THE RELATIONSHIP BETWEEN THE SUMMER FOOD OF JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, AND THE STANDING STOCK OF ZOOPLANKTON IN ILIAMNA LAKE, ALASKA[1,2]

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ABSTRACT

The foregut contents of juvenile sockeye salmon in samples taken at night by tow net in the limnetic area of Iliamna Lake consisted primarily of zooplankton and rarely of insects. The number of organisms per foregut was correlated with the estimated zooplankton density between 0 and 100 m. *Cyclops* and *Bosmina* were the dominant zooplankters in both foregut and zooplankton samples. The zooplankton hauls contained a greater percentage of calanoid copepods than the fish foreguts. Food selectivity was indicated but appeared to be minimal. Fry (age 0) foreguts contained a lesser percentage of *Cyclops* and a greater percentage of *Bosmina* than did yearling (age I) foreguts.

Juvenile sockeye salmon (*Oncorhynchus nerka*) spend 1 or 2 years in Iliamna Lake before migrating to sea. They occupy the littoral from the time they emerge from the gravel, in late winter or early spring, until mid-July, when they move to the limnetic area where they remain until migrating to sea in the spring of the following or second year (at age I or age II). A similar change in distribution was found in Lake Aleknagik in the Wood River system (Pella, 1968) and is probably common for all juvenile sockeye salmon in the lakes of Bristol Bay. Preious food studies, summarized by Rogers (1968), indicated that juvenile sockeye salmon feed primarily on insects in the littoral and on zooplankton in the limnetic area.

The standing crop of zooplankton is usually used as an indicator of food availability for zooplankton feeders. However, differences in size, agility, and visibility of the zooplankters may invalidate this assumption.

The objectives of this study were: (1) to determine the food of juvenile sockeye salmon and (2) to compare the composition of the diet with that of the estimated standing stock of zooplankton during the summers of 1966 and 1967. The diets of fry (age 0) and yearlings (age I) were also compared. The population density of juvenile sockeye salmon in Iliamna Lake was high during these years as the escapement into the Kvichak River system was exceptionally large (24.3 million fish) in 1965.

THE ENVIRONMENT

Iliamna Lake is the largest lake in Alaska, with an area of 2,622 km^2 and an average depth of 44 m. It empties into the Kvichak River, which flows into Bristol Bay. The Lake was divided geographically into four sampling areas (Figure 1). Areas I and II have a mean depth of 34 m and an even bottom of glacial till. Area III is much deeper (mean depth 74 m) and has a highly variable, glacially scoured bottom. Area IV is made up of islands and isolated bays and also has a highly variable bottom contour.

Twenty-nine fishes have been identified in the Kvichak River system (Bond and Becker, 1963), but only the sockeye salmon is of commercial importance. The threespine stickleback, *Gasterosteus aculeatus*, the most abundant of the resident species, may compete with the juvenile sockeye salmon for food.

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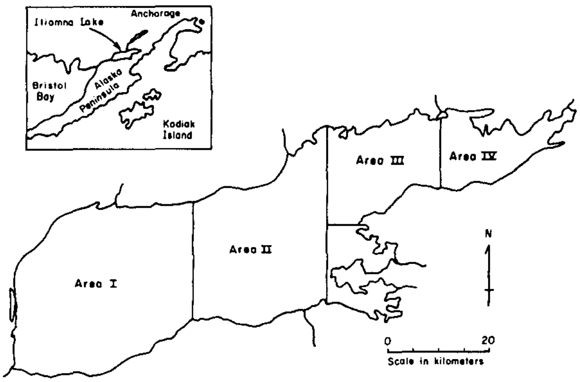

FIGURE 1.—Sampling areas of Iliamna Lake.

The following species of zooplankton occur commonly in the limnetic area of the Lake: *Diaptomus gracilis, Erytemora yukonensis, Cyclops scutifer, Bosmina coregoni, Daphnia longiremis,* and *Holopedium gibberum* (Lenarz, 1966).

