450	1,909
1954	321	1,168	60	257	1,425
1955	836	3,042	228	978	4,020
1956	358	1,303	248	1,064	2,367
1957	115	418	164	704	1,122

[1] The average fecundities of 2- and 3-ocean females are 3,639 and 4,290 eggs on the assumption of mean lengths of 490 and 560 mm., respectively (Mathisen, 1962).

The four reproductive curves, all similar, indicate that an escapement of about 0.9 million sockeye salmon to the Nushagak district will yield the highest surplus of return over parent escapement. Escapements ranging from 0.6 to 1.2 million would theoretically produce about the same surplus because the curve is nearly flat in this area (fig. 22).

A drastic decline in the returns to the Nushagak district occurred in 1946-54. In fact, the returns did not equal the parent escapements in 1946-48. The returns from the relatively large escapements of these 3 years may have been abnormally low. If data from additional years indicate that it is more common for relatively large escapements to produce large returns, the calculated optimum escapement will be higher than 0.9 million.

The escapements of sockeye salmon to the Wood system have averaged about 70 percent of the total for the Nushagak district in recent years; this fact suggests an optimum escapement for the Wood system of about 630,000 sockeye (70 percent of 900,000). The only other period when escapements were counted for the Wood system was in 1908-19, when adults were counted at a weir on Wood River by the U.S. Bureau of Fisheries (no estimates of escapements were made for the other systems of the Nushagak district during these years). Although the average catch in the Nushagak district approached 5 million fish in 1908-19, escapements to the Wood system averaged only 750,000 sockeye salmon (Bower, 1920). The escapements to the Wood system from 1908 to 1919, therefore, averaged only slightly higher than our calculated optimum based on recent data. After 1919, the average catch in the Nushagak district dropped and remained at about 3 million until 1946—we have no satisfactory explanation for the higher production in 1908-19.

INTERPRETATION OF FINDINGS AND APPLICATION TO MANAGEMENT

In this final section we consider those characteristics of the sockeye salmon populations, the spawning grounds, and the nursery lakes that bear on carrying capacity and optimum escapement and, finally, give our best estimate of the optimum escapement for each system. The Mainland Systems tributary to Nushagak Bay—Igushik, Snake, Wood, and Nuyakuk—are discussed together. The Kvichak system of the Mainland group and the Peninsula Systems are discussed individually. The Alagnak and Egegik systems are not discussed.

Igushik, Snake, Wood, and Nuyakuk Systems

The Igushik, Snake, Wood, and Nuyakuk systems are all tributary to Nushagak Bay, the source of most of the fish taken in the Nushagak fishing district. These systems have a combined area of 867 km.^{2} distributed as follows: Igushik system, two lakes and 74 km.^{2}; Snake system, one lake and 89 km.^{2}; Wood system, five main lakes and 425 km.^{2}; and Nuyakuk system, three lakes and 279 km.^{2} The Nushagak fishery operates on a mixture of stocks from the four systems, and the catch for the district is assigned to each system on the basis of age composition and escapement levels. Therefore, the several systems of the district are evaluated in part as a unit.

In the early 1900's the annual commercial catch of sockeye salmon in the Nushagak district averaged about 5 million fish. It declined to an annual average of about 3 million in 1920-45 and suffered another marked decline in the next 10 years. Since 1955 the annual catch has been generally increasing but has not yet reached the pre-1945 levels.

The recent annual escapements to systems of Nushagak Bay have been distributed about as follows: Wood system, 70 percent; Igushik system, 23 percent; Nuyakuk system, 5 percent; and the Snake and several minor systems, 2 percent. The Nuyakuk and Snake systems historically may have produced at much higher levels.

Because of the selective action of the commercial fishery (larger fish are more susceptible to capture, and the time and route of migration and, therefore, exposure to the fishery may vary among the stocks), fishing mortality has not been uniform among the stocks in the Nushagak district. In 1948-60 the percentages of the large 3-ocean adults returning to the Wood, Igushik, and Nuyakuk systems were about 30, 60, and 70 percent, respectively (from data compiled by Burgner, footnote 7).

