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COLLECTION AND ANALYSIS OF BIOLOGICAL DATA FROM THE WOOD RIVER LAKE SYSTEM, NUSHAGAK DISTRICT, BRISTOL BAY, ALASKA

WILL FERTILIZATION INCREASE GROWTH AND SURVIVAL OF JUVENILE SOCKEYE SALMON IN THE WOOD RIVER LAKES?

by

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INTRODUCTION

The catches of sockeye salmon in the Nushagak District of Bristol Bay have declined significantly since the initial buildup of the fishery, and this occurred primarily because the abundance of the Wood River stock declined. Major declines in the runs followed years of large escapements (descending limb of the spawner-return curve), thus under-exploitation in some years probably contributed more to the decline than did overexploitation.[1] Mathisen (1971) demonstrated a decline in the survival (return per spawner) of the Nushagak stocks and suggested that this decline was caused by a decline in the basic productivity of the nursery areas. Although the catches in the Nushagak declined from an annual average of 3 million to about 1 million after 1950, the catches in the other districts of Bristol Bay either remained stable, e.g., Egegik, or declined a lesser extent, e.g., Nahnek-Kvichak (figure 1).

Burgner (1964) showed that the growth of sockeye salmon fry was density-dependent and suggested that the level of salmon populations in the individual Wood River lakes was limited primarily by the rearing capacity of the lake nursery areas. Since 1952 the escapements to the Wood River lake system have been larger (relative to the surface area of the lakes) than the escapements to the other large lake systems in Bristol Bay and the runs have also been relatively larger except for the peak cycle runs to the Kvichak system (figure 2 and table 1). However, the mean rate of exploitation on the Wood River stock has been the lowest in Bristol Bay and this has caused some of the decline in the Nushagak catches although most of the decline in catches was caused by at least a 50 percent reduction in the average run after 1950.

In recent years, the number of fry produced in the Wood River system has been proportional to the parent escapement except for a slight decrease in number of fry at very high abundance of parent eggs. However, growth decreased with a increase in abundance. Thus, the biomass of fry produced decreased sharply when the abundance of eggs exceeded the average for recent years. The number of adults produced was proportional to the number of fry in the lake system when the number of fry was less than average, but there was little increase in the number of adults produced when fry abundance was higher than average. The number of adults is more closely correlated with the biomass than the number of fry.[2]

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[1]Rogers, D. E. 1974. Systems modeling of sockeye salmon in the Wood River Lakes. Annual Progress Report. Anadromous Fish Project. FRI-UW-7406.

[2]Rogers, D. E. 1975. Systems modeling of sockeye salmon in the Wood River lakes. Annual Report. Anadromous Fish Project. FRI-UW-7511.

The production of adult salmon in the Wood River lakes is presently limited by 1) the amount of spawning ground when there is a large escapement and a high proportion of creek spawning, 2) predation during lake residence and seaward migration when escapements are small to average, and 3) growth conditions in the lakes which affect the age and size at seaward migration and thus the early marine survival when escapements are average to above average. Historically, the escapements have not changed significantly since the early 1900's and it is unlikely that the amount of spawning area has decreased; therefore, the decline in the abundance of adults in the Wood River system is probably the result of a decrease in growth conditions (primary and secondary productivity) and an increase in freshwater mortality that most likely was caused by an increase in the abundance of Arctic char (Rogers et al. 1972).

The purpose of this report is to present evidence which supports the thesis that artificial fertilization will increase the abundance of adult sockeye salmon in the Wood River system by increasing growth and survival of juveniles. Freshwater growth in the Wood River lakes is compared to the growth in the other lakes in Bristol Bay for recent years and to growth in prior years in the Nushagak District. The effects of growth on survival and age at seaward migration are examined, then relationships between the growth of sockeye and the abundance of their food (zooplankton) are presented, and the evidence that the abundance of zooplankton is ultimately limited by the concentration of nutrients is discussed.

METHODS

Statistics on the abundance of adult sockeye salmon and the abundance and size of smolts in the major lake systems of Bristol Bay were obtained from the series of informational leaflets by the Alaska Department of Fish and Game. Statistics prior to 1961 were collected by the Fisheries Research Institute (since 1946) and the Bureau of Commercial Fisheries.

Data pertaining to the abundance and size of juvenile sockeye in the individual Wood River lakes were obtained from tow-net sampling conducted during mid-summer since 1958. The annual relative abundances of zooplankton were estimated from vertical hauls with a 1/2-m net of no. 6 mesh. Six hauls were made in each lake during late August to early September since 1967 and hauls were made monthly in Lake Aleknagik since 1963. Statistics on abundance and growth were examined for each lake, for combinations of adjacent lakes, and for the lake system by correlation analysis to determine the degree of association among variables and probable statistical relationships. Data were first plotted (scatter diagrams) and a linear regression was calculated if so indicated.

Possible genetic effects on growth and survival were sought by arranging statistics according to four or five-year lines depending on the predominate age at return of the stock. Ricker (1972) reviewed the evidence for hereditary and environmental effects on salmonid populations and concluded: "In almost all cases where both genetic and environmental influences affecting natural stock differences among Pacific salmon and steelheads have been searched for adequately, both have been found; though sometimes one, sometimes the other, is relatively weak, or is infrequently expressed."

Our search for the factors that control the sockeye salmon populations in the Wood River lakes has concentrated on the environmental ones (including population density) because these seemed to offer a greater potential for manipulation by fishery management than hereditary factors. The relatively large variation in age at return within Bristol Bay stocks would seem to limit the role of hereditary factors in controlling annual fluctuations in abundance.

RESULTS

The Wood River stock is characterized in Bristol Bay by a young age at maturity. The sockeye tend to spend one year in freshwater and two years at sea and thus mature at age 1.2 (4_2). The exceptions to this (probably genetic) tendency are those stocks which spawn in the two major rivers in the system and they tend to return after three years at sea (age 1.3 or 5_2) as do the stocks in the other Nushagak lake systems. Most of the other stocks in Bristol Bay tend to spend two years in freshwater though there is considerable annual variation.

Size of Smolts

Since 1955, the smolts that migrated from the Wood River lakes were much smaller than those from other districts in Bristol Bay (table 2). The Wood River smolts are smaller because they are predominantly age I and small for their age. The Wood River smolts are also poorer in condition because their average weight for a given length is less (figure 3). The small size of the Wood River smolts suggests that they experience poorer marine survival relative to the other stocks in Bristol Bay (Ricker 1962).

The age I smolts from Wood River were smaller in recent years partly because their populations were denser than those in the other Bristol Bay lakes (figure 4). However, even at relatively low densities, they tend to be smaller than the other smolts except for those from the Kvichak system. Thus, relatively poor growth conditions are indicated for the Wood River lakes, but this may not have been the case in the early history of the fishery.

The smolts migrating from the Wood River lakes in the early 1900's were probably comparable in length to those that migrated from the other Bristol Bay lakes in recent years as indicated by the following quotes:[3]

> In 1908, "At Nushagak (outlet of Lake Aleknagik), June 3, the young, with parr marks still evident, ranging in size from 95 to 115 mm, were very abundant. These were doubtless descending the rivers to the sea and were probably 20 months old."
>
> In 1911, "the salmon fingerlings leaving Lake Aleknagik are exceptionally fine fish. The average length of nearly 200 measured was 111 millimeters. The average length of something over 400 red fingerlings taken at the mouth of the Nushagak was only 51 millimeters. Further, there was a greater diversity of sizes in the Nushagak fingerlings. They varied between the extremes of 40 and 86 millimeters; the Lake Aleknagik fingerlings between 90 and 133 millimeters. Neither of these lots could have been less than a year and a half old--that is, they must have passed one winter in the lakes after hatching. An examination of the scales of the Aleknagik fish does not indicate that they are more than one year from hatching."
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> In 1912, "The movement of yearling salmon was given somewhat less attention than in 1911. But one lot of 108 Lake Aleknagik fingerlings, taken July 12, was preserved. These averaged only 92.3 mm in total length, or 8 percent less than those of 1912. On the other hand, a lot of 21 sockeye, taken at Lewis Point on the Nushagak July 28, averaged 66 mm."

The sockeye smolts that were sampled in the Nushagak were probably from the Tickchik Lakes (Nuyakuk River). These lakes are presently the poorest producers of sockeye salmon in Bristol Bay (Burgner 1964), however no recent data on the size of smolts are available.

To further examine historical changes in the size of Wood River smolts, we measured the freshwater portion of scales that were collected from adult sockeye caught by the Nushagak fishery.[4] Measurements were made in millimeters from the center of the focus, along the anterior portion of the scale, to the outer edge of the first winter check. A magnification of 226 times was used. These measurements should be proportional to the size of the surviving adults when they were age I smolts (adults of age 1.2 and 1.3) or yearlings that remained in the lake and did not migrate until age II (adults of ages 2.2 and 2.3).

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[3]Source: U. S. Bureau of Commercial Fisheries. 1908, 1911, and 1912. Alaska fishery and fur-seal industries. *In* Rep. U. S. Comm. Fish., Dec. Series.

