

THE FERTILIZATION OF GREAT CENTRAL LAKE

III. EFFECT ON JUVENILE SOCKEYE SALMON

W. E. BARRACLOUGH AND D. ROBINSON¹

ABSTRACT

Nutrient levels and rates of primary production in nursery lakes are factors which may limit production of sockeye salmon. This paper describes the effect of artificial fertilization on feeding behavior and growth of juvenile sockeye salmon in Great Central Lake, Vancouver Island, British Columbia. Under-yearling sockeye salmon grew 30% larger in 1970 than in 1969 as a result of adding 100 tons of fertilizer to Great Central Lake. The growth pattern for the whole population was complex, however, and the increase in size of juvenile sockeye was not as much as had been expected from the increase in quantity of their food organisms. The fact that the sockeye did not appear to appreciably crop the high epilimnetic concentrations of zooplankton during July and August 1970 may have been partly due to avoidance of high temperatures by the fish.

Decomposing carcasses of anadromous fish, such as the sockeye salmon (*Oncorhynchus nerka*), contribute to the fertilization of nursery lakes following spawning in the lake. In most instances the extent of this fertilization is not known but the removal of maturing sockeye by a commercial fishery may deny lake waters of their essential nutrients and contribute to lowered productivity. Particular attention has been focussed on the imbalance of phosphate in the natural fertilization of lakes from decomposing salmon carcasses (Krokhin, 1959) and the suggestion has been made (Krokhin, 1967) that a positive balance should be maintained by the artificial replacement of the phosphate with inorganic fertilizers.

Early studies carried out in a small unstratified lake in Alaska (Nelson and Edmondson, 1955; Nelson, 1958) showed that the addition of phosphate and nitrate fertilizer resulted in increased length and weight of sockeye smolts leaving the lake. The potential role of a natural imbalance of phosphate in nursery lakes on sockeye salmon is emphasized in the following quotation from Foerster (1968):

One wonders whether sufficient significance has been given to this feature of the phosphate balance. With

sockeye populations in all areas showing such evident declines, despite legislation on regulation and limitation of fishing, it might well be that some basic factor such as this may be having a much more limiting effect on productivity than seems apparent. In addition to the smaller amounts of phosphorus introduced into a lake in the carcasses of fewer sockeye spawners, there may also be occurring a steady decline in the phosphate content of the runoff waters as the phosphates of the soil and rock become leached out over the years. Future studies of the phosphate balance of sockeye-producing waters and the direction of its trend may prove most enlightening. Addition of suitable fertilizers may be found advantageous.

In recent years it has become more evident that suitable fertilizers should not only include phosphates but also other nutrients, including trace elements, in order to increase aquatic productivity (Goldman, 1960, 1964).

The theory and application of adding natural fertilizers to aquatic environments has been practiced in fish farming for many centuries. Parsons et al. (in press; 1972) have presented data on various aspects of lake fertilization studies carried out by others. In summary of these findings, there is much evidence to show that the larger the sockeye smolts at the time of seaward migration, the higher the percentage return from the sea (Burgner, 1962; Ricker, 1962). Since food supply is one of the important factors

¹ Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., Canada.

governing growth, the effect of increasing the food supply to underyearling sockeye salmon through artificial fertilization of Great Central Lake, B.C., is presented here. It has already been established (Parsons et al., in press; 1972) that the waters of Great Central Lake are relatively unproductive of sockeye salmon, the average size of yearling smolts at the time of seaward migration being much smaller than in Babine Lake, B.C. (63 mm versus 79 mm) (McDonald, 1969). The average size of yearling smolts from 14 other lakes in Washington, British Columbia, Alaska, and Kamchatka is larger than the yearling smolts from Great Central Lake (Foerster, 1968). In the following account particular attention is given to changes in size of juvenile sockeye salmon in Great Central Lake associated with changes in their food supply prior to and after the addition of inorganic nutrients (see Parsons et al., 1972; LeBrasseur and Kennedy, 1972).

STUDY AREA

Great Central Lake (Figure 1) is located in central Vancouver Island, British Columbia. The lake is about 33 km long and varies between 1 and 2.5 km in width. The shoreline length is 72 km and the surface area is ca. 51 km². Ele-

vation of the lake surface is 83 m above sea level and the mean depth is 200 m, with a maximum depth of about 280 m. The outlet of the lake runs into the Stamp River. Most of the shoreline slopes very abruptly into deep water. This feature is an important factor in regulating horizontal distribution of juvenile salmon in the lake, by providing a maximum amount of the lake surface available to juvenile sockeye.

LAKE SPAWNING

A brief account of the spawning sites of the sockeye salmon is presented here because the location of the in-lake spawning grounds is an important factor in the emergence of the alevin and dispersal of the fry at the time of their initial intake of food. Little or no published information is available on the migration and spawning of adults in the lake. Mr. F. C. Boyd of the Department of the Environment has kindly granted permission to refer to his internal manuscript reports on the subject.