Studies of migration routes and timing of adult sockeye salmon in Nushagak Bay have shown that runs to the Wood and Igushik systems are partially segregated in the fishing areas (unpublished data of the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska). There is evidence that in the past, runs to the Igushik system may have been subject to lower fishing intensity than those from the Wood system. Were the intensity of fishing the same on the two runs, a higher percentage of the fish going to the Igushik system would be captured because of the predominance of the 3-ocean fish.

Since sockeye salmon in the escapement to the Nuyakuk system are primarily 3-ocean fish, and this run of larger fish is presumably fished as intensively as the run of smaller fish in the Wood system, the run to the Nuyakuk system probably suffers a consistently heavier fishing mortality than the run to the Wood system. Over the years this heavier mortality could have caused a decline in the relative contribution of the Nuyakuk system to the Nushagak fishery.

Certain spawning areas within the Wood system consistently contain more 3-ocean than 2-ocean fish. Thus, fishing mortality may vary between groups within a system as well as between systems.

Estimates of the capacities of the potential spawning areas in each system in the Nushagak district indicate that the potential area greatly exceeds that used at the current levels of escapement.

The factors that limit production of juvenile sockeye salmon in systems tributary to Nushagak Bay appear to lie in the rearing areas of the lakes rather than in the spawning areas. Our studies of the limnology of the lakes of these Mainland Systems indicate that they are generally poorer in minerals than lakes of the Peninsula Systems and have a higher calcium-to-sodium ratio. The watersheds in Nushagak Bay have mostly sedimentary rocks, which contribute smaller amounts of minerals to the lake waters than do the igneous rocks common in the watersheds on the peninsula—an area of recent volcanism. Lakes of the Igushik and Wood systems nevertheless ranked fairly high in primary productivity. Lakes in the Nuyakuk system had the highest mineral content of lakes tested in the Nushagak district, but rates of carbon fixation were low. Lakes of the Nushagak Bay area have less of an oceanic climate than the other lakes studied—ice covers the lakes longer, and thermal stratification during the summer is more pronounced.

Although the four main lakes in the Wood system have similar limnological characteristics and similar numbers of sockeye salmon per square kilometer of lake in the escapements, they contrast sharply in the proportion of kinds of spawning grounds. The similarities in numbers per unit of lake area in the average escapements indicate that the population level is controlled by the capacity of the nursery areas in each lake.

The production of juvenile sockeye salmon in the lakes of the Wood system increases linearly as the escapement increases, up to a density of 5,000 spawners per square kilometer of lake. Above this density the relation is no longer linear, and the production of juveniles per spawner declines when escapements exceed 6,000 per square kilometer. To have 5,000 spawners per square kilometer in all lakes of the system would require an escapement of 2,125,000 fish. At this density, however, the growth of juvenile salmon is considerably reduced. The mean length of age 0 fish in September is inversely related to the size of the parent escapement in each of the lakes of the Wood system. The mean length of age I smolts leaving the system also is inversely related to numbers in the parent escapement.

The combined effect of large populations of juveniles is to increase total mortality (freshwater and ocean) by causing many juveniles to remain an extra year in fresh water and to be of smaller average size for their age when they reach the ocean. This increase in mortality tends to make the population self limiting.

Threespine sticklebacks and Arctic char are the species of fish thought to have the most important effects on juvenile sockeye salmon in the Igushik, Snake, and Wood systems. In the Wood system, threespine sticklebacks and juvenile salmon use the same food supply, and, therefore, the growth of sticklebacks and age I salmon is reduced when large numbers of age 0 salmon are present. In all three systems Arctic char is the chief predator on small fish and probably eats substantial numbers of sticklebacks and juvenile salmon. The role of sticklebacks as a competitor for food and as a buffer between Arctic char and sockeye salmon and the effect of the Arctic char in keeping stickleback populations in check are not understood.

The recent average escapement of sockeye salmon per unit area of lake has been higher in the Igushik than in the Wood system. Juveniles from the larger escapements in the Igushik system have not grown as well (the smolts have not been as long) as those from the smaller escapements, so that here also the food supply apparently limits growth. Preliminary limnological studies show no marked difference in richness between the waters of the Igushik and Wood Lakes, and the greater concentration of spawners in the Igushik system appears to be caused by differences in the intensity of fishing on the two stocks.