Juvenile sockeye salmon and zooplankton exhibit a similar diel vertical migration. Echograms have shown a movement toward the surface at dusk, a concentration usually at less than 10 m at night and a downward movement of fish at dawn. Pella (1968) described a similar diel vertical migration for juvenile sockeye salmon in Lake Aleknagik, Alaska. About half of the zooplankton population occurs above 15 m at midnight and above 50 m at noon in Iliamna Lake (Fowler and Lenarz, 1965).

MATERIALS AND METHODS

Fry (age 0) and yearlings (age I) were collected with a tow net, having an opening of 2.7 m^2 and a cod end mesh size of 0.2 cm, and suspended between two boats spaced 15 m apart with 30.5 m of tow line. Each tow was 20 min in duration at a speed of about 1.5 m/sec. Alternate tows were made at 1.5 and 6 m, and occasionally deeper tows were made when fish were observed at greater depths on the echo sounder. Most samples were taken during darkness (normally between 2100 and 0300 hr). During the day catches were very small at depths of 30 m, and major fish concentrations usually were not seen on the echo sounder. Fishing near the bottom with monofilament, small-meshed gill nets was tried without success.

Fry and yearlings were preserved separately in 10% Formalin within 15 min after capture. No regurgitation of the stomach contents was observed. The fish were measured and the stomachs removed several months later.

The stomach was divided at the major bend, and only the contents of the foregut were examined so that bias from unequal digestive rates among different food items would be minimized. The foregut contents from all the fish in a sample were combined and mixed with water of a known volume. Two subsamples were taken with a 1-ml bulb pipette, and the organisms identified and counted under a low-powered dissecting microscope. Each organism was identified as either *Cyclops, Daphnia, Bosmina, Holopedium,* calanoid copepods, or insects. Nauplii and rotifers were seldom observed and were not counted. The total number of each food item in the sample was estimated by multiplying the number of each food item in the two subsamples by the appropriate factor. The variance between subsamples was less than 1% of the total variance among samples within date and area and was ignored.

The samples ranged from 1 to 45 fish but usually contained between 15 and 25 fish. The results from each sample were weighted by the number of fish per sample and grouped by area and sampling period. The sampling periods were:

1. Late summer 1966 (August 15-September 10).
2. Early summer 1967 (June 20-July 20).
3. Late summer 1967 (August 10-September 5).

The zooplankton sampling (described by Lenarz, 1966) was undertaken for a separate study and differed spatially and temporally from the young fish sampling. Samples were taken with a conical, nylon net of No. 6 mesh attached to a 0.5-m ring by vertical hauls, either from 100 m to the surface or from the bottom to the surface if the depth was less than 100 m. The zooplankters were identified and counted similarly to the organisms in the foregut. Samples were grouped by area and sampling period. The sampling periods were:

1. Late summer 1966 (August 10-26).
2. Early summer 1967 (June 18-30).
3. Late summer 1967 (August 22-September 15).

RESULTS

The numbers of fry and yearlings and the numbers of zooplankton samples by area and sampling period are listed in Table 1. Catches of yearlings in 1966 and of fry in the early summer of 1967 were small and were excluded from the analysis. Both fry and yearlings occurred in varying numbers in nearly all samples during the late summer of 1967. The mean fork length by area and sampling period ranged from 50 to 58 mm for fry and from 71 to 96 mm for yearlings.

TABLE 1.—Summary of samples of fish and zooplankton by area and sampling period.

Sampling period	Area	Age group	Number of fish samples	Number of fish examined	Number of zooplankton samples
Late summer 1966	I	Fry	7	22	9
	II		7	62	9
	III		7	116	6
	IV		17	385	4
Early summer 1967	I	Yearling	7	14	9
	II		8	113	9
	III		7	39	6
	IV		8	81	4
	I	Fry	7	43	9
	II		8	107	9
	III		7	150	6
	IV		7	160	6
Late summer 1967	I	Yearling	8	43	9
	II		8	105	9
	III		7	120	6
	IV		7	90	6
Total			127	1,650	116

