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COLLECTION AND ANALYSIS OF BIOLOGICAL DATA FROM THE WOOD RIVER
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BIOLOGY OF THE THREESPINE STICKLEBACK
IN THE WOOD RIVER LAKES

by

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INTRODUCTION

The threespine stickleback *Gasterosteus aculeatus* L. is a very abundant species that is distributed throughout the northern hemisphere. It can tolerate a relatively wide range of environmental conditions and is well suited for rearing in aquaria. Thus sticklebacks have been the subject of much research in experimental biology, and a considerable amount of literature has been published on their behavior, genetics, taxonomy, and physiology. Fishery biologists have largely been concerned with the role of sticklebacks as potential competitors with commercially important species and their food habits have been studied in North America, Europe, and Asia.

The stickleback occurs in all of the major salmon producing lakes in Bristol Bay and their abundance is often comparable to that of the juvenile sockeye salmon. The Fisheries Research Institute has investigated the populations of stickleback in the Wood River lake system (Fig. 1) since 1958 to determine whether their abundance adversely affects the production of juvenile sockeye.

The stickleback and juvenile sockeye have similar food habits and seasonal distributions (inshore in spring and offshore in summer and fall), but a significant effect of stickleback abundance on the growth and survival of the sockeye has not been demonstrated (Rogers, 1968 and 1973). However, the annual variation in the abundance of juvenile sockeye was greater than the variation in stickleback abundance and the growth of both species was inversely related to the abundance of the sockeye. In years when the abundance of sockeye is high, the relative abundance of stickleback may have some adverse influence on their growth. However, stickleback are also eaten by the same predatory fish and birds that feed on the juvenile sockeye, thus their abundance as an alternate prey may have a beneficial influence on the survival of the sockeye.

This report summarizes our observations on the life history, relative abundance, and growth of the threespine stickleback and emphasizes those which likely influence their abundance and ecological relationship to juvenile sockeye salmon.

METHODS

Sampling was conducted in the littoral zone at Lake Aleknagik during the summers of 1959 through 1976. We generally used a beach seine that was 35 m long and had a midsection of 6-mm mesh, 7.6 m long and 3.7 m deep. Seine hauls were made only in the lower end of the lake (Area C) during 1959-1961, whereas hauls were made at 24 stations throughout the lake in

1962 and at 10 stations from 1964 to 1976 (Fig. 2). Hauls were usually made at weekly intervals from mid-June to early August.

Beach-seine hauls were made in Lakes Kulik, Beverley, and the north arm of Nerka during 1968-1972, and in Little Togiak Lake during 1973-1976. Sampling was conducted in the other Nushagak lake systems in 1964-1965.

The catches or samples from large catches were preserved in 10 percent Formalin and enumerated by species from 1 to 7 days after collection. Length was measured from the tip of snout to end of middle ray of the tail (fork length) and the length frequencies were plotted by lake area and for areas combined. Partial age compositions were determined from the length frequencies, and mean lengths were calculated for those age groups that were easily separated from the length frequencies. The mean lengths were converted to equivalent live lengths to adjust for shrinkage caused by preservation. Weight was estimated from a common weight-length regression that was determined during the early 1960's.

The abundance, size, and partial age composition of pelagic populations were estimated from tow-net sampling. Tows were made on two to three nights in each of the Wood River lakes during August 15-September 10. From 1958 through 1971, tows were made at the surface (0-3 m) and below the surface (3-6 m), and from 1972 to 1976 only surface tows were made. An echosounder was used to estimate the abundance of fish below 3 m in the later years. Population estimates were made according to the method described by Rogers (1967).

The catch data were analyzed through logarithmic transformation, and analysis of variance was used to determine the significance of observed variation associated with location, date, and year. The weight and catch data were examined through step-wise multiple regression and linear correlation techniques to determine significant relationships among physical and biological parameters.

Variation in the incidence and intensity of infection of the cestode *Schistocephalus solidus* (Muller) was studied in 1959-1961 to determine the effects of the pleurocercoid on the threespine stickleback. The number and weight of the parasite and the length, weight, sex, and fecundity of females were determined from samples collected in the lower end of Lake Aleknagik.

RESULTS

A list of references on the threespine stickleback is given in the Appendix. The stickleback in the Wood River lakes is predominantly the partially plated freshwater form, *leiurus* (Hagen and Gilbertson, 1972). The fully plated marine form (*trachurus*) has been rarely observed and then only in the lower end of Lake Aleknagik.

The literature on the life history of the threespine stickleback is somewhat contradictory, especially in regard to age and growth, e.g.,

Greenbank and Nelson, 1959; Hynes and Jones, 1950; Leiner, 1931; and Bertin, 1925. Differences among the results of these studies are probably caused by geographical variation in growth and behavior. Sticklebacks are almost exclusively carnivorous fishes that eat a wide variety of prey, chiefly crustaceans and insects. Their diets apparently depend on what is available and they probably feed only during the daytime (Beukema, 1964 and 1968).

Reproduction

Sticklebacks spawn in the spring and their maturation is a function of day length (Baggerman, 1957). In the Wood River Lakes, spawning occurs in June and July, and the annual variation in the time of spawning is related to when ice breaks up. Most fish mature at age III, although some larger individuals mature at age II. Maturation and fecundity are partly functions of their size and thus their growth during the previous summer (Rogers, 1962).

Males build a nest in which one or two females deposit eggs. The average female contains about 100 eggs. Spawning generally occurs along the shore and in bays where there is a mud bottom. Although sticklebacks commonly migrate up streams to spawn, this has not been observed in the Wood River lakes. Males guard the nests and the young which are about 6 mm long when they hatch. There is a high mortality rate of spawning males. Dead individuals are a common sight along the shoreline during the summer. The sex ratio was about 50:50 at ages I and II, females were more abundant than males at age III and all fish over 75 mm in length (mostly age IV) were females. The immature age I fish and most of the age II fish begin moving into the pelagic areas of the lake in mid-July. After that time, the populations in the littoral zone are predominantly the fry and the age II and III males (Fig. 3). The stickleback fry first appear in beach-seine catches when they are about 12 mm in length and they first appear in the tow-net catches when they are about 18 mm long.

The reproduction of the sticklebacks may be adversely affected by unusually cold conditions in the spring. Such conditions prevailed in 1971 and 1972 and subsequently the relative abundance was greatly reduced until 1974. Growth also affects reproduction because it affects age at maturation and the number of eggs in a female (Rogers, 1962).

Parasites

The life cycle of the pseudophyllidean cestode, *Schistocephalus solidus*, has been investigated in Europe by Hopkins and Smyth (1951), Clarke (1954), and Vik (1954). The life cycle is: eggs to coracidium in water, coracidium to procercoïd in *Cyclops* sp., procercoïd to pleurocercoïd in sticklebacks (*G. aculeatus* and *P. pungitius*), and pleurocercoïd to adult in fish-eating birds. The pleurocercoïd may affect the development and spawning of eggs in female sticklebacks (Jara, 1953), and kill the host by breaking through the wall of the abdomen (Vik, 1954).

There was no significant difference between sexes in rate and intensity of infection for sticklebacks of a given size. Rate of infection was related to size and thus the age of the fish. The percent infected in 1959 samples from the pelagic zone was highest in the upper lakes and lowest in Lake Aleknagik; however, in that lake there was a higher rate of infection in 1960 and the percent infected was higher for fish collected in the littoral zone in early summer than for those from the pelagic zone in late summer (Fig. 4). Sticklebacks in the Wood River lakes probably become infected at age I and older. Age I sticklebacks were examined only in 1959 and the percent that was infected was relatively low and did not change greatly during that summer (Fig. 5). The seasonal changes in the percent of ages II and older that were infected were only slightly different in 1959 and 1960 in the lower end of Lake Aleknagik. The percent infected increased to a maximum in mid-July then decreased in those fish caught in the pelagic zone but not in those caught in the littoral zone. A decrease in the percent infected would indicate that the parasite causes some mortality if the fish are all from the same population; however, there may be subpopulations, e.g., some that remain inshore and some that move offshore and the ones that move offshore are less infected.

The weight of a pleuroceroid was partly dependent on the weight and age of the fish and the number of worms it contained. On June 17, 1960 (about two weeks after ice breakup) there were three size groups of pleuroceroids in those fish which contained only one individual (Fig. 6). The smallest group weighed less than .05 gm and was present in both age II and age III fish. In an intermediate group, worms weighed from .10 to .25 gm and these were primarily present in age II fish. The maximum weight of a worm was .59 gm on June 17. Growth of the pleuroceroids occurred from June to September, however the maximum weight of a worm on September 4 was only .44 gm. This may indicate that large pleuroceroids cause mortality in the stickleback population. However, most age III sticklebacks contained two or more pleuroceroids by September and their weight was often very high relative to the weight of the fish (Fig. 7).

The maximum number of pleuroceroids in one fish was 15 and the maximum weight was 1.55 gm which was in a fish that weighed 4.37 gm (including the weight of the parasites). The pleuroceroids constituted up to 36 percent of the total weight of fish that ranged from 1.5 to 4.4 gm, and up to 55 percent of the weight of fish minus the weight of the pleuroceroids. *S. solidus* must affect the growth of fish in the population since a considerable amount of their food must end up in the parasite rather than in growth and reproduction.

In the littoral of Lake Aleknagik on September 4, 25 percent of the mature females with one or more pleuroceroids were unspawned and 7 percent contained some mature ova. None of the uninfected females were unspawned and only 4 percent contained any mature ova (diameter greater than 1 mm). The differences between infected and uninfected females were statistically significant ($X^2 = 15.93$ with 2 dif.). Therefore, the presence of the parasite can adversely affect reproduction in the threespine stickleback.