Although primary productivity is low in the Nuyakuk system, escapement densities are probably too low to produce enough juvenile salmon to tax the food supply. Spawning areas appear to be far in excess of the present need. Relatively heavy fishing pressure probably has contributed to the present low level of the runs. Lake trout are more plentiful than Arctic char in the Nuyakuk system; the lake trout may be the primary predator on young salmon and sticklebacks.

The return-escapement relations of sockeye salmon in the Nushagak district in 1946-62 indicate that the optimum escapement is about 1 million fish, but that escapements between 600,000 and 1.2 million will produce near-optimum results.

If spawners were properly distributed, production in the Nushagak fishery could probably be increased by increasing the escapements. In an escapement of 1 million, for instance, if 70 percent of the fish went to the Wood system the lakes of the system would have an average density of 1,650 spawners per square kilometer. If distribution of spawners among the lakes were even, this density could be profitably exceeded. In years of uneven distribution of spawners, escapements should be held at a lower level to avoid overstocking of some rearing areas. Further, the mesh size of the gill nets used in the fishery could be regulated so as to obtain escapements of the two primary ocean-age groups in proportions that would more fully use all of the lakes of the Wood system and would give more protection to the populations of the Nuyakuk system. All the consequences of changes in the size of the mesh must be carefully studied, however, before this change is initiated.

Kvichak System

The Kvichak, the largest sockeye salmon system in Alaska, consists principally of two lakes, Iliamna and Clark, which total 2,889 km.^{2} The sizes of the runs in this system are cyclic. The range of the escapement in 1955-63 was 250,000 to 14.6 million. In 1931-61 the annual catch of the Naknek-Kvichak fishery averaged about 7.5 million fish. During the years of very large returns the Bristol Bay catch is dominated by salmon returning to the Kvichak system.

Within the Kvichak system there are many spawning groups of sockeye salmon. Adult fish of the different spawning groups are not segregated by time of passage into Iliamna Lake. The returnees generally have spent 1 or 2 years in fresh water and 2 or 3 years in the ocean; four principal age groups result. The age composition of the adults differs among the spawning grounds. In 1962, streams, with one major exception, contained significantly higher proportions of 2-ocean spawners than did beaches. It is not known if the relative proportion of 2- and 3-ocean fish is genetic. Fresh-water age, however, is probably determined more by the environment than by genetic factors.

Sockeye salmon generally spawn within the Kvichak system from early August to mid-October—a time span that probably reflects the adaptation of the various spawning populations to the different types of environments. Fry also emerge over an extended period. An indirect measure of the relative time of emergence is the size of juveniles during their first summer. The greatest range in time of emergence in the Kvichak system is in Lake Clark, where age 0 sockeye salmon in August range from 32 to more than 60 mm.

Although estimates of the amount of potential spawning area in the Kvichak system are incomplete, the available data indicate that the carrying capacity for this system is about 20.5 million spawners. Even the largest recorded escapement —14.6 million spawners in 1960—did not approach this figure (footnote 10). Between 1955 and 1963, the escapements in terms of number of adults per square kilometer of lake ranged from 84 in 1955 to 11,890 in 1960. The escapements to Lake Clark have not been well documented but are thought to be somewhat less than 10 percent of the total for the Kvichak system.

The greatest abundance of age 0 sockeye salmon in Iliamna Lake is in the vicinity of the heaviest spawning—in the east half of the lake. As the age and size of young fish increase they spread over the whole lake, and the largest fish are found in the western part.

Our knowledge of predators and potential food competitors in the Kvichak system is scanty. We do know that the distribution of threespine sticklebacks, the main potential competitor with juvenile sockeye salmon for food, is similar to that of age 0 salmon. Large populations of lake trout, Dolly Varden, Arctic char, and rainbow trout are also present. We suspect that competition for food and predation are important factors in the production of juvenile sockeye salmon in Iliamna Lake. The effect of predation would be much heavier in years of low abundance of juveniles and, thus, would tend to maintain the cyclic pattern of the Kvichak run.

