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GROWTH OF SOCKEYE SALMON IN RELATION TO ABUNDANCE IN THE KVICHAK DISTRICT, BRISTOL BAY, ALASKA[1]

By

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INTRODUCTION

Intensive exploitation of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) by both domestic and high-seas fishing has spurred the effort to formulate rational management procedures. Regardless of approaches to the formulation, two elements are indispensable: an accurate forecast of the run of adult salmon and a reliable estimate of the escapement that will produce the largest return.

Sockeye salmon leave the Kvichak River for the sea either in the second year of life (age I smolts) or in the third year (age II smolts). Nearly all survivors from both groups return after two or three years in the sea; thus practically all of the total production from an escapement is realized in instalments of 4, 5, or 6 years after the year of spawning. (Other age groups are generally negligible in number.)

RICKER (1962) compiled the available data on ocean survival of smolts and average length at the time of seaward migration for both North American and Asian sockeye salmon stocks. Survival generally was highest for the stocks that produced the largest smolts; but within one river system survival was generally not related to size. Where there is cyclic variability in run magnitude, as in the Kvichak River stock, a new dimension is added. Since the progeny from a given year of spawning return 4, 5, and 6 years later, the cyclic pattern of salmon abundance would not persist if the survival rate of the progeny were not higher in the peak cycle year than in off cycle years. For the Kvichak stock, there is a return of more than three mature fish per spawner of the peak year class, but of only

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one or two mature fish per spawner of the off year classes or even less. On the other hand, smolts during the peak cycle year may be 10–20 per cent smaller in length on the average than smolts during the off cycle years.

The interactions between the strength of year classes of salmon, primary and secondary production in the nursery area, and abundance of predators and food competitors, which result in a cyclic run abundance in the Kvichak River, can best be studied by a simulation model. But if such a model shall be useful for predictive purposes it must be a realistic one and not only one of verisimilitude. In order to achieve this a number of functional relationships must be determined. The present paper represents an effort to this end by discussing some functional relationships between growth of salmon and population density in the Kvichak River system.

SMOLT SIZE IN RELATION TO MAGNITUDE OF PARENT ESCAPEMENT

It has been observed in many river systems in North America and in Kamchatka that an inverse relationship exists between the average size of smolts and population size (Krogius 1961, Johnson 1965, Burgner *et al.* 1969).

During the period 1953–1968, for which data are available on escapement and corresponding smolt abundance for the Kvichak stock, there were seven years in which less than one million fish escaped to the spawning grounds, three years in which escapements ranged from 2.5 to 3.7 million spawners, and three years in which escapements were exceptionally large. In 1956 the escapement numbered 9.4 million fish; in 1960, it was 14.6 million fish; and in 1965, it was 24.3 million spawners (Table 1). The total number of smolts produced increased over these last three cycle years, but the number of smolts produced per spawner declined. Nevertheless, it is informative to determine whether the average length of smolts has been a function of escapement size over the years.

The average lengths of age I smolts and age II smolts are plotted against the magnitudes of parent escapements in Fig. 1. In both cases, average length decreased as parent escapement increased until parent escapement reached a certain level, after which average length stabilized. For age I smolts this level was about four million spawners. Despite exceptionally large escapements in 1956, 1960, and 1965, the average length of age I smolts produced varied only from 82 to 86 mm. For age II smolts, the level at which the smolt length stabilized itself was about nine million fish. For the two largest escapements during the period under consideration, the average length of age II smolts was about 100 mm.

Table 1. Sockeye salmon escapements and average lengths of smolts produced, Kvichak River, 1952–1965.[1]

Year	Escapement, thousands	Average length of smolts, mm		Index catch of age I and II smolts, thousands
		Age I	Age II	
1952	5,970	—	109	—
1953	321	89	116	66
1954	241	92	120	39
1955	250	96	114	89
1956	9,443	84	99	6,045
1957	2,964	80	108	639
1958	535	91	117	72
1959	680	92	110	98
1960	14,630	82	98	5,247
1961	3,706	83	108	1,717
1962	2,581	87	109	2,206
1963	339	90	114	89
1964	957	94	118	475
1965	24,326	86	105	8,341

[1] Data for 1952–1964 are from PENNOYER and STEWART (1967) and from ALASKA DEPARTMENT OF FISH AND GAME (1968); remaining values are preliminary estimates furnished by the Alaska Department of Fish and Game.