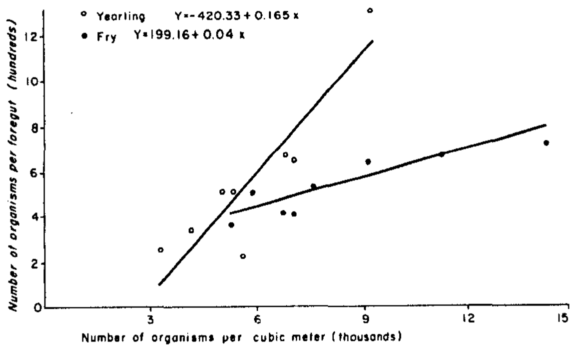

FIGURE 2.—Relationship between the number of organisms per foregut and the number of zooplankton per cubic meter.

FEEDING ACTIVITY

Most juvenile sockeye salmon (94%) contained some food. Temporal and spatial differences in the mean number of organisms in the foregut of juvenile sockeye salmon were apparent although the number of organisms per foregut varied considerably between samples within areas and sampling periods (Table 2). The number of organisms consumed per foregut increased from early to late summer and from area IV to area I.

The mean number of organisms per foregut by age group and the mean number of organisms per cubic meter in each area and sampling period are plotted in Figure 2. The positive slopes, significant at $P = 0.05$, indicate that feeding was in proportion to the abundance of zooplankton. The slope for fry is less than for yearlings probably due to the smaller foregut capacity of fry. Fry probably require a lower food concentration to become satiated, and the number of organisms per foregut may be approaching an

TABLE 2.—Mean number of organisms per foregut and variance between samples by age group, area, and sampling period.

Sampling period	Age group	Area I $\bar{x}$	Area I s_x^2	Area II $\bar{x}$	Area II s_x^2	Area III $\bar{x}$	Area III s_x^2	Area IV $\bar{x}$	Area IV s_x^2
Late summer 1966	Fry	715	72,895	685	172,641	525	113,384	502	77,863
Early summer 1967	Yearling	222	46,625	497	157,397	338	8,910	242	50,485
Late summer 1967	Fry	649	66,511	429	31,179	414	20,784	360	35,023
	Yearling	1,323	444,252	680	39,222	660	114,339	496	72,992

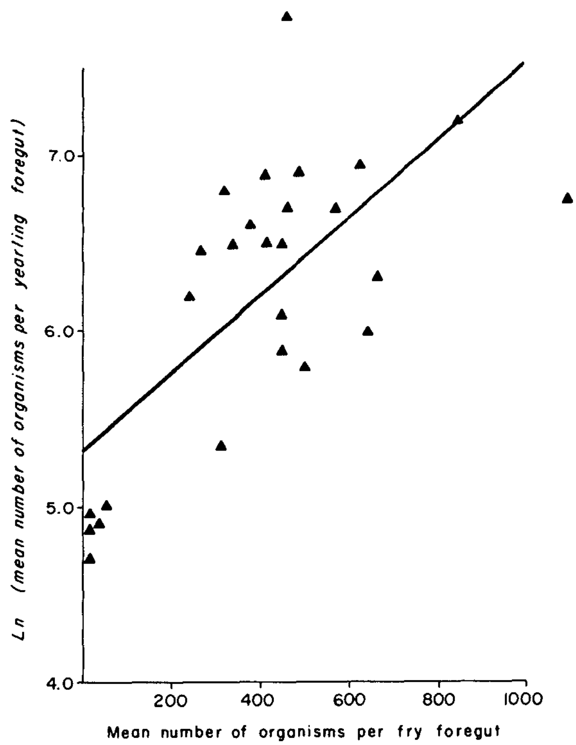

FIGURE 3.—Relationship between the mean number of organisms per foregut in fry and yearlings.

asymptotic upper limit with respect to food abundance in the Lake. The relationship might have been nonlinear for both fry and yearlings if lower and higher zooplankton densities had occurred.

The relationship between the number of organisms per foregut and fish size within each age group was not examined because size range of fry and yearlings in any sampling area was small. However, the yearlings contained an average of 40% more organisms than the fry in the late summer of 1967, probably because of their larger size and feeding capacity. The feeding intensities of both age groups are compared in Figure 3. The correlation coefficient, $r = 0.67$, between the mean number of organisms per fry foregut and the natural logarithm of the mean number of organisms per yearling foregut, significant at $P = 0.05$, indicates an exponential relationship between the feeding intensity of the two age groups. This was expected as fry tend to approach an upper limit of food intake (Figure 2).