Lakes of the Kvichak system are generally similar limnologically to lakes of the other Mainland Systems. The values for pH and concentrations of total dissolved solids and total alkalinity are intermediate among all systems. The rates of carbon fixation in Iliamna Lake were near the lower end of the range for mainland lakes, but in Lake Clark the rates were much reduced, probably because of the opacity of the water. The Kvichak system ranks in the same general position in numbers of spawners per lake area and in rate of carbon fixation per square meter, i.e., in the low range of the intermediate values.

Limnological studies in the Kvichak system span too short a time to permit comparisons between years. Future studies will determine whether dissolved minerals differ between off and peak years of the cycle; such differences could cause cyclic manifestations or, conversely, be caused by them.

Observations span too few years to indicate the relation between production of fry and parent escapement.

The relation between production of smolts and parent escapement varies, depending on whether we consider peak years or low years. The progeny of the 2 peak years studied, 1956 and 1960, had production indices of smolts of 181 and 150, respectively, although the escapement was almost 50 percent greater in 1960 than 1956. In both years, 2-ocean fish were dominant in the escapement—98 percent in 1956 and 99 percent in 1960. The maximum number of smolts is apparently produced at escapements below the 1960 level of 14.6 million (based on data collected through 1963). A reproduction curve based on the data of the 2 peak years 1956 and 1960 indicates that a range of escapements of 5 to 12 million will not drastically change the number of smolts produced.

A target escapement for peak years must be based on several factors in addition to the number of smolts produced. The data clearly show a negative linear relation between the average length of smolts produced and the escapement level—that is, growth is retarded through intraspecific competition for food when the population of juvenile salmon is too great. It is known that ocean survival is generally positively correlated with size of smolts at migration, although data do not exist to calculate the differences in survival rates for the Kvichak system.

Whether the progeny of large escapements migrate at age I or age II in the Kvichak system is probably determined by the size they attain during their first year in fresh water. The percentage of young salmon that migrate as age II increases as the population of young salmon in the nursery areas increases, although the percentage holdover to age II can be modified by the environment. Any extension of the average length of the fresh-water life in the Kvichak system will also extend the length of the reproductive cycle.

In assessing the optimum escapement for the Kvichak system, we must consider production in an entire cycle and not for just one outstanding year such as 1956. Before 1942, the returns of the peak years contained progeny of at least two (and usually three) escapements.

If we accept the thesis that the carrying capacity of the nursery areas limits the production of sockeye salmon in the Kvichak system, a rational approach to regulation would be to utilize the nursery areas to the fullest every year. This approach would require the presence of age I juveniles (fish that will migrate as age II smolts) in addition to the young-of-the-year, because only age I and older fish use the larger downlake portion of the nursery area. Historically, fish that went to the ocean as age II smolts made up almost 60 percent of the catches in the Naknek-Kvichak district (fish from the Kvichak system constituted the greater share of the catch in peak years).

If we also assume that the historical sequence of large and small escapements of the Kvichak cycle is the one which will yield the greatest return over many years, the following conclusion is unavoidable. The Kvichak system must be managed so as to provide at least two, and preferably three, successive large escapements preceded and followed by smaller escapements. The relative abundance of fish in the successive years of large escapements may be manipulated in such a manner as to provide about the same potential egg deposition each year. Because of the present conditions of the stocks, it may take two or more cycles to reestablish this pattern. Only after the historical pattern has been restored will it be possible to define an optimum escapement for the peak years, which may well be higher than that desirable during the present transition period.

Collection of vital statistics must be improved substantially to define the optimum escapement of sockeye salmon for the Kvichak system. To clarify the known vagaries of cycles of abundance and reproductive capacity, not only must better methods be devised to assess the escapement, the standing crop of young salmon in the lakes, and the smolt migration but many other factors must be evaluated.

