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FISHERIES RESEARCH BOARD OF CANADA

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DIEL VERTICAL MOVEMENTS AND FEEDING HABITS OF UNDERYEARLING SOCKEYE SALMON (*ONCORHYNCHUS NERKA*), AT BABINE LAKE, B.C.

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ABSTRACT

Sockeye underyearlings at Babine Lake, B.C. were observed to undergo diel vertical movement from July through to October 1967. This movement was more pronounced in August when the lake was most distinctly thermally stratified. The presence of a sharp thermocline (about 8 C in 10 m) did not appear to impede their movement in any substantial way. By day the sockeye inhabited cold (5-6 C), deep (35-55 m) water and at night the warm water (about 16 C) of the epilimnion. Vertical movement was closely associated with change in light levels. The sockeye rose to the surface at evening twilight, then settled to remain at about 10 m throughout most of the night. They were once again at the surface at morning twilight but then quickly descended to their daytime level between 35 and 55 m. The food of the underyearlings consisted mainly of Cladocera (Daphnia) and Calanoida (mainly Heterocope but sometimes substantial amounts of Diaptomus). Very small amounts of the Cyclopoida were found in the food. Some insects were eaten--mostly Hymenoptera and terrestrial Diptera but also a few chironomids. All, or at least most feeding, took place at or near the surface for a short period at evening and at morning twilight. Gastric digestion was essentially completed between meals. Rates were estimated to be 14% of the stomach contents per hour for the morning meal and 22 and 30% for the evening meal. The difference was attributed partly to the difference in temperature (up to 10 C) at which digestion of the morning and evening meals took place. Daily ration was estimated on three separate occasions to be 4.1, 5.1, and 6.9% of body weight. The largest ration (6.9%) was associated with an increase in weight of about 2.9% per day. It is suggested that the behaviour observed at Babine Lake may be typical of that in other lakes which become thermally stratified in the summer. The significance of certain features of the sockeye's diel activities is discussed.

INTRODUCTION

Babine Lake supports one of the major sockeye stocks in British Columbia (Larkin and McDonald 1968). The fish spawn in the outlet river, or streams tributary to the lake, in the late summer and fall. Their progeny emerge as fry from the gravel the following spring and begin a period of lake residence. After 1 year, and sometimes 2 years in the lake, they migrate to sea. Although this period of lake residence has long been the subject of study (Foerster 1968 provides a comprehensive review of the literature), much remains to be learned of the daily or seasonal activities of the underyearling sockeye. This has been due largely to the past difficulty of obtaining specimens readily and consistently. Ricker and Foerster (1948) in their pioneering studies at Cultus Lake, B.C., depended mainly on specimens taken from the stomachs of predator fishes. With the development of townetting (Johnson 1956), underyearling sockeye could be captured readily throughout the summer but usually for only an hour or so each evening. These catches provided not only samples for food and growth studies but also a relative measure of density. Still, the whereabouts of the sockeye and their activities for most of every 24 hours remained unknown, and since there was large variability in catch per unit effort (Johnson 1958), only gross differences in density could be detected.

Renewed interest in the question of the capacity of lakes to support young sockeye grew out of the work of Johnson (1956, 1958, 1961, MS 1961) at Babine Lake and Burgner (1958, 1962, 1964) in Alaska. At Babine Lake in 1965, a large development project involving artificial spawning channels and flow control was launched with the intention of increasing sockeye production by increasing fry output and making fuller use of the lake nursery area (Department of Fisheries of Canada 1965). A program to assess the results of this project and to assess the ultimate capacity of the lake to produce sockeye was initiated at the same time. In 1966, the lake population of sockeye was sampled by purse seine. Sockeye were captured readily throughout the night (but not by day) but variability in catch per unit effort was still large (McDonald 1969). Sound information about their ecology was needed not only to improve existing techniques, or to devise new ones which would provide the desired precision, but also to define the conditions necessary for good growth and survival.

Two separate studies were begun in 1967, which provide pertinent information. One study (Narver 1970) confirmed the general pattern of diel vertical movement deduced from 1966 seine catches and in addition revealed in detail other aspects of diel activity, particularly in the lake's North Arm area (Fig. 1). The study reported here was carried out in the relatively large and deep main basin of the lake. The observations complement and extend those reported previously.

METHODS

Catch and detection of underyearlings

Underyearling sockeye were captured with a purse seine and a midwater trawl. The seine was half-purse, 150 fm long (274.4 m) and hung to a depth of about 8.6 fm (16 m). The mesh size varied from 3/16 inch (0.48 cm) stretched measure in the "bunt" to 1-1/2 inches (3.81 cm) in the lead. Twenty to 30 minutes elapsed between "shooting" and pursing the net. The net probably caught sockeye which were as deep as 16 m but it would be expected that only a small proportion of those present near the bottom of the net would be enclosed. As the net was drawn up and pursed, the proportion captured would increase and probably most of those close to the surface would be taken. Further detail of methods and the catch for individual sets is given by Scarsbrook and McDonald MS 1970).

Sockeye were caught from near the surface to as deep at 58.6 m with an Isaacs-Kidd trawl. The mouth of the trawl was 6 ft (1.83 m) wide and 8 ft (2.44 m) high but when under tow the height of the opening was considerably reduced. Two mesh sizes were used: 3/16 inch (0.48 cm) and 3/8 inch (0.96 cm) stretched measure. The small mesh was used to catch the smaller early-summer fish and the large mesh to catch fish in the late summer and fall.

Both seine and trawl were fished from a 35-ft (10.7 m) drum-seiner. Trawling was done at a speed of about 4 miles per hour (6.4 km/hr) with both mesh sizes. All tows were made at mid-lake and parallel to the shore. Trawl depth was set by adjusting the length of the towing cable according to a length-depth relationship based on a number of trials using a Furano Piloto-graph echo sounder to record trawl depth. By using the midpoint of the echo, the depth of the trawl could be determined to the nearest fathom (1.83 m).

The procedure for operating the trawl was as follows. The net was "shot" over the side of the vessel while it was underway at a speed of about 2 mph (3.2 km/hr). The towing line was let out the appropriate length and the vessel brought up to towing speed. Usually, a series of tows was made starting near the surface (4.6 m or 9.2 m) and then at depth intervals of 9.2 m down to 54.9 m, or until zero or very small catches were made. The net was picked up and the catch removed and recorded after each tow which was usually 15 minutes long (i.e., from the time towing speed was reached until pick-up began). The times taken to set and retrieve the net varied with the depth of the tow. At 4.6 m, the shallowest towing depth, the average time taken to set and retrieve was 3 minutes; at 54.9 m it took about 11.5 minutes. One series of tows at 9.6-m intervals to a depth of 54.9 m took about 2.5 hours to complete.

There were four periods of observation and collection in 1967. These were July 1-7, August 18-29, September 24-October 1, and October 22-27. All fishing was done at two sites in Areas 2 and 3, except for a few seine sets made during the October 22-27 period in Areas 1 and 4 (Fig. 1). Areas 2 and 3 were chosen because they were convenient to shore facilities and because previous work had indicated that underyearlings were abundant in these areas throughout the season. Additional information on digestion rates and daily ration was obtained from 1968 seine catches. Two series of 10 sets each were made on the nights of August 17-18 and August 18-19, 1968, in Area 3.

Vertical distribution was studied by using a Simrad "Skipper" model 512-15 W:L. which operated at a frequency of 38 kHz. Transducer size was 8 × 10 cm. In order to record echoes from underyearling sockeye, which are small targets, the sounder was operated at a high level of sensitivity (gain 8 on a 1-10 scale).

Measurements of water temperature

Four temperature series were made from early summer to fall, 1967, with an electric thermister-thermometer which was accurate to the nearest 0.1 C (McDonald and Scarsbrook MS 1969). In each series, the temperature was taken 15 cm below the surface and then at every metre down to a maximum of 80 m. Up to 14 mid-lake stations were occupied in each series.

Processing of specimens

Fish were preserved in a 10% formalin solution. Processing began after 2 to 5 months in the preservative. Excess moisture was removed from each fish by blotting lightly with an absorbent paper towel. Care was taken to ensure that no moisture was left on or around the fins. To minimize the effect of dehydration, fork length and weight were recorded immediately after blotting. Next, the whole gut was removed and weighed with its contents. It was then cut into three sections corresponding to the cardiac and pyloric portions of the stomach (sections I and II) and the intestine (section III). Each section was weighed with its contents and then sections and contents were weighed separately. The contents were placed under water in a glass dish for inspection. Food items were grouped as to kind and percentage of total contents (by volume) estimated by inspection for each gut section and for the gut as a whole.

Contents of the gut were classified on the basis of their stage of digestion: stage 1 when food items were in a fresh condition; stage 2 when some breakdown of individual organisms was observed; and stage 3 when the food was broken up and contents were, for the most part, unidentifiable.

RESULTS

Diel vertical distribution

Evidence from seine catches

Catch data from each fishing period are arrayed in 24-hour sequences in Fig. 2. Times of sunset and sunrise (Pacific Daylight Saving Time) have been used to distinguish between night and day sets. For the fishing periods in July, August, and September, 1967, most of the sets were in continuous series made at the same locations. During July a series of 11 sets were made beginning 1344 hr July 5, and ending 0327 hr July 6. In August, a series of 13 sets was made between 1846 hr August 27 and 0728 hr August 28. Another series of 13 sets was made from 1022 hr September 28 to 0059 hr September 29. In this last case there was a large gap in the series spanning the afternoon of September 28. Two series of sets each spanning about 9 hours were made on consecutive days from October 22 to 24.

Seining results were similar to those of the previous year (McDonald 1969). Underyearling sockeye were seldom taken in the seine during the day, except on occasions bordering evening or morning twilight, but they could be caught at any time of the night. In both 1966 and 1967, substantial numbers of older O. nerka (anadromous and non-anadromous forms in their second year or older) were captured during the day. In 1966, 296 of these fish were taken in 7 of 13 daytime sets, and in 1967, 267 were caught in 8 of 20 daytime sets. The ready capture of these older fish suggests that by day the underyearlings were below the range of the net rather than avoiding it.

The number of underyearlings caught throughout the night varied considerably. The series made on August 27-28 is the most complete and catches show a definite pattern. The largest catch (1,194) was made shortly after sunset. This is the time when, on calm nights, underyearlings can be seen at the surface and when they can be taken readily in surface tow nets (Johnson 1956, 1958). After 2037 hr the catch decreased progressively until about 0200 hr, and then it increased to reach a second but smaller peak (686 fish) at morning twilight (0528 hr). The next set, which was shortly after sunrise, produced a reduced catch while the set made a little more than 1.5 hours after sunrise resulted in a zero catch--the typical daytime result.

These observations suggest that underyearlings rise to the surface at about sunset, subsequently settle to a lower depth, but not completely out of range of the seine. Some at least, rise to the surface again at morning twilight but shortly after they descend below the depth of the net (16 m). Ascent and descent appear to occur fairly rapidly. The evening catch rose from 0 to 1,194 in an interval of less than 2 hours. At dawn, a catch of 686 was made at 0528 hr. Catch decreased to 132 in about 1 hour, and to zero after about 2 hours.

Fewer observations were made at other periods of the season. Catches made during the night of July 5-6 were more consistent than those made in August (Fig. 2). The catch at evening twilight was not the largest, and catches remained fairly steady through most of the night. No information is available for the morning twilight period.

Catches made in late September suggest a pattern similar to that observed in August. Large catches resulted from two sets made at evening twilight. Thereafter, catches were small. No information was obtained at morning twilight.

Evidence from trawl catches

Underyearling sockeye were present in the surface layer at night and were found at considerable depth by day (Fig. 3). Before examining these data in detail, two sources of error should be examined. Catches from near surface tows and particularly those made at 4.6 m and 9.2 m probably do not reflect abundance at these levels because the trawl was towed behind the stern of the boat and the hull, propellor wash, and wake probably freightened some fish away, and thereby reduced the efficiency of the net. Also, the possibility of sockeye being caught at other than the desired towing depth while the net was being set and retrieved must be considered. It is extremely unlikely that any fish would be caught while the net was being set as it was lowered with its mouth collapsed. Probably some were caught during retrieval. The net was hauled in as rapidly as possible, but it remained in an operating condition. Retrieval took about 1 minute per 10 m of depth and for deep tows (54.9 m) it took about 5 or 6 minutes. The catch during retrieval appeared to be small both in numbers and in proportion to the total for any one series. On July 1, a series of tows was made to a depth of 58.6 m. Most fish were caught at 36.6 m or less. At the conclusion of this series of tows, the net was lowered twice to 36.6 m and immediately retrieved. Three fish were taken in the first test and 1 fish in the second (Table 1). The catch of 3 fish recorded at 58.6 m could have been made at a lesser depth during retrieval. Another and better assessment of capture during retrieval is gained from data shown in Fig. 3. Catches at the greatest depth in each series were either zero or just a few fish which usually represented a very small proportion of the total for the series. Resulting error would not cause any substantial misinterpretation of vertical distribution except when the total catch in a series was very small--such as in some series in the September and October periods. In these cases, however, most deep tows resulted in zero catches and therefore are not misleading with respect to captures during retrieval.