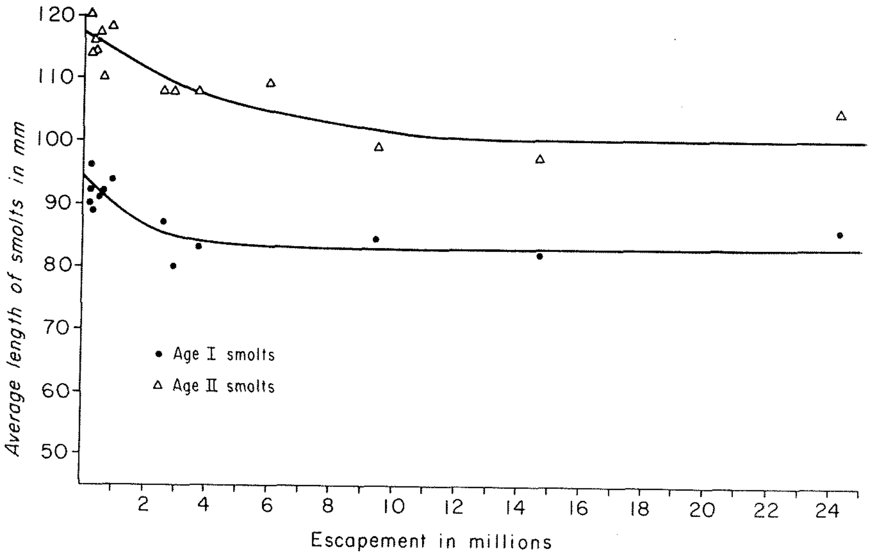

Fig. 1. Average lengths of age I and age II smolts as a function of parent escapement size in the Kvichak River, 1955–1968. Equation for the curve fitted to the age I smolt data is $y = 83.22 + 11.26 \cdot e^{-.63x}$, and that for the age II smolt data is $y = 101.02 + 16.22 \cdot e^{-.24x}$.

The observed relationships are expressed by negative exponential curves of the form $y = a + be^{-cx}$, fitted to the data by a non-linear regression technique (Gales 1964).

It may be assumed that the escapement of close to 25 million spawners in 1965 is perhaps the largest escapement to the Kvichak River since the inception of the commercial fishery. The data suggest that, for the observed escapement range, the young fish will not migrate to sea as age I smolts unless they have reached an average length of about 80–85 mm, and smolts of age II have reached an average length of about 100 mm or more. Since kokanee salmon have never been observed in Iliamna Lake and age III smolts constitute a negligible group, either the food supply is sufficient for all fish which do not migrate at age I to reach an average size of about 100 mm or the slower growing fish are more easily captured by predators.

The statement on average minimum size at time of migration as age I smolts can be verified by observations on the juvenile salmon in Iliamna Lake. Personnel of the Fisheries Research Institute have sampled the juvenile salmon in Iliamna Lake every year in August and September since 1962 (Kerns 1965, 1966, 1968). The maximum and average sample mean lengths of fingerlings calculated as of September 1 are given in Table 2. Also given is the computed daily increase in length, based on repeated sampling each year at the same locality from the latter half of the summer season; this growth rate is assumed to have been maintained from June to September. Such data may yield a higher growth rate during the first part of the summer than actually took place. In some years the maximum sample mean length of fingerlings, computed as of June 1, approached the length at which smolts migrate to sea as age I, but the computed average lengths were substantially smaller with one exception. In Iliamna Lake, the smolt out-migration is brief and essenti-

Table 2. Growth in length of yearling sockeye salmon in Iliamna Lake from June to September, 1962–1967.