Naknek System

The Naknek system consists of a series of interconnected lakes totaling 790 km.[2] Drainage to Bristol Bay is via the Naknek River into the Naknek-Kvichak fishing district. Adult sockeye salmon returning to the Naknek system mingle in the fishing area in Bristol Bay with others bound for the Kvichak and Alagnak systems. Catches were reported for the Naknek-Kvichak district as a whole until recent years, when portions of the catch were assigned to the respective river systems of the district on the basis of age composition and escapement. Since 1957 the run to the Naknek River has averaged 1.6 million fish—the commercial catch averaged 760,000 and the escapement 840,000.

The escapement of sockeye salmon to the Naknek system is composed mainly of 2- and 3-ocean fish, the relative strength of the groups varies widely from year to year. Fresh-water and ocean ages and numerical strength of the various spawning units within the system fluctuate somewhat independently of each other. The various spawning units seem to pass through the trunk river at about the same time.

Estimates of the total capacity of the potential spawning areas of the system are in excess of the average escapement for the past 10 years. Only limited data are available on the escapement of sockeye salmon per unit lake area for each lake, but great variations are known to exist among the lakes of the system. In 1961 Coville Lake received 6,600 spawners per square kilometer of lake. This density of spawners produced a catch of 150 age 0 fish per tow in 1962. North Arm had a spawner density of 55 per square kilometer of lake in 1961 and a catch of age 0 fish of 0.5 per tow in 1962. Migration of presmolt juveniles, however, results in the accumulation of young in the rearing areas of Naknek Lake regardless of the distribution of spawners. The studies have run too few years to determine the relation between the abundance of age 0 fish and various levels of the parent population.

The abundance and growth of juvenile sockeye salmon and other species and the primary productivity of the lakes varied between years and among the lakes. Differences in primary productivity between years were accompanied by marked differences in growth of juvenile sockeye salmon, independent of their abundance. The abundance of juveniles was greater in 1962 than in 1961, but the rate of growth was greater in 1962. The primary productivity, on the other hand, was greater in 1962 than in 1961 because of differences in climate. The species and abundance of fish associated with the juvenile sockeye salmon vary among the lakes and among areas within the lakes. Threespine sticklebacks were universally present, and their abundance was matched only by pond smelt in Lake Coville and pygmy whitefish in Brooks Lake. The areas of the Naknek system that yielded the largest catches of juvenile sockeye salmon or the fastest growing juveniles also yielded the largest catches of associated species. The role of the associated species as competitors or predators, or as buffers between predators and juvenile sockeye salmon, is unknown. Several potentially important predator fish are present in the Naknek system, but their significance is not known.

Lakes of the Naknek system have limnological characteristics that fall between those that are characteristic of lakes of the Mainland Systems and also the other lakes of the Peninsula Systems. Lakes of the Naknek system are richer than the mainland lakes in total dissolved solids, total alkalinity, sodium, silica, iron, and manganese and generally richer in many of the other items measured. The large quantities of igneous materials in the watershed and wind-borne materials from the ocean apparently contribute substantially to this richness. These lakes are influenced by the oceanic climate; their ice covers break up relatively early in the spring. Thermal stratification is seldom pronounced, and strong wind action mixes surface waters with deeper waters from time to time during the summer. Rates of carbon fixation by photosynthesis are relatively high, and the standing crops of phytoplankton are similar to those of other peninsula lakes. Because of differences in drainage and basin types, lakes in the Naknek system nearly encompass the range of types of sockeye salmon nursery lakes along the Alaska Peninsula, although Chignik and Black Lakes rank higher than any Naknek lakes in photosynthetic rates and chlorophyll values.

Data on the relation of smolt production to escapement in the Naknek system in 1954-60 show an increase in numbers of smolts produced with increased escapement up to about 1 million fish. Accurate determination of optimum escapement from reproduction curves based on smolt-escapement relations is dependent on knowledge of mortality rates in the ocean. For the Naknek system, estimates of total ocean mortality for sockeye salmon from 3 years of smolt migration ranged from 77.6 percent to 95.2 percent and averaged 83.5 percent (no correction for a high seas fishery).