Adult sockeye salmon bound for Great Central Lake first enter the Stamp River as early as the first week in June. This migration up the Stamp River continues through June, peaks in July, and in most years, ends in early August. The peak

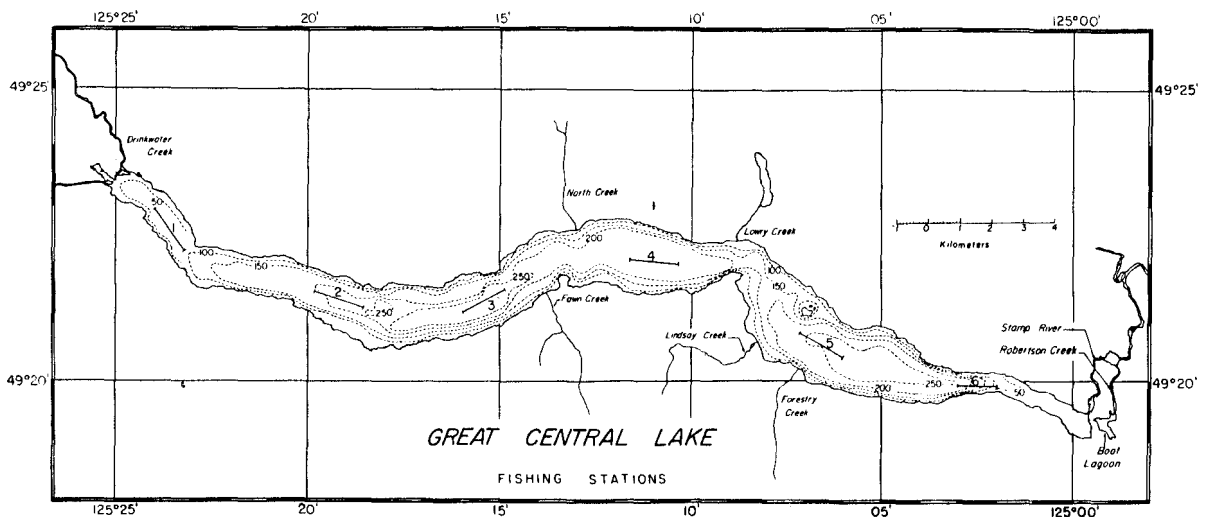


FIGURE 1.—Great Central Lake showing the six fishing stations and depth contours in meters.

of migration may not occur until the first week in September. It takes between 2 and 5 days for the sockeye to migrate up the Stamp River into Great Central Lake, depending on the water levels in the river. The fish remain in the lake but do not commence to spawn until the latter part of September. Great Central Lake is one of the few lakes in British Columbia where most of the spawning occurs in areas along the lakeshore rather than in tributary streams. Only a few hundred sockeye spawn in tributary streams a short distance away from the lake. Drinkwater, Lindsay, and Fawn Creeks (Figure 1) receive most of the stream spawners.

Lakeshore spawning commences in the last week of September, reaches a series of peaks in three principal locations during October, and ends in November. About 50% of the spawning occurs along 4.63 km of lakeshore between Lindsay Creek and Forestry Creek, 30% along 1.1 km of shoreline west of Fawn Point, and 20% along 1.6 to 4.8 km of lakeshore off North Creek. Redds were found at depths between 0.6 and 24 m but most were between 12 to 15 m. Spawnings were observed by scuba divers at depths as great as 41 m. It is now realized that the location of separate major in-lake spawning areas is important in providing the potential basis for the immediate and rapid distribution of juvenile sockeye throughout the lake, shortly after the fry emerge from the gravel and commence to feed. Two spawning areas are adjacent to the lake area where fertilizer was applied (see Parsons et al., 1972).

METHODS

LOCATION AND DISTRIBUTION OF JUVENILE SOCKEYE SALMON

A high frequency (200 kHz) moist paper recording echo sounder (Furuno model No. FNV-3000)² was used to locate the young sockeye in

² Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

the lake and monitor their horizontal and vertical distribution. During the day, young sockeye are generally distributed throughout the lake at depths between 45 and 90 m, but are most abundant at about 65 m. They commence to migrate toward the surface about half an hour before sunset. In the summer months at civil twilight, when the sun is 96° from the zenith (or 6° below the horizon) they are distributed irregularly in density between 5 and 30 m. At nautical twilight when the sun is 102° from the zenith (or 12° below the horizon) the juvenile sockeye form a layer between the depths of 10 and 20 m, with a maximum density of about 14 m. At night during the winter months they are distributed more uniformly between 20 and 60 m. In summer the downward migration commences shortly before sunrise and is usually complete 15 to 30 min after sunrise.

The young sockeye were sampled with mid-water trawls. Sampling commenced at night when the fish were in a layer between 10 and 20 m. Samples were also collected during daylight at different depths throughout the depth range of the young sockeye. The depth of trawling was adjusted to coincide with the depth of maximum fish concentration as shown by the echo sounder traces.

FISHING GEAR

A trawl net with a mouth opening 3 m wide, 6.1 m deep, and 17.7 m long was towed at 2.7 to 3.2 km/hr by a single vessel, the *Decibar*, to sample the sockeye between the depths 5 and 25 m. Three mesh sizes of knotless nylon netting were used in the construction of the net: 5 cm and 2.5 cm stretched mesh in the body and 1.3 cm in the cod end. The cod end measured 1.2 m wide by 1.8 m deep at the mouth and it tapered to a blunt end about 76 cm in diameter. A standard Henson plankton net (350 μ mesh) 76 cm in diameter at the mouth, was secured to the blunt aft end of the cod end to retain the smallest juvenile sockeye and minimize the loss

of their minute scales by abrasion against netting in the main cod end of the trawl.