Trawl catches from July 1 to 7 (Fig. 3a) include 4 daytime series made on 3 different days and 2 nighttime series made the night of July 6-7. By day, most underyearling sockeye were caught below 20 m but above 40 m. They appeared to be most concentrated at close to 30 m. At night most were caught above 20 m and the greatest proportion of them were caught around 10 m.

The same pattern was apparent in August (Fig. 3b). During the day most sockeye were taken below 35 m and at night above 15 m. The series of tows between 0407 and 0817 hr spans the time of descent of the sockeye from the surface layer to their daytime levels and the catch changed little with depth. Apparently the towing depth was increased at about the same rate as the fish descended.

A closer comparison of the catches made in the July 1-7 and August 18-29 periods reveals that the fish were concentrated at greater depths during the day in August than they were in July (35 to 55 m instead of 20 to 40 m).

Although catches in the fall periods were usually small, they were consistent enough to indicate that by day the sockeye were concentrated at about 20-30 m, and by night, above 15 m (Fig. 3c). The daytime level was much shallower than in August and somewhat less than that observed in early July. The single night series made September 24 does not suggest any substantial change from the night distribution observed earlier in the season.

<u>Evidence from trawl and seine catches combined</u>

Sufficient data are available from the August 18-29 period to show in considerable detail the changes in vertical distribution which occurred at this time (Fig. 4). Seine catches shown in Fig. 4 were made over 3 days, August 26-28, but sets beginning at 1846 hr through to 0728 hr were made consecutively on August 27-28. Trawl catches were made over several days. The dotted lines are drawn by inspection and are used only to indicate depth distribution generally. Some day-to-day differences in vertical distribution may be expected but the consistency shown by the trawl catches suggests that day-to-day differences are not large; hence arraying several days' data within one 24-hr sequence should provide a useful description of diel distribution. Almost all underyearlings were between 35 and 55 m during most of the day. Ascent probably began about 1800 hr or shortly after.

Before 1800 hr few sockeye were above 35 m. Within 2 hours sockeye were taken at 10 m to 20 m, and after 2.5 hours, the peak seine catch was made. Descent to daytime levels appears to take about the same time. The peak morning catch was made at 0528 hr. At 0656 hr, a catch of 31 fish was made at 20 m, and by 0800 hr, roughly 2.5 hours after the peak morning seine catch, the fish appeared to have established their daytime level. Both descent and ascent took up to 2.5 hours, revealing an average rate of vertical movement of about 18 m per hr.

Sockeye distribution did not remain static between dusk and dawn. Seine catches decreased after the evening twilight period and when examined together with trawl catches suggest that some fish settled to a depth of at least 12 m. Increasing seine catches after 0200 hr suggest that some fish began to move closer to the surface. By morning twilight many fish were again at or close to the surface. Some remained within the range of the net after sunrise as shown by the catch made at 0631 hr or 34 minutes after sunrise. However, no fish were caught in the seine set made at 0728 hr, or about 2.5 hours after sunrise. Trawl catches at this time confirm that sockeye were concentrated at their daytime level of between 35 and 55 m.

Evidence from echo-sounding

The Simrad 38 kHz sounder was used at Babine Lake in 1966 and 1967 in conjunction with seining. This experience had shown that the sounder would indicate the presence or absence of fish of the size of underyearling sockeye between roughly 5 and 20 m depth. Objects above 5 m were not recorded. Below about 20 m, or perhaps a little deeper, the recorder apparently cannot detect underyearlings. Sensitivity changes with depth, and underyearlings which produce dense echoes at 10 m would produce very light and scattered echoes at 20 m, and few or no echoes at greater depths.

Tracings from soundings made on August 22-23, 1967 (Fig. 5) in the same location as seine and trawl fishing, indicate the same diel vertical movement pattern of sockeye as was interpreted from the net catches. The tracings were made while cruising back and forward on a fixed course over a distance of about 1 mile. The first tracing in the series (1948 to 2203 hr) spans the time of evening twilight. At the start, an echo layer was centered at about 15 m. It rose progressively and by 2040 hr echoes were seen at the 5 m level. Apparently some fish had risen into the top 5 m. From 2100 to 2140 hr few echoes were recorded indicating that the fish were mostly in the top 5 m. By 2149 hr, an echo layer began to form again at about 10 m and then remained static throughout most of the 2216 to 0206 period. From 0206 to 0347 hr a reduction in the density of this echo layer was seen. At about 0500 to 0548 hr, few echoes were recorded. After 0548 hr the echo layer appeared once again and then progressively moved deeper and disappeared below 20 m. The absence of the echo layer from 0500 to 0548 hr can be attributed to the rise of fish into the top 5 m while the disappearance of the echo layer below 20 m occurred as a result of the decreasing efficiency of the recorder with depth.

There seems little doubt that the sounder tracings reflect movement of underyearlings within depths of 5 to 15 m. The tracings show ascent from 15 m to above 5 m from 1948 to 2040 hr. This corresponds to the time when trawl catches of sockeye below 30 m fell sharply while those in the top 15 m increased. The rise of the top of the echo layer to 5 m corresponds closely with the time (2037 hr) when the largest seine catch was made and the evening twilight period when underyearlings can be seen at the surface. The subsequent descent and formation of a static echo layer at 10 m corresponds to the decrease in seine catches after evening twilight. Disintegration of the echo layer began after about 0200 hr. Increased seine catches indicate fish were moving slowly toward the surface. Between 0500 hr and 0548 hr most fish would have been above the minimum range of the sounder and at this time the morning peak seine catch was made. The descent of the echo layer after 0605 hr corresponds to the time that seine catches dropped to zero and trawl catches showed sockeye to be present at their daytime level of between 35 and 55 m.

Diel vertical distribution and temperature

Major changes in the thermal structure of Babine Lake's main basin were observed throughout the summer and fall (Fig. 6). By early July the thermocline was not yet well developed. Surface temperatures varied from about 8 to 13 C. The lake was nearly isothermal below 30 m. A prominent feature was a wedge of relatively warm water extending from the southeast end of the lake (station 12) into the northwest end (to station 3).

In late August, the thermal structure of the lake was fairly uniform. The surface water was about 17 C and decreased to about 15 C at 10 m. A very well defined thermocline (15 to 7 C) occurred between 10 and 20 m. Below 20 m the water was 7 C or less at most stations.

By late September, the lake had cooled considerably. Surface water was 13 to 14 C. The thermocline was much reduced from the month previous. The warmest water was in the northwest end of the basin. At stations 1 to 5, water 8 C or higher extended down to 30 or 40 m. Further uplake, 8 C water extended down to only 20 m.

By late October, the lake was nearing an isothermal condition. The surface had cooled to between 7 and 9 C, but a relatively warm and deep layer of water was still evident in the northwest end of the basin.

When the diel movements of underyearling sockeye are examined together with lake temperatures (Fig. 7) it can be seen that the fish, when moving from daytime to nighttime depths and back again, experienced changes in temperature the extent of which depended upon the time of season. July 3-4 temperatures at station 8 show a gradual decrease from a surface temperature of 11 C to about 4 C at 40 m. Sockeye during the day were found between 20 m and 40 m in water of 4 to 7 C. They were most concentrated at 30 m where the temperature was about 6 C. Movement to and from the surface at twilight brought the fish into water between 8 and 11 C or 2 to 5 C degrees warmer than the water at their daytime level.

In late August, sockeye were concentrated by day well below the thermocline in water of 5 to 6 C. Movement to the surface brought them into water as warm as 17 C. The temperature at 10 m, the depth at which most sockeye appeared to spend much of the night, was about 16 C which is 10 to 11 C degrees warmer than the water inhabited during the day.

The sockeye were concentrated at about 20 m by day in late September. The water at this depth was 6 to 7 C. By night, water between 7 and 11.5 C was occupied.

By late October, the water at station 6 was nearly isothermal at close to 8 C down to 30 m. Trawling during the day indicated sockeye between 15 and 30 m. No seining was carried out at night at this site but seine sets made at other locations revealed sockeye near the surface. Evidently, at this time, vertical movement resulted in very little change in water temperature.

Feeding habits

Kinds of food

The relative amounts (by volume) of the various food items contained in the cardiac portion of the stomach have been used to provide a general description of the diet of underyearling sockeye in the study area throughout the 1967 season (Fig. 8a, b, c, d). Note that in the figure, data resulting from observations made over a period of days have been arrayed in one 24-hr sequence. Also, percentages shown are mean values for samples of usually 10 fish drawn from seine and trawl catches. Not all catches were sampled. Instead, samples were selected on the following basis: (1) the samples would provide as much as possible an hourly description of stomach contents over a 24-hr period; (2) samples would be drawn from catches made at depths where young sockeye were most abundant; and (3) a minimum sample was 10 fish (catches of less than 10 were used when no alternative source of information was available for a particular time or depth).

The data shown in Fig. 8 reveal the kinds of food ingested but not the amount in the stomach or feeding time--except that the latter is indicated by the number in each sample with empty stomachs, and by the proportion of digested material. The few fish which were found with completely empty stomachs were almost all caught at depth during the day. This fact, together with the relatively high proportion of digested material found in the daytime samples, indicated that feeding was associated mainly with nighttime and the surface layer. Further information regarding feeding times is reported in the following section.

The food of sockeye underyearlings throughout the summer and fall of 1967 consisted mainly of Cladocera (Daphnia) and Calanoida (mainly Heterocope and at times substantial amounts of Diaptomus). Very small amounts of the Cyclopoida were in the food. In addition to the Crustacea, some insects were eaten--mostly Hymenoptera and terrestrial Diptera, but also a few chironomids.

Diet changed with the season--probably in response to availability of different food organisms and from changes in food preferences associated with the increasing size of the young sockeye. Size data are summarized below:

Sampling period	No. in sample	Average length (mm)	Standard deviation	Average weight (g)	Standard deviation
July 1-7	123	33.4	4.14	0.390	0.194
Aug. 18-29	165	52.4	5.63	1.678	0.471
Sept. 24-Oct. 1	87	63.6	7.95	2.952	0.993
Oct. 22-27	80	67.2	7.90	3.375	1.156

In early July, stomach contents (Fig. 8a) consisted mainly of Heterocope (about 80% of the nocturnal contents). Small amounts of Daphnia and Epischura were eaten and only traces of other items were found.

By late August, Daphnia were the major food, and they comprised about 80% of the contents (Fig. 8b). Heterocope were still present but relatively unimportant. Only small amounts of other items were taken.

Daphnia remained the major food item until late September (Fig. 8c), but the diet was more varied than it had been earlier, and substantial proportions of Diaptomus and Epischura were noted.

In late October, almost no Daphnia were found in the stomachs (Fig. 8d). Heterocope once again predominated. The only other form taken in any substantial amount was Diaptomus. No insects were found although they had been present in all previous sampling periods.

Times of feeding

Both the quantity and condition of the stomach contents have been used to reveal feeding times (Appendix I). Contents of the whole stomach (sections and II) are given as a percentage of the body weight (total fish weight less contents of total gut). Mean, minimum, and maximum values are for samples of usually 10 fish. A relative measure of the stage of digestion of the stomach contents (called "score") was derived by assigning 1, 2, and 3 points to digestion stages I, II, and III, respectively, and summing the points for the 10-fish sample. When the sample was less than 10, the score was weighted appropriately. An empty stomach was considered to be the equivalent to stage III, and given 3 points. For a sample of 10 fish, the minimum score would be 10, i.e., the contents of all 10 fish would be in a fresh state (stage I). A score of 20 would mean that on the average the contents were partially digested (stage II), while a maximum score of 30 would mean that digestion was well advanced (stage III) for all fish in the sample. Data from each fishing period have been arrayed in 24-hr sequences (Fig. 9).

In July, stomach contents by day averaged less than 1% of the body weight and that of individuals never exceeded 1.5%. Also, during the day, the contents were found to be in an advanced stage of digestion (scores of 23 to 30). After evening twilight, average contents rose to between 3.0 and 4.0%, and one individual stomach contained 7.0%. With this increase in content there was an accompanying decrease in the stage of digestion. No samples were obtained in July to show whether feeding occurred at the time of morning twilight although this occurred in August.

The most complete series of observations was made August 18-29, and evening and morning feeding periods were clearly defined by changes in the quantity and condition of stomach contents. In the evening, the average contents increased over a period of about 2 hours from about 1.2% of body weight at 1821 hr to 5.6% at 2037 hr. Thereafter, there was a rapid and progressive decline to the mid-nocturnal low of less than 1% at 0329 hr. With morning twilight, contents increased to 3.3% of the body weight at 0631 hr from the 1.2% of about 1 hour earlier. After 0631 hr contents decreased to 1.4% by midday.

