Behaviour and Ecology of Sockeye Salmon Fry in the Babine River[1]

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ABSTRACT

In the Upper and Lower Babine rivers the fry of sockeye salmon (*Oncorhynchus nerka*) emerge and move downstream, predominately at night, before reaching low-velocity areas along the stream margins. After a period of days or weeks these fry migrate upstream, close inshore, during the day. The diel pattern of upstream movement appears to be bimodal. The seasonal periodicities of both downstream and upstream movement are related to water temperatures.

Upstream migrants were larger than downstream migrants in the Upper Babine River but not in the Lower Babine River. Upper River upstream migrants were similar in length to Lower River upstream migrants during 1964 but not in 1965. In both years Upper River fry weighed proportionately more than Lower River fry, and in both rivers 1964 fry weighed proportionately less than 1965 fry. Some possible explanations of these observations are discussed.

Early in the season, fry tend to disperse alongshore after entering the lake. Later they leave these inshore areas and become entirely pelagic.

The principal foods of fry both in the river and in the lake were copepod and cladoceran plankters.

Both fish and birds were found to be preying on sockeye salmon fry. Fry appear to be more vulnerable to predation in the river than in the lake.

The upstream movement of fry in the Babine River does not appear to differ appreciably from upstream movements in other areas. A comparison of fry movements in the Babine River and the Fulton River, where fry move only downstream, suggests that the differences in behaviour are genetically rather than environmentally induced.

It is suggested that, because of high mortalities in the prepelagic period, upstream-migrant populations will only develop where the environment of both the river and the rearing lake are especially favourable.

INTRODUCTION

THE YOUNG OF anadromous sockeye salmon, *Oncorhynchus nerka*, typically spend 1 or more years in the fresh waters of lakes before migrating to the ocean. Returning adults spawn either in lakes or in streams. Most commonly, the latter are streams flowing into the nursery lake and, upon emergence, fry move immediately downstream. In some instances, however, the parent populations spawn in the lake outlet and the young move upstream. There is a considerable body of information available describing the behaviour of sockeye fry moving downstream but, as yet, no detailed description of an upstream migration.

In two of the numerous streams utilized by spawning sockeye salmon at Babine Lake, British Columbia, large upstream fry migrations are an annual

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occurrence. During the spring and early summer of both 1964 and 1965 a study was made of the behaviour and ecology of sockeye fry in these streams, the Upper and Lower Babine rivers. Some comparisons were made with sockeye fry in the Fulton River, a Babine Lake tributary in which fry move downstream.

THE AREA OF INVESTIGATION

The accompanying map (Fig. 1) illustrates features of the Babine Lake area pertinent to this study.

The spawning grounds of the Upper and Lower Babine rivers and the Fulton River are the most heavily utilized in the Babine Lake area, receiving 23.4%, 16.9%, and 15.6% respectively of an average annual escapement of 486,000 sockeye spawners.

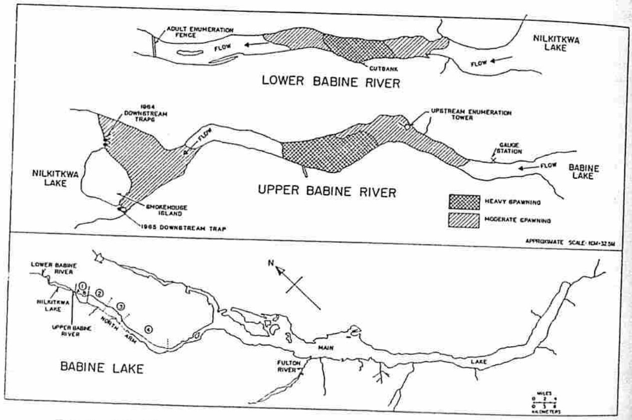

FIG. 1. The Upper and Lower Babine River spawning areas and Babine Lake.

The Upper Babine River is about 2296 m (7000 ft) long and averages 74 m (225 ft) in width. Emergent fry can enter nursery areas either downstream in Nilkitkwa Lake or upstream in the North Arm of Babine Lake. Quiet areas and grassy sloughs are common at the river outfall and along the banks, especially on the west side. Water velocities are low, generally less than 30 cm/sec (1 ft/sec). Several small streams enter the Upper Babine River but these have little effect on conditions in the river. Water temperatures in the main flow are generally lower than those at the lake surface and approximate the temperatures found between 2 and 5 m (Fig. 2). Water entering the river is probably a mixture of near-surface and deeper, colder waters. Water temperatures in the river are subject to large day-to-day fluctuations, presumably the result of wind-influenced changes in the thermal structure of the North Arm of Babine Lake.

The Lower Babine River is similar in width to the Upper Babine River but water velocities are much higher, approximately 122 cm/sec (4 ft/sec) in the main stream and up to 244 cm/sec (8 ft/sec) through the weir. There are few extensive areas of slow water along the banks to serve as refuges for holding fry and upstream migrants. Two substantial streams enter the Lower River just below Nilkitkwa Lake, one on the east and one on the west. These are frequently in flood during the period of fry migration and can markedly affect the turbidity of the main stream.

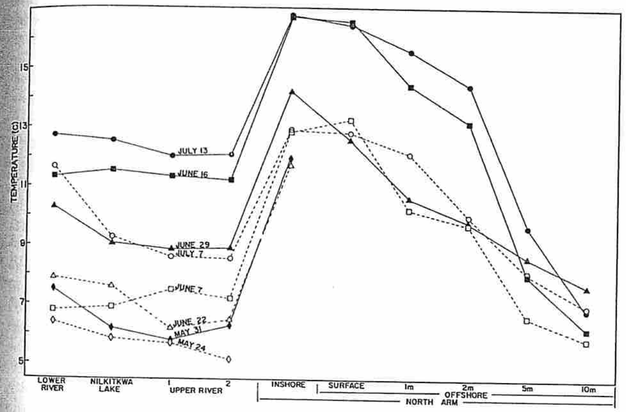

FIG. 2. Water temperatures in the North Arm, Upper and Lower Babine rivers, and Nilkitkwa Lake at various times during 1965.

Sockeye spawning in the Lower Babine River is almost entirely confined to the length of river between the enumeration weir, or fence, and the lower end of Nilkitkwa Lake, a distance of approximately 1640 m (5000 ft).

Salmon spawn over a considerable length of the Fulton River, 3281 m (10,000 ft), between Babine Lake and an impassable 13 m (40 ft) falls below Fulton Lake. The river averages 25 m (75 ft) in width and water velocities at the time of fry emergence are relatively high. Emerging fry move downstream into the main basin of Babine Lake. The river becomes turbid during extreme high water but is reasonably clear during a large part of the downstream fry run.

Fry moving upstream in the Upper Babine River eventually enter the North Arm of Babine Lake. For purposes of this study the North Arm was divided into four major sampling areas. Lake area 1, closest to the river, was further divided into subareas 1A and 1B. The lake shelves off rather rapidly throughout the area of investigation and most of it exceeds 10 m in depth. Areas of shallow littoral and emergent vegetation have a patchy distribution, generally in small bays and alongside the alluvial fans of the few, small tributary streams. Two of these streams support small sockeye spawning populations, a long-term average of less than 1400 fish between them. Movements of fry from the main body of Babine Lake into the North Arm are thought to be small so that almost all the underyearling sockeye in the North Arm are progeny of fish spawning in the Babine River.

MATERIALS AND METHODS

In the Upper Babine River, downstream migrants were sampled with traps located in relatively fast-moving water close to where the river enters Nilkitkwa Lake (Fig. 1). These traps, modifications of the type used by McDonald (1960), were constructed of 3.15 mesh/linear cm (8 mesh/linear inch) hardware cloth over plywood frames. The trap mouths measured 61 cm (2 ft) × 122 cm (4 ft).

During 1964, from May 15 to July 17, two traps fished the arm of the river to the east of Smokehouse Island. The traps were tended morning and evening at about 0800 and 2000 hr PST (Pacific Standard Time is used throughout this paper). Catches were recorded separately as *nocturnal downstream migrants*, those fish captured between 2000 and 0800 hr, and *daytime downstream migrants*, those captured between 0800 hr and 2000 hr. In fact, the period from 2000 to 0800 hr includes a number of daylight hours and a proportion of the fry classified as nocturnal migrants must have entered the traps during daylight.

Two or three times a week, hourly counts were made between 2000 and 0500 hr to determine the periodicity of nocturnal downstream movement. These counts were corrected to compensate for the period of time necessary for the removal of fry from the trap, generally about 10 min of each hour.

During 1965, a single trap was fished from May through July in the west arm of the river. As in 1964, daily counts were made at 0800 and 2000 hr. No hourly counts were made.

In both years, counts of fry moving upstream along the east bank of the Upper Babine River were obtained by estimating the number of fish passing over a 1.8 m (6 ft) square, white grid placed on the stream bottom. Fish were guided across the grid by leads constructed of hardware cloth and were viewed by an observer on a tower placed directly over the grid. Small numbers of fry were counted directly but, during periods of high activity estimates were made by groupings of 10, 100, or occasionally 1000.