An Isaacs-Kidd midwater trawl was towed from the *Decibar* to sample the juvenile sockeye at depths greater than 25 m and to evaluate the fishing capabilities of the large midwater trawl towed at the same depths. The mouth opening of this trawl was 1.9 m² and the net was constructed of 6.3 mm stretched mesh knotless netting.

FISHING STATIONS

Juvenile sockeye were sampled with trawls taken at intervals of about 3 weeks at 6 different stations (Figure 1). Most of the tows were of 30 min duration but some tows were shorter, when the echo sounder traces indicated that young sockeye were especially abundant between 12 and 14 m at night.

ANALYSES OF SAMPLES

The length of all fish was measured to the nearest millimeter from the snout to the end of the central rays of the caudal fin. This measurement is referred to as the fork length. Lengths of smaller fish were measured in a graduate tray under a binocular microscope; calipers were used for larger individuals.

All fish were weighed by fork length groups using a center-loading milligram balance (KERN Model No. T1226-1). Weights recorded are from "blot-dried" specimens. Moisture was blotted from the exterior of the fish, and gentle pressure was applied to the buccal cavity and branchial chamber to remove moisture from these spaces. Age was determined from scales using $\times 254$ projections of thermoplastic impressions.

Stomach analyses for food were done on fish selected to represent proportionally as complete a size range as possible. The food weight was measured by subtracting weight of stomach shell from weight of stomach plus food. The number of all species of food organisms were counted according to size and state of condition of each stomach examined.

RESULTS

FOOD OF UNDERYEARLING (AGE 0) SOCKEYE

During the latter part of March and up to mid-April, 1970, pre-mature fry³ (24 to 28 mm fork length) with a small portion of the yolk sac remaining were caught at night at a depth of 14 m in midlake positions off the 3 major spawning areas. A few fry (28-30 mm) with empty stomachs were caught during the day at depths between 35 and 100 m in late March, and the first actively feeding fry (28 to 33 mm) were caught at depths between 12 and 55 m at night during the latter part of April. The number of fry caught at midwater depths increased in May at Stations 3, 4, 5, and 6 and reached a maximum in June at all stations. Fry continued to be caught in July and were still being caught in trawl nets at night in late August and early September. The fry and larger underyearling sockeye ate the same food organisms throughout the year, but the larger juvenile fish had more food in their stomachs.

Figure 2 shows the number and weight of all species of food organisms per underyearling sockeye (Age 0) from August, 1969, when in-lake sampling began to April, 1970, when about 85% of the fish migrating were yearling smolts.⁴ The percentage of the total number of the six major food categories from all the fish sampled for stomach contents through the same period is shown in Figure 3. A list of the different genera of food organisms found in the stomachs of juvenile sockeye from 1969 to 1971 is given in Table 1; the smallest is listed at the top of the column and the largest at the bottom.

Epischura was the predominant form (60%) in the stomachs in August, 1969 but was almost replaced by *Holopedium* (60-80%) from September to December (Figure 3). The incidence of

³ "Embryo" is defined as a larva minus its yolk-sac. An "alevin" is a larva of an age following hatching but prior to yolk absorption. Following this stage the fish becomes a "fry" (cf. Bams, 1969).

⁴ In 1969 ca. 86% of migrant smolts were yearling, 10% were 2 year old, and 4% were 3 year old. In 1970 ca. 85% of smolts were yearling and 15% were 2 year old.

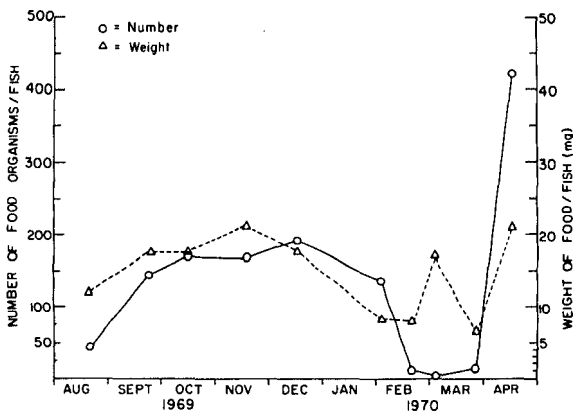


FIGURE 2.—Average number and weight of all food organisms (all species combined) per fish for underyearling sockeye salmon in Great Central Lake from August, 1969 to April, 1970.