The evidence arrayed in Fig. 9 suggests that little feeding occurred other than at the twilight periods. However, when the contents of individual fish were examined (Table 2) some daytime and nighttime feeding was indicated. Daytime samples included some fish which contained fresh-appearing food (stage I) in the cardiac section of the stomach. These samples were taken up to 12 hours or more after morning twilight; if no feeding had occurred since twilight, it would be expected that the contents would be in a more advanced stage of digestion. A few fish with fresh food were taken up to 0129 hr, or about 4 hours after evening twilight, suggesting some feeding during this time. In both day and night feeding it seems that only a fraction of the fish may be feeding and that the quantity of food ingested is extremely small relative to that ingested at the twilight periods.

Times of feeding in the fall are less clear because of infrequent sampling. In September, it appears as if feeding still remains associated with evening twilight at least. Stomach contents were minimal (about 1.0% or less of body weight) during the day and reached a maximum of about 3.0% after evening twilight. No data were obtained at morning twilight.

In late October, the largest average amount of food was found in fish sampled at about evening twilight (2.1% of body weight), but contents at 0245 hr were almost as great. The quantity and condition of the contents were fairly static throughout the night suggesting either that some feeding may have occurred or that digestion was extremely slow.

Digestion rates

Samples were obtained in the August 18-29 period with sufficient frequency to show peaks and troughs in mean stomach content (Fig. 9). These changes can be used to estimate rates of gastric digestion, i.e., rate of emptying of the stomach. Following the evening and morning meals, stomach contents decreased progressively in quantity until minimal values were observed beginning 5 to 8 hours later. At no time in August (and only occasionally at other sampling periods) were any stomachs found completely empty between meals. For instance, on the night of August 27-28, the average content decreased to 1.19% of body weight at 0129 hr and subsequent samples show little change until the morning meal at about 0631 hr.

Similarly, after the morning meal, average contents dropped to 1.52% at 1058 hr, and changed little until the evening meal nearly 10 hours later. A continuous intake of small quantities of fresh food would account for this near-static condition, as would a slowing down of digestion rate as the stomach emptied. Earlier it was suggested that a small amount of feeding occurred "between meals." However, the progressive advancement of digestion stage following the meals suggests that a slowing of digestion rate is probably the more important factor.

Estimates of the rates of digestion of the evening meal have been made using data obtained from samples drawn from catches made in consecutive hours on the night of August 27-28, 1967. These data have been supplemented by samples from seine catches made at the same location on the nights of August 17-18 and August 18-19, 1968. A continuous series of samples was not available following the morning meal. Instead, samples were drawn from catches made over several days and arrayed over consecutive hours. Instantaneous rates of digestion are estimated from the slopes of the regression of the $\log_e$ of mean weight of stomach contents (as % of body weight) on time after feeding (Fig. 10). In each case the time period begins with the evening or morning meal and ends when contents first reached the low, static, between-meals level. During this interval rates of digestion generally appeared constant. Following each of the three evening meals, digestion occurred at rates of 22% per hour (1 meal) and 30% per hour (2 meals). Digestion of the morning meal appeared to be slower and the regression line indicates a rate of about 14% per hour. This rate (slope) was significantly less than the 30% rate for two evening meals but not different from the evening meal rate of 22% ($F = 3.38$, $P > .05$).

Once the between meal low of about 1% of body weight was reached the digestion process appeared to remain static.

Daily ration

Differences in stomach content immediately before and after feeding (Appendix I) may also be used to provide some idea of the daily intake of food, or daily ration. In calculating the ration it has been assumed that no feeding occurred other than at the evening and morning twilight periods. Since this was not strictly true, the estimates are minimal.

On the evening of August 27-28, 1967, the average contents rose with the evening meal from the order of 1.0 to 5.6% of body weight--a net intake of 4.6%. Increase with the morning meal was from the order of 1.0 to 3.3% or a net intake of 2.3%. Total intake over the 24-hr period would therefore be about 4.6% (evening meal) plus 2.3% (morning meal) or 6.9% of body weight. Looking at maximum values, the highest content observed after the evening meal was 8.5%, and after the morning meal it was 4.7%. Assuming residual food prior to eating amounted to 1.0%, the maximum intake for any individual would be 7.5% + 3.7% or 11.2% of body weight.

In 1968, minimum day values are not available because the first sample was taken in the surface layer just prior to evening twilight, and probably some feeding had already taken place. To calculate the evening ration, it was assumed that the daily minimum content was 1.0%--the same as in 1967. For the two nights in 1968, the intake of the evening meal amounted to 2.5% (3.5-1.0%) and 3.5% (4.5-1.0%) of body weight. With the morning meal, contents arose from the order of 1.0 to 2.6% on both occasions for a net gain of 1.6% of body weight. Over the two 24-hr periods the total intake was 4.1 and 5.1% of body weight, compared with 6.9% for August 1967. The difference may reflect differences in times of sampling in relation to meal times rather than any real difference in food intake or perhaps changes in food supply.

Data for early summer and fall periods are too scant to warrant even rough estimates of daily ration. Information at hand (Fig. 9) suggests that in both periods the ration was smaller than it was in August.

Daily ration and growth

Size data from the three sampling periods in 1967 provide an opportunity to examine rates of growth in relation to daily ration. Using the central dates of each sampling period and the mean lengths and weights of all fish sampled, the instantaneous rates of growth were calculated using the formula:

$$g = \frac{\log_e s_2 - \log_e s_1}{t}$$

where g = instantaneous rate in growth, s_1 = initial size, s_2 = final size, and t = time in days.

Pertinent data and calculations are shown below:

Central date	t (days)	Mean length (mm) s_1	Mean length (mm) s_2	Mean weight (g) s_1	Mean weight (g) s_2	g_ℓ length	g_w weight
July 5							
	50	33.4	52.4	0.390	1.678	0.00897	0.02919
Aug. 24							
	34	52.4	63.6	1.678	2.952	0.00570	0.01635
Sept. 27							
	27	63.6	67.2	2.952	3.375	0.00207	0.00533
Oct. 24							

Fastest growth occurred during the 50 days between July 5 and August 24. Growth in weight was 2.9% per day as compared with 1.6% in the August 24-September 27 period and only 0.5% in the September 27-October 24 period.

The estimated daily ration of 6.9% of body weight is based on data obtained between August 19 and 29, or at about the end and beginning of two periods of growth in weight of 2.9 and 1.6% per day. For the purpose of estimating growth in absolute terms an intermediate rate of 2.3% has been used. Mean body weight (total weight less weight of the gut contents) of August fish was 1.678 g. A daily intake of 6.9% of body weight is the equivalent of 116 mg of food. The growth rate of 2.3% would be the equivalent of an increment in weight of 39 mg per day. These calculations suggest an efficiency of conversion from food to flesh of about 33%.

DISCUSSION

These observations confirm the description of diel vertical distribution deduced from seine catches in 1966 (McDonald 1969), and agree closely with the detailed observations by Narver (1970). However, some differences in behaviour were apparent. For instance, Narver detected two separate layers of underyearlings by day. The first was between 21-30 m, and the second more dense layer was between 41-47 m. Only one layer was evident in the lake's main basin from observations reported here and this layer corresponded roughly in depth with Narver's second layer. There was a difference also in the observed times of ascent from the nighttime level to the surface at morning twilight. Increased seine catches (Fig. 4) and echo soundings (Fig. 5) showed that ascent began several hours before dawn. However, Narver reported that ascent began soon after the first light of dawn.

These differences may be more apparent than real and merely reflect the use of somewhat different gear, techniques and different times and places of observation. It is quite possible that a narrow and sparsely populated upper layer in the main lake was missed because of the considerable vertical gap (usually 9.6 m) between midwater tows, and that further echo sounding in the pre-dawn period may have disclosed the pre-dawn ascent of the underyearlings.

But even if these differences are real, the basic pattern of diel vertical activity during the period of summer thermal stratification has been clearly established. There occurred a regular and extensive diel vertical movement to and from the lake surface. This movement was more pronounced in August when the lake was most highly stratified. By day, the underyearling sockeye were concentrated in deep, cool water and by night in relatively warm water at or near the surface. Most feeding occurred in the surface layer at evening and morning twilight. Earlier (July) and later (October), when the lake was not highly stratified, less extensive vertical movement was observed.

There is insufficient information available to establish that this behaviour is typical of sockeye in the limnetic zone of other lakes which become thermally stratified in the summer--but it seems likely. Narver (1970) points out that observations on the Wood River lakes and Iliamna Lake in Alaska, and Great Central Lake in British Columbia, indicate a similar behaviour pattern. Differences have been observed in lakes which appear to present greatly different surroundings or perhaps environmental extremes. Narver (1970) reported that young sockeye are sometimes present at the surface by day in the extremely turbid parts of Naknek Lake, Alaska, and in Owikeno Lake, British Columbia. Presumably light penetration influences the amplitude of vertical movement. He notes that turbidity also appears to influence vertical distribution in Black Lake, Alaska, but here, vertical movement must be drastically reduced as a result of very shallow water (maximum depth of 6 m). A possible example of the influence of temperature is also noted by Narver. He suggests that high epilimnion temperatures in Lake Washington (they frequently exceed 20 C in midsummer) may restrict the ascent of underyearlings to depths no less than 15 m below the surface.

From July through October the sockeye fed mainly on zooplankton. Major food items changed with the season. During July mostly Heterocope were eaten. In August, Daphnia were dominant but by October Heterocope were again the major item. Insects were eaten in July and August but they never formed a large part of the diet as was observed by Narver for fish from the main basin in August (Narver 1970).

Feeding took place mainly at evening and morning twilight. A comparison of the quantities of food contained in the stomachs at these times revealed that a larger ration was eaten in the evening than in the morning. There was some evidence of daytime feeding. This lends support to Narver's observation of a sparse upper layer of underyearlings in the main basin between 21-30 m that may feed during the day. However, available evidence suggests that few fish occupy this layer relative to the deeper one and that the amount of food ingested by day is small.

Johnson (1961) when considering the association of underyearling sockeye and their food supply believed that the fish at Babine Lake remained close to the surface (above 5 m) during the day, together with the zooplankton. Consequently, both fish and food were subject to horizontal transport by wind-driven surface currents with the result that food and feeder were in continuing contact. Although most zooplankters were concentrated near the surface throughout 24 hours (Johnson 1965; Narver 1970), the young sockeye were in this layer only at night and feeding usually for only a short period at twilight. Obviously the association of food and feeder must be re-examined. The relative strengths and directions of the currents in the epilimnion and at the depths occupied by sockeye during the day have not been measured, but probably the deeper current would be the lesser and, in the classic case, would flow in the reverse direction. In any event, it would be extremely unlikely that, under the circumstances, any particular bodies of sockeye and zooplankton would remain in close contact for more than one night. Rather, one might expect the sockeye to be relatively static (they are exposed to surface currents only about 1/4 to 1/3 the time). In this case they would ascend each evening into an entirely "new" food supply. One possible advantage of this behaviour would be to minimize the search for food. Movement to and from the surface may require a smaller expenditure of energy than would lateral searches for food. Of course, each night's "new" supply may have been grazed upon by fishes "upstream," but this would also happen if lateral search was employed.

Rates of digestion and daily ration estimated from the August data are not considered to be precise but may be useful in that they indicate their magnitude in a natural situation. Studies elsewhere have involved mainly laboratory or hatchery environments with fish held at near constant temperature. Direct comparison with Babine results are therefore difficult. Ricker (1937) found that hatchery-reared underyearling sockeye, when held at 11.5 to 13.5 C, had mostly empty stomachs 8 hours after feeding upon live zooplankters. He speculated that in the wild, digestion would take about a day because wild sockeye ate more and spent most of their time in colder water. The work of Krogius and Krokhin (1948) on Lake Dalnee sockeye indicated a range of digestion time from about 5 hours at 15 C to 20 hours at 5 C. At Babine, the rate of digestion appeared to vary between the evening and morning meals, but in both cases digestion was essentially completed (stomach contents the order of 1% or less of body weight) before the next meal was taken. Digestion of the evening meal occurred in 5-7 hours at 11 to 17 C, with most of the fish in water of about 15 C most of the time. Digestion of the morning meal took place while the temperature of the surrounding water changed from 17 C at the surface to between 5 and 6 C at the fishes daytime level; a difference of 11-12 C. In view of the much lower temperature at which at least some part of digestion of the morning meal occurred, the rate of digestion of this meal would be expected to be less than that for the evening meal.