On 7 days in 1964, records were kept of the speed at which fry moved upstream across the counting grid. These speeds were corrected by the addition of the speed of the water flow across the grid to give the true speed of the fish through the water. For each date the speeds of several hundred individual schools were averaged. The swimming speed of fry may have been affected somewhat by the presence of the grid but there was no apparent change in their behaviour or speed of movement.

During 1964, counts of upstream migrants were continuous throughout an 18- to 20-hr period, generally from 0200 to 2200 hr. In 1965 the daily counts were for 4 hr only, 1600 to 2000 hr. The 4-hr index was adopted to obtain a better measure of seasonal variation in upstream movements than was provided by the infrequent 20-hr counts made in 1964. In 1964, an average 27.5% of the daily run passed upstream during these 4 hr, ranging from a low of 3.4% on July 14 to a high of 65.2% on July 17. Figure 3 illustrates the relationship of counts made between 1600 and 2000 hr and the total daily count for 22 days in 1964. This relationship, though variable, is close enough for the purposes for which it was intended, the identification of extremes. In no case was a very high total count associated with a low 4-hr count nor a very low total count with a high 4-hr count.

In both years, samples of fry were taken in the Upper and Lower Babine rivers and in the North Arm of Babine Lake for length-frequency studies. Downstream samples were obtained from the traps in the Upper Babine River; in the Lower River (1964 only), with dip nets lowered into the water at various positions along the adult counting fence. Upstream migrants were captured in the area called the "cutbank" in the Lower Babine River and in the area close to the upstream enumeration tower in the Upper River. These were occasionally dipnetted but in most instances a small-mesh, nylon marquisette seine was used. The same seine was used to capture fry along shore in the North Arm of Babine Lake. In 1965, a few samples of fry were also taken offshore in a 2.74 m (9 ft) square townet similar to that used by the Fisheries Research Institute of the University of Washington in Alaskan lakes. All townetting was done at the water surface at dusk and shortly thereafter.

All lengths and weights were obtained from live fish anaesthetized in a 0.02% solution of 2-phenoxyethanol. Individual *standard lengths* were recorded as pin pricks on millimeter graph paper. Fry were blotted with paper towelling to remove excess moisture and then weighed in air on a Mettler K 7 balance. The weight was recorded adjacent to the appropriate pin prick. These techniques, a modification of those described by Parker (1963), were identical in both years.

Many of the fry emerging from the gravel in the Upper Babine River still retained a portion of the larval yolk supply. Anticipating that there might be differences in the behaviour and ecology of fry with and without

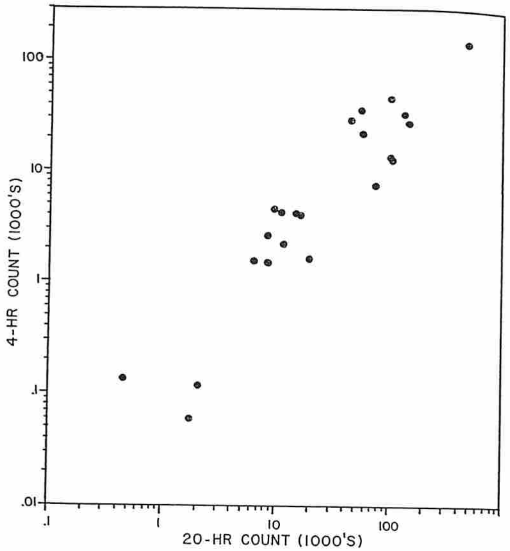

FIG. 3. The relationship of counts made between 1600 and 2000 hr to the total daily upstream count (20 hr). Data for the Upper Babine River, 1964.

yolk, records were kept of the presence or absence of an external yolk sac in fry from samples taken for various purposes. In most instances, fry with yolk sacs were further classified as having either large yolk sacs (large enough to be seen laterally) or small yolk sacs (a slit visible from the ventral surface only). Some fry without externally visible yolk sacs were examined after preservation to determine whether they still contained vestiges of yolk internally.

During 1965, samples of fry were taken for food studies at approximately weekly intervals at a number of localities in the Upper and Lower Babine rivers and in the North Arm of Babine Lake. On two occasions, fry were captured at 2-hr intervals, over a total period of 24 hr, along the shores of Smokehouse Island where the Upper River enters Nilkitkwa Lake. The numbers of food organisms were counted directly or, where very large numbers of organisms were involved, estimated with aid of a counting grid. In addition to counts of individual organisms, visual estimates were made of the percentage of the total food volume falling into each of the following groups: unidentified insects, unidentified plankters, all insects, and all plankters.

Plankton samples were taken on the same or the following day for comparison with the stomach contents of fry. These were taken using Clarke–Bumpus samplers with No. 10 standard nets. Water temperatures were taken at the same time using an electronic thermistor. The methods of counting plankters were the same as those used in stomach analysis.

Samples of predatory fishes were taken either in gill nets or in a large beach seine. The monofilament nylon gillnets were assembled in standard gangs with six 7.6 m (25 ft) × 2.6 m (8 ft) panels of the following sizes: 2.5, 3.8, 5.1, 6.3, 7.6, and 10.2 cm (1, $1\frac{1}{2}$, 2, $2\frac{1}{2}$, 3, and 4 inch) stretched mesh. The seine, 39.3 m (120 ft) long and 2.6 m (8 ft) deep, varied from 5.1 cm (2 inch) stretched mesh on the wings to 2.5 cm (1 inch) in the bag. Predators were weighed, measured, and sexed, and scale and stomach samples were taken. The stomachs, preserved in 10% formalin, were examined later under a binocular microscope.

In both years, water levels were recorded daily at a gauging station established by the Department of Energy, Mines and Resources on the Upper Babine River. A thermograph nearby kept a continuous record of stream temperatures. On occasion, changes in light intensity were followed with a Photovolt 200 photometer recording directly in foot candles.

Howard Smith of the Fisheries Research Board, working on the Lower Babine River, provided valuable data on environmental conditions and the movements of fry in the Lower Babine River. The Resource Development Branch of the Department of Fisheries of Canada provided similar information for the Fulton River.

GENERAL DESCRIPTION OF BEHAVIOUR

During both years of the study, frequent observations were made of the distribution and behaviour of sockeye fry in the Babine Rivers. These observations, largely qualitative, are presented here to acquaint the reader with the general pattern of fry movement before the more detailed aspects of the study are discussed.

The activities of fry in the Babine River can be conveniently divided into three phases: downstream movement, holding, and upstream movement.

BEHAVIOUR OF FRY MOVING DOWNSTREAM

Large numbers of fry moved downstream in both the Upper and Lower Babine rivers. This movement was predominantly nocturnal but some daytime movement did occur. The behaviour of fry moving downstream after dark was not observed but, on several occasions, downstream migrants were seen during the day from a boat anchored in midstream in the Upper Babine

River. Of 76 fry seen on June 29 and July 2, 1965, all but 10 were single individuals. There was one group of 4 scattered about 30 cm apart and 3 pairs with 30–60 cm separating individuals. Seventy-two fry were at the surface; 4 others at depths of 15–30 cm. Of the 76, 33 were swimming actively downstream, 8 were drifting down tail first, 33 were heading obliquely across the current, and 2 were swimming upstream. All these fry were small and some had visible yolk sacs. Such behaviour was observed on a number of other occasions. The behaviour of daytime downstream migrants was similar to that of the nocturnal migrants described by Hartman et al. (1962) which "migrated as individuals, facing downstream, and usually exhibited swimming movements." A significant departure was the frequent occurrence of fry which, though moving downstream, were swimming at a considerable angle to the main current. This tendency may be an important mechanism enabling fry to reach the edges of the river before being swept very far downstream.

J. Roos (personal communication) of the International Pacific Salmon Fisheries Commission, New Westminster, B.C., reports an interesting experiment which emphasizes the ability of sockeye fry to reach the stream margins. He released a number of dyed upstream migrants at night in the middle of the Chilko River. The following day some of these fry were recaptured moving upstream, alongshore, at a point opposite the point of release suggesting that the fry had not moved very far downstream before reaching the river's edge. These fry were not newly emerged but the ability of recent emergents to reach the river's edge may not be at all inferior. In the broad, fast-moving Lower Babine River, millions of fry reach the banks before they have passed downstream as much as a mile.

Another possibility was entertained, that fry reach the edges of the stream by swimming along the stream bottom, but not a single fry was located offshore along the bottom in the course of an underwater (scuba) search in the Upper Babine River. At the moment, the behaviour of fry at first emergence and the manner in which they reach the stream edge is still very much a matter of conjecture.