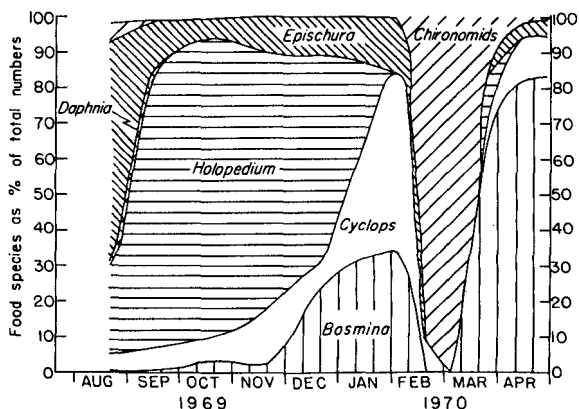


FIGURE 3.—Food of underyearling sockeye salmon expressed as a percentage of the total number of organisms from August, 1969 to April, 1970.

TABLE 1.—List of organisms found in juvenile sockeye stomachs.

Size range	Organism
mm	
0.3-0.6	<i>Bosmina</i> , usually <i>B. coregoni</i>
0.6-1.1	<i>Cyclops</i> , usually <i>C. bicuspidatus thomasi</i> and <i>C. vernalis</i>
0.9-1.2	<i>Holopedium gibberum</i>
0.9-1.5	<i>Daphnia</i> , usually <i>D. longiremis</i>
0.8-1.3	<i>Diaptomus</i> , usually <i>D. oregonensis</i>
2.0-2.5	<i>D. kenai</i>
1.1-1.9	<i>Epischura nevadensis</i>
3	Insects of the order Diptera (other than Chironomidae)
3-5	Insects of the family Chironomidae—larvae
8-11	Insects of the family Chironomidae—larvae
6-11	Larvae of the sculpin, <i>Cottus asper</i>

Bosmina and *Cyclops* increased gradually from less than 5% in August to a peak of 30 to 50% in January-February, 1970. Chironomid larvae were the only organisms eaten from February to early March and in turn were replaced by *Bosmina* (80%) in late March and April. The percentages of *Epischura* and *Holopedium* in the stomachs by number (Figure 3) and by weight (Figure 4) were similar from August to December. There was a pronounced difference between the percentages by number and by weight of *Cyclops* and *Bosmina* per fish. Although the percentage by numbers of both organisms per fish increased markedly between December, 1969 and February, 1970, the percentage weight per fish remained less than 7% for *Bosmina* and never exceeded 20% for *Cyclops*. The importance of the chironomid larvae in the diet of underyearling sockeye from February through March to early April, 1970 is more indicative when expressed as a percentage by weight (Figure 4) than by number of organisms (Figure 3).

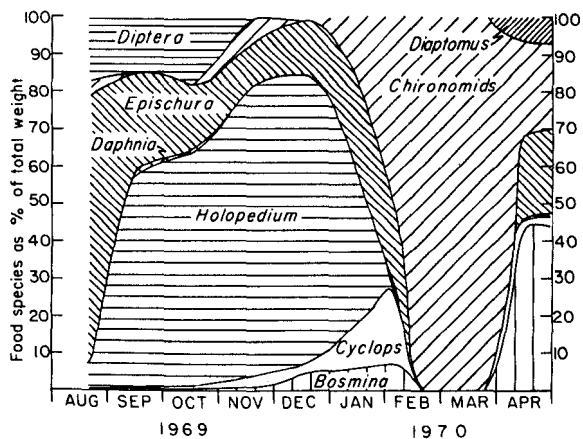


FIGURE 4.—Food of underyearling sockeye salmon expressed as a percentage of the total weight of organisms from August, 1969 to April, 1970.

The fry which emerged in late March and April, 1970 commenced to feed actively by mid-April and, as juvenile sockeye, they continued to increase their intake in number and weight of all food organisms throughout the summer,

reaching a peak in September-October (Figure 5). In August, 1970, 3 months after lake fertilization began, the underyearling sockeye had twice the number of organisms per stomach as in August, 1969 and contained about 60% more food by weight. The high consumption in September-October, 1970 represents an increase of about 45% in number of organisms, and 40% by weight, compared to the stomach contents per fish in the same period in 1969. A slight decline in number and a significant decline in weight of food organisms per fish was shown from November, 1970 to February, 1971; an abrupt increase occurred to a second high in March, which represented an increase manyfold over March, 1970. This increased food consumption occurred 1 to 2 months prior to their emigration from the lake as yearling smolts.

Five species of food organisms contributed chiefly to the diet of underyearling sockeye in Great Central Lake in 1970. In April and May *Bosmina* contributed about 50% of both the total number (Figure 6) and total weight (Figure 7) of all organisms found in their stomachs. The numbers of *Bosmina* consumed were insignificant throughout the rest of 1970 and the first 3 months of 1971. *Epischura* was the most important food organism from May to July (Figures 6 and 7) and was probably the principal source of energy for the rapid growth of the underyearlings during this period (see Figures 11 and 12). There was a transition in late July and August when *Cyclops*, *Holopedium*, and *Daphnia* gradually became more abundant in the stomach samples. In the 3 months which followed, September to November, *Cyclops* and *Holopedium* were the predominant genera. *Cyclops* continued in importance and formed about 50% of the number of food organisms to the end of January, 1971. However, during this period of 6 months *Cyclops* formed only 15 to 30% of the food by weight whereas *Holopedium* constituted 30 to 80% by weight. *Diaptomus* was first observed in the stomachs in the latter part of October, increased markedly in December and January, and was the predominant food organism by number in February and March, 1971. Thus *Diaptomus* was the most numerous food organism in the stomach samples just before