[4]Scales provided by the Bureau of Commercial Fisheries.

Means, standard deviations, and standard errors of the measurements are given in table 3. There are several sources of error in these data with respect to inferences about changes in freshwater growth, e.g., the exact location from which the scales were taken from the fish, the fish were from a mixture of Nushagak stocks not just Wood River, and the measurements represent the freshwater growth of those individuals that survived to adulthood and perhaps not those that migrated if, indeed, survival was growth dependent.

The measurements indicate that freshwater growth declined slightly from the early 1900's to the 1930's, declined significantly in the mid-1940's, and then increased in the early 1950's when escapements were small. The age 1.2 fish in the Nushagak are predominately from the Wood River system and the mean scale radius for this age group in 1959 (the last year of measurements) was significantly smaller than the means from the years prior to 1940. Thus, these data provide some evidence that the size of sockeye salmon smolts in the Wood River lakes has declined since the establishment of the commercial fishery. Smolts migrating from the Wood River lakes in recent years are probably smaller than before and therefore are subjected to a higher mortality rate during their early marine life.

Effects of Growth on Survival and Age at Migration

Growth of sockeye fry in the spring is largely determined by the date of ice breakup and water temperature, whereas their growth during the summer is density-dependent and presumably controlled by the abundance of food (Rogers 1968 and 1973). The fry attain about 50 percent of their first year's growth in weight by September 1 and their size then is correlated with their size the following spring when they are age I.

Parent spawner density, the mean weight of fry on September 1, and the percentage of age 2. fish in adult returns from the 1957-1969 brood years are given in table 4 in order of the estimated survival from number of pelagic fry to number of returning adults. Large adult runs are associated with average to large fry and a low percentage return of age 2. fish, whereas poor returns from average to large escapements are associated with average to small fry and a relatively high percentage of age 2. fish in the returns. The estimates of survival from fry to adults in Lake Kulik are significantly lower than the estimates in the other lakes but this may be caused by a difference in the availability of fish to the sampling, i.e., there are possible biases in the estimates of abundances.

The survival from fry to adults is directly correlated with the mean weight of fry in each of the Wood River lakes; however, the correlation for Lake Aleknagik is not statistically significant, and if observations from years of low escapements are omitted, no correlation is evident (figure 5). The lack of correlation in Lake Aleknagik is probably because the largest mean weight of fry observed was only 2.2 gm.

The statistics for the lake system are most influenced by those for Lake Nerka because it is the largest lake and contains about 42 percent of the fry populations in an average year. The relationships between survival and mean weight of juveniles in the lake system are shown in figure 6. The correlations are statistically significant even though there is considerable variation in survival and mean weight of fry among the lakes in a given year. The yearlings from the 1965 brood year averaged only 3.2 gm yet 5.5 percent of them survived to returning adults. About 58 percent of the yearlings and 75 percent of the returning adults (ages 2.2 and 2.3) were in Lake Aleknagik. Excluding the 1965 brood year, the survival of small yearlings (less than 6 gm) is less than the mean survival of age 0 fish (2.1 compared to 2.4 percent). The small yearlings were from relatively large populations and usually produced from above average escapements. The fact that their survival is no better than the survival of fry is probably the reason why the sockeye salmon of the Wood River lakes tend to migrate to sea at age I.

Effects of Sockeye Abundance on Zooplankton

Density-dependent growth implies that there is a limited food supply. Juvenile sockeye feed on chironomids and zooplankton during the spring and early summer and then predominantly on zooplankton during the remainder of the year. If the reproduction of zooplankton is relatively constant from year to year then we would expect their abundance to decrease with an increase in the abundance of their predators. Of the four major categories of zooplankton that are eaten by sockeye, *Cyclops* and *Bosmina* are the smallest in size and usually the most abundant in the zooplankton as well as in sockeye stomachs (Rogers 1968). However, the annual variation in the abundances of the larger but less abundant forms (Calanoid copepods and *Daphnia*) are more closely correlated with the relative abundance of sockeye (figure 7).

The annual compositions of zooplankton in the Wood River lakes during August 16 to September 9, 1967-1976, were compared to the composition in the stomachs of sockeye fry collected in 1959 (table 5). The fry apparently select cladocerans and particularly *Daphnia*. The seasonal abundance of *Daphnia* in Lake Aleknagik is correlated with the abundance of sockeye spawners in the previous year (figure 8). When sockeye escapements were small, the abundance of *Daphnia* increased almost linearly from June to September, but when escapements were average or large, the abundance of *Daphnia* increased at a lesser rate and often decreased by September (about 90 days after breakup).

Effects of Zooplankton Abundance on Sockeye Growth

The mean weight of sockeye fry on September 1 is directly correlated with the abundance of *Daphnia* about September 1 in each of the large Wood River lakes (figure 9). Significant correlations between mean weight and the abundance of calanoid copepods are evident only in Lakes Aleknagik and Nerka. There is some indication that the relationships are not linear; however the size of sockeye fry on September 1 is obviously not determined solely by the abundance of food at that time, rather by the average abundance of food and water temperatures up to September 1. This information is only available for Lake Aleknagik where we have sampled the zooplankton at monthly intervals and the size of the fish at weekly intervals.

The absolute growth of sockeye fry when they are in the limnetic region of Lake Aleknagik is correlated with the average number of large zooplankton or the average volume of zooplankton (figure 10). The correlations are remarkably high when the relative low precision of most biological measurements is considered. The abundance or volume of zooplankton accounts for 76 to 79 percent of the annual variation in growth during the period of the year when the growth rate of the juvenile sockeye is maximum. Although growth of sockeye, sockeye abundance, and zooplankton abundance are correlated with each other, it is most likely that the abundance of fish influences the abundance of zooplankton which in turn controls the growth of the fish.

The growth of sockeye fry should be more closely correlated with the production rather than the standing stock of zooplankton, but we have not estimated the reproductive rates of zooplankton. If the production of zooplankton is some positive function of the abundance of phytoplankton, then the growth of sockeye fry should be greater than predicted from the abundance of zooplankton, when phytoplankton abundance is higher than average. Conversely, the growth should be lower than predicted from zooplankton abundance when phytoplankton abundance is lower than average.

Effect of Phytoplankton Abundance on Sockeye Growth

The abundance of phytoplankton in Lake Aleknagik was estimated from monthly samples of chlorophyll a. Sampling was conducted at relatively fixed dates each year; however the seasonal abundance of phytoplankton varies according to days after ice breakup rather than calendar dates. The abundance of phytoplankton is low at ice breakup, increases to a peak abundance at about 30 days after breakup (usually late June or early July), and then decreases until September when there is usually a small increase.

The amounts of chlorophyll a in the upper 20 m in July and August are plotted by days after ice breakup in figure 11. Sockeye growth was greater than predicted from zooplankton in 1969-1971 and 1973 (figure 10). The growth was highest in 1973 and lowest in 1967. The amount of chlorophyll was also relatively high in 1969-1971 and 1973 and lowest in 1967. Although the observations in 1967 were somewhat suspect from problems with chlorophyll determinations, and there is not a significant correlation between the average density of chlorophyll and sockeye growth; there is some evidence that standing crop of phytoplankton, and presumably primary production, affects the production of zooplankton, hence the growth of the fish.

Effect of Phosphorus on Phytoplankton Production

Phosphorus is the biogenic nutrient that most frequently limits production in oligotrophic lakes. In 1963-1965, the phosphorus in salmon carcasses contributed 2 to 60 percent of the phosphorus input to Lake Iliamna. In a year with a large escapement, the salmon carcasses provided the major source of phosphorus to the lake ecosystem. Although the primary loss of phosphorus from the lake was from sedimentation, there were losses of 2 to 19 percent of the phosphorus from the outmigration of smolts (figures calculated from data in Donaldson 1967).

The nutrients from salmon carcasses may cause the small increase in phytoplankton that is observed in early September in Lake Aleknagik. Most of the spawning in the lower half of that lake occurs in early August, however the spawning in the remainder of the lake system occurs from mid-August to early October. Thus, the phosphorus in salmon carcasses probably benefits their progeny in the following year but may have little effect on the amount of nutrients available to adjacent brood years.

With the establishment of the commercial fishery, about 1900, there must have been a drastic reduction in the annual input of phosphorus to the Wood River lakes because the fishery removed about 81 percent of the runs from 1900 to 1919. Prior to the fishery, the mean annual number of spawners in the lakes must have been about five times greater than at present. It is unlikely that the spawning grounds of the Wood River lakes could have accommodated such large numbers, and the mortality from eggs in females to fry in the lakes must have been very high. However, the surviving fry probably had an environment that was rich in nutrients and thus they experienced good growth and survival to the adult stage. At the onset of the fishery there was probably a shift from a high mortality at the egg stage to a high mortality at the adult stage. The spawners were fewer in number, their efficiency increased, and production of adults remained high for about 20 years (four to five generations). However, the reduction in nutrient input may have gradually decreased the rearing capacity of the lakes and subsequently the freshwater and early marine survival of the sockeye stocks. The predator control program during the 1920's and 1930's may have slowed the decline in the production, but five years after this program was terminated the production of adult sockeye dropped to its present low level.