BEHAVIOUR OF HOLDING FRY

After reaching the river margin, fry may pass several weeks before completing their journey upstream. These fry accumulate in backeddies, sloughs, and other areas of quiet water along the river's edge. In the Upper River thousands more gather in areas bordered by brush and emergent vegetation around Smokehouse Island and the river outfall. These "holding" fry were observed on many occasions. There is also some indication that many Upper River upstream migrants have lived for a time in Nilkitkwa Lake before entering the river and moving upstream.

Early in the season, schools of holding fry were small and scattered (a maximum of about 200 fry) and solitary individuals were common. Later, groups of several hundred thousand fry often accumulated in favoured holding areas.

During the day, undisturbed fry swam near the water surface. Schools were loosely organized and there was a great deal of individual activity, generally associated with feeding. The orientation of schools was basically rheotactic but where currents were slight there was much wandering about.

The behaviour of sockeye fry in response to disturbances, either by observers or predators, appeared to change after schooling. Some of the single individuals observed holding along the stream edges very early in the season buried themselves in the bottom material when disturbed. Fry in groups were never seen to do this. When mildly disturbed they moved as a group, away from the disturbance, often sounding, and in among brush and vegetation alongshore. When violently agitated they scattered wildly; however, schools soon formed again.

At night, schools of fry in fast water generally remained close to the bottom but were frequently observed near the surface in quieter areas. Observations of single schools indicated that the majority of these remained in the same area throughout the night even at temperatures as low as 5 C. This contrasts with the behaviour of schooling sockeye fry described by Hartman et al. (1962) in Hidden Creek at Brooks Lake, Alaska. In this stream, holding areas were completely evacuated during the nightly outmigration and filled again at dawn.

The holding period, during which fry are concentrated in a narrow strip along the edges of the stream, is undoubtedly one of high mortality. Hartman et al. (1962) have discussed the survival value of protected, inshore holding areas as refuges from piscivorous predation. Observations on the Upper Babine River suggest that there are additional advantages to fry inhabiting these areas for extended periods of time. Currents immediately alongshore are slow, often negligible, and, as Fig. 4 shows, water temperatures are comparatively high. These conditions were most exaggerated in some of the small sloughs along the west bank of the Upper River. On June 3, 1965, a temperature of 14.8 C was recorded in a flooded grassy area where there were many fry. The temperature of the main stream 6 m away was 5.3 C. Together, higher water temperatures and slower currents probably encourage rapid growth.

BEHAVIOUR OF FRY MOVING UPSTREAM

Sockeye fry moving upstream did so almost entirely in daylight. The movement was confined to the stream edges. The first, early morning migrants were individuals or, more rarely, small groups of up to 10 fish swimming in a characteristic manner: a series of short, quick spurts followed by periods of holding or of downstream movement during which fry drifted tail-first. The fish appeared to have difficulty in maintaining position and the movements of fry in groups were not well synchronized. As light intensities increased, so did the size of groups and hesitant, individual, swimming movements were replaced by highly organized schooling behaviour.

Where they were unhindered, migrants moved in tightly knit schools at the surface close to shore, often in water only a few centimeters deep. The

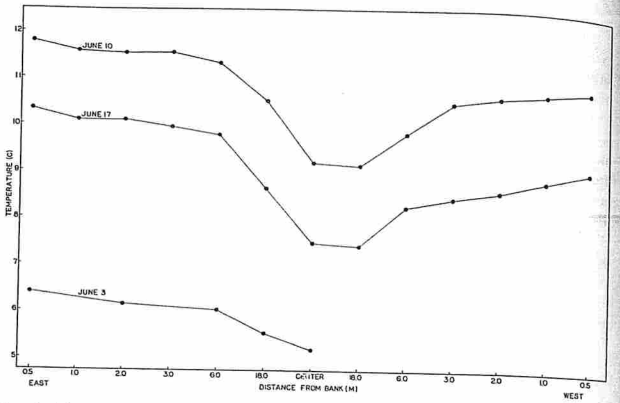

FIG. 4. Mean water temperature across the Upper Babine River on three occasions in 1965.

average school numbered from 100 to 200 individuals but many were larger. On June 26, 1964, an almost continuous band of fry moved across the counting grid for a period of 26 minutes.

The average speed of schools on the 7 days when records were kept ranged from 18.3 to 32.1 cm/sec with a mean of 24.9 cm/sec. The average speeds for 6 of the 7 days exceed the mean maximum sustainable cruising speed of from 15.3 to 20.1 cm/sec given by Brett et al. (1958) for fish of similar size (30 mm) in water of similar temperatures (6–10 C) but are comparable to the average 24.4 cm/sec recorded by Andrew and Geen (1960) for Chilko River upstream migrants. Possibly Brett's laboratory-reared fry had less stamina than natural fry. Another possibility is that upstream migrants are able to maintain a speed in excess of their maximum sustainable swimming speed by alternating periods of rapid upstream movement with periods of holding and resting.

Fry usually swam around rather than under floating objects. After a period of hesitation during which the school moved back and forth searching for alternate routes, the fry either rounded the obstruction at good speed and continued upstream (after moving back into shallow water) or, occasionally, retreated downstream.

In some instances (especially in the Lower River) fry encountered short stretches of extremely fast water. Here, fry spread out over the bottom close behind, and frequently in contact with, protruding stones and vegetation, apparently taking advantage of small eddies and areas of turbulence. Individuals and small groups moved upstream from holding point to holding point in a series of short, quick spurts. In one particularly fast section of the Lower River, fry were observed moving along the bottom as much as 5 m offshore, at a depth of 1.5-2.0 m.

Current direction was an important factor in the orientation of migrants while they were still in the river. In some situations where current patterns were confused in the immediate inshore area (as they were in large backeddies) actively migrating fry moved upstream along the current interface even when this took them 10 m or more offshore over deep water. Similarly, fry moving past flooded grassy verges or the entrances to sloughs usually remained along the edges of the main current rather than taking advantage of the adjacent areas of dead water. They avoided the areas frequented by holding fry. Current responses of this sort would eventually bring fry up into the lake. Occasionally, however, fry were observed moving alongshore, into and through large backeddies, with no apparent hesitation even though the direction of the current changed through 180°. This, and the fact that, especially early in the season, many schools maintained their southward orientation for many miles up the lake, suggest that there may be other important orientational cues.

As light intensities fell toward evening, the behavioural changes observed during the morning were reversed. Fish moved in smaller and smaller units and upstream movement became erratic. Loosely knit groups of fry accumulated in suitable holding areas alongshore and mass movement of fry ceased. That fry were then unresponsive to visual stimuli is indicated by the fact that they did not react to a hand waved repeatedly only 30–40 cm above them. In the Upper Babine River few fish were seen to lose position in the dark. Most of the groups holding either on the grid or upstream from it appeared to maintain their integrity throughout the night although on occasion fry were observed fleeing downstream under attack by predators.

During May and June 1965, many of the schools of fry entering the North Arm of Babine Lake continued to move southward close inshore. Fry were seen inshore, moving southward, as far uplake as Halifax Landing, a straight-line distance of approximately 32.2 km. During July, however, it appeared that only a small proportion of the fry entering the lake behaved in this way. The numbers of fry seen inshore declined to almost zero within 400 m of the river and a number of large schools were observed swimming directly out into the lake a few hundred meters beyond the river.

SEASONAL PERIODICITY OF FRY MOVEMENTS

Both the upstream and downstream movements of fry in the Upper Babine River were characterized by a succession of peaks or surges (Fig. 5). In 1964, downstream movement was underway when trapping began in mid-May. In 1965, the first captures were made on the second night of trapping. In both years there was a gradual increase in nocturnal downstream catches up to mid-June and then two prominent peaks. Catches declined thereafter

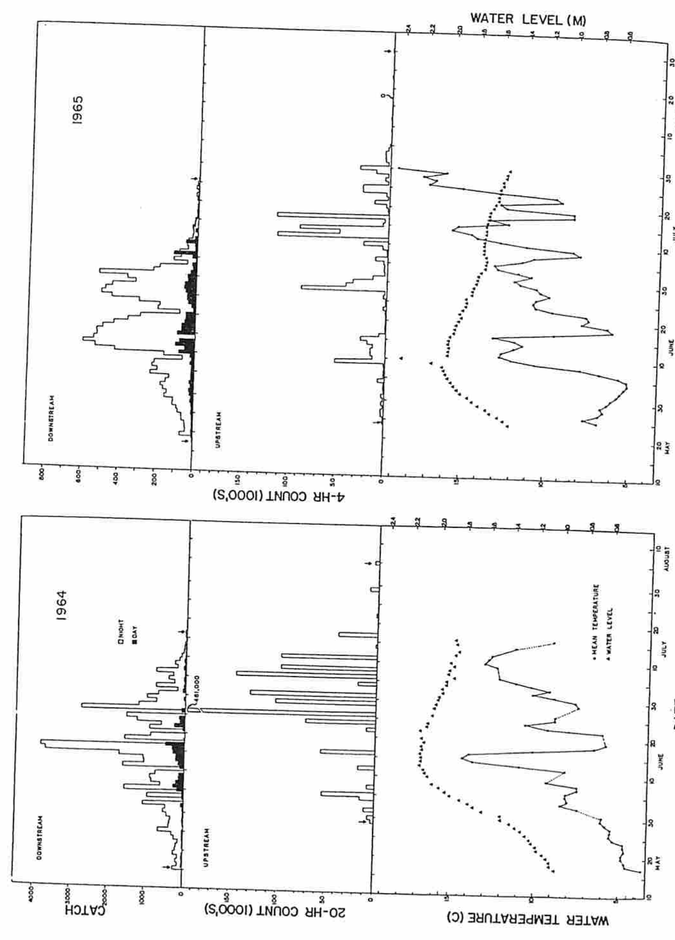

Fig. 5. Major trends in the seasonal periodicity of sockeye fry movements in the Upper Babine River in 1964 and 1965. Data are recorded separately for nocturnal downstream migrants (those captured between 2000 and 0800 hr), daytime downstream migrants (0800–2000 hr), and upstream migrants and are shown along with the seasonal fluctuations in water level and water temperature. Arrows indicate the dates between which observations were made. Except for one occasion, August 17, 1965 (indicated by a zero), some movement was recorded during each day of observation. Where gaps appear, no observations were made.