If total ocean mortalities range around 83.5 percent, maximum yields may be realized with escapements of 0.6 to 1.0 million. The presently known spawning areas have a capacity of about 1.3 million spawners. Escapement levels do not appear to have any effect on the size of age I smolts or the percentage of the progeny that migrates seaward as age II smolts. The Naknek lakes are richer in basic nutrients and generally have higher rates of phytoplankton production than the mainland lakes. Major differences in climate between years probably influence the growth of young sockeye salmon more strongly than do differences in their density. At present we do not know whether the upper limit on the production of smolts is imposed by the capacities of the spawning areas, the capacities of the nursery areas, or a combination of several factors that may or may not include these two.

Ugashik System

The Ugashik system on the Alaska Peninsula is the southernmost of the major river systems that drain into Bristol Bay. The system consists of two lakes, Upper and Lower Ugashik, which total 385 km.^{2} Our studies in the Ugashik system included limnological observations, continuation of studies of smolts, catch, and escapement, and analysis of data previously collected.

Commercial fishing began in the Ugashik district in 1889 when several small salteries were established. Unlike the other districts of Bristol Bay, the Ugashik fishery developed rapidly and experienced a decline in the catch several years before peak production was achieved in the Egegik and Naknek-Kvichak districts.

The Ugashik also differs from the other Bristol Bay systems in that it has had several periods of peak production of sockeye salmon. The first was early—from 1899 to 1903—when the annual catch averaged 1,114,400 fish. A period of gradual decline followed, and in 1911 the catch reached its lowest point—about 113,000 fish. Between 1904 and 1916 the annual catch averaged 368,400; from 1917 to 1923, it rose to about 882,000. The 1924-42 period was characterized by generally low catches. A regulatory closure of the fishery occurred in 1935. Fishing effort in the district was greatly curtailed in 1940 and 1941 because of the war. Annual catches in 1942-48 averaged nearly 1 million fish. Since 1949, with a few exceptions (1953, 1954, and 1960) the annual catch has averaged less than 500,000.

Escapement counts were obtained for the Ugashik system in 1925-32 and 1949-63. Escapements during the earlier period ranged from 149,000 in 1929 to 1,380,000 in 1931 and averaged about 533,000 fish; escapements in the later period varied from 77,000 to 2,294,000 and averaged about 574,000.

The Ugashik system, in common with other Peninsula Systems, is currently supporting escapement densities that average about 1,300 sockeye salmon per square kilometer of lake. This density is about one-sixth of that observed in the Chignik and Karluk systems and about one-half of that of the Wood system. Most of the sockeye salmon of the Ugashik system spawn in tributary streams that drain the foothills of the Aleutian Range.

Limnological observations, though not as extensive as those made in other systems, indicate that the Ugashik lakes rank low in total dissolved solids, phytoplankton abundance, and primary productivity.

Estimates of the numbers, ages, and sizes of smolts have been obtained annually since 1958. We cannot see a relation between the size of smolts and parent escapement nor between the proportions of each year's progeny that migrate seaward at age II and escapement. It is possible that relationships are masked by year-to-year variations in environmental conditions.

Although the size of smolts in the Ugashik system apparently is not related to escapement, the number of smolts produced is. The greatest recorded escapement (2.3 million fish in 1960) produced the greatest recorded smolt migration (31.40 million). Low escapements of 215,000 in 1957 and 219,000 in 1959 resulted in 4.33 million and 4.08 million smolts, respectively. The escapement of 425,000 fish in 1956 produced about 12 million smolts. Because no escapements have been of intermediate size, it is not possible to define precisely the smolt-escapement relation over the entire range. All that can be determined now is that smolt production increases markedly with increasing escapement up to about one-half million. The results from the large 1960 escapement show only that increases in numbers of smolts can be realized from escapements greater than one-half million.

The best that can be inferred from the suggested form of the smolt-escapement relation is that the target escapement should be at least 500,000.

Chignik System

The history of the fishery on sockeye salmon runs of the Chignik system is similar to that of the Nushagak district in that the catch remained high until the 1920's, then dropped to a lower level from which it has never recovered.