Primary production in the Wood River lakes can be increased by the addition of phosphate fertilizers.[5] A precise estimate of the effect of fertilization on the growth and survival of juveniles and the adult return to the Wood River lakes can only be obtained from direct experimentation. However, based on the work by Nelson (1959), Donaldson et al.

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[5]Rogers, D. E. 1976. Fertilization of Little Togiak Lake. Final Report to Alaska Department of Fish and Game. FRI-UW-7602.

(1971), and Barraclough and Robinson (1972) a given percentage increase in primary production can result in a comparable increase in the average weight of juvenine sockeye. In the Wood River lakes, for example, an increase in the average weight of fry (1.7 gm) from an average population of 60 million to an average weight of 2.4 gm could increase the adult return from 1.4 million to 1.9 million, an increase of 500,000 fish (valued at about $1 million). A unit increase in average weight results in a unit increase in survival (figure 6), thus the maximum benefit from fertilization in the Wood River lakes would be achieved by fertilizing when and where the fry populations are most abundant.

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Table 1. Escapements and returns for the 1952-1970 brood years divided by surface area (km^2) of lake system and grouped by escapement

Lake system	n	Geometric means Escapement	Geometric means Return	Geometric means R/E	Arithmetic means Escapement	Arithmetic means Return
Kvichak	7	140	273	1.95	159	426
(2992)	3	901	664	.74	903	987
	3	1189	924	.78	1192	1102
	1	1995	5789	2.90[1]	1995	5739
	1	2805	1694	.60	2805	1694
	3	4158	9655	2.32[1]	4234	10778
	1	8130	13235	1.63[1]	8130	13235
	Means	751	1061	1.41	1738	3279
Naknek	5	304	1363	4.48	328	1486
(790)	5	901	1891	2.10	903	2013
	5	1151	2467	2.14	1157	2966
	2	1630	2495	1.53	1632	2516
	2	2518	2408	.96	2534	2408
	Means	856	1965	2.30	1067	2220
Wood	2	603	1564	2.59	607	1828
(425)	5	1251	2307	1.84	1257	2607
	4	1654	2509	1.52	1657	2602
	3	2231	4729	2.12	2235	4817
	3	2701	3742	1.39	2704	4035
	2	4113	5788	1.41	4226	6264
	Means	1723	3002	1.74	1968	3483
Egegik	6	321	950	2.96	334	1082
(1132)	11	780	1449	1.86	791	1652
	2	1424	3787	2.66	1432	4230
	Means	628	1493	2.23	714	1743
Ugashik	3	248	191	.77	267	233
(385)	6	680	1128	1.66	692	1306
	4	1142	1269	1.11	1145	2880
	3	1817	2080	1.14	1819	2743
	2	2666	1731	.65	2667	1846
	1	6081	6943	1.14	6081	6943
	Means	979	1107	1.13	1390	2048

[1]Peak cycle years

Table 2. Mean lengths (live measurements in mm) of sockeye salmon smolts in annual migrations from Bristol Bay river systems, 1955-1969

	Age I					Age II				
Year	Wood	Kvichak	Naknek	Ugashik	Egegik	Wood	Kvichak	Naknek	Ugashik	Egegik
1955	85	89	--	--	--	102	109	--	--	--
56	82	92	--	--	101	95	116	--	--	116
57	77	96	111	--	107	93	120	112	--	120
58	82	84	91	93	--	102	114	114	112	--
59	88	80	97	90	99	105	99	106	120	116
60	88	91	99	90	106	114	108	109	108	115
61	82	92	103	90	--	102	117	113	112	--
62	80	82	105	88	--	98	110	112	112	--
63	83	83	98	90	--	102	98	114	104	--
64	84	87	97	92	--	104	108	110	118	--
65	86	90	99	94	--	106	109	114	114	--
66	77	94	106	--	--	101	114	118	--	--
67	78	86	113	88	--	90	118	119	113	--
68	77	88	99	93	--	96	104	108	113	--
69	89	92	100	97	99	92	109	112	121	119
Means	83	88	94	91	102	100	110	112	113	117

	All ages				
Year	Wood	Kvichak	Naknek	Ugashik	Egegik
1955	85	108	--	--	--
56	85	107	--	--	118
57	80	103	111	--	119
58	89	85	92	93	--
59	89	98	99	94	111
60	88	106	104	97	114
61	83	99	105	108	--
62	83	84	109	93	--
63	86	98	108	98	--
64	84	103	106	97	--
65	87	108	105	108	--
66	79	96	114	--	--
67	82	88	116	100	--
68	78	102	104	94	--
69	89	100	105	107	113
Means	84	99	106	99	115

Table 3. Means and standard deviations of scale radius measurements of the first year growth of sockeye salmon from the Nushagak fishery

Year	Age	n	$\bar{x}$	S.D.	S.E.	Year	Age	n	$\bar{x}$	S.D.	S.E.
1917	1.2	211	75.2	10.23	0.7	1947	1.2	21	51.6	8.94	1.9
	1.3	7	74.4	11.97	4.5		1.3	151	50.0	8.11	0.7
	2.2	24	61.2	14.80	3.0		2.2	11	46.6	8.02	2.4
	2.3	0					2.3	0			
	1.4	1	62.0	--	--		1.4	0			
1919	1.2	48	76.5	13.87	2.0	1949	1.2	9	50.2	12.69	4.2
	1.3	107	67.3	14.21	1.4		1.3	141	44.9	10.08	0.8
	2.2	41	49.7	15.02	2.3		2.2	16	33.7	9.05	2.3
	2.3	9	52.7	10.90	3.6		2.3	12	30.4	6.67	1.9
	1.4	6	60.3	10.52	4.3		1.4	14	52.2	8.77	2.3
1927	1.2	19	72.1	15.15	3.5	1951	1.2	31	72.5	10.16	1.8
	1.3	160	68.5	14.26	1.1		1.3	136	67.2	11.19	1.0
	2.2	7	58.9	7.34	2.8		2.2	21	58.2	11.32	2.5
	2.3	26	54.3	10.53	2.1		2.3	20	51.5	8.66	1.9
	1.4	2	60.5	--	--		1.4	3	69.0	--	--
1928	1.2	312	67.9	10.94	0.6	1957	1.2	47	80.9	9.50	1.4
	1.3	30	73.4	10.30	1.9		1.3	139	71.6	10.36	.9
	2.2	23	57.7	11.40	2.4		2.2	17	62.8	6.64	1.6
	2.3	6	58.7	5.85	2.4		2.3	16	54.7	8.01	2.0
	1.4	0	--				1.4	0			
1937	1.2	127	72.0	11.13	1.0	1959	1.2	284	65.9	11.78	.7
	1.3	25	67.7	8.00	1.6		1.3	108	65.5	9.38	.9
	2.2	7	58.0	7.53	2.8		2.2	131	55.4	9.92	.9
	2.3	2	50.0	--	--		2.3	15	56.1	13.54	3.5
	1.4	0					1.4	0			

Table 4. Spawner density (thousands per km^2 of lake area), mean weight of fry on September 1, and the percentage of ages 2.2 and 2.3 in adult returns ordered according to the estimated survival from mid-summer fry populations to adult returns

Lake	Spawner sensity	Fry to adult survival (%)	Fry mean weight (gm)	Age 2 in adult return (%)	Lake	Spawner density	Fry to adult survival (%)	Fry mean weight (gm)	Age 2 in adult return (%)
Alek.	0.4	4.7	1.98	1	Bever-ley	0.1	9.0	2.09	42
	1.8	4.0	1.43	5		0.4	6.3	2.12	7
	0.6	3.0	2.15	0[1]		0.3	4.0	1.82	26[2]
	0.8	2.5	2.22	1		0.7	1.8	1.62	8
	1.1	2.3	1.75	4					
	3.5	2.2	1.54	15		3.9	5.1	1.60	8
	1.0	2.2	.74	14		3.1	4.4	1.52	0
	1.9	2.1	1.85	51[2]		2.3	4.3	1.57	2
	1.9	1.6	1.39	61		1.3	3.8	2.37	3
	2.7	1.4	.97	25		4.6	2.5	.92	35
	2.1	1.4	2.09	1		3.6	2.4	1.17	13
	1.1	1.0	2.15	0		4.6	1.8	1.53	16[1]
	2.5	.6	1.54	15		3.1	1.5	1.08	9
Nerka	2.0	7.2	2.38	2	Kulik	0.4	7.8	2.32	42[2]
	1.4	5.1	2.14	5		0.1	1.7	2.12	10
	2.7	3.4	1.93	1		0.6	1.5	1.55	7
	0.9	3.2	2.08	7		0.7	1.5	2.25	0
	1.6	3.2	1.45	3					
	1.2	3.1	1.88	3		1.4	2.7	3.23	7
	1.5	2.9	2.06	1		1.6	1.6	2.21	0
	1.1	2.8	2.47	2		6.3	1.4	1.37	29
	1.9	2.8	2.23	23[2]		2.3	1.3	1.48	8
	1.5	1.7	2.11	2[1]		2.2	.9	2.05	2
	2.9	1.5	1.67	8		1.8	.9	1.52	17[1]
	2.1	1.3	1.45	21		3.2	.5	1.20	26
	6.4	1.2	1.55	14		3.0	.3	1.06	50

[1]Ice breakup in spring of age I smolt migration was two weeks later than average; 1962 brood year (1) and 1969 brood year (2).