and nocturnal movement was essentially finished by mid-July. This long period of downstream activity, of presumably newly emerged fry, probably reflects the long spawning period of the parent fish, from late September to December.

The daytime downstream catch constituted an important segment of the total (9.0% in 1964 and 13.7% in 1965), even exceeding the nocturnal catch on a number of occasions during the latter part of the 1965 season. Its actual importance may be even greater than the figures indicate in that trap avoidance probably affected catches more during daylight than in the dark and because an unknown number of fry which had actually moved downstream in the early morning daylight were included with the nocturnal segment of the downstream run.

Although the 1964 data are incomplete, there was, in both years, a general correspondence between the peaks of daytime and nocturnal trap catches. Several obvious exceptions are the relatively large daytime catches made subsequent to July 5, 1965. These catches may reflect an increased tendency to daytime emergence during the latter part of the season. The fact there is little correspondence between the numbers of fish moving downstream during the day and the counts of upstream migrants suggests that the former were not simply fry displaced while moving upstream. On several occasions in 1964, daytime and nocturnal downstream migrants taken on the same day were compared. There was no apparent difference in either the degree of development of the fry or their length-frequencies.

The only comparable rate of daytime downstream movement in sockeye fry under stable natural conditions is that recorded by Heard (1965) for the Brooks River in Alaska, 11.0%. Heard (1965) suggests that these large daytime catches resulted from the fact that the traps were located on or immediately adjacent to gravels from which fry were emerging and that these were caught while making short excursions out of the gravel during daylight. The traps in the Upper Babine River were located close to the spawning gravels. However, daytime downstream migrants were readily observable in this river and their behaviour, already described, did not appear to support Heard's suggestion. On occasion, the paths of individual fry could be followed for 30 to 40 m. The fry were at the water surface, sometimes over considerable depths, and were not seen to make any attempt to hide or rebury themselves. Some were seen swimming with the current on into Nilkitkwa Lake.

The 1964 upstream data are incomplete. The tower counts, together with visual surveys of the stream edge, indicated that few fry were moving upstream when counts began in late May and early June; that fry were most abundant and active from about June 20 to July 15; and that few fry were present in the river from late July on into August. This would suggest that most of the upstream movement took place when downstream movements were already in decline.

Except for one day (July 11), the 1965 upstream data are complete from May 24 to August 5. There were three distinct surges in upstream movement, the first two of which overlapped the two large peaks in downstream movement. The third and largest occurred in mid-July at a time when the downstream run was almost over. Daily counts were terminated on August 5, when it appeared the major movements of fry were past. Counts were made occasionally up to August 30 but very few fry were moving.

The existence of surges in both the downstream and upstream movements of fry and their close correspondence on two occasions during 1965 is especially striking. Water levels in the Upper Babine River are rarely subject to sudden changes and have little effect on either the velocity or turbidity of the river. The changes that did occur during the period of this study had no apparent effect on the periodicities of fry movements. The Upper Babine River is, however, subject to very marked fluctuations in water temperatures and the 1965 data suggest a relation of these fluctuations to the seasonal periodicity of both downstream and upstream movements. All of the major movements occurred during periods of relatively high water temperatures.

Figure 6 illustrates the seasonal periodicity of downstream movement in fry having external yolk sacs. The percentage of yolk-sac fry in the total daily trap catch varied considerably throughout both seasons. In interpreting seasonal changes in the percentage of yolk-sac fry in the catches, two factors must be considered: first, the relative availability of yolk-sac and fully developed fry and second, the possibility of differing responses to environmental variables in fry of the two types. The high incidence of sac fry at mid-May of both years probably reflects the fact that at this time of year there are few completely developed fry in the gravel and not that there is a greater tendency for yolk-sac fry to emerge early in the season at low temperatures. The slight increase in the proportion of yolk-sac fry at the end of the 1964 season and the large peak in mid-June 1965, were both associated with temperature surges. The 1965 peak occurred several days later than the peak movement of fully developed fry during this surge so that yolk-sac fry were most abundant when the numbers of fully developed fry were declining. Yolk-sac fry continued to move downstream in considerable numbers for several days after water temperatures had fallen. The difference of several days in the timing of the peaks of yolk-sac and other fry may represent the time it takes for the former to reach the gravel surface. Yolk-sac fry were still present in the 1964 trap catches when trapping ceased but in 1965 none were taken after July 15 though trapping continued for several additional weeks.

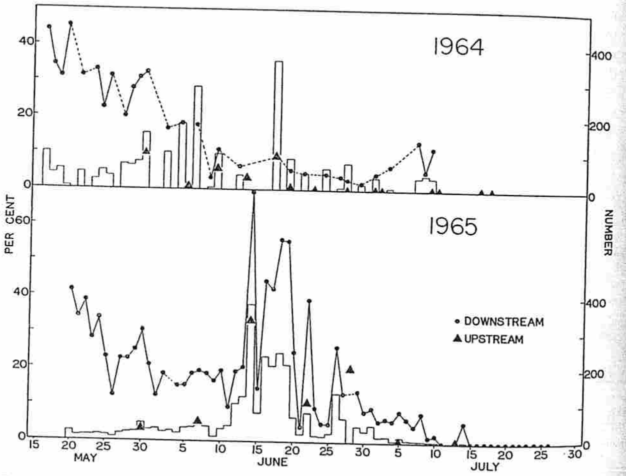

FIG. 6. Seasonal periodicities of movements of yolk-sac fry in the Upper Babine River during 1964 and 1965. Downstream data are presented as the numbers of yolk-sac fry captured daily (columns) and as the percentages of yolk-sac fry in the total daily catches (curves). The triangles give the percentages of yolk-sac fry in various samples of upstream migrants.

Changes in the proportion of yolk-sac fry in samples of upstream migrants tended to parallel those in the downstream catch, though at a lower level. Considerable numbers of fry with yolk sacs moved upstream in 1965 during the peaks of abundance in the downstream samples. The difference in the degree of development of upstream and downstream migrants is actually greater than indicated because only the presence of an externally visible yolk sac is shown and not the degree of absorption, which was considerably greater in upstream migrants. Over the 2 years of the study, nearly 20% of the downstream migrants sampled had yolk sacs classified as "large" whereas only 5% of the upstream migrants fell into this category, most of these early in the season.

In 1965, a few fry with small yolk sacs were captured about a quarter mile up the North Arm on June 7 and June 15, 1.9% and 0.7% respectively of the total samples. None were taken at this location later in the year and none were ever taken further uplake.

Much remains to be done in identifying the factors affecting the seasonal periodicity of emergence and downstream movements in sockeye fry. There is a broad relationship between the seasonal periodicity of emergence and the spawning pattern of the parent population. At Karluk Lake, Alaska, for instance, the bimodal spawning periodicity of summer and fall spawners in Meadow and Canyon Creeks is mirrored in early and late peaks of downstream fry movement; in Grassy Point Creek where there is only a single summer spawning peak, there is also a single seasonal peak of fry outmigration (C. J. DiCostanzo, personal communication). Various studies of downstream fry migrations in streams at Lakelse and Babine Lakes suggest a direct relationship between the length of the parental spawning period and the seasonal duration of downstream fry movements. However, very little is known about the factors which result in the short term fluctuations in emergence and downstream movement. Three possibilities are light intensity, stream discharge, and water temperature.

Northcote (1962) observed that larger numbers of rainbow trout fry tended to move downstream on foggy or overcast nights than on bright moonlight nights. In trough experiments with sockeye fry, McDonald (1960) got exactly the opposite result. However, many of McDonald's fry had been holding over the gravel during the day before the experiment and their behaviour may not have been that of fry emerging directly from the stream bottom. The effect of natural variations in nocturnal illumination has not, to my knowledge, been otherwise investigated.