Food Habits

Cyclopoid copepods and midges (tendipedids) are the most important food items for threespine sticklebacks in the spring and early summer when they are in the littoral zone (Rogers, 1968). Age I sticklebacks consumed a higher proportion of copepods and nauplii than older fish which fed more on the adult copepods. The age I fish also consumed a higher proportion of midge larvae than pupae, whereas older sticklebacks consumed about equal proportions of larvae and pupae. The main difference in the diets of the sticklebacks and sockeye fry was that the sockeye fry consumed many adult insects whereas the sticklebacks did not. Otherwise the diets of the species were similar.

Cyclopoid copepods were the most important food item in the diet of sticklebacks in the limnetic regions of the lakes during August and September, whereas insects were of minor importance (Table 1). Sockeye fry consumed about 2.5 times more food than sticklebacks of comparable length (age II), and the amount of food in stickleback stomachs was proportional to the size of the fish. About 7 percent of the sticklebacks and sockeye fry had empty stomachs; whereas, in the littoral zone, 6 percent of the sockeye and about 3 percent of the sticklebacks had empty stomachs.

The composition of the zooplankton in the stomachs of the sticklebacks was similar to the typical composition in net plankton except that *Holopedium* was more abundant in the stomachs than in net hauls (Table 2). In contrast, the sockeye fry apparently select cladocerans, particularly *Daphnia*, and the percentage of copepods in their stomachs was lower than typically occurs in net plankton hauls.

The diet of age I sticklebacks is more similar to the diet of sockeye fry than is the diet of the older sticklebacks and the seasonal distribution of the age I sticklebacks is also more similar to that of the sockeye fry. Thus, the young sticklebacks are potentially greater competitors for food with the sockeye fry although the older sticklebacks consume a greater amount of food.

Relative Abundance

Estimates of the relative abundance of threespine stickleback in the littoral zones of lakes in the Nushagak district were confined to the period June 20-July 19 because most of the populations in the Wood River lakes move offshore in midsummer. Threespine stickleback were the most abundant or second most abundant species in all lakes sampled except two of the Tikchik Lakes (Table 3). Lakes Nuyakuk and Chauekuktuli have very restricted littoral zones and are deeper than the other lakes in the district.

The relative abundance and growth of age I threespine stickleback in the littoral of Lake Aleknagik during 1962-1972 was discussed by Rogers (1973). The observations collected in 1973-1976 did not change most of the conclusions

of that study in regards to seasonal and annual fluctuations in abundance. Significant differences were detected in the mean catches by year for all species, but the absolute and relative variation (coefficient of variation) were highest for sockeye fry. The COV for annual mean catches of sockeye fry was 81 percent compared to 60 percent for annual mean catches of threespine stickleback. No significant correlation was evident between the annual mean catches of threespine stickleback and those of sockeye fry either in the same year or the previous year.

Annual mean catches of age I stickleback tended to be higher following years when the ice breakup was early and water temperatures in the spring were warm and lower following years when ice breakup was late and water temperatures were cold; however, there was not a statistically significant correlation between these environmental measurements and the catches of sticklebacks. The successive cold springs of 1971-1973 were followed by low catches of sticklebacks in the littoral of Lake Aleknagik from 1972 through 1975 (Fig. 8). Cold weather in the spring may have an adverse affect on the reproduction of the stickleback. In addition, spring weather affects the offshore movement of sticklebacks. They tended to move offshore earlier when water temperatures were warmer than average and ice breakup was early, whereas they showed up later in the catches and moved offshore later in the summer when ice breakup was late and temperatures were colder than average.

Pelagic populations of threespine stickleback and juvenile sockeye salmon were estimated during the period of mid-August to early September in each year from 1958 through 1976. On the average, the populations of both species were larger in Lake Aleknagik and the north arm of Lake Nerka than in the other lakes in the system¹. The density of fish in the upper 6 m was estimated by the mean tow-net catches (Table 4). The distribution of threespine stickleback throughout the pelagic areas of the lake system generally corresponds to the distribution of sockeye salmon fry, and the average size of sockeye fry and age I stickleback was inversely proportional to their density.

The annual abundances of threespine sticklebacks in the lake system are shown by 5 mm length intervals in Figs. 9 and 10. The relatively low abundance in 1971 was probably not representative of the abundance of the total population. An unusually high proportion of the population was probably located inshore in August of that year and perhaps also in August of 1972. The annual abundances of threespine stickleback and sockeye salmon fry were not correlated.

Relatively large populations of age 0 sticklebacks occurred in 1968 and 1974 which were years when the spring weather was warmer than average. The abundance of age 0 fish in the pelagic areas of the lakes are usually not

¹Rogers, D. E. 1975. Systems modeling of sockeye salmon in the Wood River lakes. Univ. of Washington Fish. Res. Inst. Annual Report. Anadromous Fish Project. FRI-UW-7511. 51 pp.

indicative of their actual abundance in the lakes, because they tend to remain inshore in August and are not fully available to tow-net sampling. Age I fish were particularly abundant in 1964, 1968, and 1975. These years followed the warm years of 1963, 1967, and 1974 when the age I fish were hatched. Very large sticklebacks occurred in the populations in 1958-1960, and they were particularly abundant in the upper lakes of the system. Based on the seasonal length frequencies of sticklebacks in Lake Aleknagik these fish were probably age III in 1958, age IV in 1959, and perhaps some individuals were age V in 1960 (Fig. 11).

Growth

The growth of age I sticklebacks is partly density dependent (abundance of sockeye) and partly dependent on water temperature and the area of the lake system where they are caught. Their growth is lowest at high densities, cold temperatures, and in deeper areas of the system, whereas their growth is highest at low densities, warm temperatures, and in shallow areas of the system.

Growth rates of threespine stickleback are highest at age 0, then decrease at older ages (Fig. 12). Most of their annual growth occurs during July and August, whereas growth of sockeye fry continues through at least September. Annual variation in the size of age I sticklebacks was greater at the end of the summer than at the beginning and in some years they were smaller on September 1 than they were on August 1 of other years (Fig. 13). The summer growth of the age I sticklebacks determines their size the following spring and thus determines the proportion of the population that matures and spawns at age II. In 1960, the smallest sexually mature female was 50 mm long, and in most years the mean length of age II fish was less than 50 mm in mid-June.

The calculated mean weights of threespine sticklebacks in Lake Aleknagik on June 20, July 20, and September 1 are given by year class in Table 5 and by year of sampling in Table 6. Growth from June 20 to July 20 occurs primarily in the littoral zone and growth from July 20 to September 1 occurs in the pelagic zone. An explanation of the observed annual variation in the mean weights and increases in weights of age I sticklebacks was sought through step-wise multiple regression. Two sets of regressions were used one for data from all years ($n = 15$) and one for data only from 1967-1976 ($n = 10$). The later was done because the accuracy of some data prior to 1967 was poor.

The mean weight of age I threespine stickleback on June 20 was related to 1) days after ice breakup, 2) water temperature on June 21-27, 3) relative abundance of large zooplankters in June, 4) beach-seine catches of sockeye fry in the year of sampling and in the preceding year, and 5) the escapement of adult sockeye two years prior to sampling.

Although all variables, except catch of sticklebacks, were somewhat correlated with the mean weight on June 20, the escapement two years prior to sampling was the most highly correlated variable ($r = -.76$, $n = 10$). The

abundance of sockeye fry was correlated with the abundance of parent spawners, thus the growth of age 0 sticklebacks was inversely related to the abundance of sockeye fry.

The mean weight of age I stickleback on July 20 was inversely correlated with the mean catch of sockeye fry in the same year. The relationship was curvilinear and the best correlation was obtained by regressing the mean weight on the logarithm of the sockeye catch during 1967-1976 ($r = -.72$, $n = 10$). The absolute growth or increase in weight from June 20 to July 20 was most highly correlated with the relative abundance (1,000's per m^2) of large zooplankters (calanoid copepods, *Daphnia* and *Holopedium*) during that period of the summer ($r = .88$). However, the relative abundance of sockeye fry (geometric mean catch) explained a significant amount of the residual variation and the following multiple regression had a correlation coefficient of .95 ($n = 10$):

Increase in weight
from 6/20 to 7/20 (gm) = $.044 + .003 (\text{Zoop.}) - .00014 (\text{sockeye catch})$.

About 80 percent of the summer growth of the age I stickleback occurs between July 20 and September 1 when they are feeding in the pelagic area. Their growth during this period was correlated with the growth of sockeye fry and the volume of zooplankton (Table 7). About 64 percent of the annual variation in the growth of age I stickleback was associated with the volume of zooplankton and none of the other variables explained a significant part of the remaining variation. The linear regression was:

Increase in weight
from 7/20 to 9/1 (gm) = $.055 + .003 (\text{vol. of Zoop.})$.

SUMMARY

Annual variation in the abundance and growth of threespine stickleback in the Wood River lakes was studied because this species is a potential competitor with the commercially important sockeye salmon. The growth of juvenile sockeye salmon is density dependent and is a function of the abundance of zooplankton. The survival of juvenile sockeye is partly determined by their growth, thus competition for food can limit the survival and ultimate production of adult salmon.

The juvenile sockeye salmon apparently have the advantage in the competition between the species, because the growth of both species was more closely related to the abundance of the sockeye than to the abundance of sticklebacks. The reproduction of sticklebacks was indirectly affected by the abundance of sockeye because their maturation was partly a function of their growth. However, the reproduction of sticklebacks was more affected by spring weather conditions and the parasite *S. solidus*, than it was by the abundance of sockeye.

Quantitative estimates of the effects of stickleback abundance on the growth of juvenile sockeye were not possible because there was a considerable

degree of correlation among most of the variables examined. Growth of sockeye fry, growth of age I stickleback, relative abundance of each species, and the abundance of zooplankton were all interrelated. Growth of sockeye fry would probably increase if stickleback were less abundant, but just how significant the increase would be is as yet undetermined in the Wood River lakes.