Table 5. Comparison between the composition (percent) of net zooplankton in the Wood River lakes in 1967-1976 and the composition in sockeye fry stomachs in 1959

Year	Cyclops	Calanoid	Bosmina	Daphnia	Holopedium
Zooplankton					
1967	39	22	28	10	1
1968	46	10	31	13	1
1969	33	16	37	13	1
1970	31	23	30	14	1
1971	44	19	26	9	2
1972	40	18	34	6	2
1973	39	22	29	9	1
1974	31	23	29	15	2
1975	41	15	37	3	4
1976	37	17	38	5	4
Mean	38	18	32	10	2
Sockeye stomachs					
1959	29	4	44	22	1
Ratio (zooplankton/stomachs)	.76	.22	1.37	2.20	.50

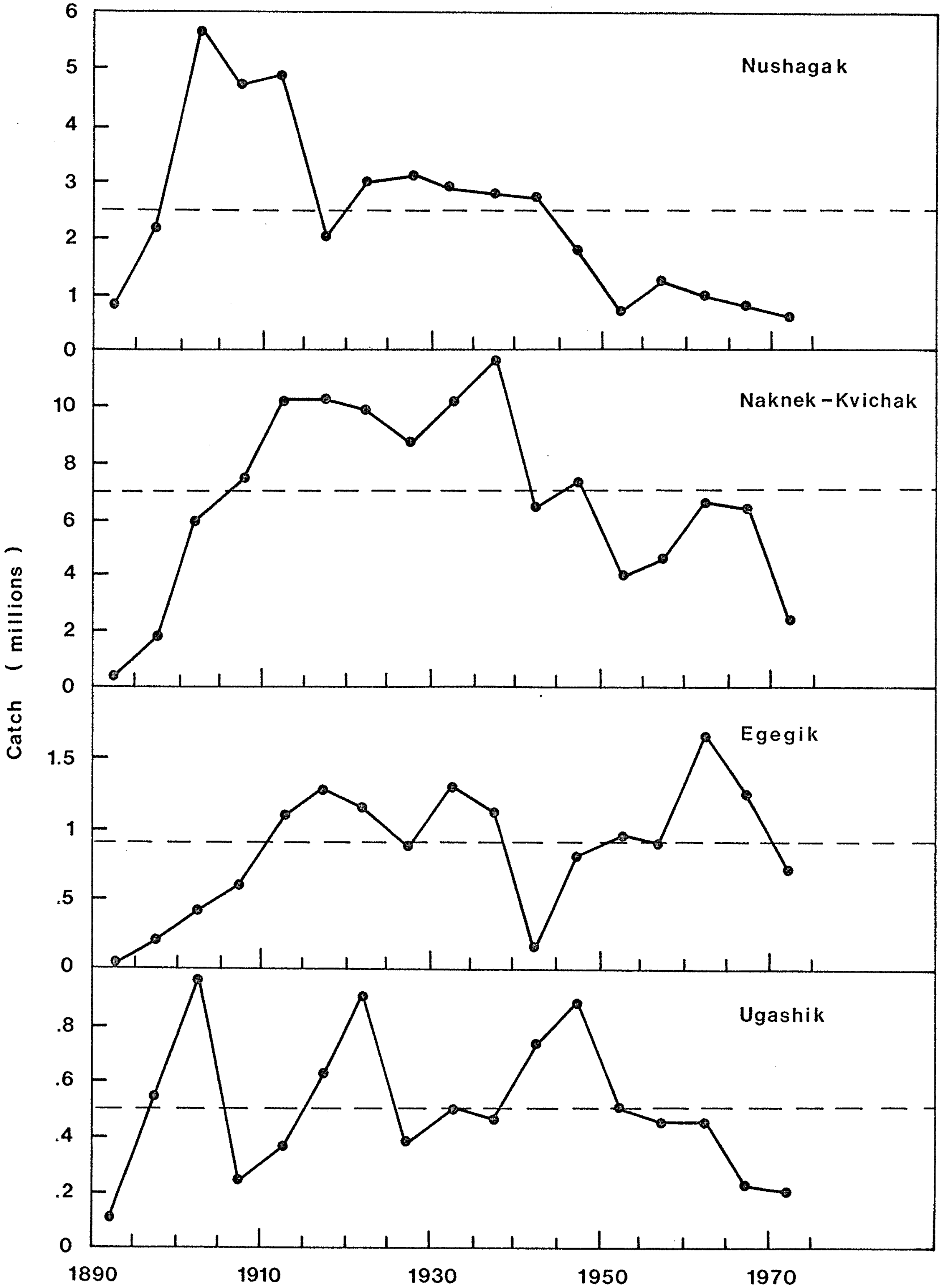


Fig. 1. Catches of sockeye salmon in the major fishing districts of Bristol Bay by 5-year means. Dashed lines at the 80-year means, 1896-1975.

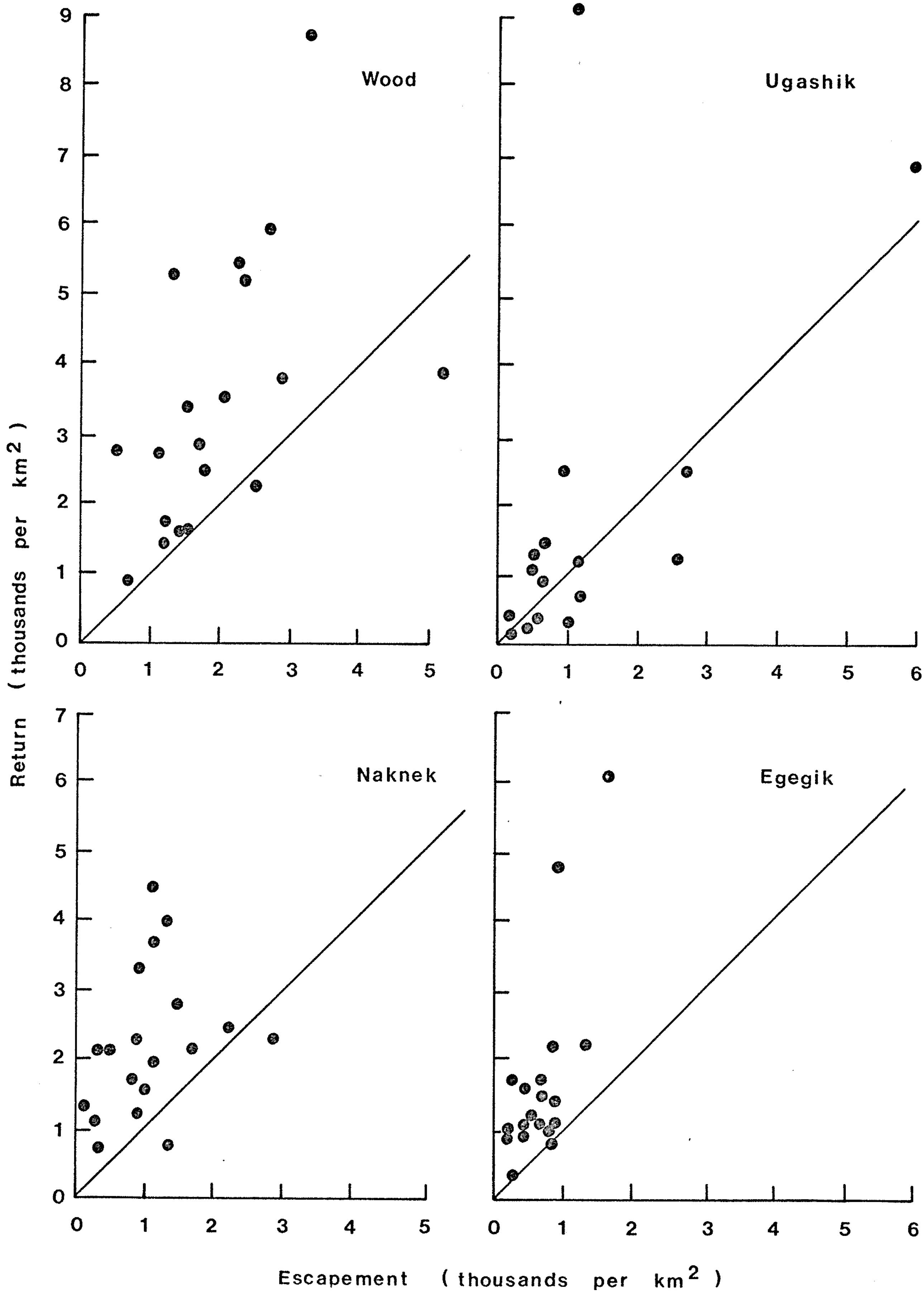


Fig. 2. Plots of adult returns on escapements adjusted by surface area of lake systems.