Year	Sample mean length on Sept. 1, mm		Estimated average daily increase in length, mm	Calculated length on June 1, mm	
	Maximum	Average		Maximum	Average
1962	102.1	90.8	.18	85.9	74.6
1963	104.1	100.0	.20	86.1	82.0
1964	108.8	96.2	.37	75.5	62.9
1965	117.3	110.3	.58	65.1	58.1
1966	114.8	110.7	.56	64.4	60.3
1967	104.0	90.4	.27	79.7	66.1

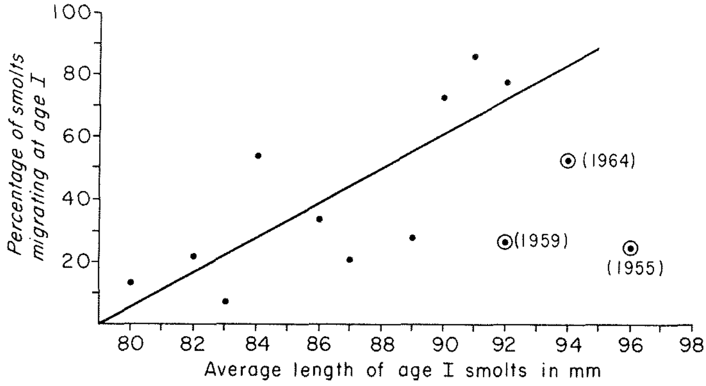

Fig. 2. Regression line of percentage of smolts migrating at age I on the average size of age I smolts, 1953–1965. Data for the years 1955, 1959, and 1964 are not included in the calculation of the regression line $y = -437.3 + 5.54x$.

ally over by the first week of June, unlike in some other lakes of Bristol Bay, where migration may extend through the month of June and part of July. In the Kvichak River system, therefore, it is possible to specify the time at which smolts must average a minimum size to migrate.

Finally, one could expect the proportion of age I smolts produced from an escapement to increase with an increase in average length of age I smolts. Data published by PENNOYER and STEWART (1967) on average smolt length and proportions of smolts of age I and age II produced from an escapement have been plotted in Fig. 2. At first glance a linear relationship seems to be nonexistent. However, when the three aberrant points representing the proportions of smolts from the spawnings in 1955, 1959, and 1964 migrating at age I are excluded, a reasonably well-defined relationship emerges. The larger the average length of age I smolts, the larger the proportion of the year class that migrated at this age.

An explanation for the three aberrant points must be sought elsewhere. All three represent production from a pre-peak year class of the Kvichak River sockeye salmon cycle. The low percentages of age I smolts produced from the spawning in 1955, 1959, and 1964 should be viewed perhaps as a result of the cyclic variability in run magnitude. The age II smolts spent their last year of freshwater residence together with the fry of the subsequent peak year, and they may have survived better than smolts in the other years of the cycle since the rate of primary production shows a tendency to increase in the year following a peak cycle year (BAXTER 1968).

Furthermore, the proportion of fish migrating to sea as age I smolts may only increase linearly with length of the juvenile salmon over a certain size range. In years with a low biomass of juvenile salmon and a high growth rate and average length, the proportion of age I smolts produced from an escapement may decrease in a parabolic manner. This presumably was the case for the three aberrant years prior to the peak cycle year. Krogius (1961) has presented similar data from Lake Kuril pointing to a prolonged freshwater residence in years with low biomass of juvenile salmon relative to the food supply and hence increased growth rate. The secondary production in Iliamna Lake has remained fairly stable since observation started in 1962. Such suggestions can only be verified by further studies, but the substantially identical relationship for the three pre-peak years for which data exist strongly suggests that such a mechanism must be operating.

LENGTH AT MATURITY OF THE KVICHAK SOCKEYE SALMON

Since 1957 the mean length of the returning mature sockeye salmon to the Kvichak River has varied from about 540 to 580 mm for three-ocean females and from about 480 to 520 mm for the two-ocean females. Although the males are larger, a similar range of size variation has been observed for the males (Table 3). Length is defined as the distance from the middle of the eye to the fork of the tail.

Population density has been expressed as the total size of the run in any one year by combining the catch and escapement of all age groups which returned to the Kvichak River in a year. A negative exponential

Table 3. Average lengths of Kvichak sockeye salmon in the escapements, 1957–1968 (mm).