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Table 1. Average number of food items in the stomachs of sockeye salmon fry and threespine sticklebacks from the limnetic zone of the Wood River lakes in 1959

Food item	Sockeye fry	Threespine stickleback		
		Age I	Age II	Age III+
Copepods				
Cyclopoids	27.0	9.1	15.6	29.4
Calanoids	3.2	2.9	7.5	14.5
Copepodids and nauplii	6.2	1.1	1.4	1.1
Cladocerans				
<i>Bosmina</i>	41.2	7.9	8.2	10.7
<i>Daphnia</i>	20.1	2.4	3.2	4.5
<i>Holopedium</i>	1.2	2.9	5.4	5.5
Chydorids	0	0.1	0	0
Insects				
Diptera adults	2.8	0	0	0
Other	0.5	0.1	0.2	0.3
TOTAL	102.2	26.5	41.5	66.0
Sample size (n)	995	662	763	757
Mean lengths (mm)	55.7	43.7	55.6	67.1

Table 2. Percent composition of adult zooplankters in the stomachs of sockeye fry and threespine sticklebacks in 1959 and the composition in zooplankton hauls during 1967-1976

	Net zooplankton	Sockeye fry	Threespine stickleback		
			Age I	Age II	Age III+
Cyclopoids	38	29	36	39	46
Calanoids	18	4	12	19	22
<i>Bosmina</i>	32	44	31	21	17
<i>Daphnia</i>	10	22	10	8	7
<i>Eolopedium</i>	2	1	11	13	9

Table 3. Geometric means of beach-seine catches made during June 20-July 19 in lakes of the Nushagak district of Bristol Bay

Lake system	Lake	Year	n	Sockeye salmon		Stickleback		Sculpin	Arctic char age 0
				Age 0	Age I+	three-spine	nine-spine		
Wood River	Beverley	1968	4	26	2	23	44	22	10
		1969	9	78	3	220	36	38	5
		1970	9	59	0	89	12	27	11
		1971	9	71	1	105	8	37	9
		1972	9	85	3	83	4	34	8
Kulik		1968	4	339	0	48	15	28	37
		1969	9	36	1	88	7	30	3
		1970	9	50	1	231	8	30	34
		1971	9	234	0	174	11	26	7
		1972	9	77	2	46	5	13	11
N. Nerka		1969	4	33	5	565	85	27	4
		1970	5	73	0	115	30	30	33
		1971	5	21	0	75	14	30	3
		1972	5	146	2	154	12	37	6
		1973	24	63	0	34	2	17	19
Little Togiak		1974	24	12	1	35	7	7	12
		1975	28	135	0	65	6	17	39
		1976	28	130	0	74	8	12	23
		1962	40	278	3	222	12	38	6
Aleknagik		1964	40	171	2	277	20	45	4
		1965	40	565	1	199	8	31	2
		1966	40	380	3	228	4	18	6
		1967	40	335	10	369	22	19	6
			40						

Table 3. Geometric means of beach-seine catches made during June 20-
July 19 in lakes of the Nushagak district of Bristol Bay - continued

Lake system	Lake	Year	n	Sockeye salmon			Stickleback		Sculpin	Arctic char age 0
				Age 0	Age 1+	three- spine	nine spine			
Wood River (continued)	Aleknagik (continued)	1968	40	35	6	193	32	24	5	
		1969	40	85	2	212	22	26	2	
		1970	40	127	2	132	16	29	4	
		1971	40	405	4	202	11	40	2	
		1972	40	131	2	40	3	34	4	
		1973	40	22	3	24	6	30	5	
		1974	40	26	1	34	8	12	10	
		1975	40	97	1	51	16	22	2	
		1976	40	204	2	211	22	12	3	
		Tikchik	Tikchik	1964	6	36	1	44	3	3
Nuyakuk	1964		12	22	0	6	2	25	1	
Chauekuktuli	1964		9	118	1	3	1	27	8	
Igushik	Amanka	1965	12	288	1	937	9	8	4	
		1966	4	408	14	605	8	6	1	
		1965	11	92	0	165	2	22	12	
Nunavaugaluk		1965	12	17	2	557	2	6	1	
		1966	6	16	0	34	0	2	4	
		1973	18	3	2	16	3	11	2	

Table 4. Geometric means and annual ranges in mean tow-net catches, and the mean lengths and annual ranges in mean lengths on September 1, 1958-1976, arranged by area of the lake system from the outlet to the uppermost lake

Lake	Sampling area	Surface area (km ²)	Mean depth (m)	Catches (no. per 5 min. tow)		Lengths (mm)	
				Sockeye salmon fry mean range	Threespine stickleback mean range	Sockeye salmon fry mean range	Age I stickleback mean range
Aleknagik	C	28	22	38 5,521	59 7,195	58 44,69	44 40,51
	B	33	56	28 1,478	51 1,502	57 44,65	43 40,51
	A	23	52	25 1,377	43 2,377	54 42,62	42 38,49
S. Nerka	C	23	29	3 0,15	2 0,16	63 57,75	46 42,54
	B	20	33	8 1,101	4 0,95	61 51,72	45 39,51
	A	20	48	8 0,260	3 0,114	60 52,67	45 42,49
C. Nerka	C	20	40	10 0,60	5 0,278	58 48,64	44 40,48
	B	22	66	10 2,62	6 0,125	58 50,67	44 38,49
	A	9	86	3 0,37	1 0,99	55 42,70	46 41,52
No. Nerka	A	32	39	22 2,69	10 0,243	57 46,65	43 39,50
	B	31	28	28 3,490	9 0,112	59 45,69	43 37,51
	C	23	15	19 2,140	18 2,79	58 44,67	44 39,52
Beverley	C	38	36	5 0,68	9 1,108	61 48,69	44 39,48
	B	26	55	7 0,117	6 0,82	55 45,66	44 35,49
	A	26	78	14 0,163	12 0,68	54 43,61	44 38,48
Kulik	A	13	70	10 1,92	9 0,107	57 46,69	43 39,52
	B	17	94	8 0,42	5 0,63	56 46,72	44 40,48
	C	15	62	17 0,130	6 1,108	58 41,66	43 38,47
Little Togiak	C	2	35	21 0,68	39 2,247	55 43,66	43 39,49
	B	2	32	35 3,304	57 4,858	54 45,62	43 36,48
	A	2	18	39 0,550	21 2,126	53 44,63	42 37,48

Table 5. Mean weights (gm) of threespine stickleback in Lake Aleknagik by year class

Year class	Age 0	Age I (year + 1)			Age II (year + 2)			Age III (y + 3)
	9/1	6/20	7/20	9/1	6/20	7/20	9/1	6/20
1961	.11	.18	.29	.62	(.80)	1.30	1.53	1.97
62	.12	.20	.38	.75	.88	1.04	1.62	1.70
63	.12	.23	.29	.60	.68	.83	1.39	1.70
64	.12	.17	.24	.46	.60	.75	1.10	1.25
65	.12	.15	.21	.46	.60	.78	1.25	1.79
66	.08	.17	.23	.53	.64	.99	--	2.26
67	.11	.21	.33	.61	.78	1.18	1.54	1.70
68	.17	.24	.33	.65	.73	1.10	1.46	1.79
69	.11	.23	.37	.67	.85	.94	1.20	--
70	.15	.22	.27	.61	.68	.83	1.46	--
71	--	.16	.26	.66	.88	1.25	2.16	2.36
72	.07	.18	.33	.95	.99	1.39	2.06	--
73	.10	.26	.47	.94	1.12	1.39	--	--
74	.17	.23	.31	.57	.64	.88	1.12	--
75	.09	.14	.24	.44	--	--	--	--
76	.15	--	--	--	--	--	--	--

Table 6. Mean weights (gm) of threespine stickleback in Lake Aleknagik, 1961-1976.

Year	Age 0	Age I			Age II		
	9/1	6/20	7/20	9/1	6/20	7/20	9/1
1961	.11	--	--	.56	--	--	1.45
62	.12	.18	.29	.62	.64	.76	1.23
63	.12	.20	.38	.75	(.80)	1.30	1.53
64	.12	.23	.29	.60	.88	1.04	1.62
65	.12	.17	.24	.46	.68	.83	1.39
66	.08	.15	.21	.46	.60	.75	1.10
67	.11	.17	.23	.53	.60	.78	1.25
68	.17	.21	.33	.61	.64	.99	--
69	.11	.24	.33	.65	.78	1.18	1.54
70	.15	.23	.37	.67	.73	1.10	1.46
71	--	.22	.27	.61	.85	.94	1.20
72	.07	.16	.26	.66	.68	.83	1.46
73	.10	.18	.33	.95	.88	1.25	2.16
74	.17	.26	.47	.94	.99	1.39	2.06
75	.09	.23	.31	.57	1.12	1.39	--
76	.15	.14	.24	.44	.64	.88	1.12
Means (1962- 1976)	.12	.20	.30	.63	.77	1.03	1.47

Table 7. Correlation coefficients from 15 observations, 1962-1976 (lower left-hand corner), and from 10 observations, 1967-1976 (upper right-hand corner). Statistically significant correlations are underlined