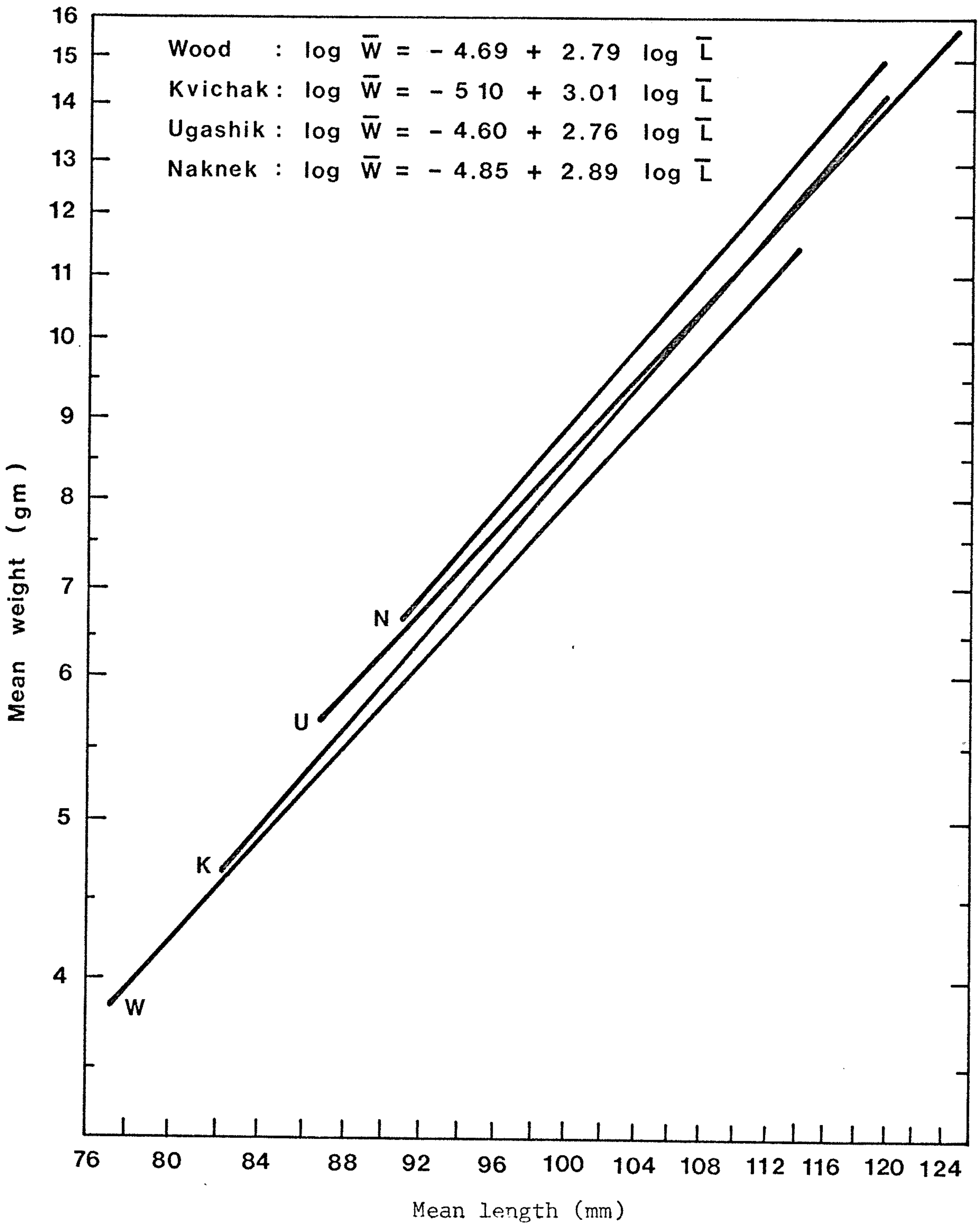


Fig. 3. Weight-length regressions from annual mean weights and lengths of age I and age II sockeye smolts.

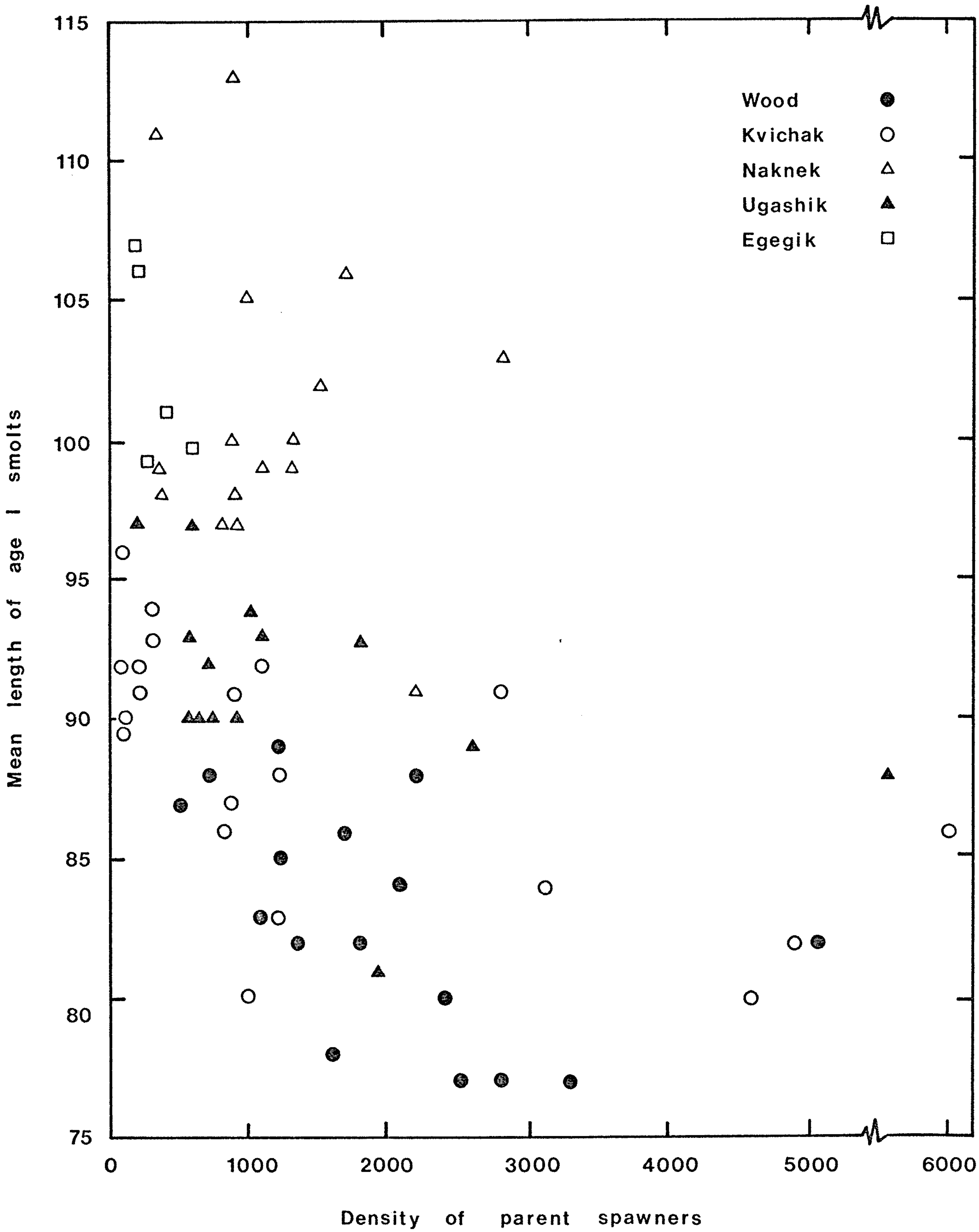


Fig. 4. Plot of the mean length of age I smolts on the density of parent spawners.