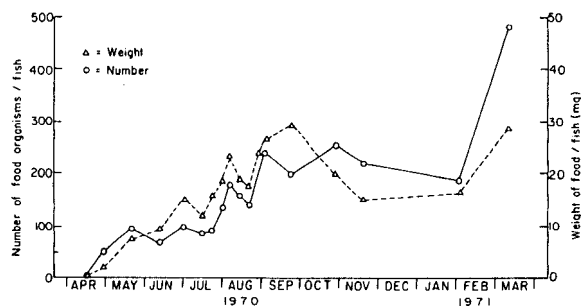


FIGURE 5.—Number and weight of all food organisms per fish, for underyearling sockeye salmon from April, 1970 to March, 1971.

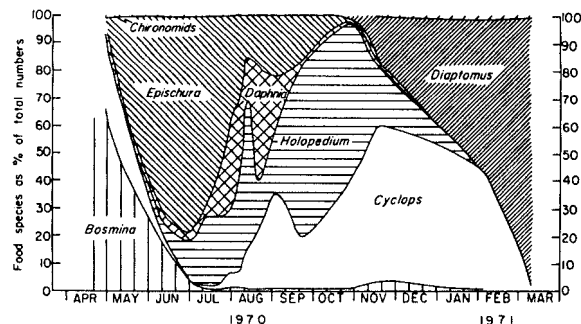


FIGURE 6.—Food of underyearling sockeye salmon expressed as a percentage of the total number of organisms from April, 1970 to March, 1971.

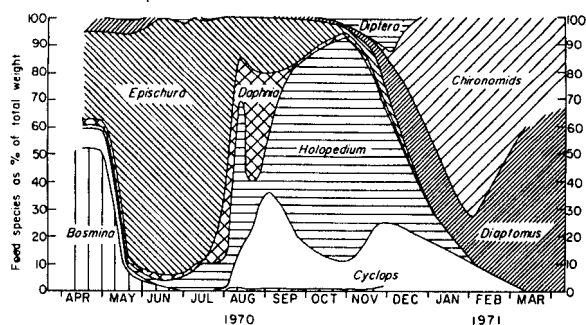


FIGURE 7.—Food of underyearling sockeye salmon expressed as a percentage of the total weight, from April, 1969 to March, 1971.

smolt migration in 1971. *Bosmina* was the most numerous in the previous year. The few chironomid larvae (Figure 6) in the diet of juvenile sockeye from December, 1970 to March, 1971, formed 30 to 70% by weight of all the food organisms (Figure 7). The importance of chironomid larvae during the winter months was observed also in the previous winter (Figures 3 and 4).

FOOD OF YEARLING (AGE 1) SOCKEYE

Those underyearling sockeye in Great Central Lake in 1969 which did not migrate to sea as yearling smolts in 1970, but remained in the lake for a second year, attained a mean length of only 51 mm and weight of 1.1 g between the latter part of April and May, 1970, whereas the migrating smolts had a mean length of 70 mm and weighed 3.5 g. The yearling sockeye which remained in the lake were collected from samples taken at all six stations and not from the end of the lake where smolts were schooling and heading seaward. Reference will be made later to the fact that the smallest size smolt, caught in the Robertson Creek weir (Figure 1) or in the nets set to capture smolts in the Stamp River, measured 55 mm and weighed 1.5 g.

Food organisms found in the stomachs of the yearling sockeye were similar to those eaten by the underyearlings during most of the year in 1970, but the yearling sockeye were more selective in cropping the larger forms of zooplankton (Figure 9). Both the underyearling and yearling sockeye fed heavily upon *Epischura* from May to July (Figures 6 and 9), but it was evident from the large numbers and weight of food organisms per fish (Figure 8) that the yearling sockeye elected to feed or were able to prey more heavily upon *Epischura* (Figure 9) than the underyearlings during September and October. Few yearling sockeye were caught in the trawls during the winter months of 1970-1971 prior to their migration as 2-year-old smolts. *Diaptomus*, *Holopedium*, and *Cyclops* were in the stomachs of these fish.

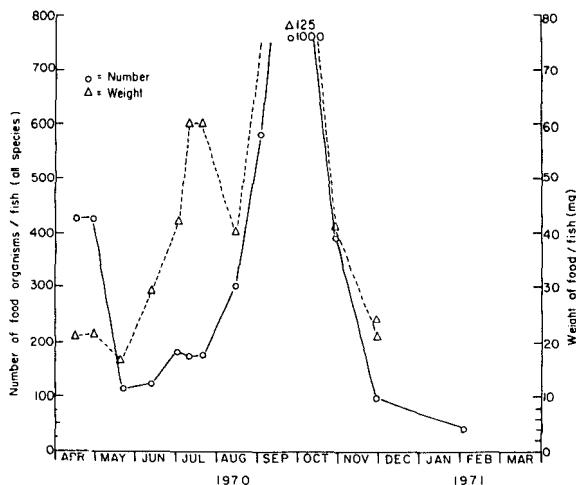


FIGURE 8.—Number and weight of food organisms of yearling sockeye salmon from April, 1970 to February, 1971.