Variable	1	2	3	4	5	6	7	8	9
1. Stickleback growth 7/20 to 9/1 (gm)	1.00	<u>.80</u>	.23	-.06	<u>.73</u>	<u>.80</u>	-.38	-.57	-.55
2. Sockeye growth 7/20 to 9/1 (gm)	<u>.76</u>	1.00	.32	.06	<u>.90</u>	<u>.86</u>	<u>-.73</u>	<u>-.67</u>	<u>-.74</u>
3. Days from ice breakup to 9/1	.27	.06	1.00	<u>.76</u>	.26	.14	-.47	-.03	-.46
4. Water temperature 7/20 to 9/1 (C)	-.02	-.13	<u>.69</u>	1.00	.06	-.01	-.44	.14	-.28
5. Large zooplankton (1,000S/m ²)	<u>.58</u>	<u>.76</u>	.18	-.03	1.00	<u>.93</u>	<u>-.81</u>	<u>-.86</u>	<u>-.75</u>
6. Volume of zoo- plankton (ml/m ²)	<u>.79</u>	<u>.87</u>	.17	.03	<u>.81</u>	1.00	<u>-.75</u>	<u>-.87</u>	-.57
7. Beach-seine catch of sockeye	<u>-.51</u>	<u>-.58</u>	-.34	-.24	<u>-.52</u>	<u>-.63</u>	1.00	<u>.65</u>	<u>.67</u>
8. Beach-seine catch of stickleback	<u>-.57</u>	<u>-.60</u>	-.17	.14	<u>-.68</u>	<u>-.81</u>	<u>.51</u>	1.00	.40
9. Sockeye escape- ment year-1 (1,000S)	-.40	<u>-.59</u>	-.22	-.28	<u>-.65</u>	-.47	.38	.13	1.00

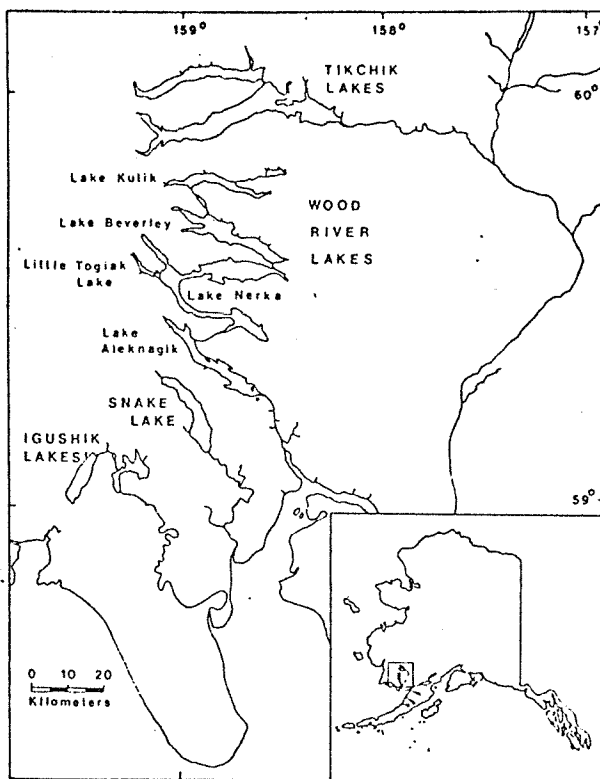


Fig. 1. Map of Nushagak lakes.

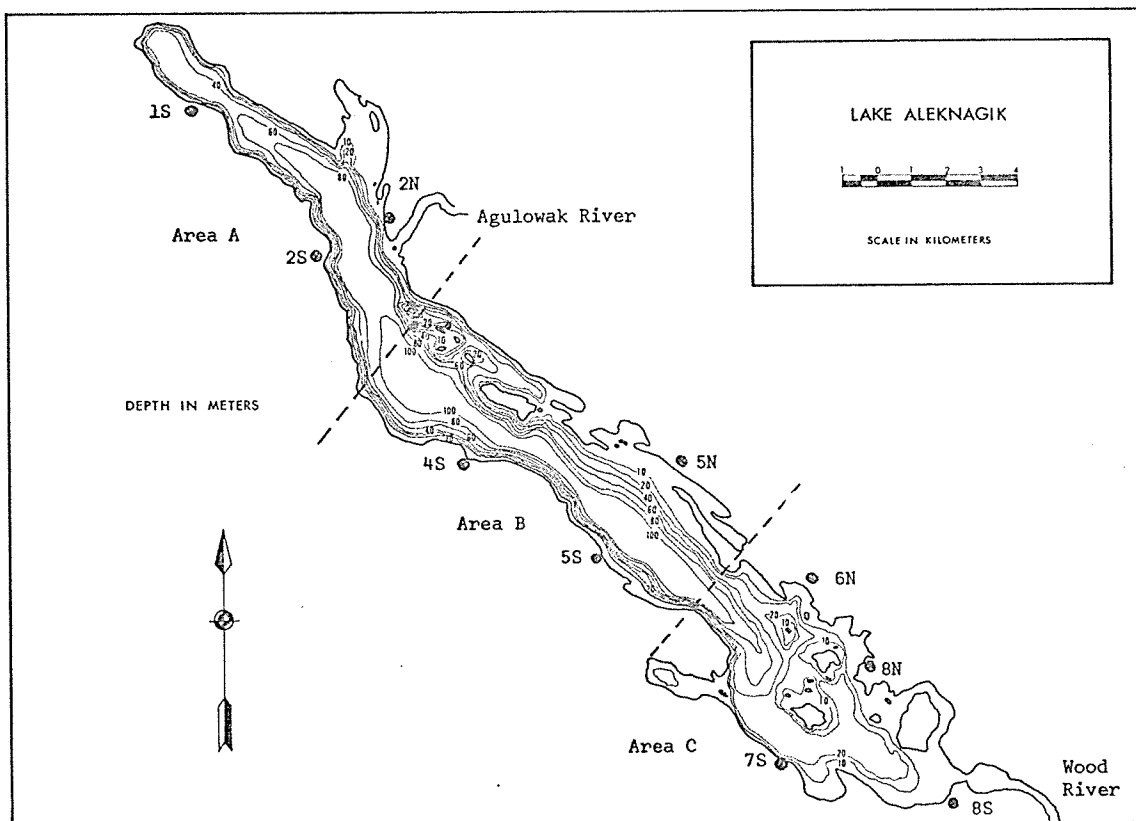


Fig. 2. Map of Lake Aleknagik.

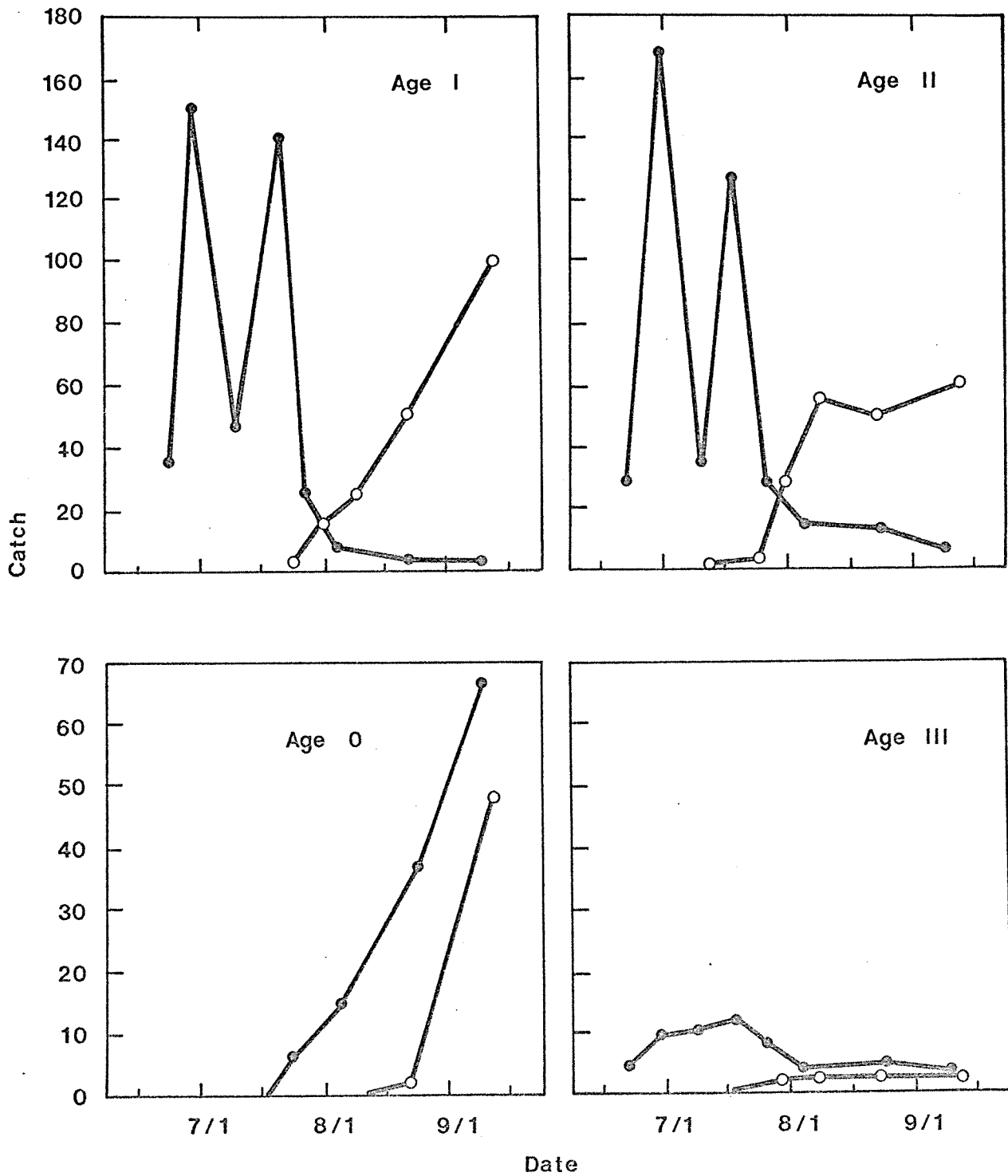


Fig. 3. Geometric means of catches of threespine stickleback in Lake Aleknagik, 1962. Solid points for beach seine and open points for tow net.