In some streams, where changes in river discharge and turbidity are quite marked, the periodicity of fry movement is most closely related to total river discharge. At Babine Lake, the Fulton River (Fig. 7) and Gullwing Creek (Withler, 1952) are of this type. Some of these fry are undoubtedly removed from the gravel by scouring but there is some evidence that the mere presence of mud and silt in the water percolating through the gravel will stimulate increased activity and emergence in sockeye fry even when water levels and temperatures are relatively constant (Coburn and McCart, 1967).

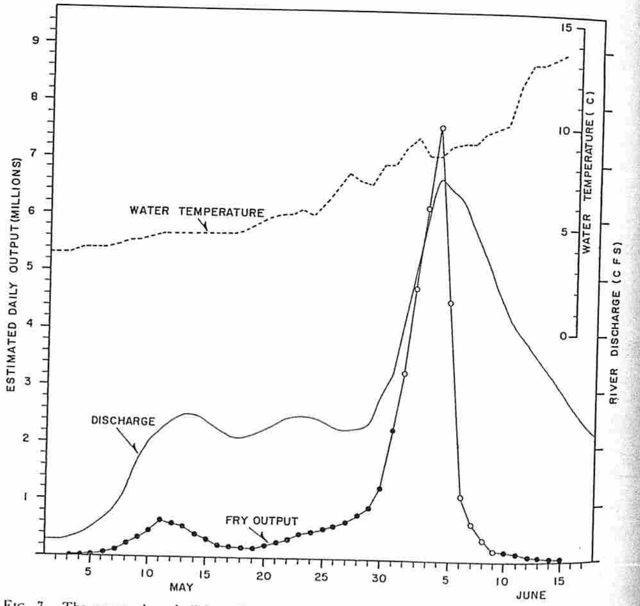

FIG. 7. The seasonal periodicity of downstream fry movement in the Fulton River, 1964.

Most studies of downstream movement in sockeye fry have been done in small tributary streams in which temperature fluctuations are much smaller than those in the Upper Babine River and in which fluctuations in other environmental variables complicate the pattern of emergence. There is consequently no clear evidence of thermal regulation of emergence and downstream movement comparable to that for the relatively stable Babine River.

The available evidence suggest that, once the fry have reached a certain stage of development, anything that stimulates them to increased activity—changes in water quality, sharply increased temperatures, dark nights—will bring them out of the stream bottom in large numbers.

The increase in upstream movement with rising water temperatures also appears to be the result of activity stimulation. Runnström (1957) and Northcote (1962) found similar relationships in brown trout and rainbow trout respectively. Both authors were impressed by the fact that, after a sharp increase in upstream movement coincident with a rise in water temperature, fry counts often fell even though water temperatures continued to rise. Runnström suggests that this may occur when temperatures exceed the level for maximum activity (10–12 C in brown trout, Brown, 1946). Northcote (1962) felt that in many instances such declines were the result of a decreased "supply" of animals ready for upstream movement. Brett et al. (1958) found that the performance of sockeye fry in swimming tests reached a maximum at 15 C. This temperature was rarely exceeded during the temperature peaks in the Upper River and it would therefore appear that the early declines in the number of fry moving upstream were primarily the result of a depleted supply.

DIEL PERIODICITY OF FRY MOVEMENTS

Figure 8 illustrates the hourly distribution of nocturnal downstream trap catches and upstream grid counts for six representative periods in 1964 along with data on light intensity and water temperatures.

The periodicity of nocturnal downstream migration assumed the sharply peaked form previously described by McDonald (1960) and Hartman et al. (1962) in other populations of sockeye fry. Peak captures were made in the hours immediately after dark, and numbers declined thereafter to very low levels shortly after sunrise. Light intensity appeared to be of primary importance in regulating this periodicity. McDonald (1960) and Hartman et al. (1962) (op. cit.) found the relationship of downstream movement and light intensity to be so close that the nightly period of downstream movement became progressively restricted as the season advanced due to changes in

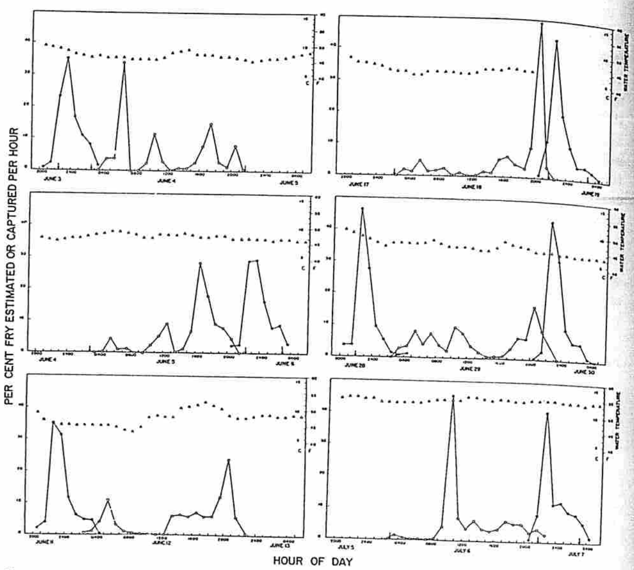

FIG. 8. The diel periodicity of fry movements in the Upper Babine River during six representative periods in 1964. The data are shown as percentages of the total downstream (black circles) and upstream (white circles) movement occurring in each hourly period. The mean hourly temperature is shown by the triangles. The arrows indicate, where data is available, the times at which light intensity reached .01 ft-c in the evening and rose above it in the morning.

the hours of darkness. At the same time, the peak of nocturnal migration came progressively later.

To determine whether similar seasonal trends were characteristic of the diel periodicity of downstream movement in the Upper Babine River and to partially obviate variability due to chance fluctuations in environmental factors, the data have been grouped by 1-week periods and are presented in Fig. 9 as the average percentages of the largest single hourly catch that were taken between 2000 and 0500 hr (2000–0400 hr for the week May 31–June 6).

There are two definite trends: first, a tendency for the distribution of catches to become more sharply peaked; second, a shift in this peak from the period 2300–2400 hr to an earlier period, 2200–2300 hr. These trends continue through the summer solistice (June 21). The latter trend is the reverse

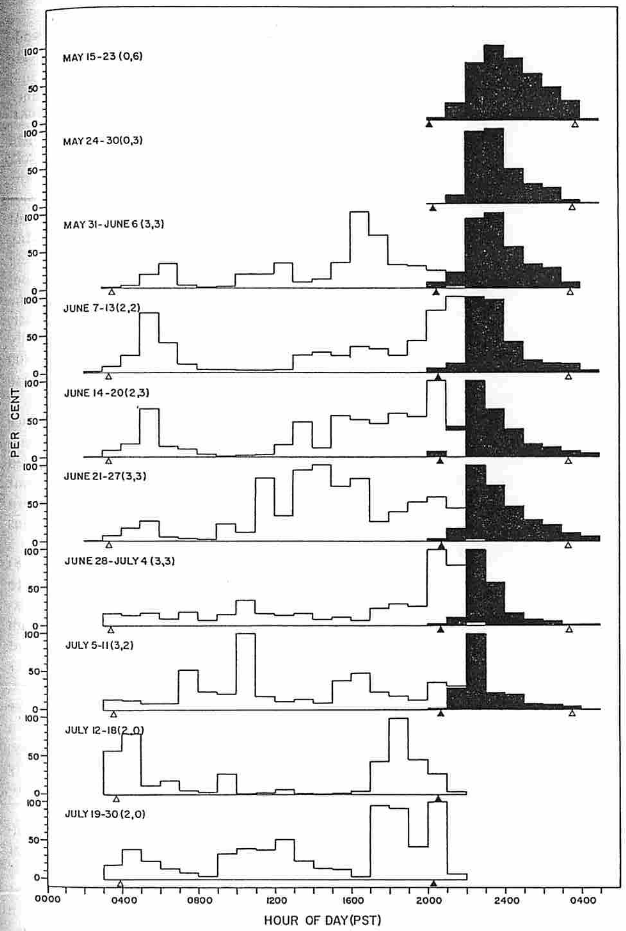

FIG. 9. Weekly changes in the diel periodicity of fry movements in the Upper Babine River during 1964. The data for each hour are expressed separately for downstream (black columns) and upstream (white columns) movements, as the average percentage of the largest single hourly catch. The numbers in parentheses indicate first, the number of days in each week for which upstream data are available and second, the number of nights for which downstream data are available. The triangles indicate the average times of sunrise and sunset during each week.

of that previously described for downstream migrant sockeye. Similar trends apparently occur in the Lower Babine River (Fig. 10). The data indicate a progressive decline in the importance of catches taken after midnight and a corresponding increase in those taken before midnight. The significance of this pattern is not clear. It may be related in part to the fact that in 1964, fry moving downstream early in the season tended to be less well developed than those moving later. There is some evidence that fry with external yolk sacs have a diel pattern of emergence different from that of fry in which the yolk is fully enclosed.