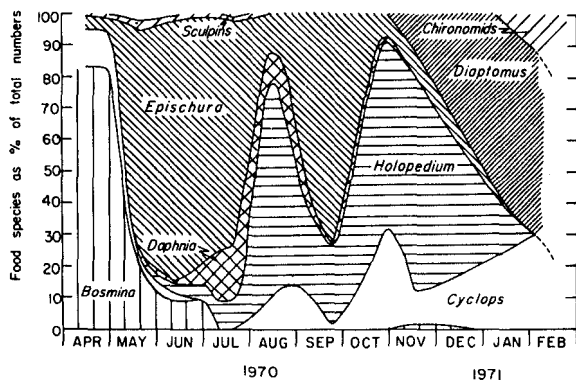


FIGURE 9.—Food of yearling sockeye salmon expressed as a percentage of the total number of organisms from April, 1970 to February, 1971.

DIEL FEEDING OF JUVENILE SOCKEYE

From midafternoon on June 17 to midday on June 18 a series of 11 tows, each of 15 min duration, were made with an Isaacs-Kidd midwater trawl. The trawl was towed through the middle of the densest portion of the stock during their

diel migration. The tows were made to determine what portion of different food organisms contributed to the salmon's ration during the day and night, as well as during the period of their diel migration. Data on depth and time of each tow, the number, size range, and mean length of sockeye caught, together with those sampled for the number and species of food organisms, and the weight of the food as a percentage of the body weight are given in Table 2.

The degree of freshness of food organisms was arbitrarily determined as fresh, fragmented, or largely unidentifiable. Fresh food was designated when no indication of digestion had occurred. The percentage of fresh zooplankton in the stomachs is given in Table 2. Depth of the densest portion of the layer of juvenile sockeye at different times of the day and night is indicated in Figure 10a by a broken line. The depth and time of each trawl tow relative to the depth of the fish is also indicated in Figure 10a.

The 24-hr data collection shows that in the day the densest portion of the layer of juvenile sockeye was formed at 75 m where the temperature of the water was 4° C; of the fish examined for stomach contents (Table 2) from tow No. 1, few food organisms per fish (Figure 10b) were noted and only 5% of the species were in fresh condition (*Bosmina*). The remaining species, *Epischura*, *Cyclops*, and *Daphnia*, were digested. Tow No. 2, through a less dense sec-

ondary layer at 105 m, indicated the same feeding pattern. Young sockeye commenced to migrate upward from 75 m between 1700 and 1800 hr. No differentiation in migration between underyearling or yearling sockeye could be detected at any level in the layer, either by net sampling or from high frequency echograms.

A tow just after sunset at a depth of 35 m revealed that the fish were eating *Bosmina* and *Cyclops* (Figure 10c) as they moved upward and 22% of the contents were in fresh condition. At 2200 hr the sockeye had passed 25 m where the heaviest concentration of *Cyclops* and *Daphnia* was located (LeBrasseur and Kennedy, 1972); in passing they had eaten *Cyclops* (Figure 10c). It should be recognized, however, that there is a natural time lag between feeding at any depth and the time the fish was captured by the trawl at a shallower depth, as they migrated toward the surface.

At nautical twilight, most of the fish had completed their upward migration and were distributed in a layer between 10 and 20 m where temperatures ranged from 6° to 12°C (Figure 10a). Echograms indicated many of the juvenile sockeye salmon appeared to spend brief periods between 0 and 10 m at temperatures ranging from 14° to 23° C, during which time the young fish fed heavily upon *Epischura* (Figure 10c). In the 4 hr between the beginning and end of nautical twilight no feeding occurred (Table 2).

TABLE 2.—Diel feeding of juvenile sockeye; tows made with an Isaacs-Kidd midwater trawl, each of 15 min duration, over a 24-hr period from June 17 to 18, 1970 at Station 4 in Great Central Lake.

Tow No.	Depth of tow (m)	Time (PST) at start of 15 min	Number fish caught	Size range underyearling	Mean length	Mean weight	Size range sampled for food	Mean length	No. sample fish for food	Total no. food organisms	No. of organisms per fish	% fresh	Weight of food as % body weight
				mm	mm	mg	mm	mm					
1	75	1449	47	23-40	32	292	28-40	33	10	190	19	5.5	1.1
2	105	1538	17	27-36	30	212	27-36	31	9	112	12	--	1.0
3	55	1820	21	27-38	32	272	27-38	33	10(1) ¹	67	7	--	1.0
4	35	2018	11	27-36	31	263	27-36	32	10	164	16	22	1.0
5	18	2142	6	26-36	31	282	26-36	31	6(2)	132	22	46	1.6
6	14	0023	71	26-41	32	315	26-41	33	11	537	49	6	1.7
7	19	0254	50	26-39	32	296	28-39	34	10(1)	257	26	--	1.5
8	62	0517	14	28-39	32	271	28-39	32	14(4)	586	41	64	2.1
9	68	0738	10	29-37	33	320	29-37	33	9	447	50	84	1.6
10	70	0945	9	29-39	33	278	29-39	33	9	543	60	34	1.6
11	75	1159	6	31-39	35	353	31-39	35	6	324	54	2	2.1
						Time of sunset	2011	Time of sunrise	0350				
						Time of nautical twilight	2201	Time of nautical sunrise	0200				

¹ Number in parentheses is number of items in sample which contained no food in stomachs.