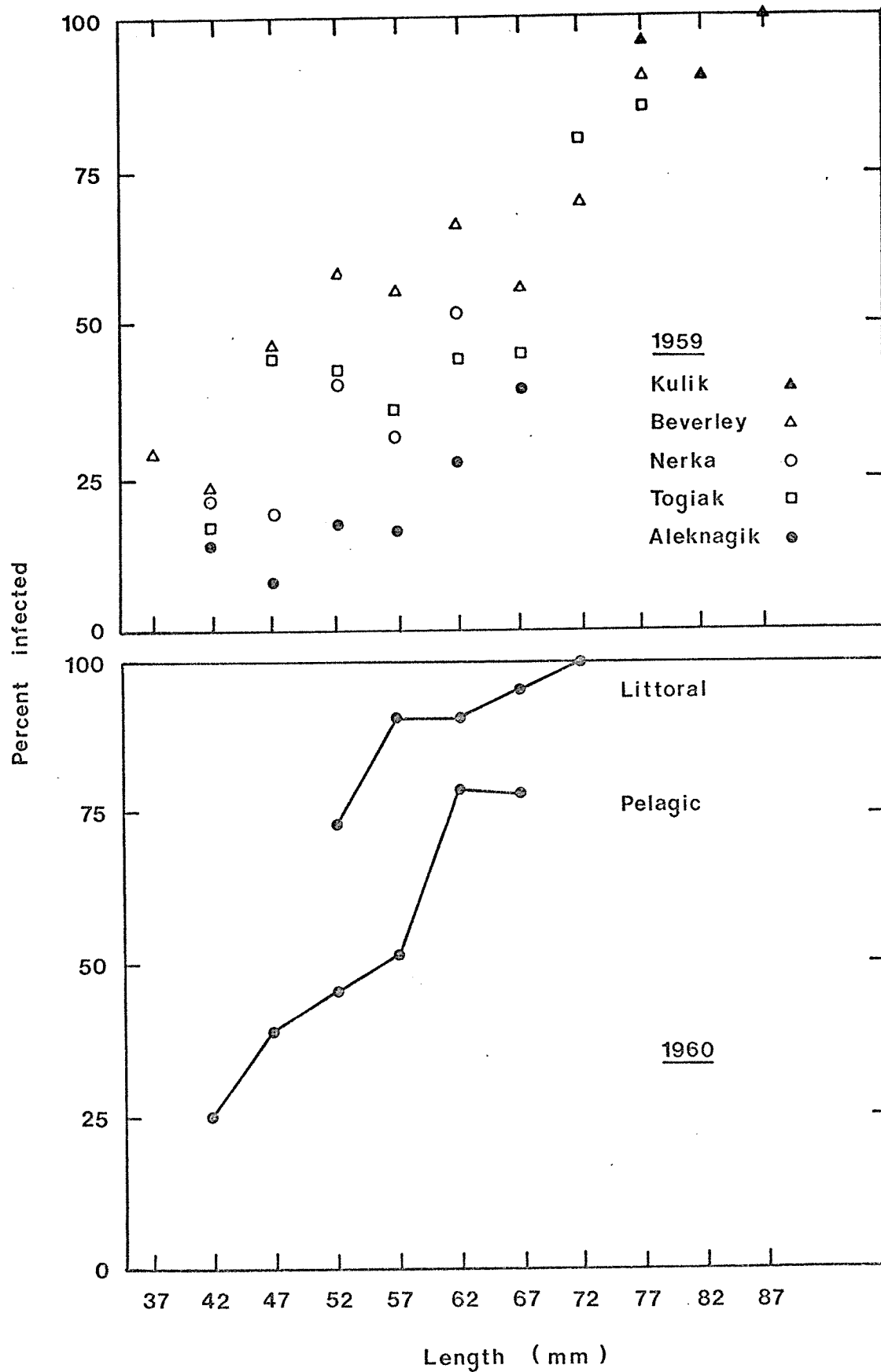


Fig. 4. Percent infected with *S. solidus* in the pelagic areas of the Wood River lakes in 1959 and in the littoral and pelagic areas of lower Lake Aleknagik in 1960 (bottom).

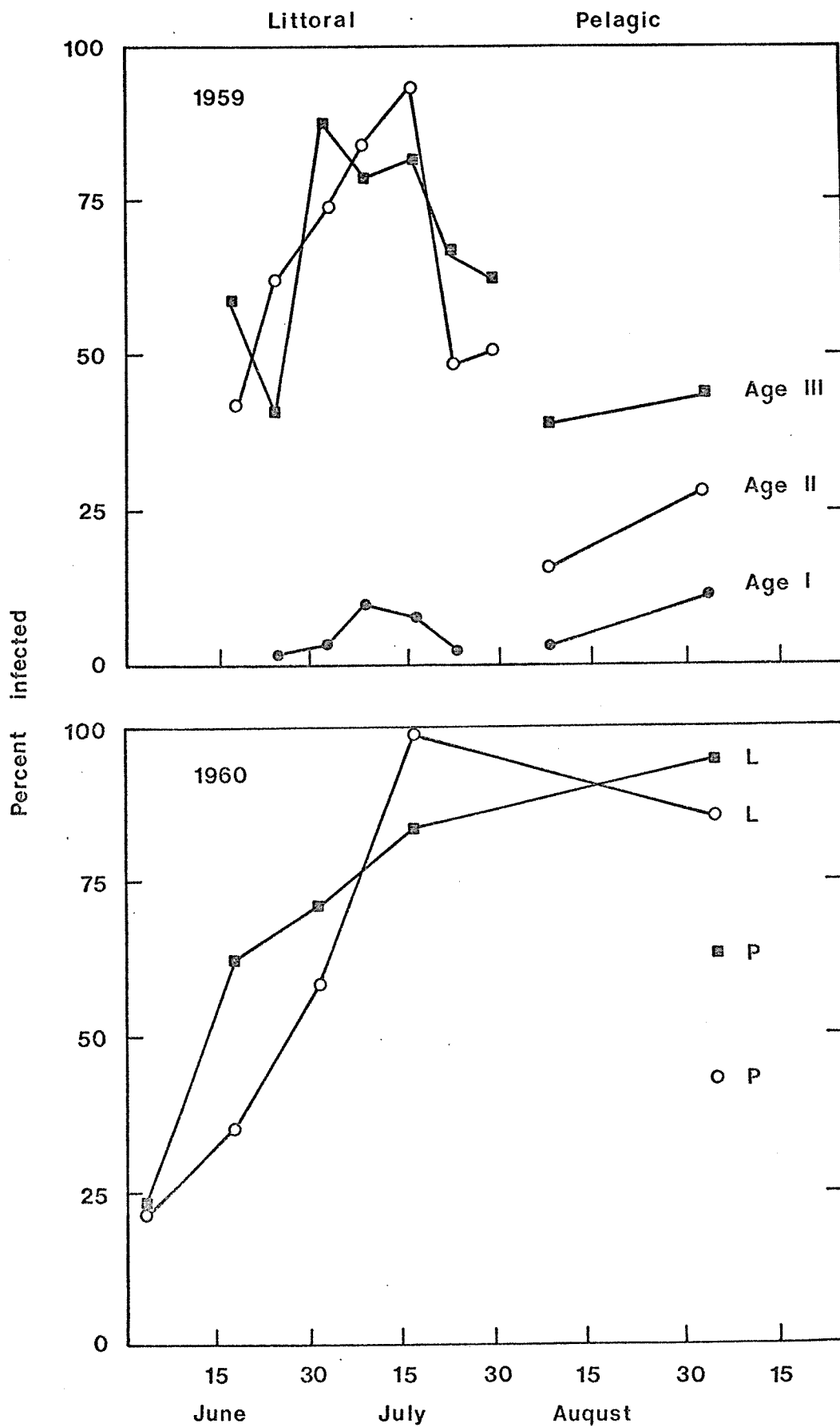


Fig. 5. Percent of threespine stickleback infected with *S. solidus* in area C of Lake Aleknagik in 1959 and 1960.