One of the first studies of daily ration of sockeye was made by Ricker and Foerster (1948) who estimated that Cultus Lake sockeye ingested about 7-8% of their body weight in food daily during the summer period of fast growth. This intake was based on the stomach contents of sockeye taken from predator stomachs, together with an arbitrary estimate that the contents at any one time represented about one-quarter of the total daily intake. Krokhin (1957) estimated the daily ration of Lake Dalnee sockeye by measuring their oxygen consumption and determining the equivalent caloric content of food organisms. His estimates of daily ration were 11.7% and 7.6% of body weight for July and August when the fish grew from 2.3 to 4.3 g (a rate of 2.1% per day). Brett et al. (1969) studied the influence of temperature and ration (amount) on the growth of laboratory-reared Lakelse Lake sockeye. When fed to excess (about 10% of dry body weight per day), 5- to 7-month-old fish of about 5 g grew fastest (2.6% per day) at 15 C as compared to 1, 5, 10, and 20 C. Older (7 to 12 months) and larger fish grew more slowly (1.6% per day) but again best at 15 C. In another test, groups of sockeye were subjected to different rations and temperatures. Fastest growth (about 1.4% per day) occurred at 15 C on the two largest rations offered (6% of body weight and an "excess" ration). The efficiency of food conversion also varied with temperature and ration. The maximum gross efficiency (ratio of intake to weight gain) was 25% at 11.5 C on a ration of 4% of dry body weight per day. For purposes of comparison, the Babine Lake ration has been converted to a dry weight basis by assuming a moisture content of 88% for the food and 80% for the fish. The 88% was the average moisture content of 15 zooplankton samples from Babine Lake. The moisture content of Babine Lake sockeye has not been determined, but Brett et al. (1969) found that, roughly, 5-8 g sockeye ranged from 71.3-86.9% moisture depending upon temperature and ration. Babine Lake fish being younger and smaller would probably fall into the upper half of this range, and for present purposes the moisture content has been assumed to be 80%. On this basis, the weight of Babine Lake fish in August averaged 336 mg and the daily intake of food was 14 mg or 4.2% of dry body weight. This ration is considerably less than the observed maximum ration for the two daily meals (23 mg or 7.7% of dry body weight). Apparently, on the average, the sockeye were feeding below their capacity. However, the ration was sufficient for good growth. The 14 mg of food was accompanied by a daily increment in weight of 8 mg--a gross efficiency of food conversion of 56%. This is a much higher percentage than the highest (25%) observed by Brett et al. (1969), although the daily rations were both about 4%. The Babine figure is probably maximal, because small amounts of food may have been eaten between meals. But a rate of efficiency approaching 56% may not be unreasonable since Babine fish were younger and smaller than Brett's fish and a greater conversion efficiency could be expected. Also, Babine fish by virtue of their diel vertical movement maintain low light levels which may serve to reduce their activities and minimize maintenance requirements. Their activities appeared to involve mainly vertical movement between day and night depths and two short feeding periods every 24 hours. The remainder of the fish may be relatively static. Certainly little feeding occurs and there is no suggestion of extensive vertical movements. Extensive horizontal movement, except from displacement by currents, appears unlikely but cannot be discounted.

Further advantage would result from the different temperatures at which the activities took place. McLaren (1963), after examining the relation of temperature and growth of zooplankton, proposed that under certain conditions of thermal stratification, animals would feed most efficiently in the warm surface waters but would digest their food and direct it to growth more efficiently in the colder, deeper water. The situation at Babine Lake in August meets the conditions set by McLaren although only part of the morning meal is digested in cool water. There is no doubt, however, that by remaining for much of the day (nearly half) at this low temperature, the fishes metabolic rate, and thus maintenance requirements, would be minimized leaving more energy for growth.

Other studies of temperature and growth were made by Donaldson and Foster (1941) and Rounsefell (1958). Donaldson and Foster found that Baker Lake sockeye (initial size about 2.3 g) lost weight and experienced considerable mortality when held at 73 F (22.8 C). At 70 F (21.1 C), the fish were able merely to maintain themselves. Optimum conditions for growth and survival were provided by temperatures averaging between 48.5 F and 52.4 F (9.2-11.3 C). Rounsefell used the Donaldson and Foster data to plot a dome-shaped curve relating summer surface temperature to growth efficiency (ratio of food intake to growth). The curve described a decrease in efficiency above or below an optimum range of 48-56 F (8.9-13.3 C). Rounsefell compared the productive capacity of Karluk Lake, Alaska, and Cultus Lake, British Columbia, and concluded that Cultus Lake was less productive due to above-optimum surface temperatures. Foerster (1968) compared a number of lakes, including Babine Lake, by using Rounsefell's curve. The relationship appears inapplicable to Babine Lake or other lakes where sockeye undergo extensive diel vertical movements. It is possible that warm surface water enhances, rather than limits, production by increasing the fishes food supply. Because of their diel vertical movements, the sockeye can take advantage of the food supply but avoid continuous contact with high temperatures which may inhibit growth or even prove to be lethal. Ricker (1937) reported as follows: "Experimental retention of artificially-fed fingerlings in the epilimnion for long periods has resulted in their deaths, presumably from high temperature, but this would not necessarily prevent the wild fingerlings making foraging expeditions into the warm water as the food available would warrant." Observations at Babine Lake have also suggested that constant exposure to high temperature may be detrimental to fingerlings. In 1967, sockeye were held for up to 2 months (June and July) in large tanks supplied with water from Fulton River which drains Fulton Lake, a tributary lake to Babine. In July, the temperature rose as high as 17 C--close to the maximum (18 C) observed at the surface of Babine Lake that summer. Accompanying this temperature was a very high rate of mortality of the sockeye. However, coho fry (O. kisutch) held in the same tanks thrived and grew rapidly, suggesting that sockeye mortality was related to temperature. On the other hand, Brett (personal communication) found little difficulty in holding sockeye at 20 C for considerable periods. Obviously further work is needed to determine if descent to cooler, deeper waters by day is in part at least a response to unfavourable epilimnial temperatures.

Certainly light appears to be a primary controlling factor of diel activity, but temperature seems to have a modifying influence in that the most extensive vertical movements coincided with the greatest degree of thermal stratification. Several possible advantages of diel vertical movement have already been touched on. There are others--avoidance of predation is an obvious one to consider--but present information is too scant to really add to existing theories about vertical migration.

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Table 1. Catch of underyearling sockeye in the midwater trawl, by depth and duration of tow, for the series of July 1, 1967.

Depth of tow (m)	Duration of tow (minutes)	Catch
9.2	15	0
18.3	15	3
23.8	15	31
29.3	15	6
36.6	15	21
47.6	15	0
58.6	15	3
36.6	0	3
36.6	0	1

Table 2. Number of sockeye underyearlings sampled which contained fresh food (Stage I) in the cardiac section of the stomach, August 18-29, 1967.

Time (night)	No. in sample	No. with contents in Stage I condition	Time (day)	No. in sample	No. with contents in Stage I condition
2037	10	10	0631	10	10
2129	10	10	0656	10	10
2329	10	3	0748	10	10
0129	10	3	0907	10	8
0329	10	0	1153	10	1
0541	10	0	1257	10	3
0528	10	6	1502	7	2
			1606	10	4
			1821	10	3

Appendix I. Quality and quantity of the stomach contents of underyearling sockeye as percent of body weight, Babine Lake, 1967 and 1968.

Period	Date	Time	Depth (m)	No. in sample	Body weight (g)[1] Mean	Body weight (g)[1] Min.	Body weight (g)[1] Max.	Stomach contents as percent of body weight[2] Mean	Stomach contents as percent of body weight[2] Min.	Stomach contents as percent of body weight[2] Max.	Relative stage of digestion[3] (score)
July 1-7, 1967	July 4	1218	36.6	9	0.389	0.186	0.703	0.54	0.16	1.46	29
		1417	18.3	7	0.198	0.150	0.237	0.47	0.05	1.05	30
		1513	27.5	10	0.306	0.177	0.818	0.28	0.00	0.71	27
		1545	36.6	7	0.341	0.154	0.548	0.16	0.00	0.48	30
	July 5	2142	16.0	10	0.315	0.217	0.415	3.00	1.28	4.40	15
		2246	12.8	10	0.613	0.429	1.012	3.32	1.85	4.53	15
		2341	16.0	10	0.319	0.243	0.522	3.65	2.04	7.05	15
	July 6	0027	16.0	10	0.349	0.250	0.524	2.35	1.03	4.76	15
		0123	16.0	10	0.626	0.381	1.341	2.09	1.35	2.55	20
		0235	16.0	10	0.517	0.343	0.649	1.96	1.22	3.06	21
		0327	16.0	10	0.378	0.275	0.577	1.32	0.62	2.81	17

Appendix I - cont'd.

Period	Date	Time	Depth (m)	No. in sample	Body weight (g)[1] Mean	Body weight (g)[1] Min.	Body weight (g)[1] Max.	Stomach contents as percent of body weight[2] Mean	Stomach contents as percent of body weight[2] Min.	Stomach contents as percent of body weight[2] Max.	Relative stage of digestion[3] (score)
July 1-7, 1967 (cont'd.)	July 4	1119	27.5	10	0.230	0.178	0.297	0.64	0.00	1.42	24
		1149	22.9	10	0.296	0.229	0.459	0.50	0.00	1.21	23
	Overall			123	0.396	0.150	1.341				
Aug. 18-29, 1967	Aug. 25	1257	36.6	10	1.217	0.684	2.679	1.54	0.41	3.31	21
	Aug. 19	1502	36.6	7	1.169	0.642	2.187	0.96	0.45	1.68	22
	Aug. 18	1606	36.6	10	1.435	0.839	2.265	0.99	0.30	2.16	21
	Aug. 29	1821	36.6	10	1.453	0.998	2.250	1.18	0.47	1.99	22
	Aug. 27	2037	16.0	10	1.620	1.125	2.274	5.60	1.50	8.49	15
		2129	16.0	10	1.692	1.280	2.218	4.52	3.09	6.43	15
		2329	16.0	10	1.714	1.109	2.054	2.00	1.39	2.85	19
	Aug. 28	0129	16.0	10	1.799	1.416	2.624	1.19	0.39	1.79	21
		0329	16.0	10	1.970	1.535	2.633	0.77	0.44	1.19	24

Appendix I - cont'd.

Period	Date	Time	Depth (m)	No. in sample	Body weight (g)[1]			Stomach contents as percent of body weight[2]			Relative stage of digestion[3] (score)
					Mean	Min.	Max.	Mean	Min.	Max.	
	Aug. 24	0451	4.6	10	1.736	1.141	2.456	0.90	0.42	1.52	23
	Aug. 28	0528	16.0	10	1.801	1.295	2.697	1.20	0.79	1.79	17
		0631	16.0	10	1.905	1.192	2.429	3.30	1.91	4.69	15
	Aug. 24	0656	20.1	10	1.542	1.174	2.083	2.98	2.05	4.20	15
		0748	45.8	10	1.888	1.435	2.305	2.69	1.73	4.65	15
	Aug. 29	0907	36.6	10	1.786	1.305	2.385	2.59	0.84	4.65	16
	Aug. 25	1058	41.2	8	1.383	0.662	2.035	1.52	0.88	2.22	21
	Aug. 19	1153	36.6	10	1.256	0.814	2.115	1.40	0.88	2.94	20
	Overall			165	1.658	0.642	2.697				
Sept. 24-Oct. 1, 1967	Sep. 26	1416	18.3	7	2.326	0.813	3.478	0.59	0.00	1.16	27
	Sep. 29	1932	16.0	10	2.884	1.395	4.163	2.81	1.18	3.61	15
	Sep. 24	2031	9.2	10	2.080	1.274	2.888	3.10	1.67	5.23	16

Appendix I - cont'd.

Period	Date	Time	Depth (m)	No. in sample	Body weight (g)[1] Mean	Body weight (g)[1] Min.	Body weight (g)[1] Max.	Stomach contents as percent of body weight[2] Mean	Stomach contents as percent of body weight[2] Min.	Stomach contents as percent of body weight[2] Max.	Relative stage of digestion[3] (score)
	Sep. 28	2041	16.0	10	2.997	1.591	4.830	2.60	1.25	4.30	15
		2147	16.0	10	2.659	1.347	3.810	1.89	1.30	2.54	15
		2251	16.0	10	2.747	1.328	4.105	2.45	1.23	3.94	16
		2352	16.0	10	3.040	1.076	4.839	1.85	1.04	3.19	18
	Sep. 29	0059	16.0	10	3.021	1.388	5.524	1.71	1.04	3.00	19
	Sep. 26	0943	18.3	10	3.802	2.915	4.442	1.13	0.41	2.49	16
	Overall			87	2.840	0.813	5.524				
Oct. 22-27, 1967	Oct. 27	1607	18.3	10	3.577	1.584	5.190	0.88	0.45	1.70	19
	Oct. 22	1849	16.0	10	2.903	1.958	4.297	2.11	0.45	3.92	18
		1930	16.0	10	3.275	1.919	5.066	1.68	0.99	2.80	19
		2024	16.0	10	3.406	1.802	4.876	1.12	0.74	1.75	19
		2107	16.0	10	3.606	1.555	4.545	1.40	0.91	2.47	16
		2156	16.0	10	2.892	1.470	4.759	1.69	0.17	5.40	18

Appendix I - cont'd.