COMPOSITION OF THE DIET AND THE ZOOPLANKTON SAMPLES

The food of juvenile sockeye salmon in the limnetic area of Iliamna Lake consisted primarily of zooplankton. Insects averaged less than 1% of the total number of organisms in the foregut except for yearlings from area I during the early summer of 1967, when they constituted 42.6%. *Cyclops* and *Bosmina* were usually dominant in the zooplankton hauls and in the fish foreguts, and averaged 75% in the zooplankton hauls and 90% of zooplankton in the fry and yearling foreguts (Table 3). Yearlings contained a higher percentage of *Cyclops* and a lower percentage of *Bosmina* than fry in late summer 1967 when both age groups were sampled. The percentage of calanoid copepods averaged higher in the zooplankton hauls (13%) than in the fish foreguts (3%) and was consistently higher for all areas and sampling period. *Daphnia* and *Holopedium* occurred in most samples but only constituted 11% of the organisms in the zooplankton hauls and 7% in the fish foreguts.

To compare the percentage composition of organisms in the zooplankton hauls with that of the foregut contents, a "two-way crossed" analysis of variance (fish-zooplankton by area) was performed for each sampling period and for each organism (*Cyclops*, *Bosmina*, and calanoid copepods). *Daphnia* and *Holopedium* were not tested. Mean squares and degrees of freedom are shown in Table 4. The percentage composition of the foregut contents and the zooplankton hauls (Table 3) were significantly different except for *Cyclops* in late summer 1966 and early summer 1967. However, differences in the zooplankton hauls and the foregut contents were not consistent in all areas for *Cyclops* and *Bosmina* as indicated by the significant interaction between the fish-zooplankton samples and areas. Interaction was not significant for the calanoid copepods.

A modification of Tukey's test (Snedecor, 1956, p. 251) showed a significant difference

(P = 0.05) in the percentage of *Cyclops* and *Bosmina* in fry foreguts, yearling foreguts, and zooplankton hauls in late summer 1967. The percentage of calanoid copepods in fry and yearling foreguts did not differ significantly, but both differed significantly from that in the zooplankton hauls.

Spatial and temporal changes in the composition of the zooplankton catches were compared with changes in the fish foreguts. In the zooplankton hauls, the percentage of *Cyclops* generally decreased and the percentage of *Bosmina* generally increased from early to late summer and from area IV to area I. The composition

TABLE 3.—Mean percentages of *Cyclops*, *Bosmina*, and calanoid copepods in the foregut of fry and yearlings (insects excluded) and in the zooplankton samples by area and sampling period.

Sampling period/ area	*Cyclops*			*Bosmina*			Calanoids		
	Fry	Year ling	Zoo-plankton	Fry	Year ling	Zoo-plankton	Fry	Year-ling	Zoo-plankton
	%	%	%	%	%	%	%	%	%
Late summer 1966									
Area I	45.1	--	42.0	45.6	--	38.1	4.0	--	7.1
Area II	29.4	--	41.0	55.5	--	40.9	4.9	--	6.5
Area III	38.1	--	47.5	49.6	--	38.6	1.2	--	6.8
Area IV	26.8	--	62.0	64.5	--	24.9	1.0	--	7.0
Early summer 1967									
Area I	--	58.9	72.4	--	28.9	5.7	--	7.5	13.1
Area II	--	79.0	78.5	--	4.6	3.2	--	1.1	11.0
Area III	--	87.9	84.6	--	4.2	1.2	--	1.7	9.4
Area IV	--	92.3	77.8	--	1.8	1.0	--	4.5	17.9
Late summer 1967									
Area I	21.0	47.2	27.5	68.3	44.0	34.6	2.5	2.3	17.0
Area II	34.6	54.7	14.0	54.3	34.4	45.7	2.3	2.4	16.4
Area III	75.2	84.8	38.4	18.2	6.8	27.0	2.8	2.6	21.1
Area IV	77.6	84.7	36.1	18.0	9.9	23.5	2.3	3.7	24.0
All sampling periods/area	43.5	73.6	51.8	46.8	16.8	23.7	2.6	3.2	13.1

TABLE 4.—Mean squares and degrees of freedom for a "two-way crossed" analysis of variance by sampling period and zooplankton.