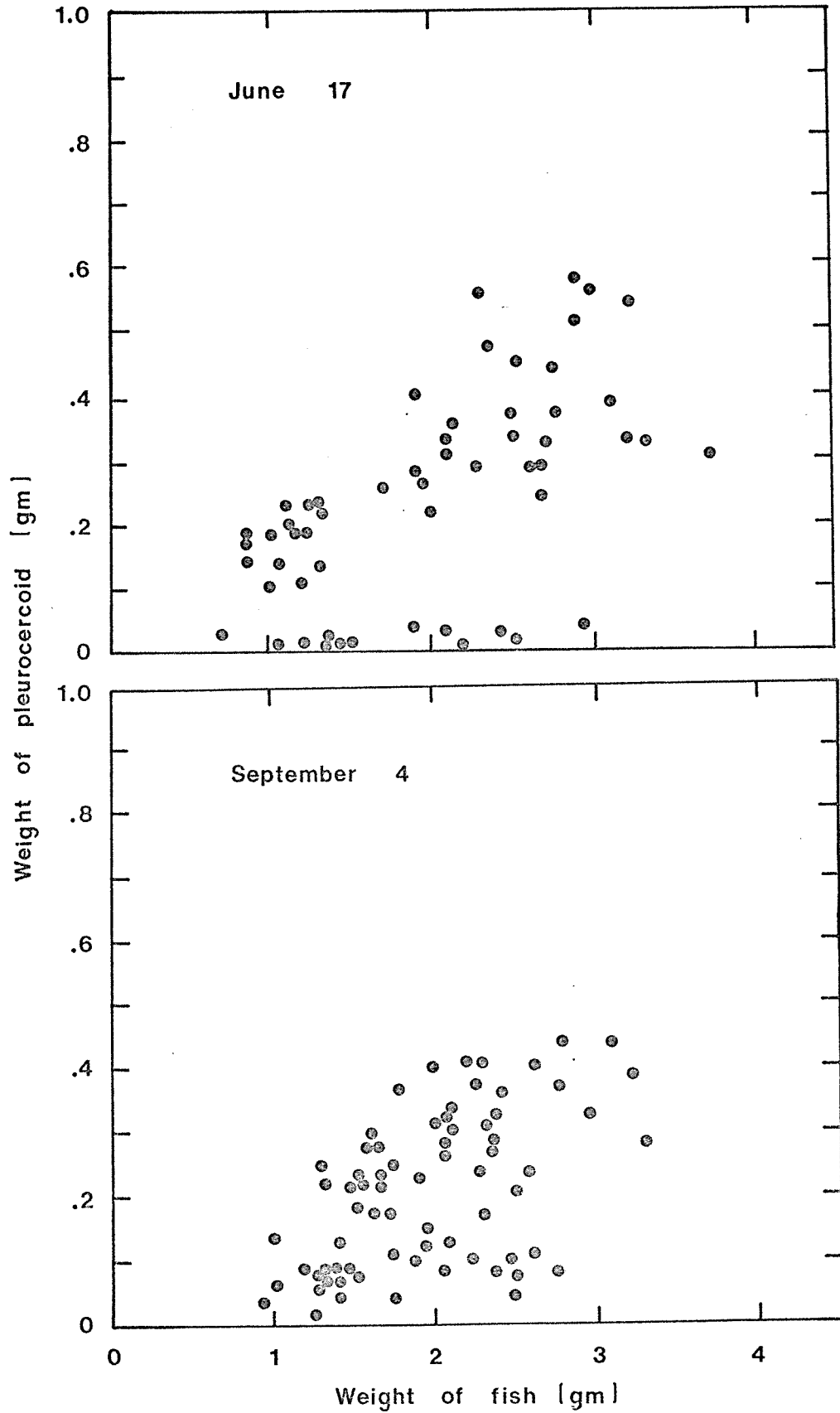


Fig. 6. Weight of a pleurocercoid on the weight of the fish for those fish with one pleurocercoid. Lower Lake Aleknagik, 1960.

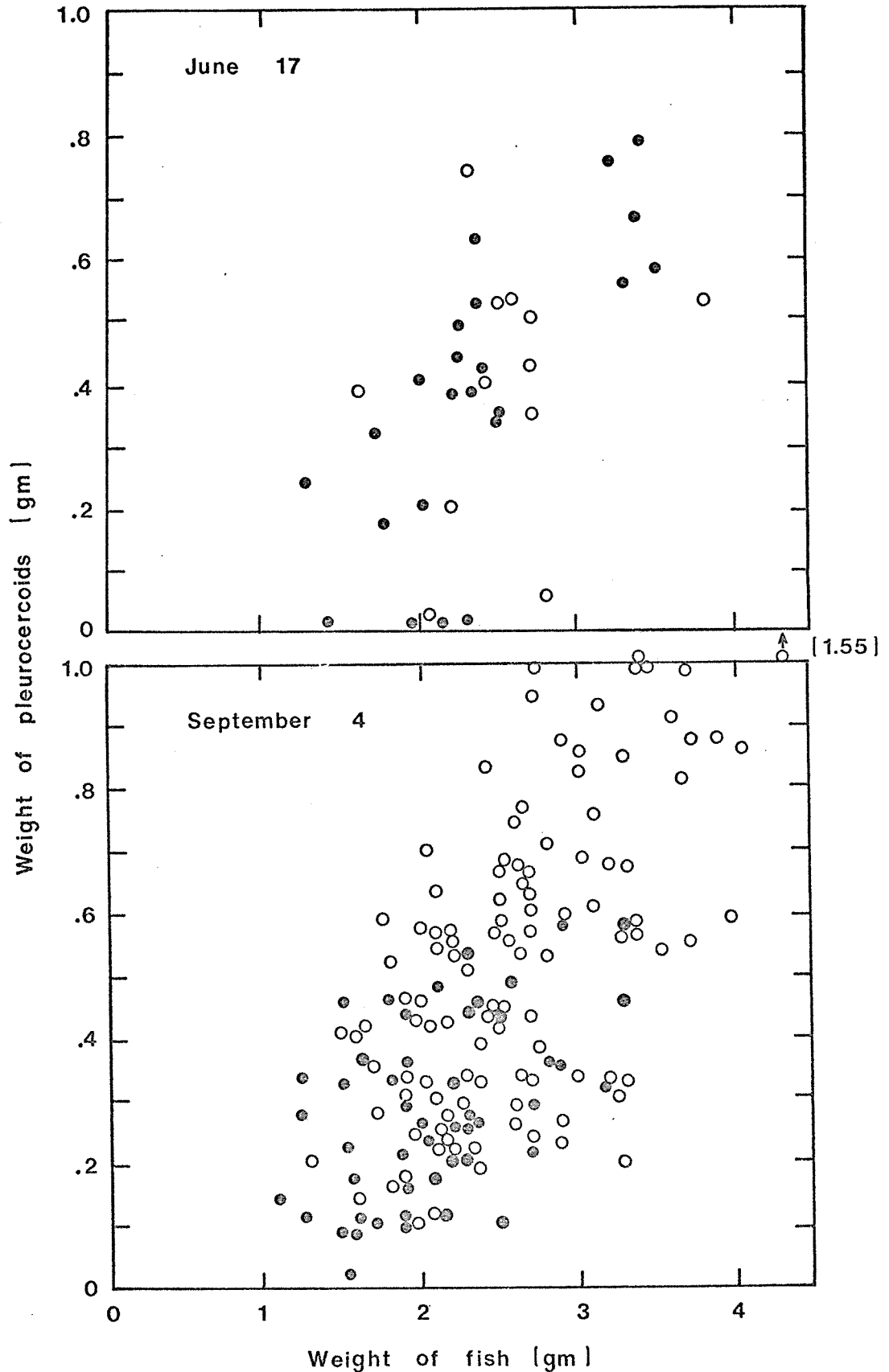


Fig. 7. Weight of pleurocercoids in fish with two (solid points) and three or more (open circles) pleurocercoids plotted against the weight of a fish.

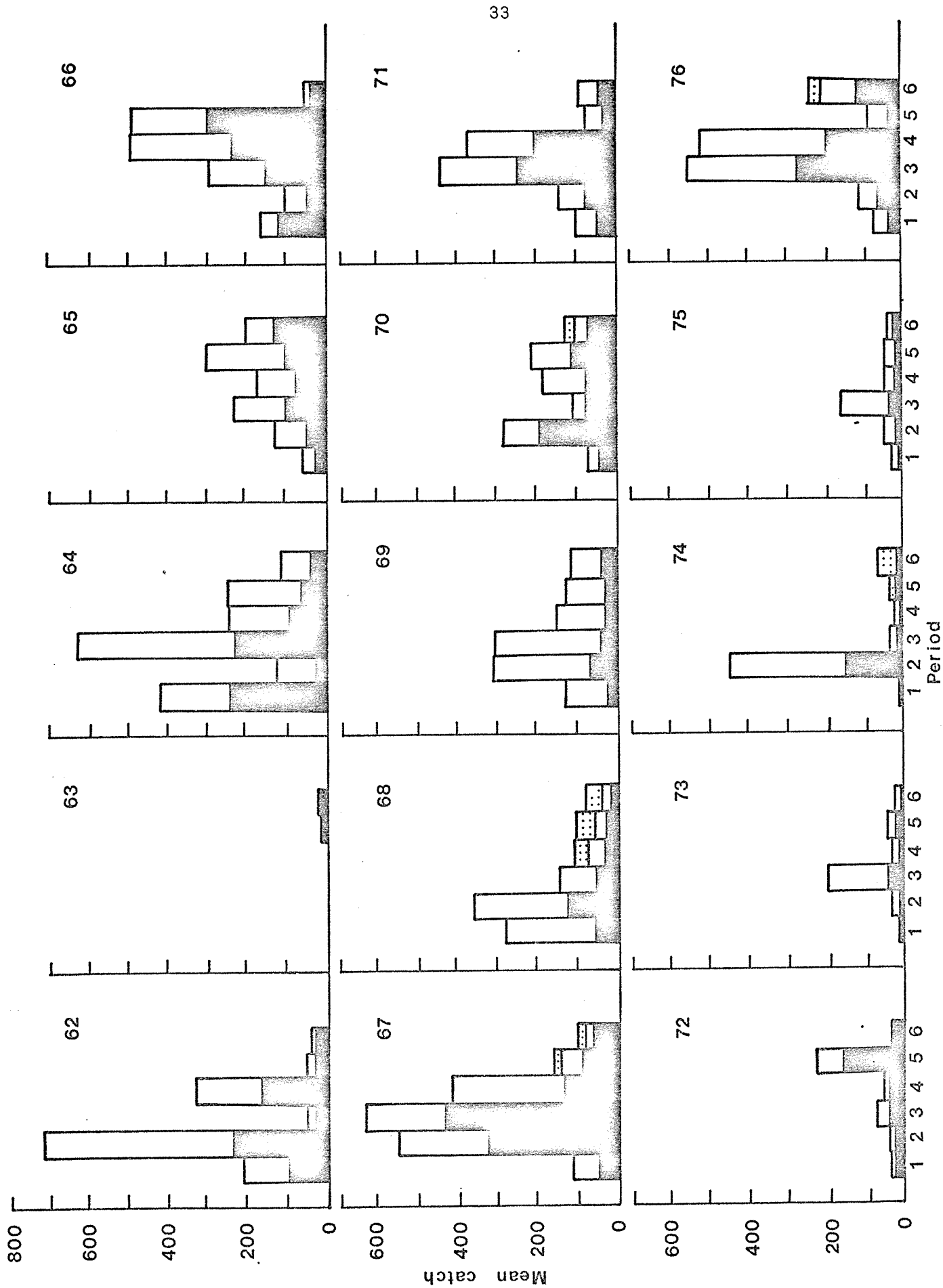


Fig. 8. Geometric means of beach-seine catches of threespine stickleback in Lake Aleknagik by period, June 20 to August 5, 1962-1976.