Period	Date	Time	Depth (m)	No. in sample	Body weight (g)[1]			Stomach contents as percent of body weight[2]			Relative stage of digestion[3] (score)
					Mean	Min.	Max.	Mean	Min.	Max.	
	Oct. 24	0205	16.0	10	3.860	2.048	6.343	1.13	0.40	2.08	17
		0245	16.0	10	3.447	1.886	5.713	1.97	0.37	5.53	17
	Overall			80	3.371	1.470	6.343				
Aug. 17-18, 1968	Aug. 17	2028	16.0	10	1.592	0.663	2.627	1.58	0.89	2.94	17
		2127	16.0	10	1.734	0.726	3.626	3.47	2.53	5.31	15
		2228	16.0	10	2.506	0.987	4.286	2.86	1.57	5.50	17
		2328	16.0	10	1.851	0.898	2.552	2.68	1.37	4.11	17
	Aug. 18	0028	16.0	10	1.578	1.174	2.055	2.18	0.46	3.37	18
		0128	16.0	10	1.612	0.854	3.693	1.61	0.64	2.23	20
		0229	16.0	10	1.609	1.097	2.181	1.34	0.70	2.20	22
		0328	16.0	10	1.624	1.159	2.211	0.91	0.54	1.66	21
		0430	16.0	10	1.596	0.873	2.600	0.79	0.40	1.14	22
		0530	16.0	10	1.604	1.118	2.006	2.55	1.57	4.90	16

Appendix I - cont'd.

Period	Date	Time	Depth (m)	No. in sample	Body weight (g)[1]			Stomach contents as percent of body weight[2]			Relative stage of digestion[3] (score)
					Mean	Min.	Max.	Mean	Min.	Max.	
Aug. 17-18, 1968	Overall			100	1.731	0.663	4.286				
Aug. 18-19, 1968	Aug. 18	2059	16.0	10	1.676	1.138	2.591	2.98	1.09	4.72	16
		2158	16.0	10	1.746	1.400	2.197	4.52	2.59	6.52	15
		2258	16.0	10	1.556	0.884	2.587	2.93	2.14	4.50	15
		2358	16.0	10	1.686	1.336	2.020	2.57	1.50	3.71	18
		0058	16.0	10	2.151	1.111	2.541	1.57	0.95	2.18	21
		0158	16.0	10	1.924	1.416	2.609	1.37	0.77	1.71	20
		0259	16.0	10	1.488	1.011	2.194	1.00	0.67	1.37	20
		0358	16.0	10	1.735	1.186	3.130	1.14	0.43	1.92	20
		0459	16.0	10	1.825	1.239	2.371	1.17	0.69	1.61	20
		0559	16.0	10	1.874	1.091	2.354	2.57	1.44	4.08	15
	Overall			100	1.766	0.884	3.130				

[1] Total wet weight less weight of gut contents
[2] Contents of sections I and II
[3] Adjusted to sample of 10 fish

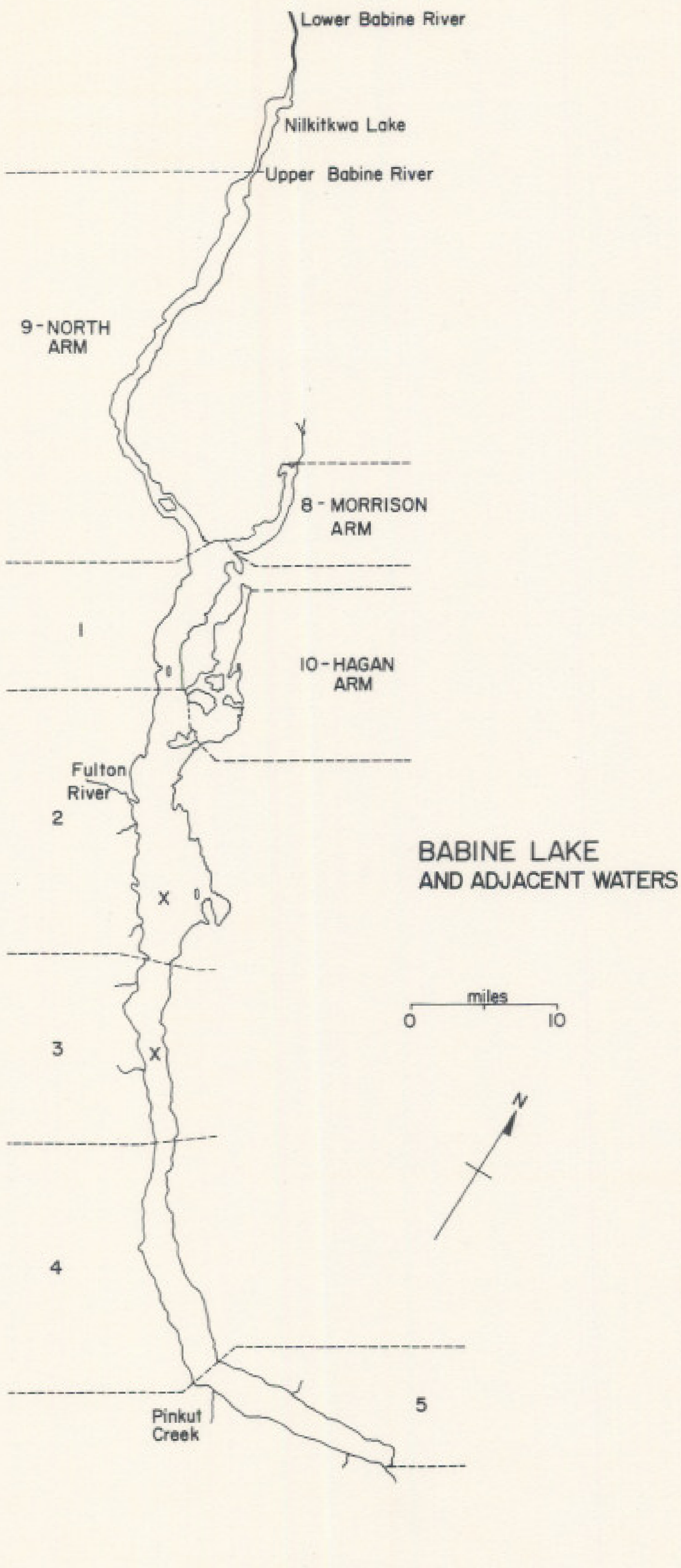

Fig. 1. Babine Lake showing lake areas and fishing sites (X's).

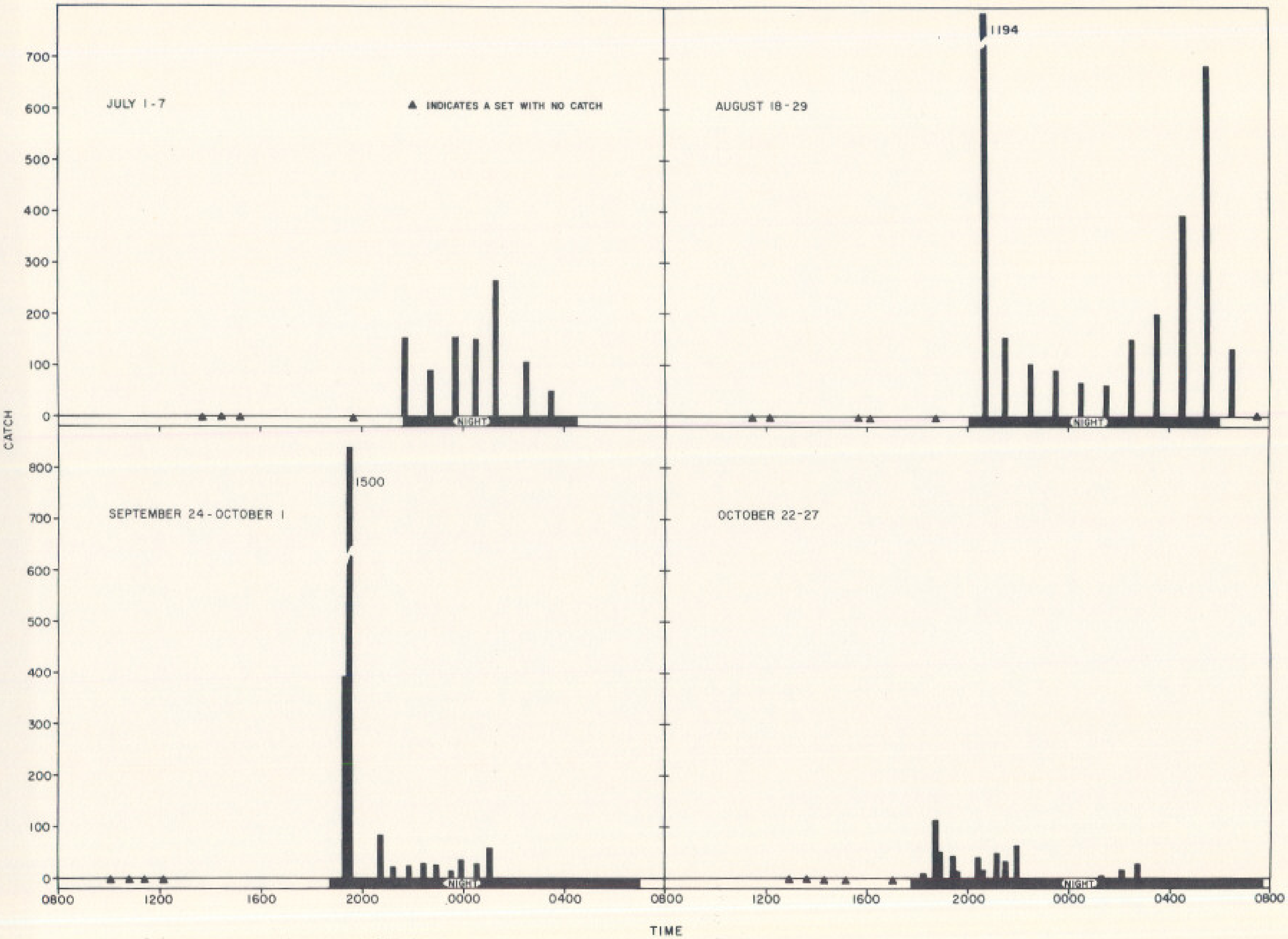

Fig. 2. Catches of underyearling sockeye in seine sets made at different times of day in four periods, July to October, 1967.

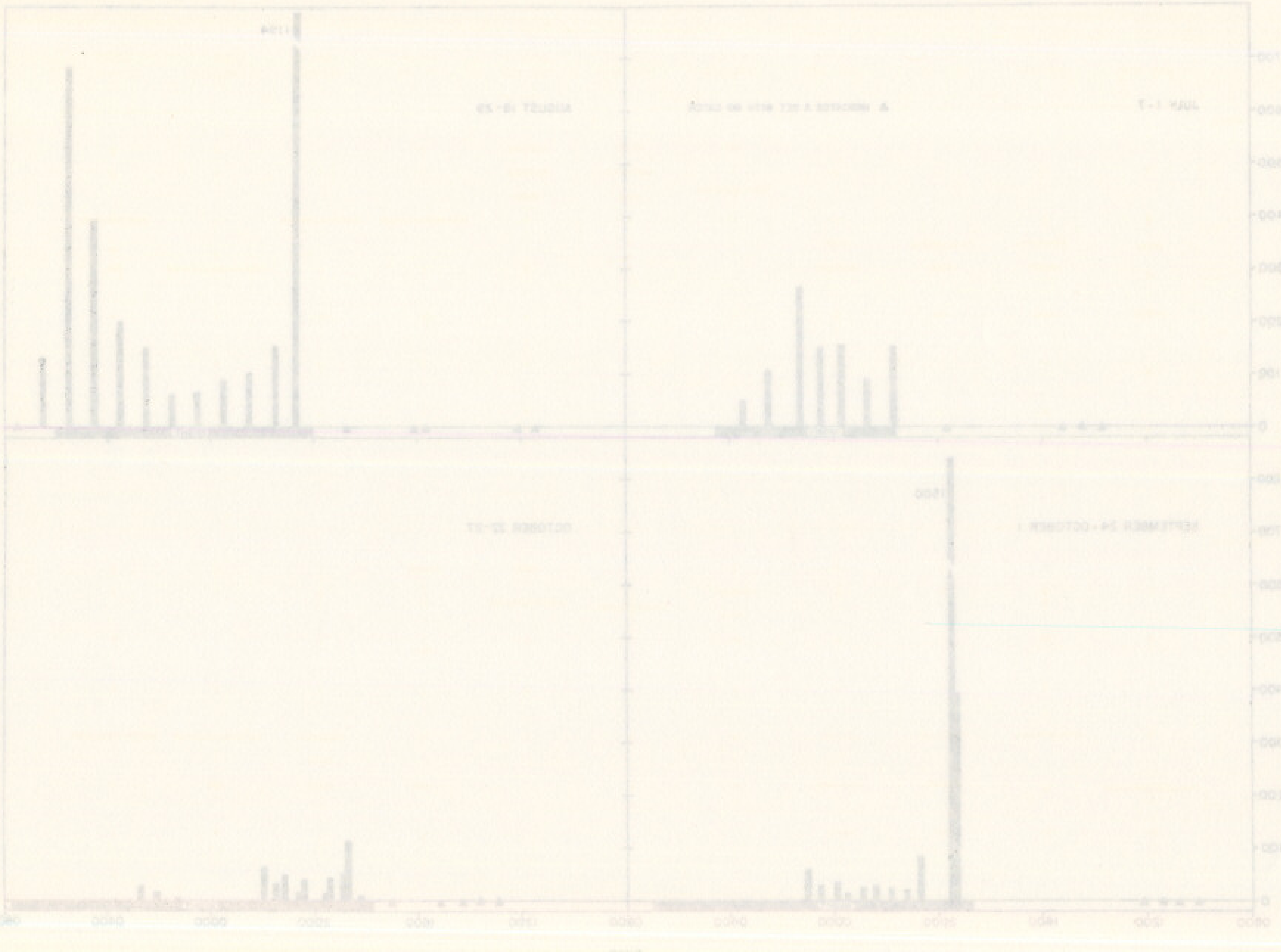

Fig. 2. Catches of underyearling sockeye in seine sets made at different times of day in four periods, July to October, 1957.