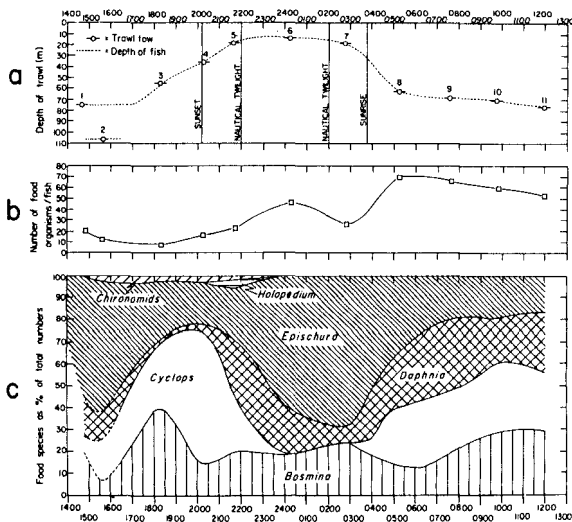


FIGURE 10.—(a) Depth of the densest portion of the layer of juvenile sockeye salmon at different times of the day and night from June 17 to June 18, 1970 is indicated by a broken line. A secondary layer is shown at 105 m for a 2-hr period. The depth of each tow with a midwater trawl is shown relative to the depth of the fish. (b) Number of all food organisms of underyearling sockeye. (c) Food species of underyearling sockeye salmon expressed as a percentage of the total number of organisms.

A second feeding period was noted at the time of the diel migration downward. Stomach samples from juvenile sockeye collected during this period contained many fresh *Daphnia* and *Cyclops* in tows 8 to 10. Only 2% of the zooplankton in the stomachs of sockeye caught at midday were in a fresh condition (Table 2), which indicates a marked reduction in feeding activity.

GROWTH OF UNDERYEARLING SOCKEYE

The average size of underyearling sockeye (Age 0) in 1969 and 1970 in Great Central Lake is shown in Figures 11 and 12. A total of 1,760 underyearling sockeye were caught in 1969 and 20,783 fish in 1970 from all six stations. A complete record of all data on which this analysis is based has been reported by Barraclough and

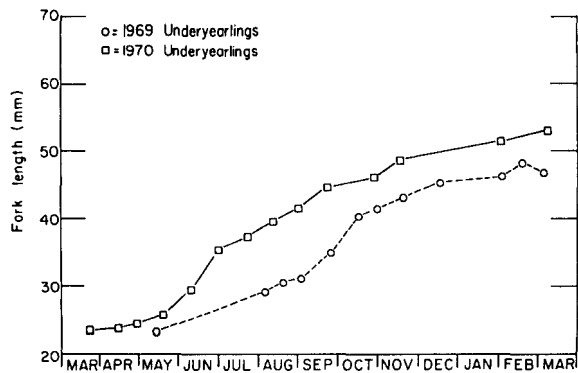


FIGURE 11.—Average length of underyearling sockeye salmon in each month, 1969 and 1970.

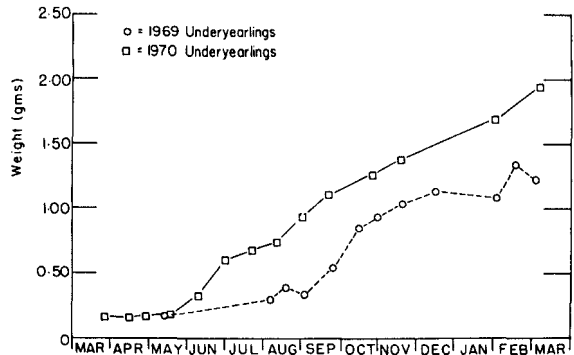


FIGURE 12.—Average weight of underyearling sockeye salmon in each month, 1969 and 1970.

Robinson (1971).⁶ Although little data on the size of in-lake juveniles prior to August, 1969 are available, it is evident that a marked initial increase in length and weight of underyearlings occurred from June to July, 1970 at a time when sustained additions of nutrients were made to the lake. Growth continued steadily during the rest of 1970 and through winter months in 1970-1971.

⁶ Barraclough, W. E., and D. G. Robinson. 1971. Length, weight, age and food of juvenile sockeye salmon (*Oncorhynchus nerka*) from Great Central Lake, British Columbia, May 1969 to February 1971. Fish. Res. Board Can., Manusc. Rep. No. 1128, 268 p.

In October, 1970, when fertilization was discontinued, the underyearling sockeye salmon were about 30% heavier than the fish caught in October of 1969.