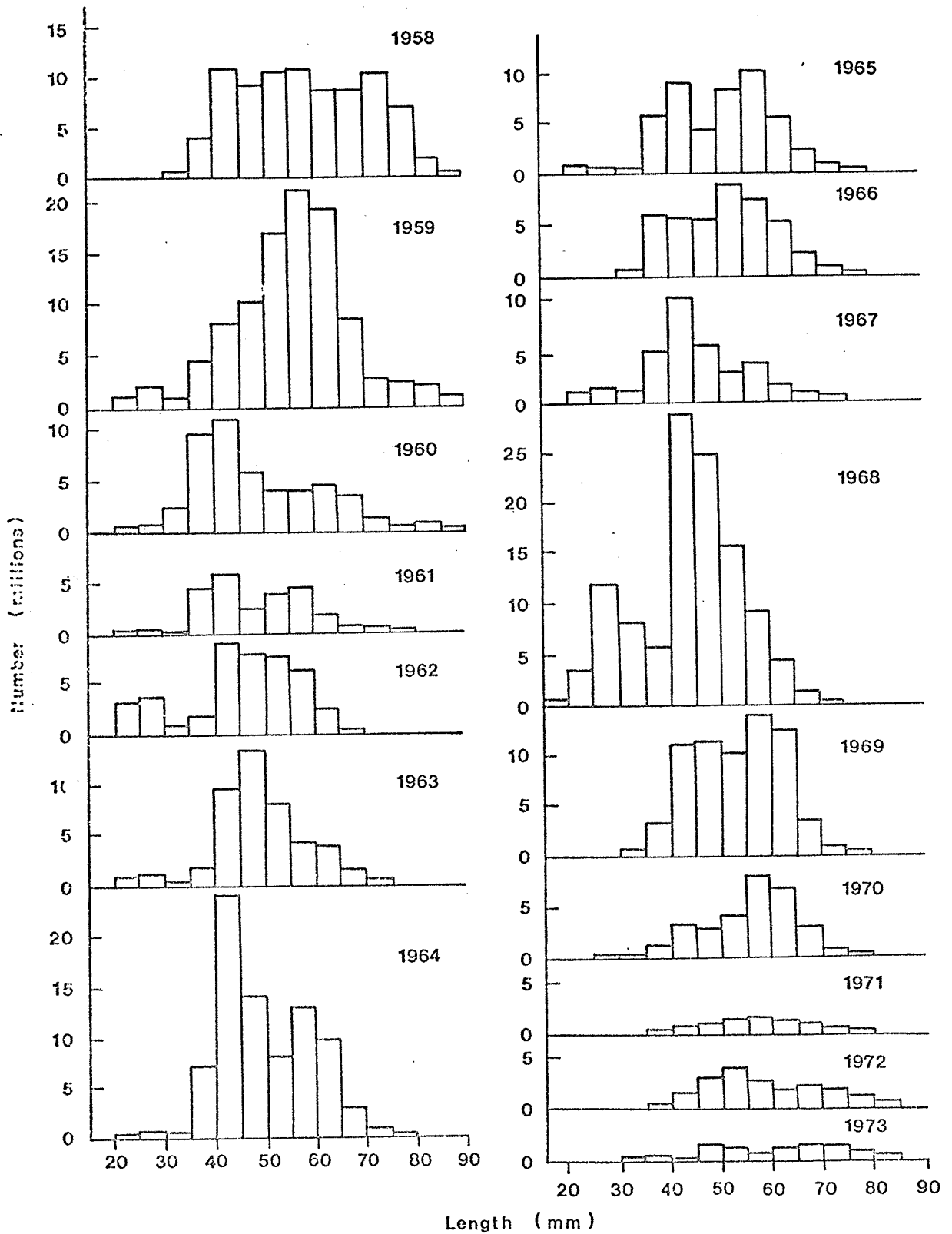


Fig. 9. Abundance of pelagic populations of threespine stickleback in the Wood River Lakes by 5 mm length intervals, 1958-1973.

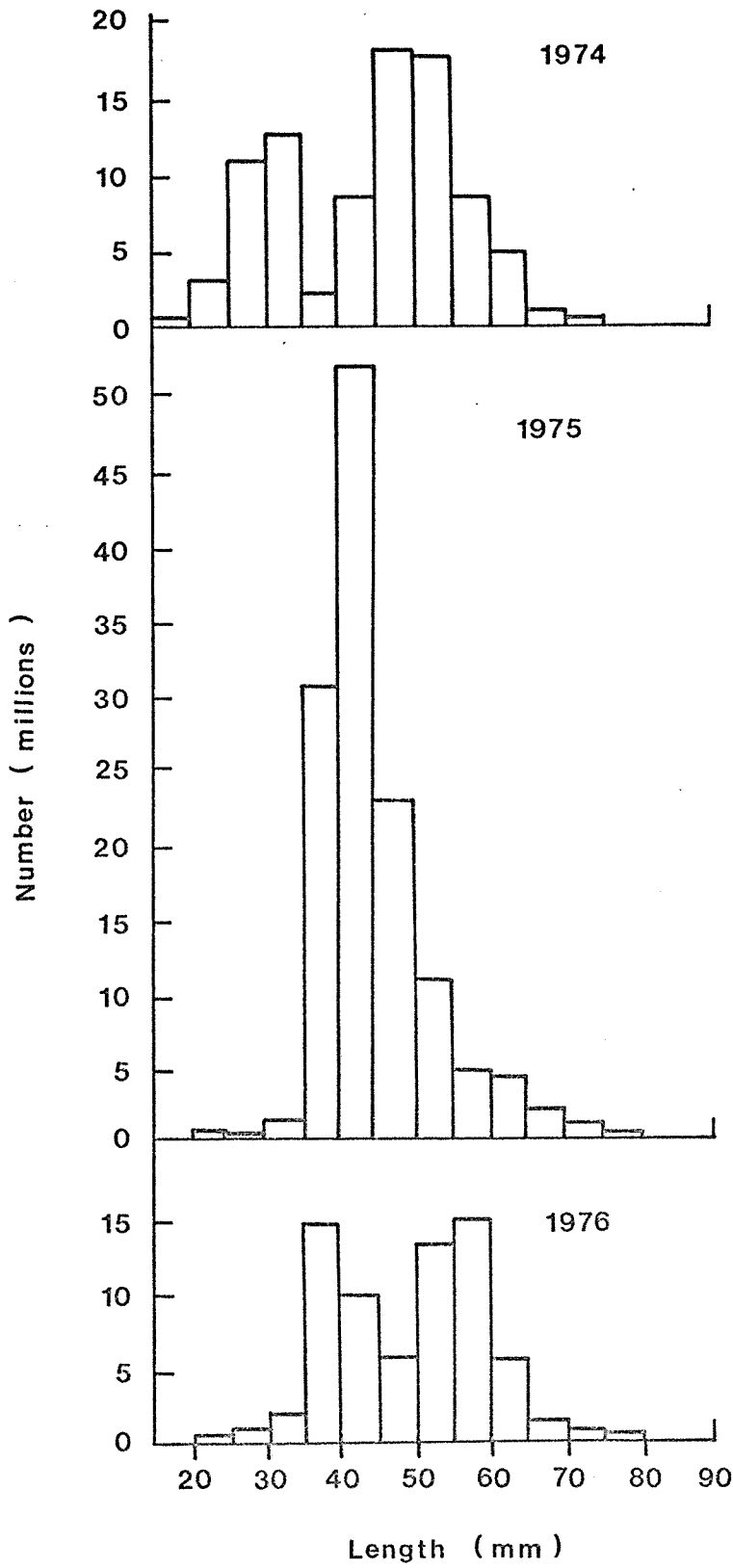


Fig. 10. Abundance of pelagic populations of threespine stickleback in the Wood River Lakes by 5 mm length intervals, 1974-1976.