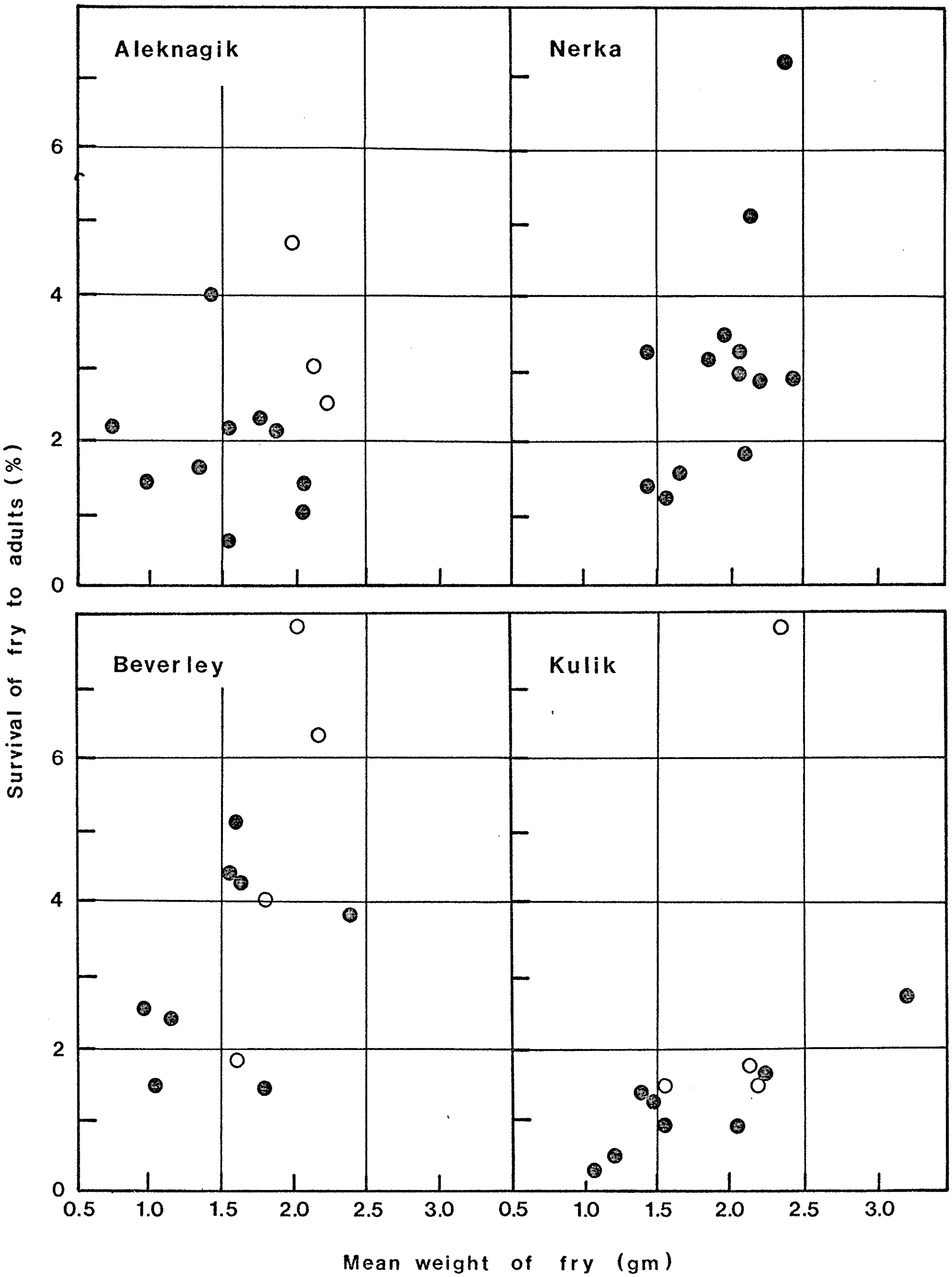


Fig. 5. Survival from number of fry in mid-summer to returning adults versus the mean weight of fry on September 1. Open circles indicate years when parent escapement was low, less than 800 per km^2 of lake.

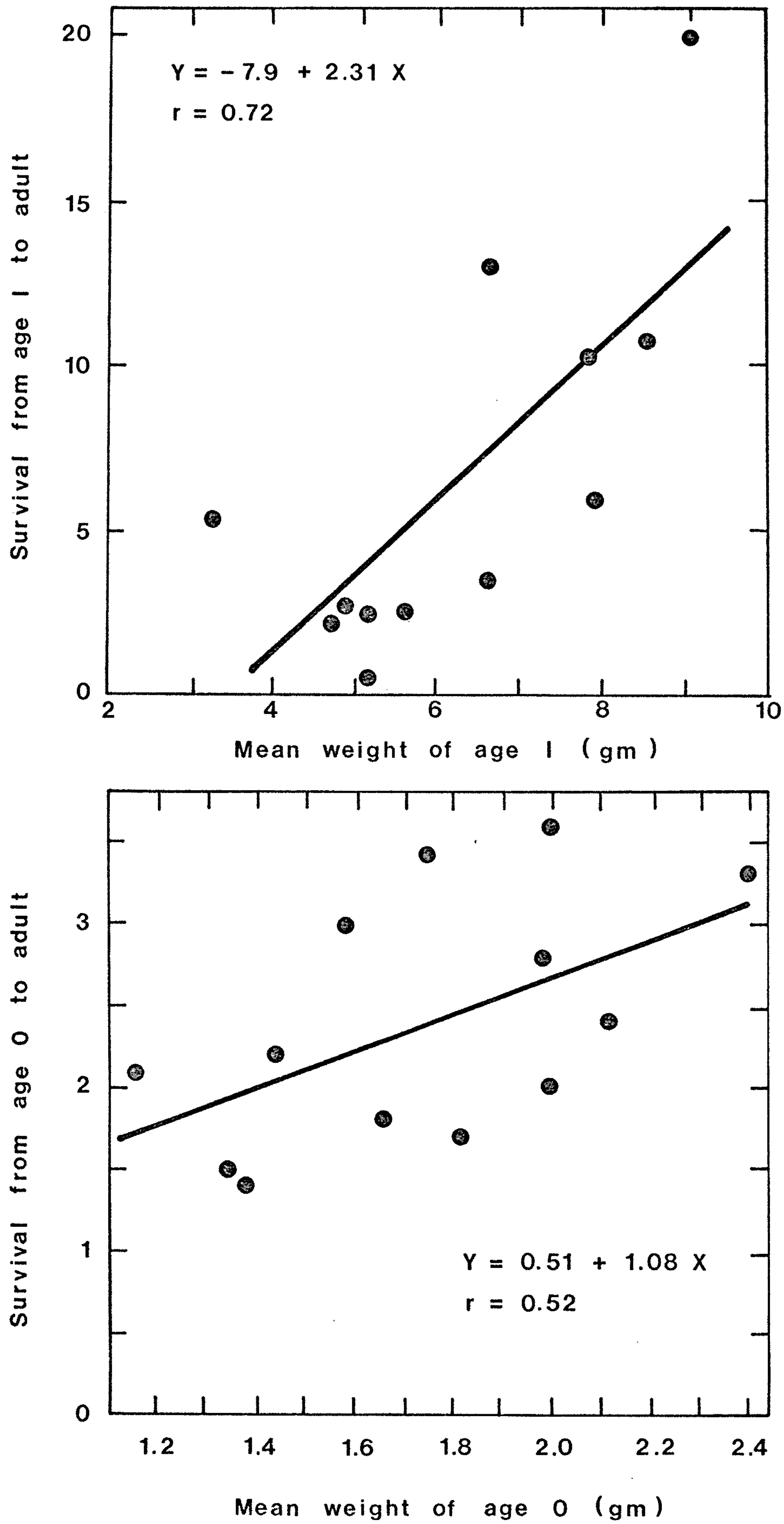


Fig. 6. Relationships between survival to adult returns and mean weight of juveniles on September 1 in the Wood River lakes.