	Cyclops		*Bosmina*		Calanoids	
	Mean square	Degrees of freedom	Mean square	Degrees of freedom	Mean square	Degrees of freedom
Late Summer 1966						
Treatments (zooplankton, fry)	65.9	1	644.3**	1	33.0**	1
Areas	117.4**	3	14.0	3	1.5	3
Interaction (treatment × area)	127.7**	3	106.8*	3	1.6	3
Residual	20.6	58	28.1	58	.6	58
Early summer 1967						
Treatments (zooplankton, yearlings)	3.4	1	100.7**	1	166.6**	1
Areas	178.6**	3	109.2**	3	16.8*	3
Interaction (treatment × area)	67.8	3	57.2**	3	5.8	3
Residual	30.8	50	10.6	50	4.8	50
Late summer 1967						
Treatments (zooplankton, fry, yearlings)	1,514.5**	2	615.0**	2	386.1**	2
Areas	1,086.8**	3	887.5**	3	6.0	3
Interaction (treatment × area)	121.0**	6	97.5**	6	3.5	6
Residual	26.9	77	25.0	77	3.5	77

* F test significant at P = 0.05.
** F test significant at P = 0.01.

TABLE 5.—Rank correlation coefficient (r_d) for percentage of five organisms in fish foreguts and zooplankton hauls by area and sampling period.

Sampling period	Samples	Area			
		I	II	III	IV
Late summer 1966	Fry-zooplankton	0.975***	0.975***	0.800*	0.800*
Early summer 1967	Yearling-zooplankton	.675	.425	.300	.700
Late summer 1967	Fry-zooplankton	.700	.225	.900**	1.00***
	Yearling-zooplankton	.600	—.025	.825*	1.00***

* Significant at $P = 0.20$.
** Significant at $P = 0.10$.
*** Significant at $P = 0.05$.

of organisms in the yearling foreguts showed a similar change; for *Cyclops* and *Bosmina* $r = 0.66$ (significant at $P = 0.10$) and 0.71 (significant at $P = 0.05$), respectively. Correlation was not significant for fry ($r = 0.01$ and 0.22, respectively). The percentage of calanoid copepods in the fish foreguts remained constant in spite of an increase from early to late summer in the zooplankton hauls (Table 3).

Although differences were significant in the percentage composition of organisms in the zooplankton hauls and in the fish foreguts, the fish fed predominantly on those organisms which were most abundant in the zooplankton hauls. Rank correlation coefficients (r_d) were used in comparing the percentage of *Cyclops, Bosmina,* calanoid copepods, *Daphnia,* and *Holopedium* in the zooplankton hauls and in the foreguts, and showed very good correlation in several areas and sampling periods and, with one exception, were always positive (Table 5).

COMPARISON OF FRY AND YEARLING DIETS

Cyclops and *Bosmina* were the major food items in the diet of both fry and yearlings although the percentage of the former was greater and the percentage of the latter smaller in the yearling foreguts than in the fry foreguts (Table 3). Differences in the foregut contents may result from slight differences in habitat and hence from differences in available food.

To minimize this possibility only those samples that included at least five fry and five yearlings were examined. The relationship between the two age groups in the percentage of *Cyclops* and *Bosmina* in the foreguts appeared linear (Figures 4 and 5) and a regression analysis was performed. The slope (b) was significantly greater than zero ($P = 0.05$) for both zooplankters; thus, the two age groups have similar food habits. However, the hypothesis $b = 1$ was rejected ($P = 0.05$); therefore, I concluded that fry consume more *Bosmina* and less *Cyclops* than yearlings. The positive intercept in Figure 4 and b less than 1 in Figures 4 and 5 indicate that the percentage of *Cyclops* and *Bosmina* vary less in yearling than in fry foreguts.