Year	Total Kvichak/Naknek run in millions	Male		Female	
		2-ocean	3-ocean	2-ocean	3-ocean
1957	8.183	518.6	571.6	503.2	552.0
1958	1.830	537.2	591.1	516.8	567.7
1959	5.427	521.4	582.4	510.5	558.9
1960	26.547	488.1	567.5	471.4	535.0
1961	12.314	515.1	574.1	503.6	563.2
1962	5.676	524.0	578.3	511.3	562.3
1963	2.405	529.3	599.1	513.7	571.7
1964	4.799	501.7	577.4	487.1	567.2
1965	44.358	493.9	560.8	477.2	540.4
1966	10.364	521.8	577.4	503.8	556.0
1967	6.512	537.6	597.1	518.6	578.1
1968	4.963	510.9	591.1	493.3	574.8

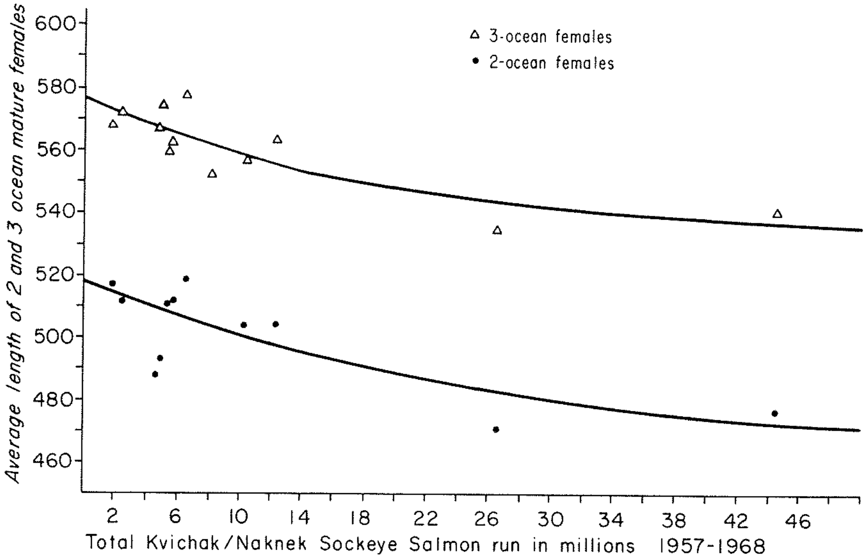

Fig. 3. Average length of returning female sockeye salmon as a function of total return, 1957–1967. Equation for two-ocean females is $y = 462.64 + 53.64 \cdot e^{-.037x}$ and that for three-ocean females is $y = 532.23 + 44.61 \cdot e^{-.53x}$.

relationship was found between the two variables for runs up to 26 million fish; but no further reduction in average length was observed, for example, in 1965 when 44 million fish returned (Fig. 3).

Changes in average length of a given age group of mature salmon have been described for other populations. Krogius (1960) describes regular periodic fluctuations in length of sockeye salmon from Lake Dalnee. Birman (1964) brings out the interesting fact that not only is length of the salmon feeding in the sea inversely related to population density, but the total quantity of feeding salmon of all species affect the final size of a species, even in a year where this species may not be particularly abundant. He demonstrated that the size of the mature Bolsheret chum salmon was inversely related to the magnitude of the pink salmon runs in the same year. Egorova (1964) relates age at maturity of the Ozernaya sockeye inversely to the magnitude of the runs.

The authors cited above relate these manifestations to competition for food. However, it does not seem reasonable to postulate a general shortage of food in the ocean since the two ocean age groups of Kvichak sockeye salmon together number in any year at most between one and two hundred million individuals which migrate widely. Even if all species of salmon were considered together the magnitude is small compared with the abundance of other marine species. Still this does not preclude the existence of local shortage of food.

Table 4. Average index catches and weights of pelagic fish in Iliamna Lake, 1962–1967.

Year	Fry		Yearlings		Threespine sticklebacks		Relative total biomass
	Average catch per set	Average weight, in g	Average catch per set	Average weight, in g	Average catch per set	Average weight, in g	
1962	21.8	1.3	93.3	9.4	141.3	.8	1018
1963	27.8	2.1	12.0	9.0	24.3	.8	186
1964	.9	1.5	20.6	8.0	96.3	.9	253
1965	4.4	2.2	3.6	11.2	86.7	.9	128
1966	151.7	1.5	.9	13.1	40.4	.7	268
1967	67.6	2.1	80.9	6.6	38.3	.7	703
Average for all years		1.78		9.55		.8	

In the sea it is a difficult task to ascertain the abundance of food at one specific place and at a specified time. But, since growth of juvenile salmon in the Iliamna Lake nursery area and length at seaward migration seemingly follow the same pattern as growth of maturing salmon and their length at maturity in the sea, these problems can better be studied in a restricted freshwater ecosystem such as that of Iliamna Lake.