The two lakes in the Chignik system—Black and Chignik—have dissimilar physical characteristics. Black Lake (mean depth, 3 m.) is the shallowest of the lakes we studied. Chignik Lake has less area than Black Lake but has six times the volume. The total area of the two lakes is 61 km.^{2}

Chignik Lake supports an unusually large escapement of sockeye salmon per unit lake area. The average escapement of 14,000 per square kilometer of lake for 1955-62 is the highest for the lakes studied. Black Lake had an average escapement of about 4,600 per square kilometer over the same period.

Chignik and Black Lakes had the highest primary productivity and chlorophyll *a* concentrations of the lakes studied. The richness of the lakes is undoubtedly the main reason that the

Chignik system has been able to produce large numbers of sockeye salmon per unit lake area.

Although spawning in the Chignik system is primarily in streams, about one-third of the spawning in Chignik Lake is on the beaches. Most of the stream spawning is in the longer streams. No estimates have been made of potential spawning area, but the level of sockeye salmon production by the Chignik system does not appear to be controlled by the capacity of the spawning grounds.

The runs to Black and Chignik Lakes are segregated in time of passage through the fishery. This segregation is significant because it permits control of the escapement to each lake by regulation of the fishery.

The adults returning to the Chignik system are predominantly 3-ocean fish.

The average time juvenile sockeye salmon remain in fresh water is different in the two lakes; the smolts from Black Lake are mostly age I, and those from Chignik Lake are mostly age II.

Age 0 sockeye salmon are reared in three major areas in the Chignik system—Black Lake, Chignik Lake, and Chignik Lagoon. Most of the juvenile sockeye salmon that originate in Black Lake remain there to the smolt stage, although some age 0 fish migrate into Chignik Lake. The brackish water of Chignik Lagoon is the rearing area for a significant part of the Chignik Lake progeny.

The growth of juvenile sockeye salmon is inversely related to the density of the parent population within each of the two lakes. Accurate indexing of the abundance of migrating smolts has not been achieved in the Chignik system, but studies of the size and age composition of the smolts and of abundance and growth of juveniles in the lakes are in agreement. Both studies indicate an increase in abundance, a reduction in growth rate, and an increase in average length of fresh-water residence for progeny of larger escapements. Also, the density of spawners is generally lower, and the juveniles grow faster in Black Lake than in Chignik Lake.

The juvenile sockeye salmon produced by the Chignik system are larger than those of the Wood system at comparable parent population densities—an indication that growing conditions are more favorable in the Chignik system.

Several species of fish other than sockeye salmon are also present in the system. Threespine and ninespine sticklebacks and pond smelt are present and are potential competitors of sockeye salmon for food; they also may act as buffer species between sockeye salmon and predators. The potential competitors are much more abundant in Black than in Chignik Lake; possibly they are held in check in Chignik Lake by the great abundance of young sockeye salmon. Young coho salmon and Dolly Varden, also present, are the system's principal predators on juvenile sockeye salmon. Arctic char and lake trout are not present.

The abundance of associated species and the growth of juvenile sockeye salmon indicate that recent escapements in the Chignik system as a whole have been adequate, but apportionment of the escapement to the two lakes must be considered. Low escapements to Black Lake and the resultant underutilization of its nursery areas by juvenile sockeye salmon may be one reason for the large populations of potential competitors in this lake. In contrast, the relatively high escapements to Chignik Lake have resulted in a shortage of food that has undoubtedly led to the reduced growth and survival of juvenile sockeye salmon and perhaps kept the populations of potential competitors low. The optimum escapement to Black Lake, therefore, is greater than the present level of escapement; to Chignik Lake it is considerably less than the larger escapements of recent years.

Suggested target escapements for each lake are based on the relative success of recent escapements and the effective rearing areas of the lakes. Although the total area of Black Lake is 39 $km.^2$, the effective rearing area is only about 30 $km.^2$ because of extensive shoals not utilized by juvenile salmon. We recommend that escapements to Black Lake should be increased from the recent average of 4,600 per square kilometer of effective rearing area to 6,000 to 8,000, or a total of 180,000 to 240,000 fish.[18] The effective rearing area of Chignik Lake as determined from tow net catches includes the entire surface area of 22 $km.^2$ The suggested escapement to Chignik Lake is 8,000 to 10,000 per square kilometer or a total of 180,000 to 220,000 fish. This escapement is a reduction from the average in

[18] Recent studies of distribution and growth of species which compete with juvenile sockeye salmon for food and space in the Chignik system suggest that the populations of competitors would be reduced by larger populations of juvenile salmon. Therefore, the attainment of the recommended escapements might make it possible to increase escapements considerably above 240,000.

recent years of 14,000 adults per square kilometer.