DISCUSSION AND CONCLUSIONS

Cyclops and *Bosmina* were the most abundant, and calanoid copepods, *Daphnia*, and *Holopedium,* the least abundant zooplankters in the fish foreguts and in the zooplankton hauls. However, the percentage composition of organisms in fish foreguts differed significantly from those in the zooplankton hauls in that: fry contained more *Bosmina;* yearlings contained more *Cyclops;* fry and yearlings contained less calanoid copepods than the zooplankton hauls.

Discrepancies in estimates of available food and diet are due to sampling error and selective feeding. Spatial and temporal differences in the sampling of zooplankton and fish, and diel and depth variations in available food and feeding activity probably accounted for some discrepancy. Fowler and Lenarz (1965) established diel and depth variations in the percentage composition of the standing zooplankton stock in the lake. Northcote and Lorz (1966) showed diel changes in the food of resident sockeye salmon (kokanee) in Nicola Lake, British Columbia,

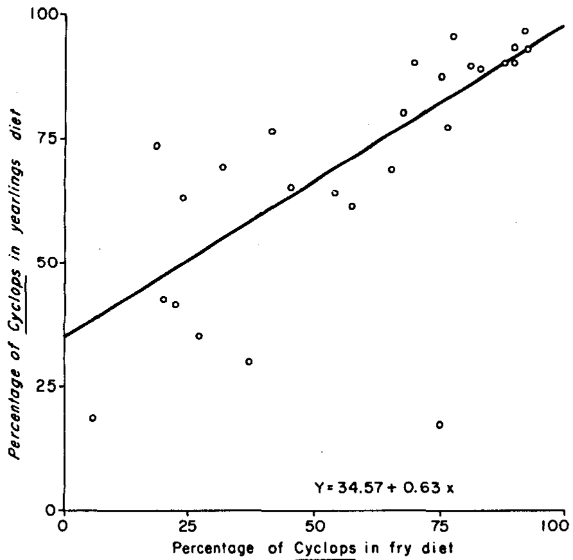

FIGURE 4.—Relationship between the percentage of *Cyclops* in the foregut of fry and yearlings.

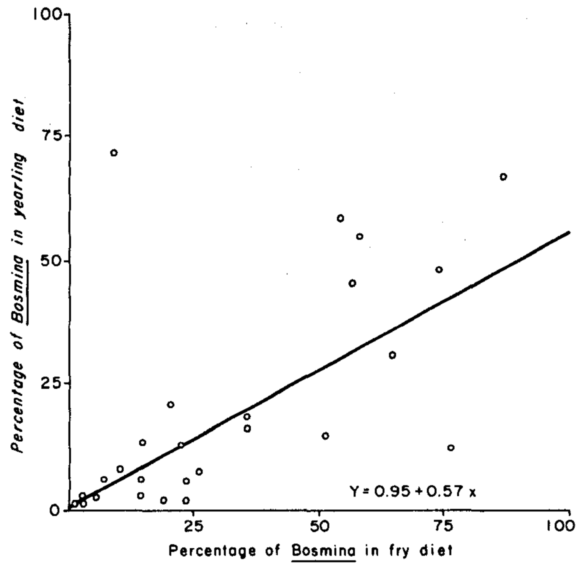

FIGURE 5.—Relationship between the percentage of *Bosmina* in the foregut of fry and yearlings.

and Narver (1970) showed diel and depth changes in the food of juvenile sockeye salmon in Babine Lake, British Columbia.

Food selection depends on characteristics of the feeder and food items (Ivlev, 1961) and probably occurs in some degree for all species. In this study, the cause of the discrepancy between the composition of the foregut and zooplankton samples cannot be attributed specifically either to sampling error or to selective feeding. Whatever the cause, the degree of discrepancy was small, and I concluded that the zooplankton samples generally reflect available food in Iliamna Lake. This is in contrast to Narver (1970), who found that juvenile sockeye salmon strongly selected numerically less abundant zooplankters in Babine Lake.

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