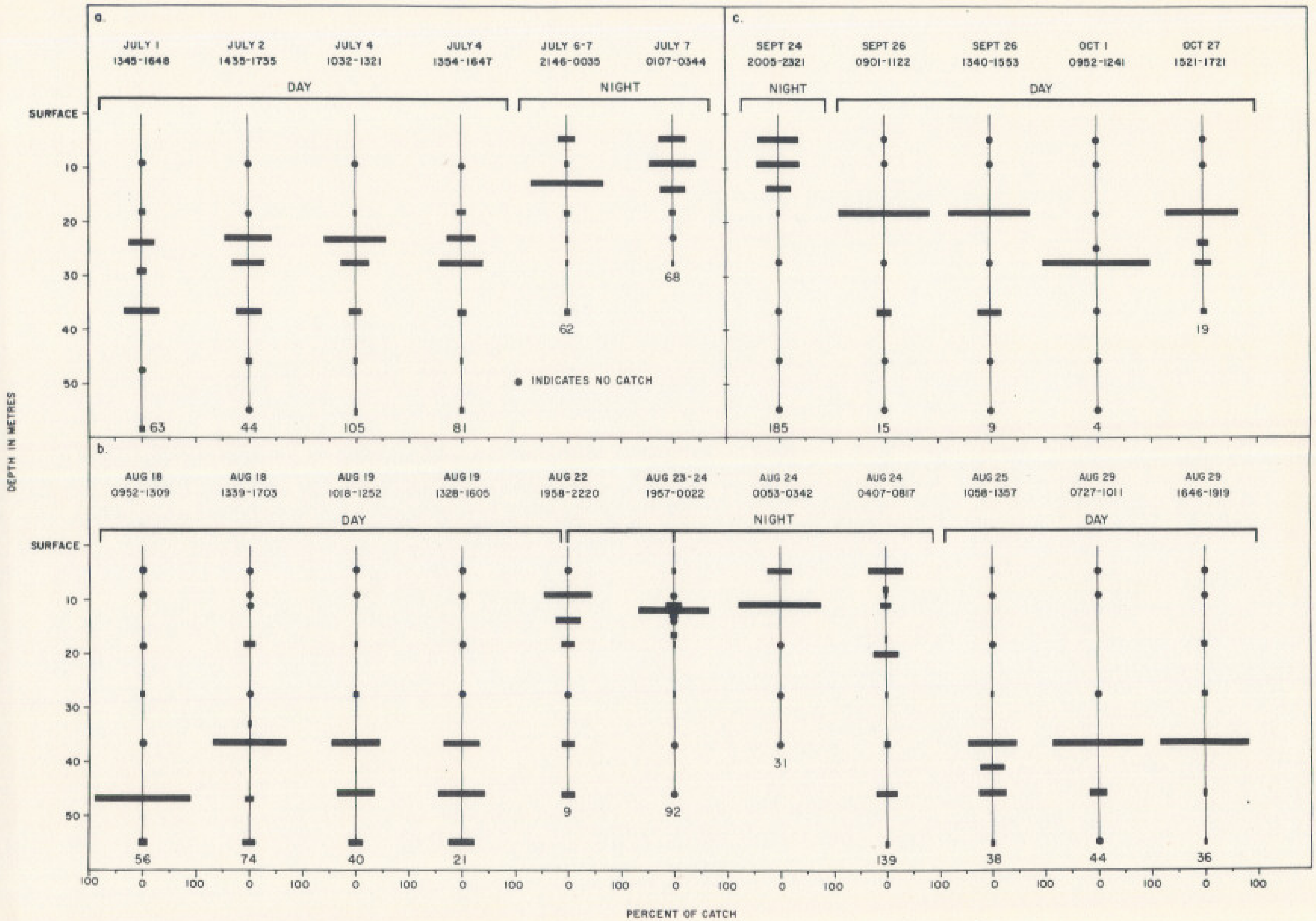

Fig. 3. Catches of underyearling sockeye in trawl series at different times of day, July to October, 1967. Number below the vertical line is total catch for the series. Horizontal bars represent proportions of the catch made at the various depths.

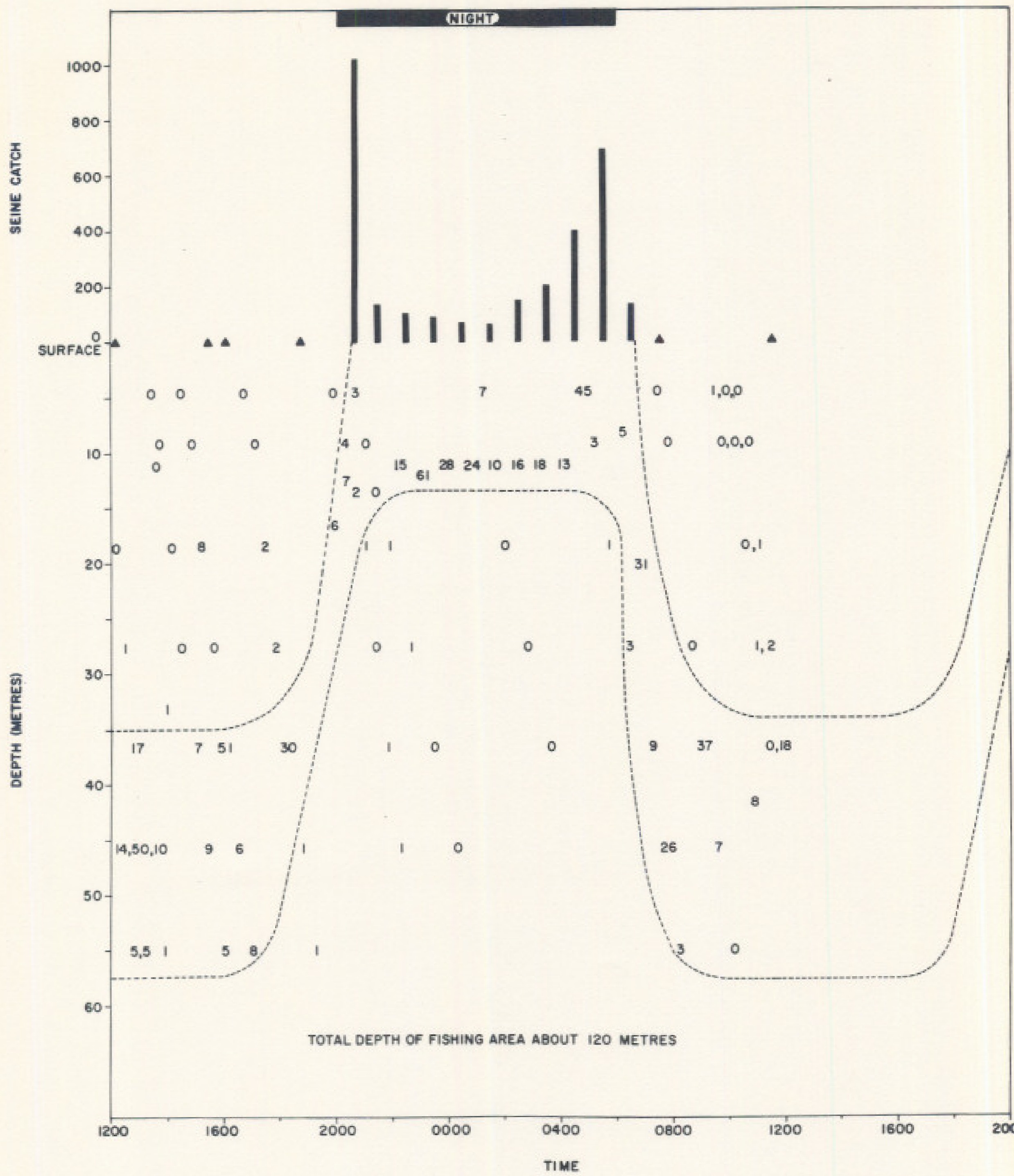

Fig. 4. Catches of underyearling sockeye by seine and trawl by time of day and depth, August 18-29, 1967. Surface is used as zero baseline for seine catches. Trawl catches are shown in the body of the figure by depth of tow and by time.

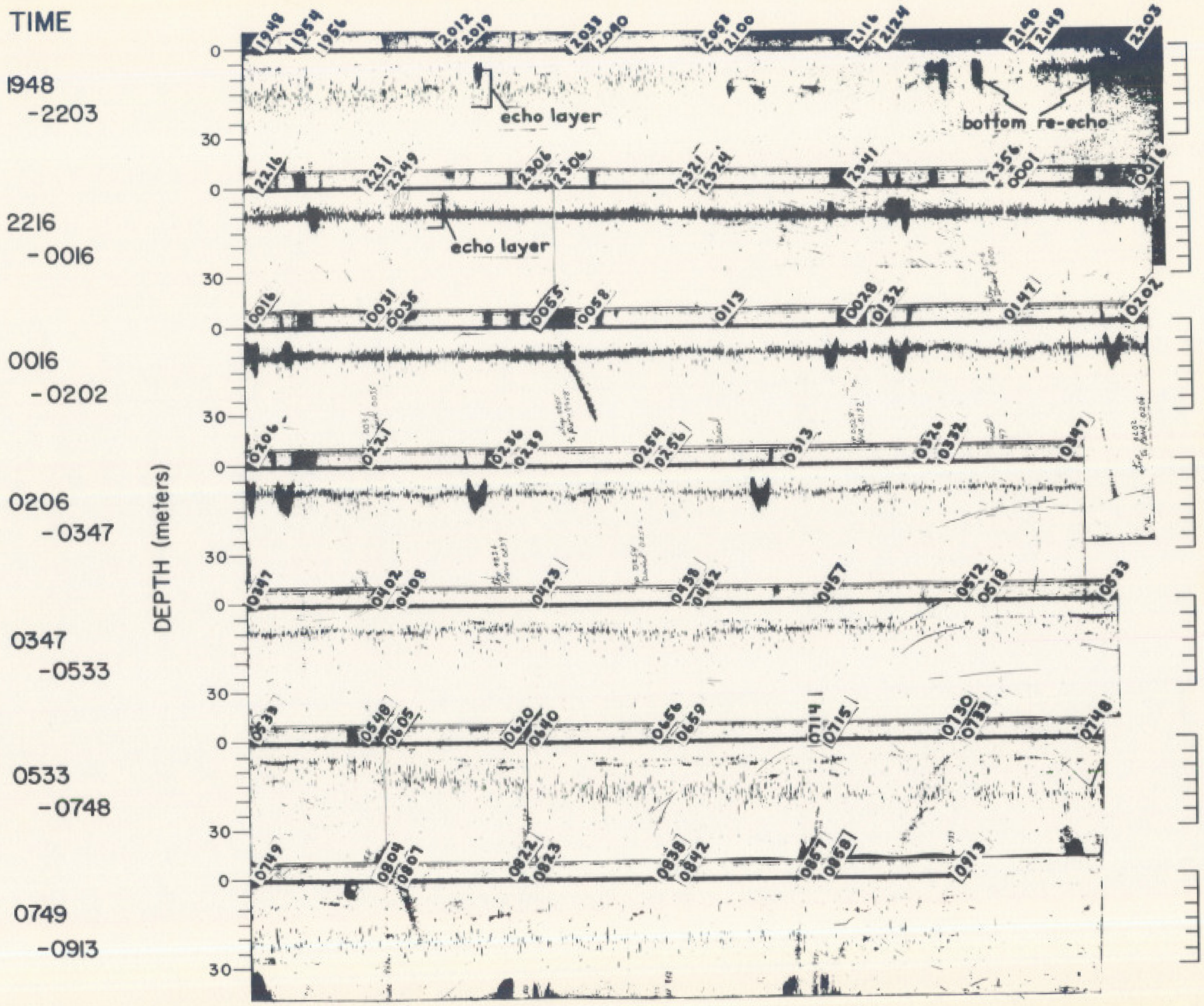

Fig. 5. Echo soundings at Babine Lake, August 22-23, 1967.