Figure 11 compares the periodicity of nocturnal downstream movement of fry with and without yolk sacs on 4 nights between May 16 and May 29, 1964. Fully developed fry were more abundant than yolk-sac fry during both the first (2100–2200 hr) and last (0300–0400 hr) hour of observation, possibly an indication of a greater tolerance for daylight. Captures of the former increased to a sharp peak between 2300 and 2400 hr. In contrast, the periodicity of captures of fry having external yolk sacs was more broadly peaked with nearly equivalent catches made during the 3 hours from 2200 to 0100 hr. Finally, a greater proportion of fully developed than yolk-sac fry emerged before midnight. Together with a seasonal decline in the proportion of yolk-sac fry moving downstream, differences of this kind might produce a seasonally changing pattern of diel periodicity such as has been described. However, the fact that the diel pattern of downstream movement continued to change even when the proportion of yolk-sac fry remained fairly constant (from June 10 on) suggests that this is not the whole answer. The pattern may reflect some major difference between the Babine River populations and others in the behaviour of fry at the time of emergence.

The diel periodicities of downstream and upstream movement (Fig. 8) were nearly mutually exclusive with the latter almost entirely confined to the hours between dawn and dusk. The pattern of upstream migration exhibited much more day-to-day variability than did the pattern of downstream movements. Although the initiation and termination of upstream movement were certainly light regulated, the factors resulting in the several daily peaks are not easily identified. One of the difficulties with this kind of data is that, as Northcote (1962) points out, nothing is known of the supply of fry available to move upstream. None of the observed environmental variables showed a corresponding periodicity. Water temperature, the most likely possibility, was obviously unrelated to hourly grid counts: peaks occurred as frequently during periods of stable or decreasing temperatures as during periods of increase.

When grouped by weeks (Fig. 9), the data still show considerable variability but there is some indication of a regular pattern. During at least 5 of the 8 weeks there was an identifiable morning peak of movement followed by a mid-morning depression; a more prolonged afternoon peak was apparent during 6 weeks. These observations suggest that the basic activity pattern of upstream migrants was bimodal. Hoar (1958) described a midday depres-

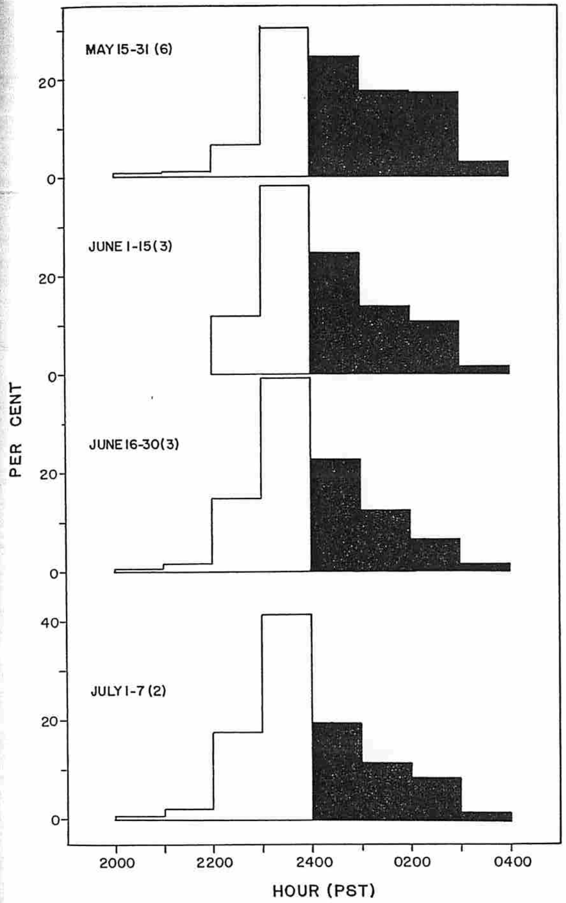

FIG. 10. Biweekly changes in the diel periodicity of downstream movement in the Lower Babine River during 1962. The data are presented as the percentage of the total nightly catch moving downstream during each hourly period from 2000 to 0400 hr (2200 to 0400 hr from June 1–15). The hours before and after midnight are distinguished to facilitate comparison. The number in brackets indicates the number of nights during each 2-week period for which data are available.

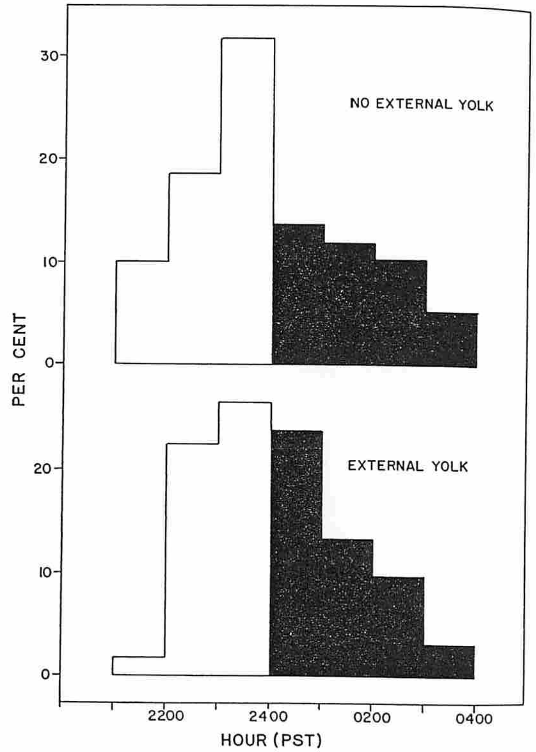

FIG. 11. Periodicities of nocturnal downstream movement of fry with and without externally visible yolk sacs. The data, expressed as percentages of the total captures between 2100 and 0400 hr, are the averages for the hourly catches on 4 nights between May 16 and May 29, 1964.

sion in both the swimming activity and current responses of sockeye fry. Groot (1965), commenting on the dawn–dusk periodicity of activity in migrating smolts notes "There is some evidence that this is the basic diel activity rhythm of sockeye salmon, young or old, migrating or not."

LENGTH-FREQUENCIES

Length-frequency information is most complete for fry taken in the Upper Babine River and the North Arm of Babine Lake. The length-frequencies of these fry will be considered first and then compared with those of fry in the Lower River.

In 1964, the major emphasis was on a comparison of the length-frequencies of downstream and upstream migrants. The length-frequencies of the samples, taken at intervals of a few days, grouped by weekly periods, are presented in Fig. 12. Initially, the length–frequencies of the two groups were similar but although there was a marked seasonal increase in the lengths of the upstream samples, there was virtually no change in the length composition of the downstream samples other than the occurrence of a few larger fish in samples taken during the last week of the season. A comparison of the length-frequencies of downstream migrants and fry taken from the stream gravel during the same period (May 22 to May 26, 1964) revealed that the downstream migrants were larger and better developed (Fig. 13)

In 1965 also, there was a seasonally increasing disparity in the lengths of downstream and upstream migrants (Fig. 14). Once again, a few larger fry were taken during the latter stages of the downstream run.

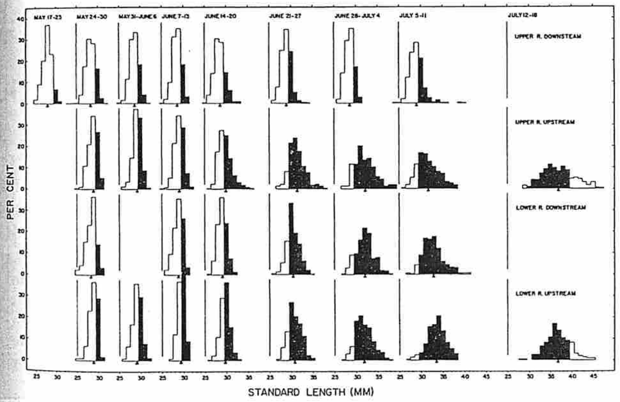

FIG. 12. Length distributions of fry captured in the Upper and Lower Babine rivers during 1964 expressed as the percentage of the total sample in each millimeter length class. The percentages between 30 and 40 mm have been blackened to facilitate visual comparison of samples taken on various dates. The triangles indicate the mean lengths of samples.