GROWTH OF JUVENILE SOCKEYE SALMON IN RELATION TO FOOD SUPPLY

Threespine sticklebacks, sockeye salmon fry and yearlings inhabit the limnetic zone of Iliamna Lake. Ninespine sticklebacks, smelts, and a few fish of other species are found also; but they make up a negligible part of the biomass of pelagic fish and can be ignored. The average weights of age I threespine sticklebacks and sockeye fry and yearlings in index catches in the years 1962–1967 are given in Table 4, based on data published by Kerns (1965, 1966, 1968). Whereas the average weight of age I sticklebacks has remained almost the same in the last 6 years, the weights of fry and yearlings have varied and have reflected changes in total biomass of limnetic fish. For all years, the average weight of fry was 1.78 and that of yearlings 9.55, or a ratio of 5 : 4. But within the lake

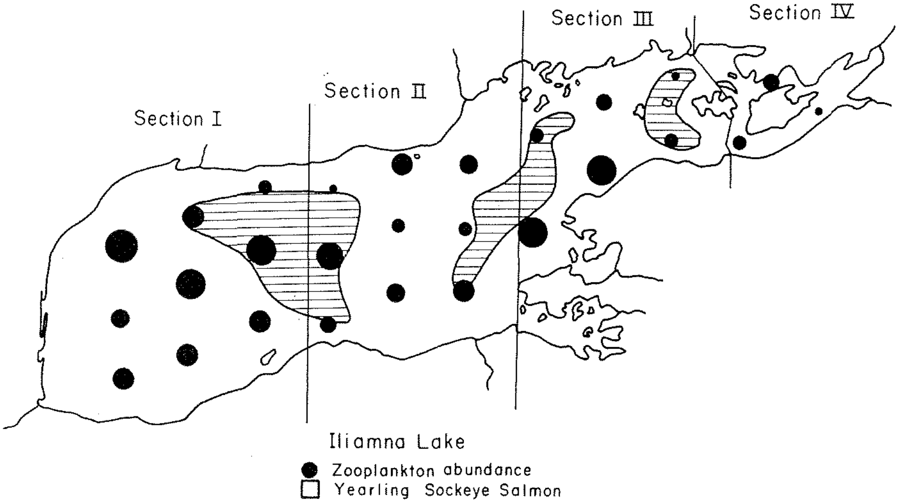

Fig. 4. Standing crop of zooplankters and maximum density of sockeye salmon yearlings in Iliamna Lake, August, 1967. Cross-hatched areas correspond to average catches of 300 yearlings or more per tow. Smallest circle indicates 3–4,000 and largest circle, 12–14,000 zooplankters per cubic meter. (Data on fish abundance given by Kerns (1968) and plankton abundance from unpublished data provided by Mr. T. Gunnerød.)

there are great differences in length. For the sake of convenience the lake is divided into four main sections, numbered I to IV, from west to east (Fig. 4). It has been known for some time that the average length of yearlings in any one year in the western part of the lake (section I) is greater by about 20 per cent than that of fingerlings in the eastern part (section IV) (Kerns *et al.* 1963). These differences can be related to the standing crop of zooplankton which has been estimated from samples taken with a No. 6 mesh, $\frac{1}{2}$-m open net from bottom or 100 m to surface. Although such a sampling does not yield any absolute estimate of the rate of production, the standing crop of zooplankters toward the end of August, when sampling of juvenile sockeye salmon normally takes place, serves as a relative measure of the food potential at this time of the year.

The average number of zooplankters per cubic metre in sections I to IV for the years 1963–1968 were 10,050, 8,938, 7,196, and 6,201 respectively. This seemingly direct relationship to average length of yearling sockeye salmon which decreased from section I to section IV for the same years disappears when the average length of yearlings within a section is plotted against the standing crop of zooplankters there in any one year (Fig. 5). If a regression line is fitted between observed average length and corresponding zooplankton abundance, the hypothesis that the slope