DISCUSSION

The period of freshwater growth is a very important stage in the natural production of juvenile sockeye. It is one in which mortality may be high, particularly in the very early stages of their growth. An abundant food of the optimum size readily available for the fry to prey upon is one factor which increases their survival rate (LeBrasseur et al., 1969). LeBrasseur and Kennedy (1972) determined that the biomass of zooplankton in May, 1970 before fertilization was greater than at the same time in 1969. At this time the numbers of fry caught in the mid-water trawls began to increase and the catches were greatest, reaching a maximum in June at all stations shortly after fertilization commenced. LeBrasseur and Kennedy (1972) have demonstrated that the phenomenal increase in standing stocks of zooplankton in 1970 over 1969 was attributable to the sustained additions of nutrients. It is evident that the young sockeye fed very heavily (Figures 6 and 7) upon the increased number of *Epischura* in the lake (LeBrasseur and Kennedy, 1972). *Epischura* reached their greatest abundance in the upper 10 m in June when the average surface temperatures was about 15°C which was ca. 5° lower than that in July. In their diel migration, the young sockeye are able to take advantage of the most favorable temperature for food conversion for sockeye, which lies between 5° and 17°C, with a general physiological optimum at 15°C (Foerster, 1968; Brett et al., 1969). This may account for the rapid rate of growth in June compared with July.

Although the increase in length was greater in any one month in 1970 than it was in the same month in 1969, the increase in weight of about 30% in October, 1970 was less than expected from the 10-fold increase in zooplankton abundance reported by LeBrasseur and Kennedy (1972). The underyearling sockeye in the lake in 1970 were the progeny of a large escapement

of 72,000 adults in 1969 and a large number of new recruits could be expected. Since most of the spawning occurred along the lakeshore it was not possible to determine the number of fry that entered the lake, particularly when it was discovered that fry were always caught in the trawls from March to August. An estimate of the total numbers of sockeye in the lake was calculated from the fish targets recorded on the high-frequency echo sounder during surveys of the lake conducted once every 3 weeks throughout the year. From this analysis, coupled with pertinent catch data from each tow, a maximum estimate of 1×10^7 juvenile sockeye was determined. Johnson (1961) suggests that above a threshold concentration of 5,000 fish per hectare crowding may affect growth. LeBrasseur and Kennedy (1972) have demonstrated that the lake is sufficiently large that density of even a maximum estimate of 1×10^7 juvenile fish could not have been a limiting factor in their growth. However, the movement over a distance of 8 km in 1 day of large layered masses of juvenile fish in August (observed with high-frequency echo sounder) from one locality where the food source became depleted (O.D. Kennedy, personal communication) to another where food was abundant suggests that fish density may have been a seasonal factor.

The size of the yearling smolts leaving the lake from April to June each year was always larger than the same year class of juveniles caught at the six regular trawling stations during the same period because the migrating smolts school near the outlet of the lake. In 1969 the 781 yearling smolts caught in the Robertson Creek weir averaged 67.5 mm in length and 2.6 g in weight. In 1970 the average length of 1,423 yearling smolts was 71 mm and 3.5 g. In 1970 the average length of the yearling smolts decreased from 72 mm in April and May to 68 mm in June. The largest yearling smolts migrated first in April and May together with the 2- and 3-year-old smolts, and in June, almost all the smolts were smaller yearlings.

In April, 1971, 589 yearling smolts were sampled from the weir at Robertson Creek. Their average length and weight was 79 mm and 4.8 g. During this period the largest yearling smolts

ever recorded from the weir were taken, ranging from 90 to 95 mm. In May, 1971 the average length of 1,582 yearling smolts was 71 mm and a weight of 3.7 g. This average length and weight was the same as that of all yearling smolts sampled in 1970. In June, 1971, 3,012 yearlings were sampled and the smolts averaged 66 mm in length and 3.3 g in weight. It has been noted already that the smallest yearling smolt ever caught at Robertson Creek weir was 55 mm.

In conclusion, from the data presented here it is apparent that the total lake population of young sockeye salmon took advantage of the extra zooplankton ration (mainly *Epischura*) and that the average weight of individual fish of the in-lake population was 30% larger than in the previous year. However, the mechanism whereby this overall average increase in growth was observed is complex. The explanation offered is that the first fry to enter the epilimnion of the lake in April and May could take the greatest advantage of the increased zooplankton standing stock in June, when the average surface temperature was ca. 15°C. The following year (1971) this resulted in the migration of a group of 1-year-old smolts which were the largest (90-95 mm) ever observed from the lake. Fry which entered the lake in June and July could not take the same advantage of the zooplankton standing stock because the surface temperature was >16°C, and this reduced their feeding efficiency (Foerster, 1968). Thus increases in temperature of the epilimnion through the long period of fry emergence decreased the apparent benefit to late-hatching fish. However, in spite of this, most of the fry hatching later in the year achieved a length greater than 55 mm and migrated from the lake in June 1971; under normal conditions it is believed that these fry would not have reached 55 mm and would have migrated the following year as 2-year-olds. Preliminary examination of the scales from juvenile sockeye in 1971 reveals an absence of a winter check on many scales which suggests that the high concentrations of zooplankton persisting through the winter enabled many fish to smoltify and leave the lake. The combination of an early run of very large 1-year-old smolts, combined with this later run of much smaller smolts,

tended to reduce the overall apparent effectiveness of lake fertilization. Thus the real effects of fertilization seem likely to be greater than would be judged from considering only changes in overall mean size of smolts.

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