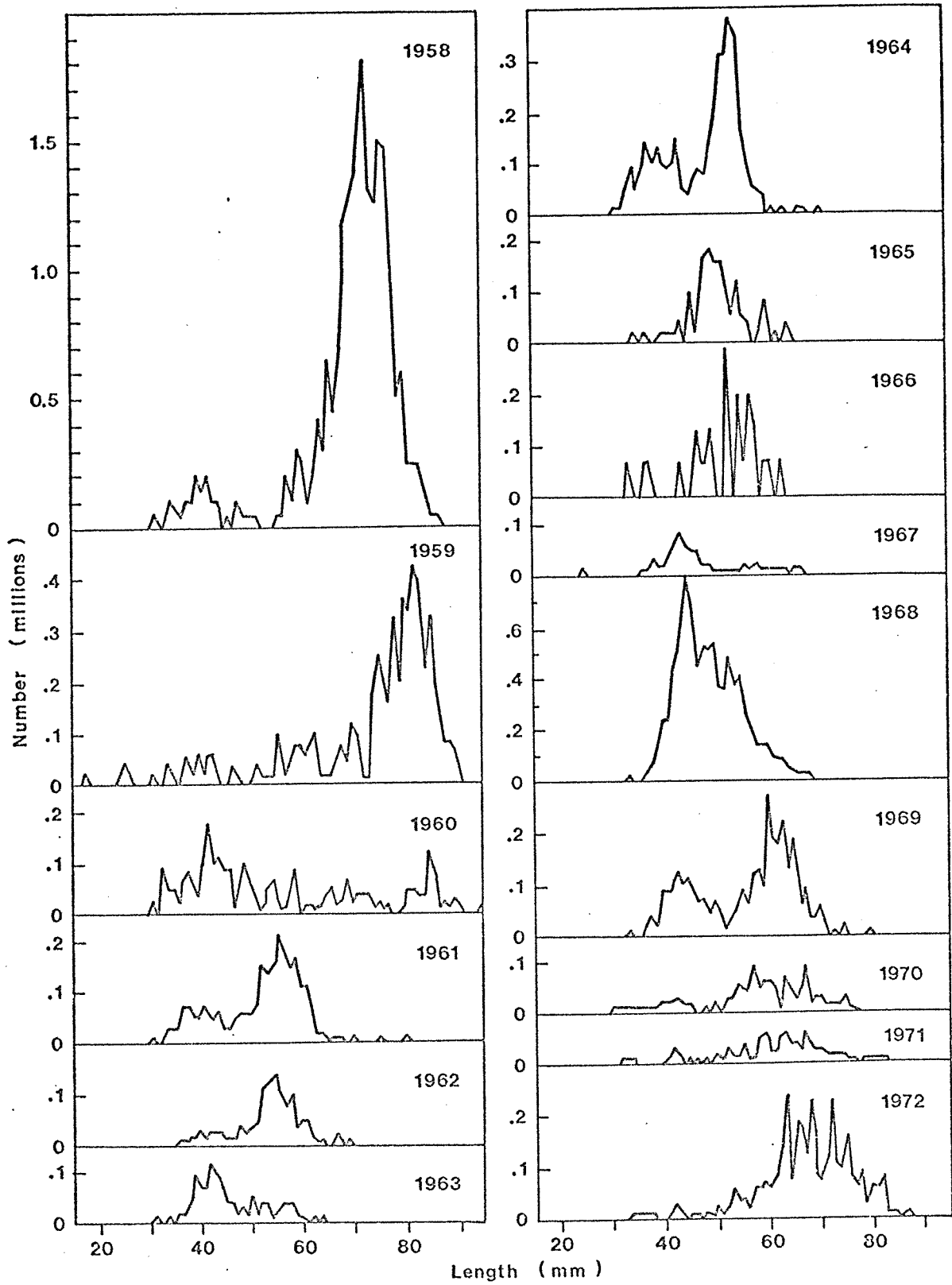


Fig. 11. Abundance of pelagic populations of threespine stickleback in Lake Kulik by length, 1958-1972.

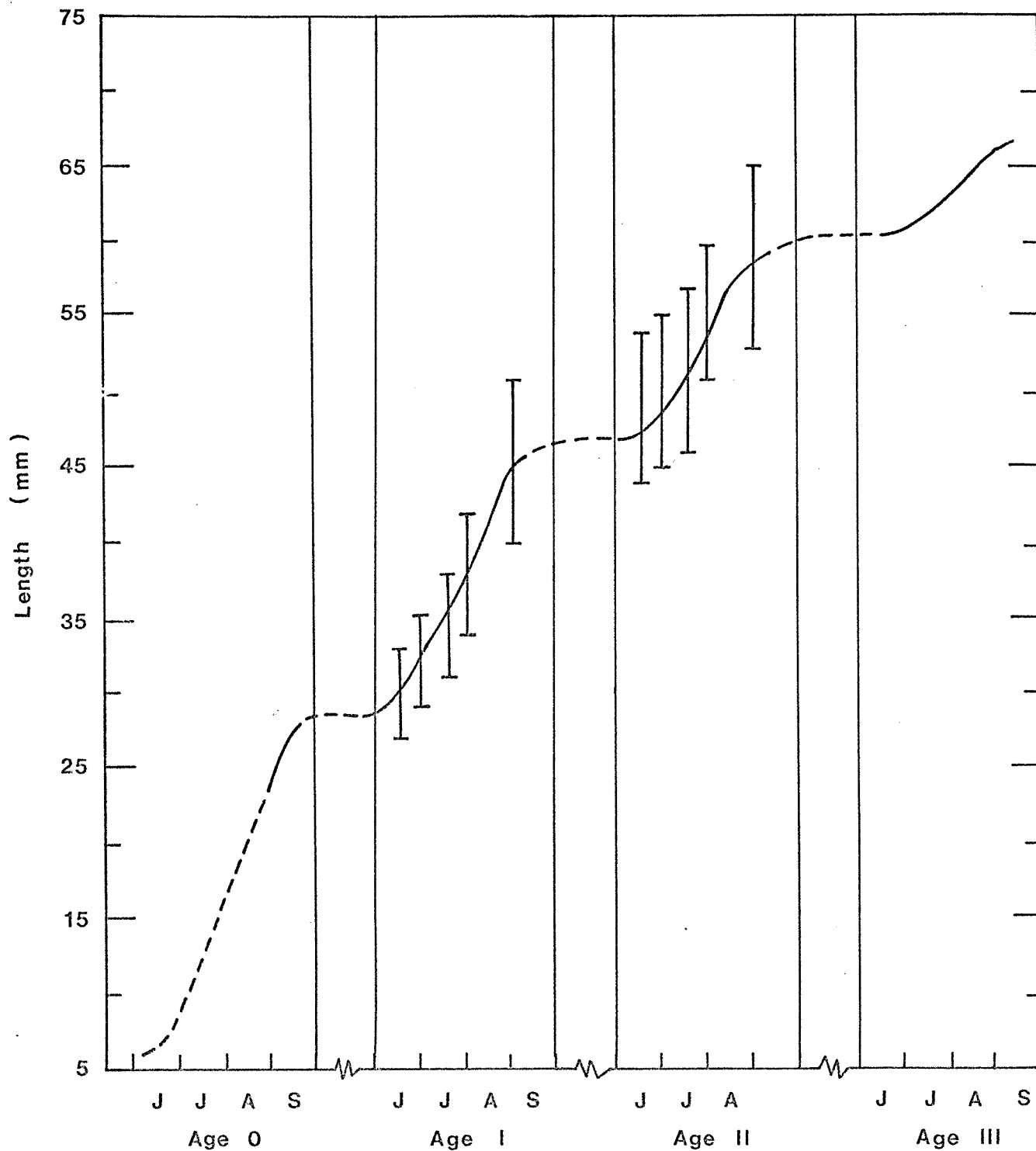


Fig. 12. Average growth in length of threespine stickleback in area C of Lake Aleknagik during 1959-1976. Vertical lines indicate ranges in annual mean lengths at selected dates.

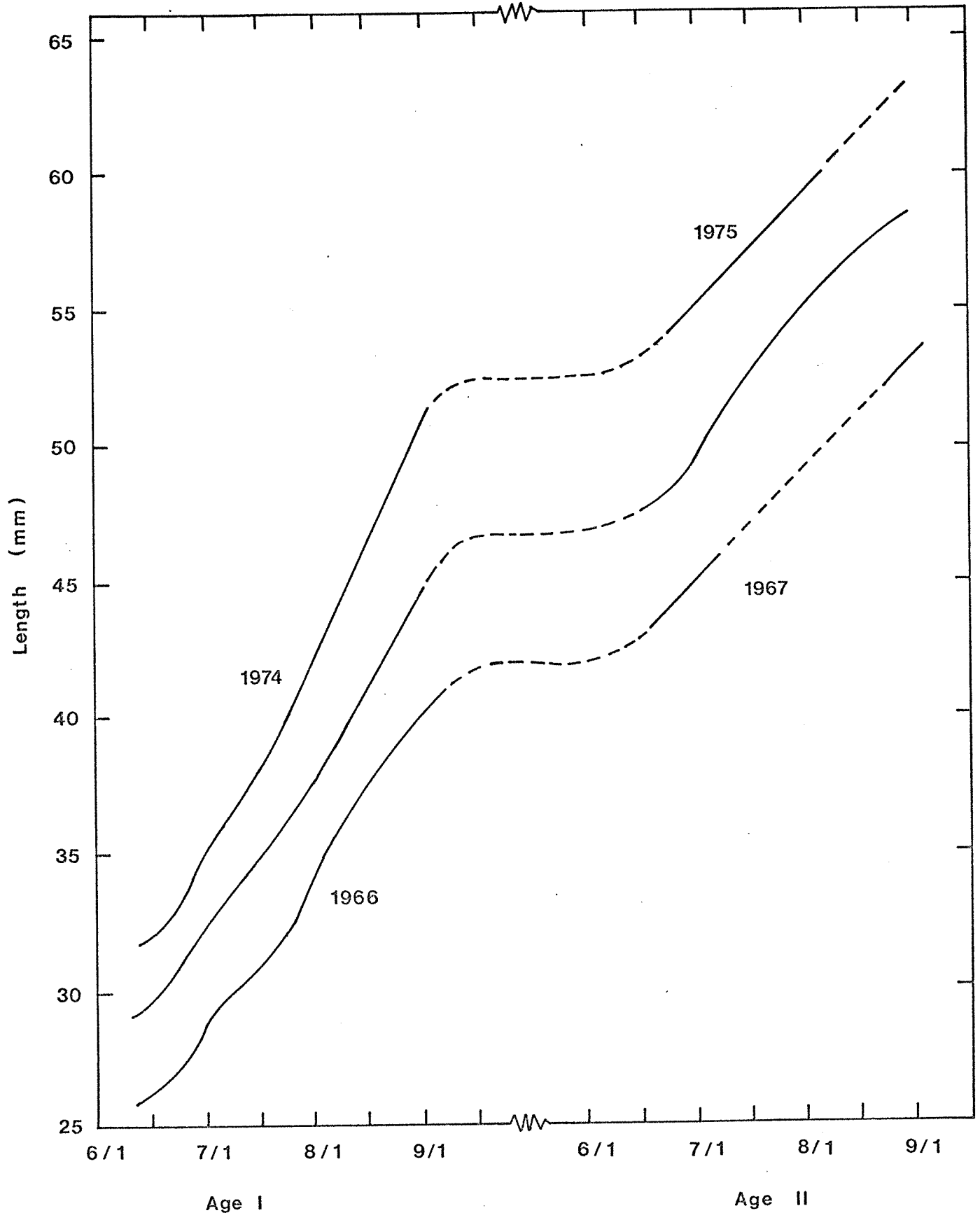


Fig. 13. Average growth trajectory for age I and age II threespine stickleback in area C of Lake Aleknagik during 1959-1976 and the trajectories for the brood years when growth was largest (1973 brood) and smallest (1965 brood).