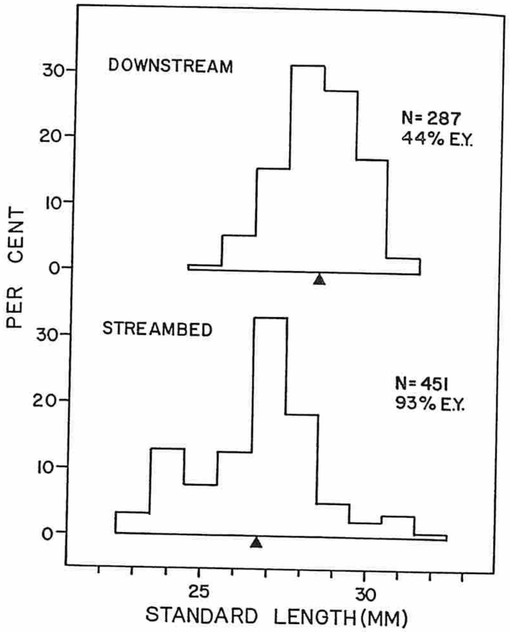

FIG. 13. Length distributions of pre-emergent and downstream migrant fry in the Upper Babine River, May 22 to May 26, 1964. The percentages of fry having external yolk sacs (E.Y.) are indicated.

Early in the season, fry captured moving upstream were no larger than those moving down during the same period. However, many fry, if not most, remained for a time feeding and growing along the river edges or in Nilkitkwa Lake. It is these larger fry which dominate the upstream samples later in the season.

On one occasion in 1964, July 2 and 3, a series of length-frequency samples was taken in the Upper Babine River and along the east shore of the North Arm of Babine Lake (Fig. 15). There was a direct relationship between the mean length of fry and distance uplake, exactly what would be expectde were fry dispersing from a single source and growing as they dispersed. In

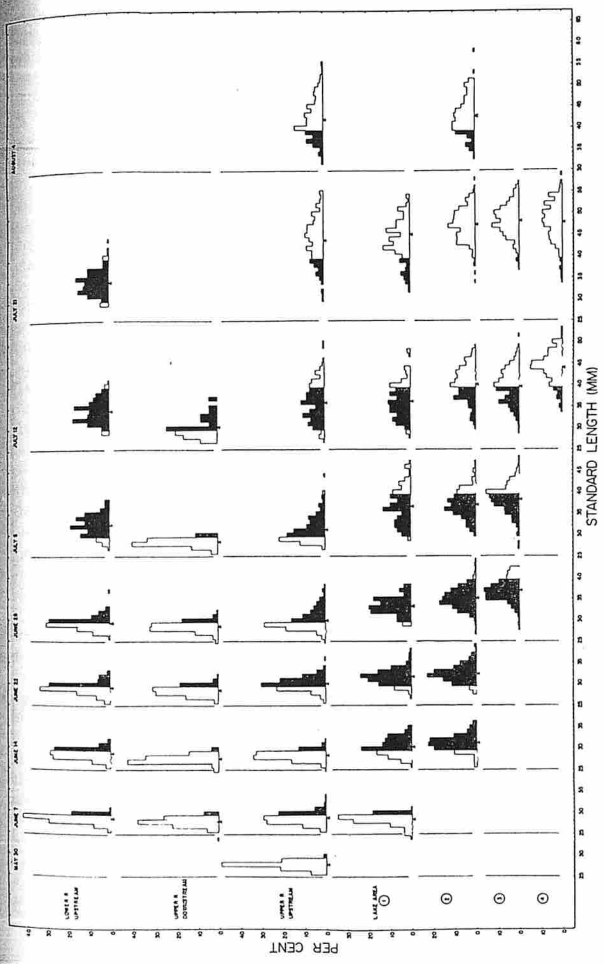

FIG. 14. Length distributions of sockeye fry captured in the Upper and Lower Babine rivers and the North Arm of Babine Lake during 1965. Format as in Fig. 12.

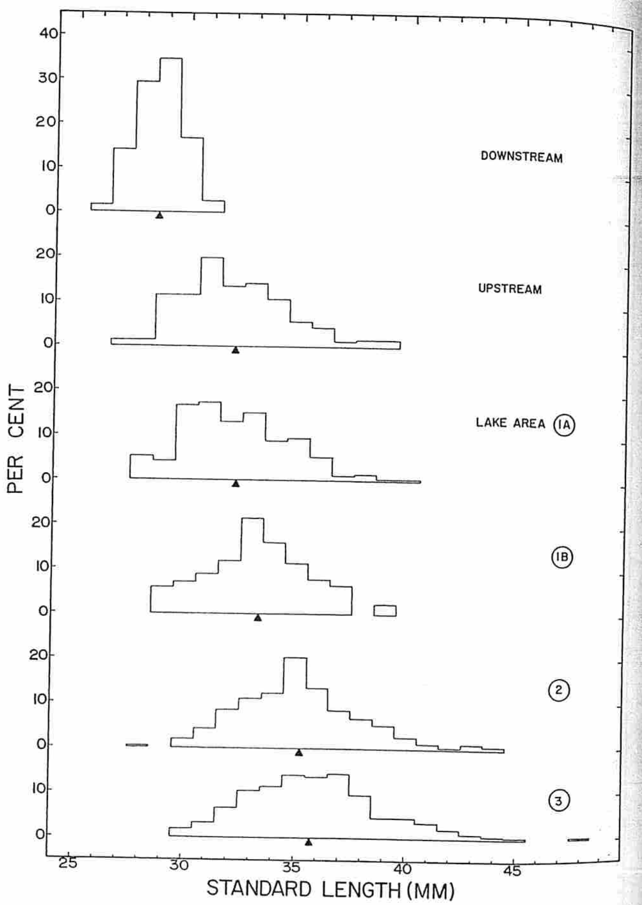

FIG. 15. Length distributions of sockeye fry captured in the Upper Babine River and the North Arm of Babine Lake on July 2 and 3, 1964. Format as in Fig. 12.

1965, North Arm samples showed a similar relationship up until early July (Fig. 14). On July 12, however, the pattern began to break down and on July 21 the length-frequencies of fry collected in the three areas farthest uplake were almost identical, suggesting that considerable mixing had taken place. By August 4, fry were scarce in the littoral area of the lake and were taken in only one locality. These fry were smaller than those taken in the same area the previous week. Apparently most fry had abandoned the lake edges and become entirely pelagic by this time.

The length-frequencies of downstream and upstream migrants captured in the Lower River during 1964 (Fig. 12) were more alike than those of comparable fry taken in the Upper Babine River. Fry of both kinds gradually increased in length and there was only a hint of the increasing disparity so obvious in the Upper River samples. There are several possible explanations for this. In the first place, spawning in the Lower River precedes that in the Upper River by several weeks and there is some suggestion that this difference is reflected in the respective periods of fry emergence. This would account for the almost complete absence of small fry in collections made during the last 2 or 3 weeks of downstream sampling. The high proportion of larger fry taken during this same period may have resulted from the comparatively difficult environment with which the Lower River fry must contend. In this river, where currents are strong and where there are few good holding areas, even well-developed fry might have difficulty in maintaining position. A particularly unfavourable location is an island in midstream about 100 m above the weir. Many of the large fry captured at the fence may have been those swept down while attempting to move upstream from this island.

In 1964, the length-frequencies of fry moving upstream in the Upper and Lower Babine rivers were similar during the period from May 24 to July 18. In 1965, the mean lengths of fry in the two groups (Fig. 14) were similar up through July 5 but the Upper River fish were considerably larger thereafter. The explanation of this may lie in the fact that fry moving upstream in the Lower Babine River spend the period between emergence and eventual entry into Nilkitkwa Lake entirely along the edges of the river. On the other hand, several lines of evidence suggest that many of the fry moving upstream in the Upper Babine River spend a period of time in Nilkitkwa Lake and that some of them originate in the Lower Babine River. For instance, large upstream migrations were observed on several occasions in 1965 the day after surveys indicated that there were very few fry holding along the edge of the river itself. This was after the period of significant downstream catches and the sudden increase in the numbers of fry in the river could not have been due to the recruitment of newly emerged fry. On other occasions, continuous bands of fry have been seen moving out of Nilkitkwa Lake into the Upper River (F. Jordan, personal communication). The fry moving upstream on these occasions were often very large. Further evidence of a movement out of Nilkitkwa Lake comes from townetting studies which indicate that sockeye populations in Nilkitkwa Lake decline precipitously from June to October (F. Jordan, personal communication).

In both the Upper and Lower rivers, fry taken during 1964 averaged slightly larger than those taken during comparable time periods in 1965 (Fig. 16).

LENGTH–WEIGHT RELATIONSHIP

The mean weights of fry in each millimeter length class were used in calculating the length–weight relationships of sockeye fry in the Upper and Lower Babine rivers and the North Arm. The means and the calculated regression lines are illustrated in Fig. 16. Although the mean weights of each length class are indicated, only data for fry 31 mm or longer were used in calculating the regression statistics because smaller fry appeared, in some instances, to have a markedly different length–weight relationship. This difference is thought to be due to the presence of yolk in many of the smaller fish, particularly those most recently emerged.