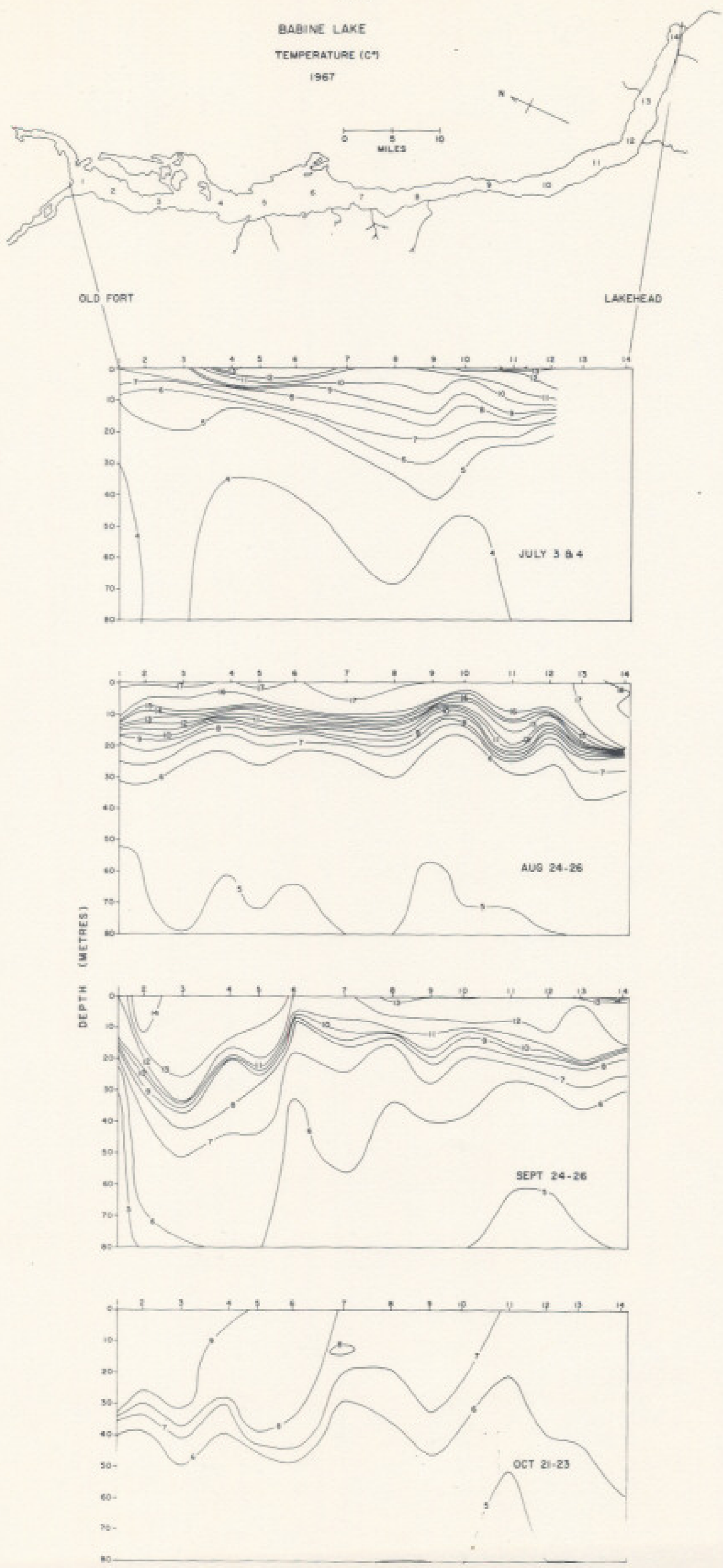

Fig. 6. Thermal structure of Babine Lake's main basin, 1967 as indicated by observations at stations 1-14 (shown on the map).

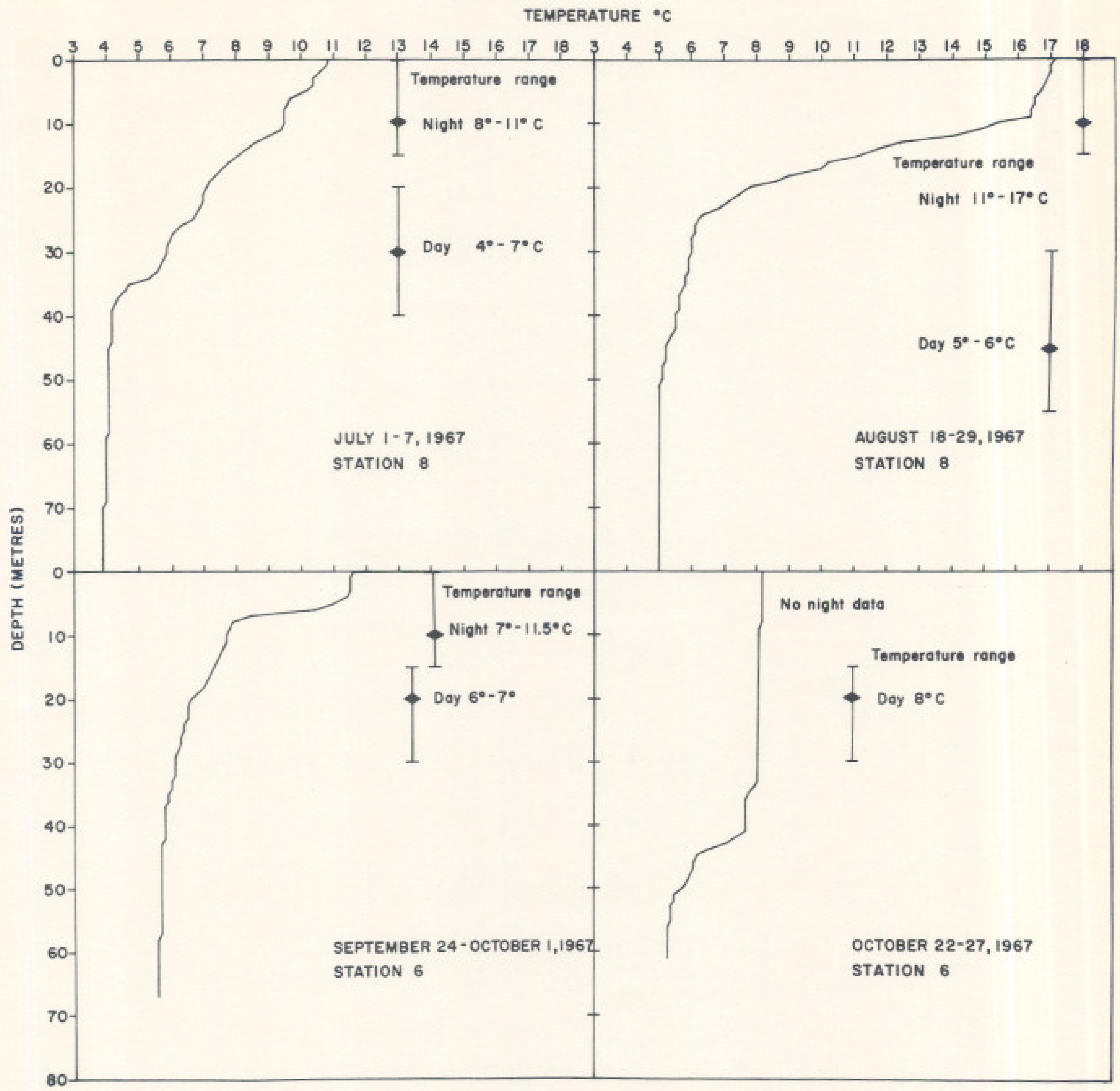

Fig. 7. Day and night distribution of underyearling sockeye and lake temperature, July to October, 1967. Vertical lines represent range of depth, and "diamonds" the level of greatest concentration. Depth ranges are from inspection of net catches (Fig. 2, 3, and 4) and echo soundings (Fig. 5). Temperature profiles are from stations 6 and 8 (Fig. 6) which are located at the netting and sounding sites.

Fig. 8. Stomach contents of underyearling sockeye captured at different times and depths in four periods, July to October, 1967.

8(a). July 1-7

8(b). August 18-29

8(c). September 24 to October 1

8(d). October 22-27

JULY 1-7, 1967

TIME OF CAPTURE	DEPTH OF CAPTURE (m.)	NO. IN SAMPLE	NO. STOMACHS EMPTY
1218	36.6	9	2
1417	18.3	7	2
1513	27.5	10	5
1545	36.6	7	6
2142	<16.5	10	0
2246	<16.5	10	0
2341	<16.5	10	0
0027	<16.5	10	0
0123	<16.5	10	0
0235	<16.5	10	0
0327	<16.5	10	0
1119	27.5	10	2
1149	22.9	10	4
OVERALL		123	21

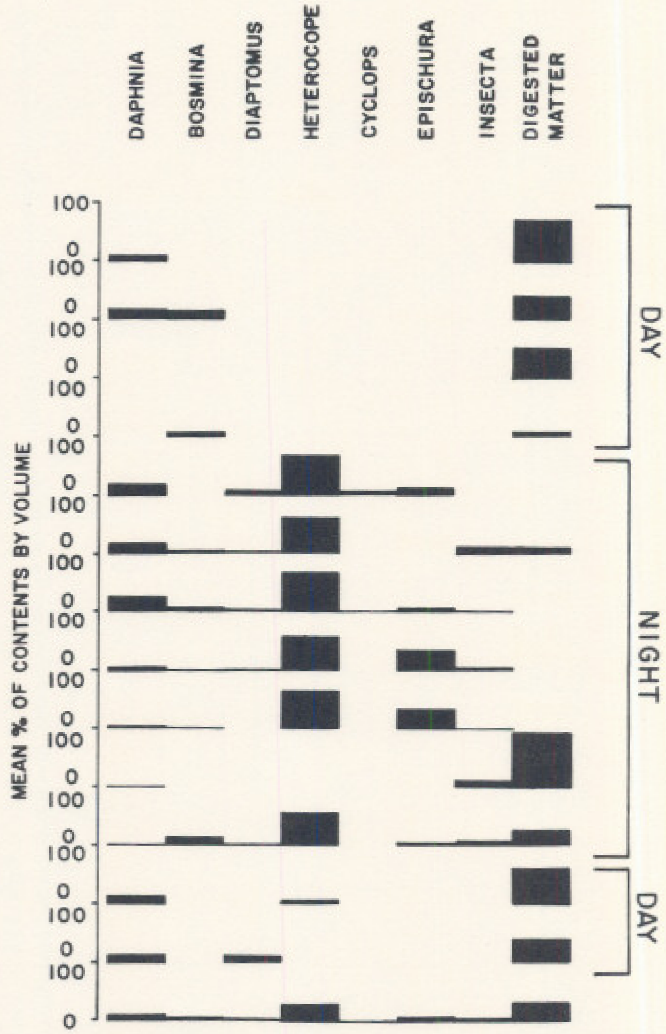

Fig. 8(a).

AUGUST 18-29, 1967

TIME OF CAPTURE	DEPTH OF CAPTURE (m.)	NO. IN SAMPLE	NO. STOMACHS EMPTY
1257	36.6	10	0
1502	36.6	7	0
1606	36.6	10	0
1821	36.6	10	0
2037	<16.5	10	0
2129	<16.5	10	0
2329	<16.5	10	0
0129	<16.5	10	0
0329	<16.5	10	0
0451	4.6	10	1
0528	<16.5	10	0
0631	<16.5	10	0
0656	20.1	10	0
0748	45.8	10	0
0907	36.6	10	0
1058	41.2	8	0
1153	36.6	10	0
OVERALL		165	1

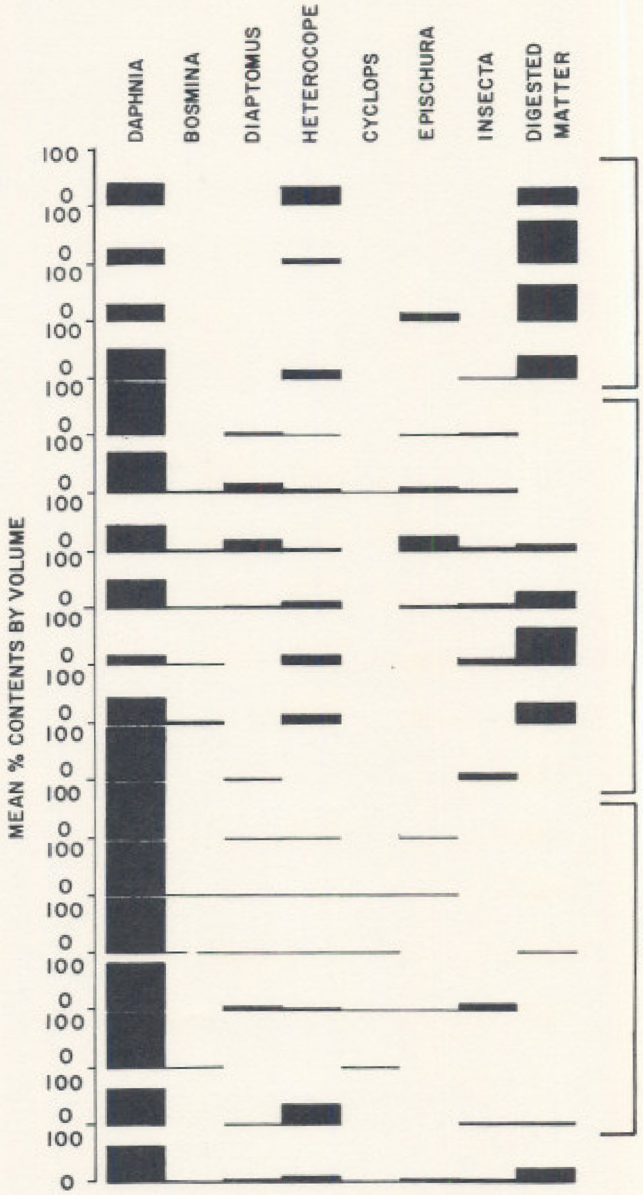

Fig. 8(b).