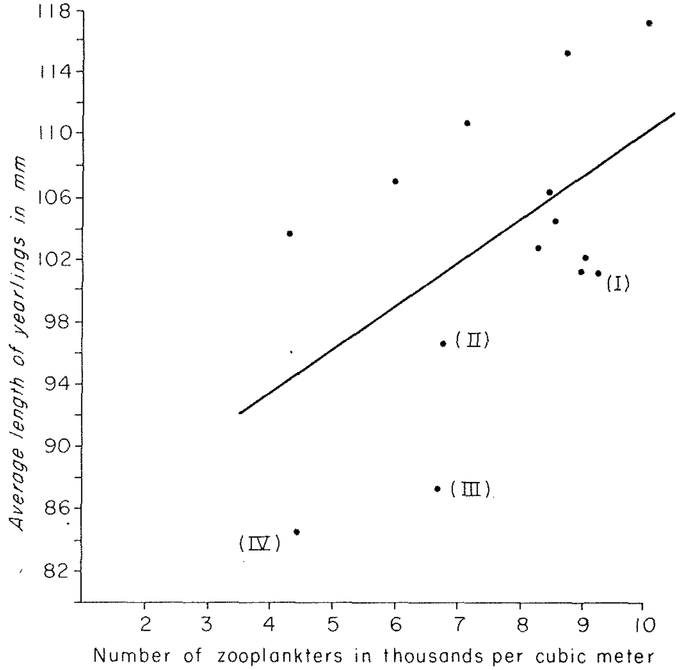

Fig. 5. Regression line of average lengths of yearling sockeye salmon and standing crop of zooplankters by lake sections (sections indicated in parentheses for 1967).

of this line is zero is barely rejected at the 95 per cent confidence level. (t = 2.33, 15 d.f.) and the hypothesis is accepted at the 99 per cent level.

Two factors add to this variability. First, the larger average lengths of yearlings in the two lower sections I and II may be due to an immigration of the fastest growing fish from the two upper sections III and IV and length may not be directly related to observed plankton abundance. A majority of fish spawn in sections III and IV and the resulting progeny move down Iliamna Lake to the outlet in the western end of section I during their freshwater residence.

Secondly, the distribution of yearlings in 1967 (Fig. 4) in relation to observed plankton abundance registered at the different stations in that year include heavy abundance of yearlings at places both with high and low abundance of zooplankton. This raises doubt as to the suitability of an average zooplankton abundance for a section as an index of food potential unless the juvenile salmon constantly and rapidly move around feeding. It is difficult to pass judgment on this question from the existing tow net data which give fish abundance only once during each season. A rapid dispersal of the juvenile salmon is not apparent. Since 1962 a centre of heavy yearling concentration in the lower part of Iliamna Lake has been associated with a large biomass of juvenile salmon and ensuing population pressure which forces a more widespread dispersal.

Too many factors are therefore confounded at the present time to state clearly the dependence of growth of juvenile salmon upon the availability of food except in a rather approximate manner.

There are indications that other growth inhibiting factors related to population density are operating. Two points deserve mention. In 1967, a year with the largest biomass of juvenile salmon present for those years where corresponding plankton data are available, the average length of the yearlings in all sections were substantially lower (sections I, II, and III) or equal (section IV) to the smallest average length observed in other years at a corresponding plankton density. Secondly, there is an asymptotic lower limit for average length of migrating smolts, both of age I and age II smolts. Both facts lead one to hypothesize that the depression of growth rate in years with a high biomass of juvenile salmon is due to space factors. The same may be true for the immature fish feeding in the sea. These results are in accord with those presented by JOHNSON (1965) from Babine Lake. As to the nature of such growth inhibiting factors related to population density JOHNSON summarized pertinent studies. But to date the proposed factors are merely indicative of those operating in sockeye populations and worthy of further investigations. It should be illustrative to study not only the total number of zooplankters but also their availability to sockeye salmon under different fish densities.

As a consequence, the capacity of the nursery area in Iliamna Lake can be measured adequately by the number of smolts produced from an escapement, especially since the survival rate of smolts to mature salmon is not closely tied to average length of the smolts.