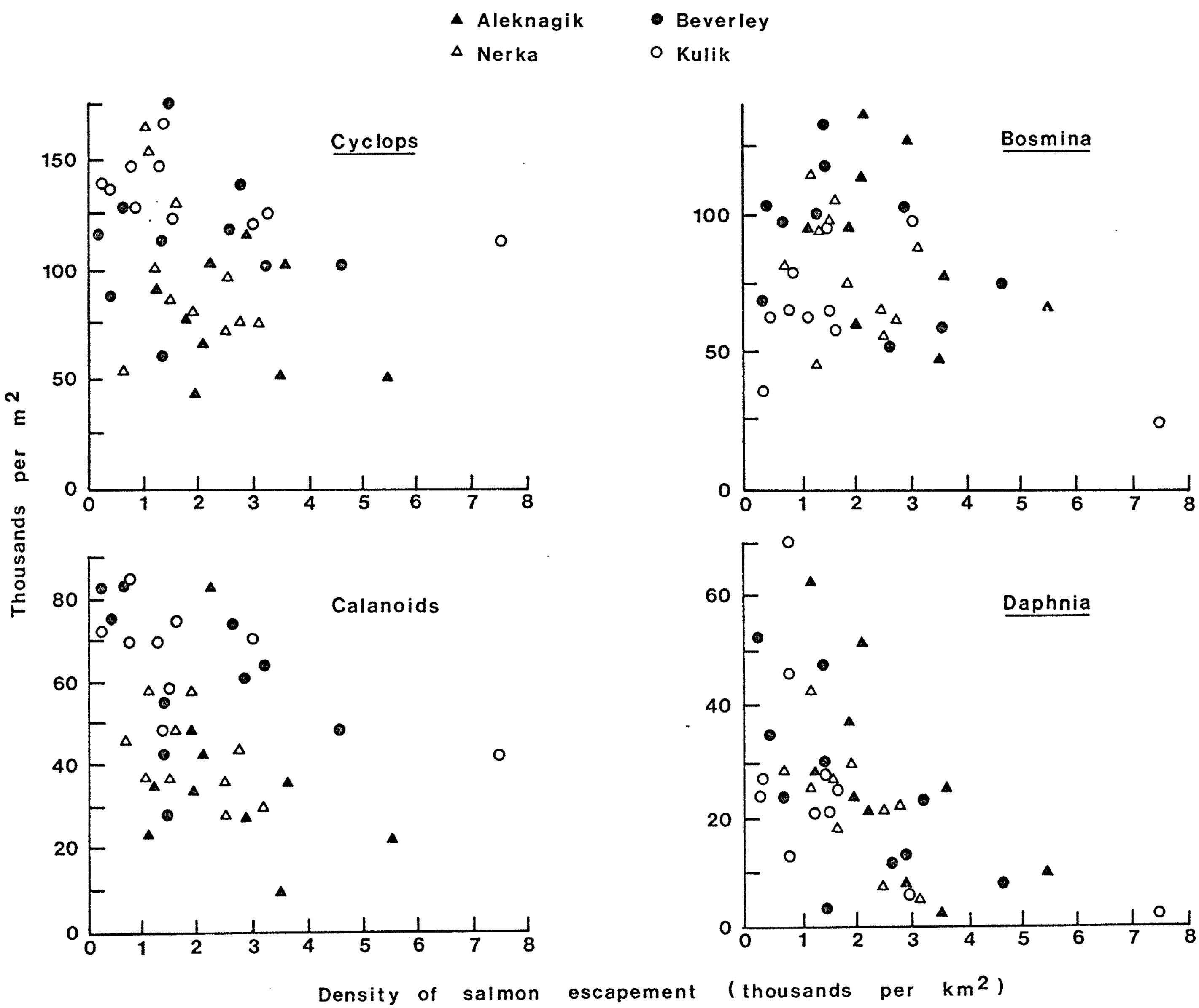
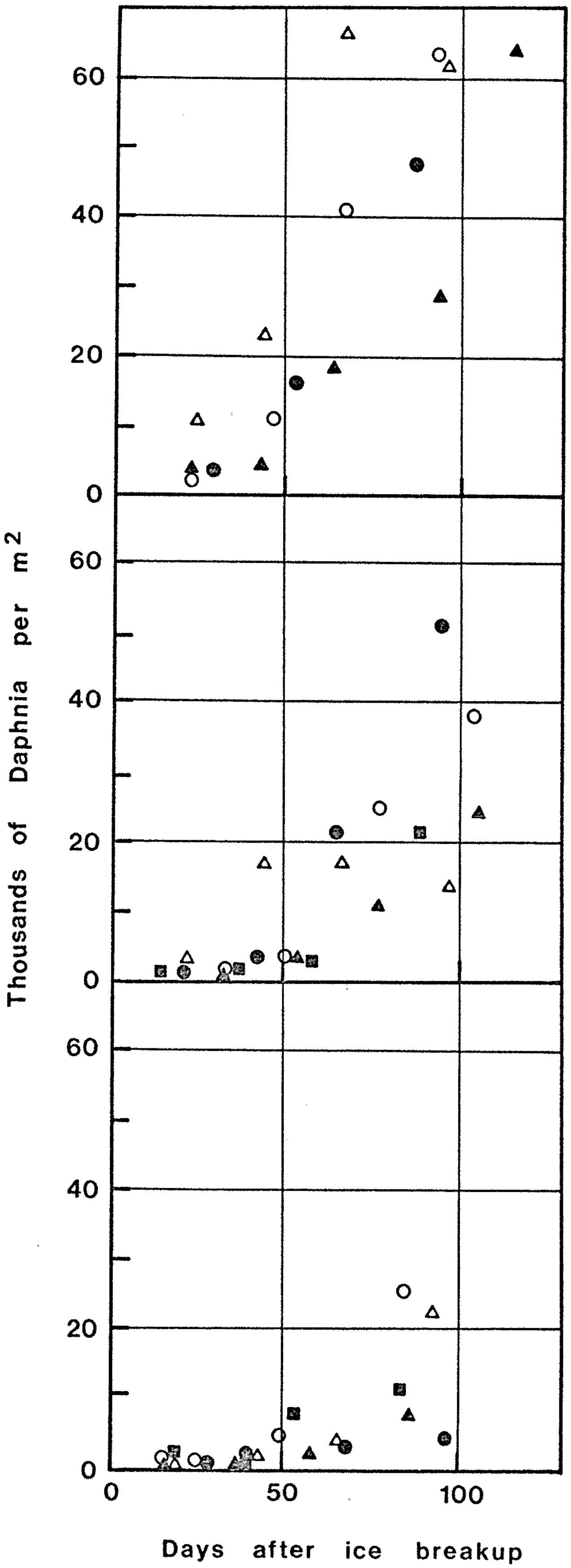


Fig. 7. Plots of zooplankton abundance during late August to early September on the density of salmon escapements in the previous year.



Year	Escapement in year-1 (thousands)		Mean weight of fry (gm) on September 1
1963	△	48	2.15
1964	◉	31	1.98
1968	○	92	1.75
1973	▲	97	2.72

1965	△	155	1.39
1969	◉	177	2.09
1970	○	160	1.85
1972	■	182	1.48
1974	▲	162	2.23

1966	△	220	0.97
1967	◉	287	0.74
1971	○	302	1.45
1975	▲	242	1.72
1976	■	459	1.11

Fig. 8. Seasonal abundance of *Daphnia* in Lake Aleknagik according to days after ice breakup in years when sockeye abundance was low (top), average (middle), and high (bottom).

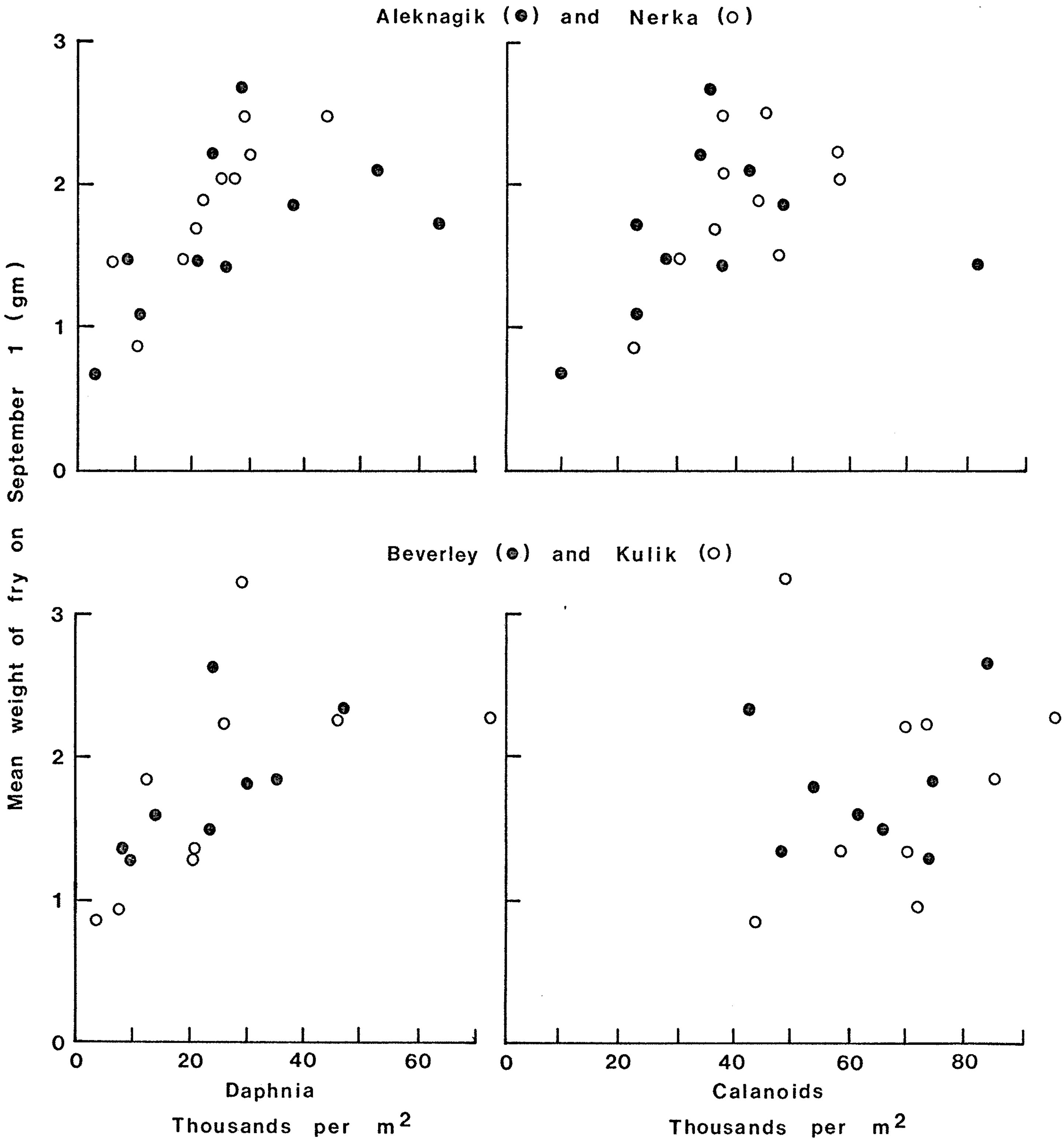


Fig. 9. Plots of the mean weight of sockeye fry on the abundance of *Daphnia* and calanoid copepods in Lakes Aleknagik and Nerka (top) and Beverley and Kulik (bottom).