SEPTEMBER 24-OCTOBER 1

TIME OF CAPTURE	DEPTH OF CAPTURE (m.)	NO. IN SAMPLE	NO. STOMACHS EMPTY
1416	18.3	7	3
1932	<16.5	10	1
2031	9.2	10	0
2041	<16.5	10	0
2147	<16.5	10	0
2251	<16.5	10	0
2352	<16.5	10	0
0059	<16.5	10	0
0943	18.3	10	0
OVERALL		87	4

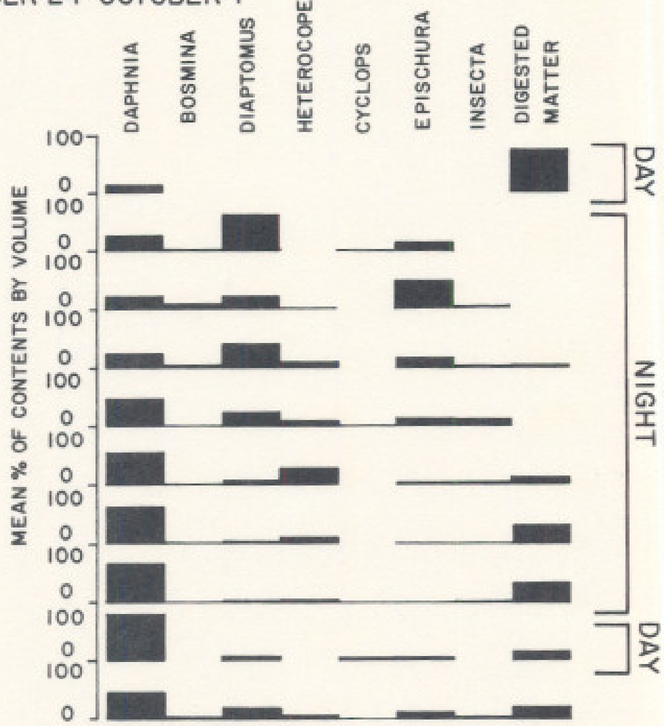

Fig. 8(c).

OCTOBER 22-27

TIME OF CAPTURE	DEPTH OF CAPTURE (m.)	NO. IN SAMPLE	NO. STOMACHS EMPTY
1607	18.3	10	0
1849	<16.5	10	0
1930	<16.5	10	0
2024	<16.5	10	0
2107	<16.5	10	0
2156	<16.5	10	1
0205	<16.5	10	0
0245	<16.5	10	0
OVERALL		80	1

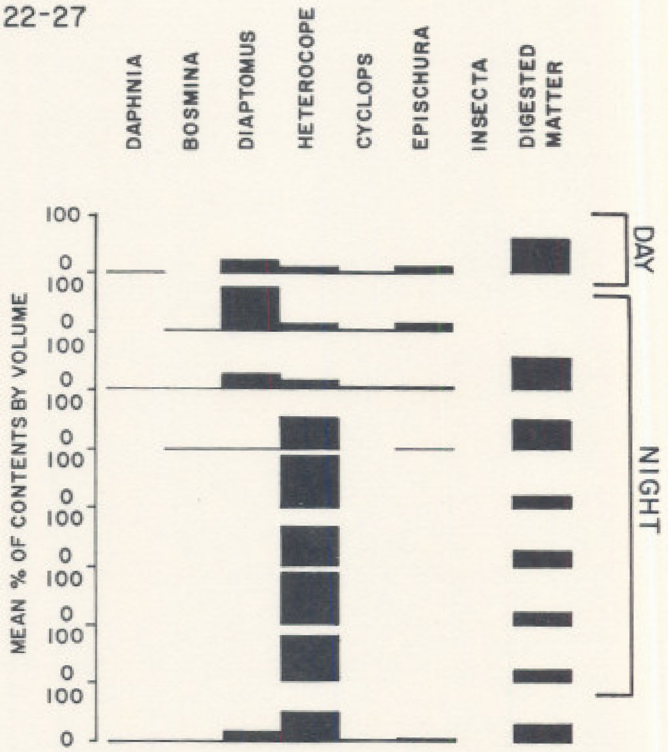

Fig. 8(d).

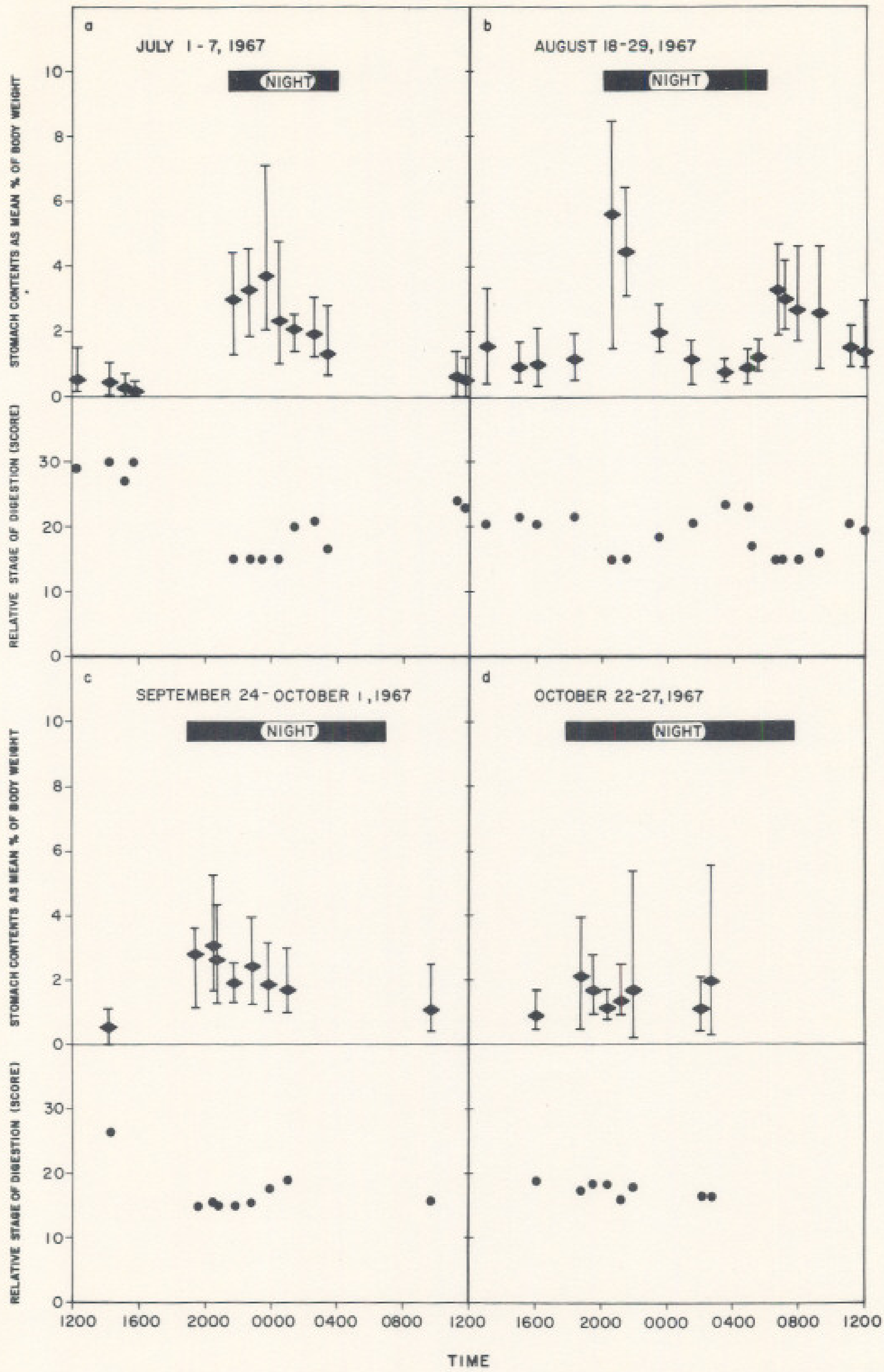

Fig. 9. Quantities and condition of food contained in the stomachs of underyearling sockeye captured at different times, July to October, 1967. Mean quantities are indicated by the "diamonds," vertical lines indicate minimum and maximum values for individuals.

Fig. 9. Quantities and condition of food contained in the stomachs of underyearling sockeye captured at different times, July to October, 1967. Mean quantities are indicated by the "diamonds," vertical lines indicate minimum and maximum values for individuals.

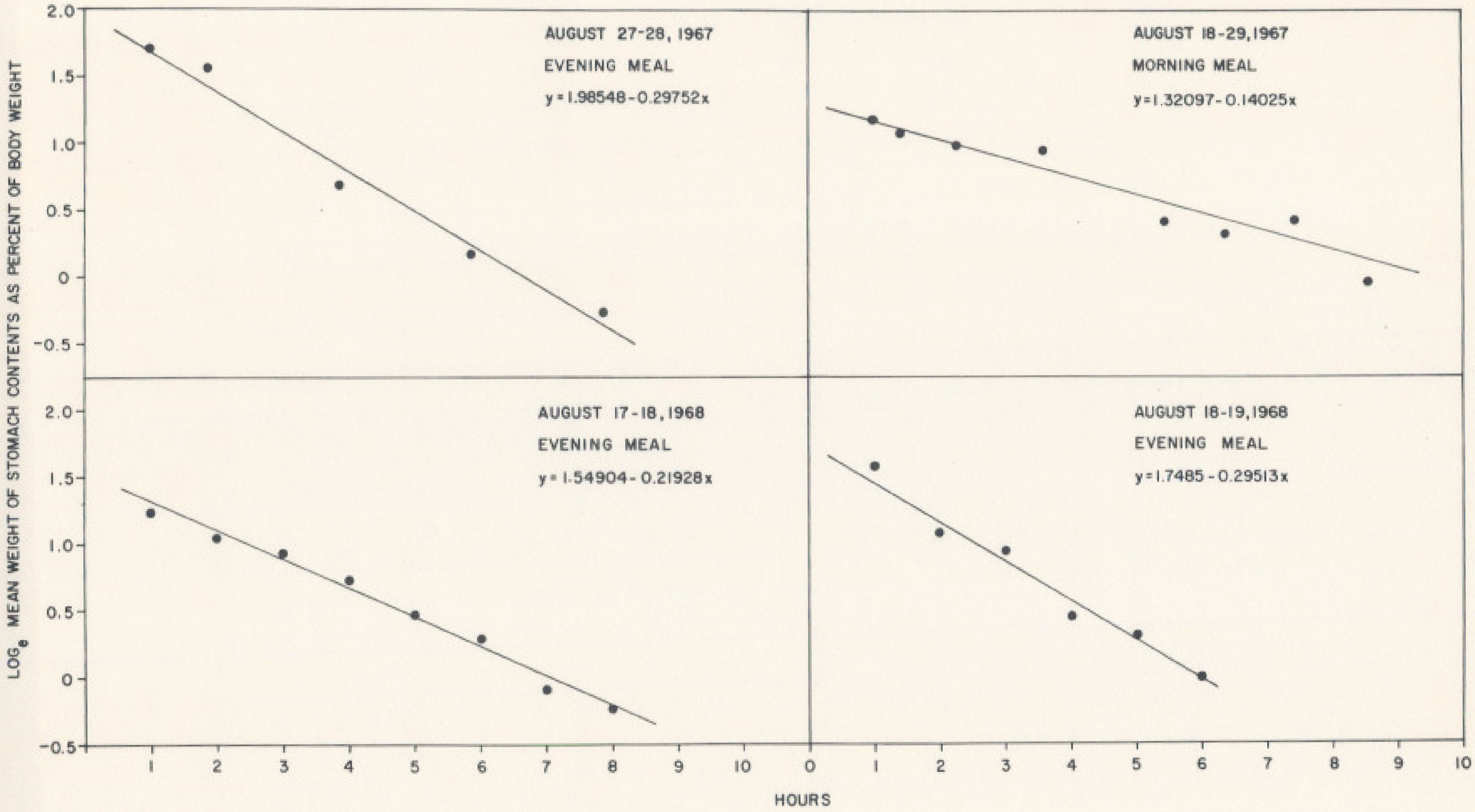

Fig. 10. Regressions of stomach contents on time after feeding (plus 1 hr), August, 1967 and 1968.