SMOLT PRODUCTION IN THE KVICHAK SYSTEM IN RELATION TO MAGNITUDE OF PARENT ESCAPEMENT

Basically, two groups of points are available for placing an upper limit on the nursery capacity. One group includes the numbers of smolts produced from a series of small escapements, and another group the numbers of smolts produced from three peak years. In Fig. 6 are plotted the numbers of smolts produced and the magnitudes of the corresponding parent escapements for all years. The smolt production from the 1960 escapement may have been underestimated because heavy iceflow prevented sampling for extended periods when age II smolts migrated to sea in spring of 1963. Another estimate can be made by assuming that the ratio between index catches of smolts by fyke net in 1963 and 1968 should approximate the ratio of the average number of fingerlings caught by tow net in Iliamna Lake in the previous fall. In 1962, an average of 93.3 fingerlings was caught per haul, whereas an average of 80.9 yearlings was taken per haul in 1967. Thus, the expected index catch for age II smolts in 1963 would have been 7.7 million instead of the observed index catch of 5.2 million; the true value may lie somewhere between.

Two logistic curves of the form $y = a/(1 + e^{-(b + cx)})$ were fitted to the data, and the two values for the smolt index for 1963 were used. Smolt production increased as magnitude of parent escapement increased until an asymptotic limit was reached. In both cases it appears that the asymptotic limit for the number of smolts that can be produced from one

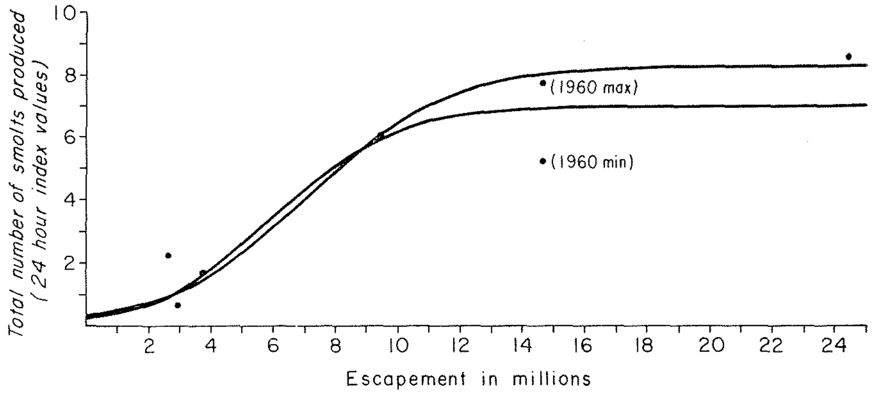

Fig. 6. Total numbers of smolts produced from escapements in the Kvichak system, 1953–1965. Equations for the two logistic curves are $y = 8.14/(1 + e^{3.20-.46x})$ and $y = 6.83/(1 + e^{3.19-.55x})$.

escapement in Iliamna Lake is close to the 1965 production value, although substantially smaller escapements will yield about the same number of smolts. Some confirmation may be derived from historical data for the Kvichak stock. In order to arrive at an escapement of 25 million spawners, it is necessary to postulate unrealistic low fishing mortalities except for the period 1936–1938. In 1936 the Kvichak catch numbered 16.8 million fish, in the following year 14.0 million, and in 1938 21.0 million; and the escapements must have been at least the same size (MATHISEN 1965). In other years the commercial catches never reached such magnitudes and it is not reasonable to suspect the escapement to have reached the 1965 value.

It is an important fact that during the period 1936–1938 the pattern of the Kvichak cycle changed from a peak run and one or two very strong subdominant runs to one exceedingly strong peak run and small runs. The latter pattern has persisted to the present. Were several strong year classes to be produced again in succession, there would be a sustained cropping rate of zooplankters and the total standing crop may decline drastically relative to the present-day situation. Zooplankton production may then exert a more direct effect on growth and survival of the juvenile sockeye salmon than observed today.

SUMMARY

1. Catch and escapement of Kvichak River sockeye salmon (*Oncorhynchus nerka*) and smolt production from Iliamna Lake, the nursery area, have been determined annually since 1955. Since 1962, information has been collected on growth and abundance of fry and yearlings and zooplankton production in Iliamna Lake.
2. Growth in length of smolts can be expressed as a negative exponential function of population density. A similar relationship exists for maturing salmon on their return from the ocean to the Kvichak River.
3. There is no strong correlation between the growth of juvenile salmon in Iliamna Lake nursery area and the standing crop of zooplankters. Other effects of crowding on growth need to be investigated.
4. An asymptotic limit for the number of smolts produced in the nursery area has been computed, but it may be valid only for a single-peak cycle, the current pattern of run variability in the Kvichak River.

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