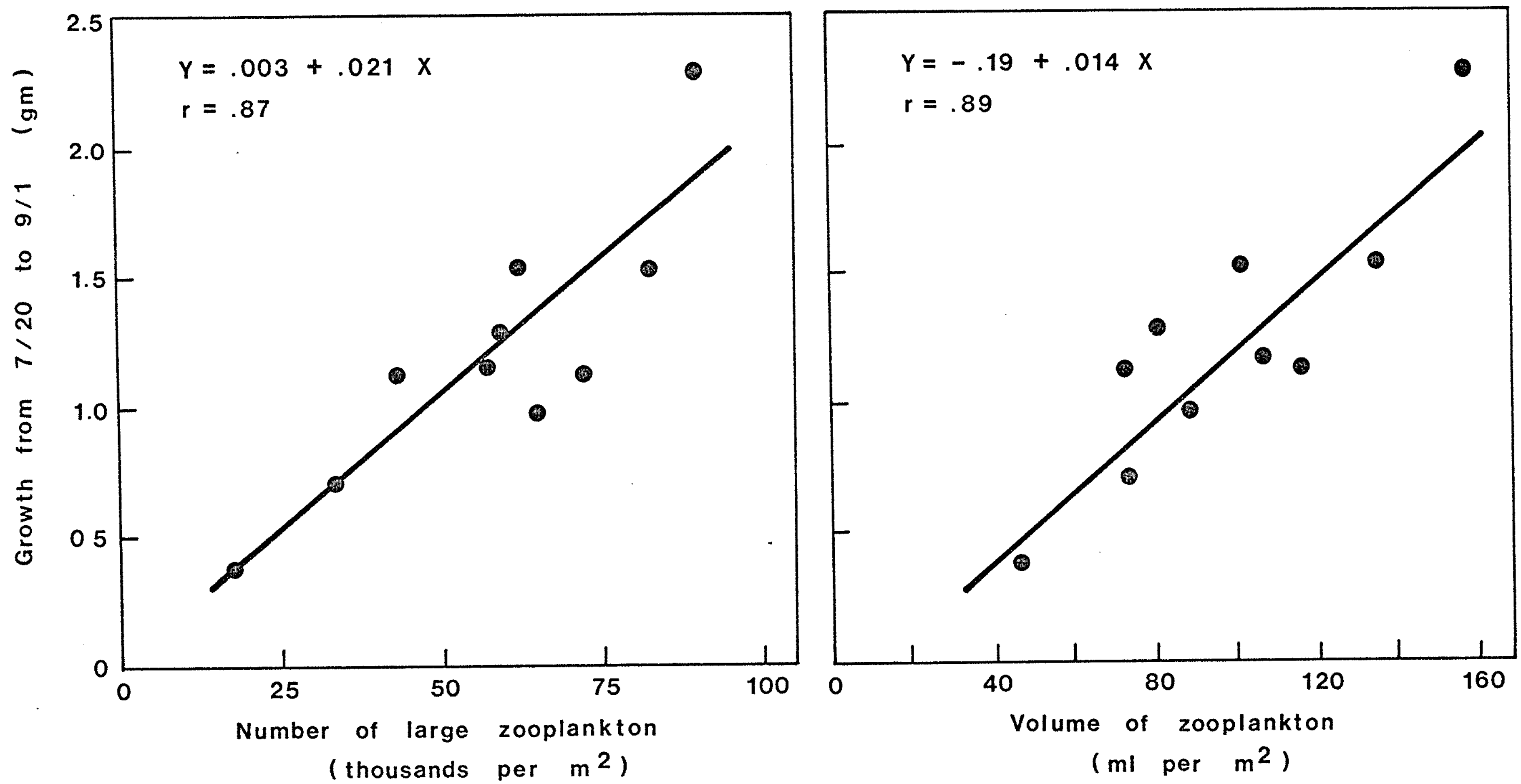


Fig. 10. Growth of sockeye (increase in weight from 7/20 to 9/1) in Lake Aleknagik as functions of the number of large zooplankton (*Daphnia*, *Holopedium*, and calanoid copepods) and the settled volume of zooplankton during the same periods in 1967-1976.

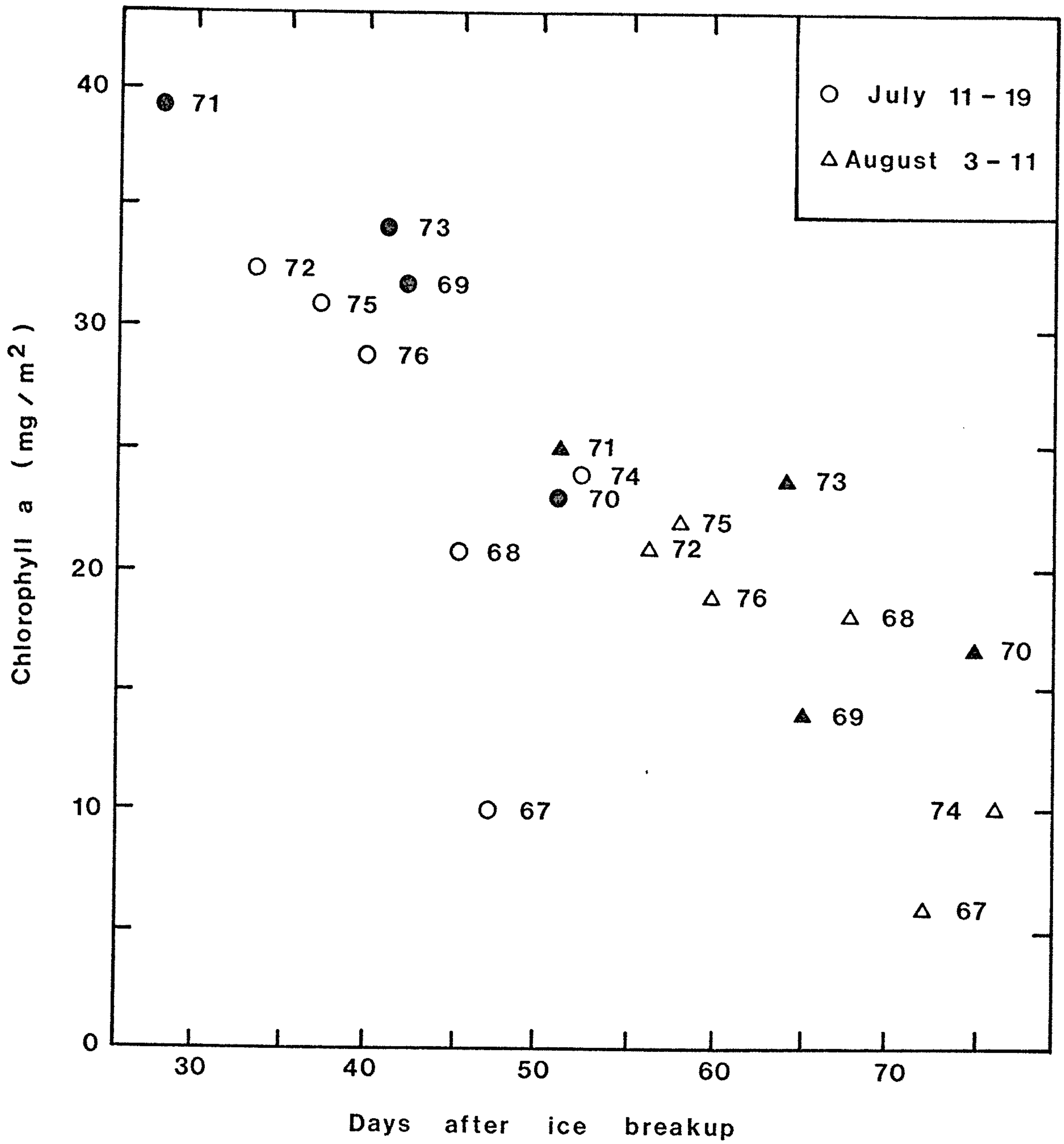


Fig. 11. Plot of the amount of chlorophyll *a* in the upper 20 m of Lake Aleknagik in July and August on the number of days after ice breakup when measurements were made. Solid symbols indicate years in which the growth of sockeye fry was greater than predicted from the abundance or volume of zooplankton.