Karluk System

The Karluk River sockeye salmon run has been historically among the more valuable in Alaska. Commercial fishing began at Karluk in 1882. Several million fish were harvested annually in the early years of the fishery (1885-95), but a long-term decline began after the turn of the century. This declining trend continued in spite of attempts to maintain escapement levels; in recent years, the total run seldom has exceeded 1 million fish.

The timing of the run of adult sockeye salmon to the Karluk system is similar to that of the Chignik system in that it extends 4 to 5 months. The Karluk run has late spring and fall peaks. Beach spawning is insignificant in most years, and most of the spawners are dispersed over the lateral and terminal tributaries and the outlet, Karluk River. Occasionally, however, as much as 25 percent of the escapement may use beach areas. Certain terminal streams and beach areas are used by both spring and fall spawners. The lateral tributaries, however, are used almost exclusively by spring spawners.

The individual spawning areas in the Karluk system are occupied continuously for about 5 weeks to 5 months by a succession of spawners, with the result that many more spawners are accommodated than could be if they all spawned in 2 or 3 weeks. This occupation by successive waves of spawners introduces questions as to the effect of superimposition of redd sites on the success of spawning. We do not know the answers.

The Karluk Lake watershed is composed of sedimentary rock and is so situated as to be strongly influenced by the oceanic climate. The lake waters originate from snowmelt and surface runoff. Two small lakes, Thumb and O'Malley, drain into separate arms of Karluk Lake.

The concentrations of most of the chemical constituents in Karluk Lake are similar to those of lakes of the Alaska Peninsula, particularly the high concentration of sodium and the low levels of nitrate nitrogen and total alkalinity. Of all the lakes studied, however, Karluk Lake is second only to those of the Chignik system in productivity as measured by rate of carbon fixation and content of chlorophyll *a*. The very high productivity is paralleled by the rank of the Karluk system as first in density of spawners per unit lake area.

The growth of juvenile sockeye salmon was correlated positively with changes in lake productivity and negatively with the abundance of juveniles in 1961 and 1962. Because of varying numerical strength of young from a protracted period of fry emergence and migration, growth data are difficult to interpret.

The only abundant potential competitor with juvenile sockeye salmon for food in Karluk Lake is the threespine stickleback. Arctic char and Dolly Varden are the most abundant predators.

The estimate of numbers of smolts produced in Karluk Lake each year in 1961-63 was about 1.5 million. Numbers of smolts and numbers of adults in the parent escapements were not related; the parent escapements ranged from 210,000 to 435,000 fish.

Data on fluctuations in abundance of sockeye salmon in Karluk Lake have been analyzed in some detail by Barnaby (1944) and Rounsefell (1958). Portions of these data that deal specifically with the return-escapement relation have been reported in a bulletin of the International North Pacific Fisheries Commission (1962), where it is concluded that in the past, escapements of about 750,000 fish have produced the largest surplus of return over escapement. The expanded research in 1961 and 1962 did not yield new information that would alter this conclusion. Recent work serves, however, to emphasize that restoration of the Karluk runs to former high levels will require considerably more than mere manipulation of numbers of spawners in the escapement. Evidence suggests that the average reproductive capacity of the sockeye salmon in the Karluk system was reduced while the run was in decline. Current research at Karluk is directed toward determination of the cause of this reduction.

ACKNOWLEDGMENTS

The salmon canning industry made substantial contributions of additional operating funds for FRI programs, which it had been supporting partially, and provided funds for equipment, camp, and laboratory facilities in the Nushagak, Kvichak, and Chignik areas. This support made possible a larger and more detailed program of research.

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