Figure 17 indicates the percentages of fry in a total sample of 375 fry between 25 and 35 mm in which the yolk was externally visible in the form of a yolk sac and in which vestiges of the yolk could be identified internally after the body cavity had been opened. Many fry in which the yolk sac had been completely enclosed retained some yolk internally. All of the 25-mm fry examined contained yolk material. In 46% of these, the yolk sac was visible externally. Between 25 and 30 mm there was a sharp decline in the propor-

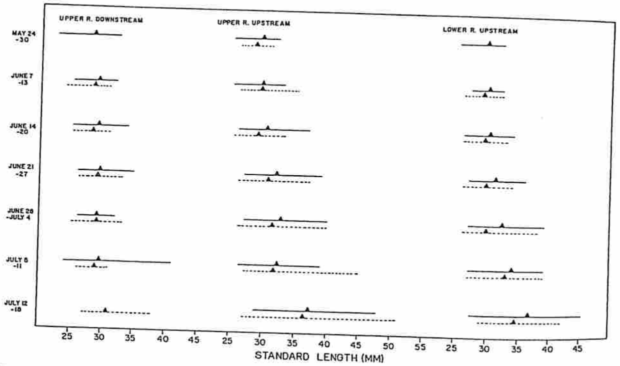

FIG. 16. Length ranges and mean lengths (triangles) of sockeye salmon fry captured in the Upper and Lower Babine rivers during comparable periods in 1964 (solid lines) and 1965 (broken lines).

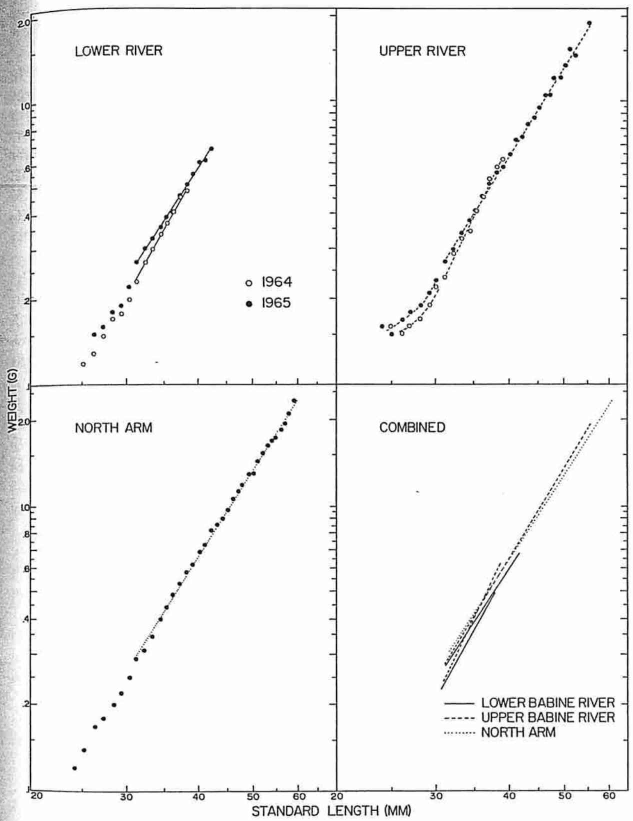

FIG. 17. Length–weight relationships of fry captured in the Upper and Lower Babine rivers during 1964 and 1965 and in the North Arm of Babine Lake during 1965. The regression lines are reproduced together in the lower right quadrant.

tion of fry containing yolk material, paralleled at a lower level by a decline in the proportion of fry having an external yolk sac. No fry 31 mm or larger had yolk either externally or internally discoverable.

An inflection in the length–weight relationship was most apparent in samples taken in the Upper Babine River. These samples included a large number of recently emerged, downstream migrants in the sub-31 mm length classes and, as the dotted trend lines indicate, fry of these lengths were proportionately heavier than larger fish. The length–weight samples from the Lower River were predominantly upstream migrants in 1964 and entirely so in 1965. The length–weight relationship of sub-31 mm Lower River fry is closer to that of larger fish than is the case in the Upper River. The lengths and weights of the well-developed North Arm fry appear to fall on the same line on either side of 31 mm.

The regression formulae are given in Table I. Also included are the results of some comparisons made using covariance techniques. The length–weight relationships being compared were tested first for differences in slope and, where these did not differ ($P = 0.01$), for differences in adjusted mean. Each of the comparisons made revealed significant differences in the length–weight relationships tested.

In both the Upper and Lower Babine Rivers, the 1964 fry in the shorter length classes weighed less than those in the same size-classes in 1965. The distribution of points in the sub-31 mm groups suggests that this difference was already established at the time of emergence. However, in both rivers the increase of weight with length was much greater in 1964 than in 1965 so that the lines for the 2 years converge; for the Upper Babine River they eventually cross.

When the length–weight relationships of Upper and Lower River fry are compared within years a common pattern emerges. The weights of fish from the two rivers are very similar at 31 mm but diverge with increasing length. In both years Upper River fry weighed proportionately more.

Covariance analysis indicated that in 1965 the length–weight relationships of Upper Babine River and North Arm fry differed ($P = 0.01$) but the obvious irregularities in the fit of individual points, especially those of the longer length classes, suggest caution in interpretation.

The significance of the length–weight data is difficult to determine. We have first to consider the factors which influence the length–weight relationship up to the time of emergence and second, those which affect the relationship after the fry leave the gravel.

As indicated, in both rivers, fry of the shorter length classes weighed less in 1964 than fry of the same lengths in 1965. There is also some evidence (Fig. 16) that in both rivers the mean lengths of fry were slightly greater in 1964 than in 1965. Possibly the factors which produced the observed differences in the lengths and weights of the two year-classes of fry were common to both rivers.

TABLE I. Results of linear regression and covariance analysis of logged length–weight data for fry captured in the Babine River and the North Arm of Babine Lake.

Locality	Year	Intercept (a)	Slope (b)	L.R.[a] '64		L.R. '65		U.R. '64		U.R. '65		N.A. '65	
				S.	A.M.[b]	S.	A.M.	S.	A.M.	S.	A.M.	S.	A.M.
Lower River	1964	–5.0059	3.6092	–[c]	–	**	–	*	**	–	–	–	–
	1965	–4.1238	3.0551	**[d]	–	–	–	–	–	**	–	–	–
Upper River	1964	–5.8407	4.1798	*[e]	**	–	–	–	–	**	–	–	–
	1965	–4.5114	3.3212	–	–	**	–	**	–	–	–	**	–
North Arm	1965	–4.1843	3.1262	–	–	–	–	–	–	**	–	–	–

[a] L.R. = Lower Babine River; U.R. = Upper Babine River; N.A. = North Arm.
[b] S. = slope; A.M. = adjusted mean.
[c] – = No test made.
[d] ** = Significant at $P = 0.01$.
[e] * = Significant at $P = 0.05$.

Various aspects of the physical environment have been shown to affect the growth and development of salmonid embryos: oxygen concentration, water velocity, water temperature, and daylight have been implicated in various studies (Garside, 1959; Silver et al., 1963; Shumway et al., 1964; Brannon, 1965). There is no information available about physical conditions in the Upper or Lower rivers during the winters which produced the 1964 and 1965 fry. However, one other interesting possibility has been explored: that year-to-year differences in length–weight relationship may be related to the size of eggs from which the fry develop.

Martin (1949) identified five relative growth stanzas in the life history of Atlantic salmon, delimited by inflections occuring at approximately the eyed egg stage, hatching, ossification, and sexual maturity. The length–weight relationship is a form of relative growth constant. Martin (1949) comments, "Differences in fish size, at growth inflection, is shown to be one of the factors important in the control of relative heaviness." It can be demonstrated that there probably were differences in the size of 1964 and 1965 Babine River fry at several critical periods in their early development.

Table II presents the proportions of 4- and 5-year-old female sockeye on the spawning grounds of the Upper and Lower Babine rivers during the years which produced the 1964 and 1965 fry. Females 4 years old predominated in the 1963 spawning run, 5-year-olds in 1964. Females of 4 years were considerably smaller than those of 5. Recent investigations on the Lower River have shown that there is a direct relationship of parent size to egg size and, because 4-year-old females are smaller, their eggs are, on the average, also smaller than those of 5-year-olds — .1448 and .1718 g respectively, in 1965 (T. Bilton, unpublished data). Thus, when 4-year-old females predominate, the average size of the eggs deposited in the gravel should be smaller than when 5-year-olds predominate. There is some additional information suggesting that fry resulting from large eggs may weigh proportionately more than those from small eggs when raised under similar experimental conditions (Fig. 18). Here then, perhaps, is a mechanism which might produce the observed year-to-year differences in the length–weight relationships of fry in the rivers. The argument does not, however, take into account that at emergence the 1965, large-egg fry were apparently shorter as well as proportionately heavier than the 1964 fry. In unpublished experiments conducted by the author and T. Bilton, fry from large eggs were consistently longer than those from small eggs when raised under similar conditions. The factors determining the length–weight relationships of emerging fry are obviously complex and egg size is certainly not only, or even the most important, consideration. It is, however, one which warrants further investigation. It might for example, explain Skud's (1955) observation that pink salmon fry migrating out of Sashin Creek during March weighed proportionately more than those migrating later, in April and May. He comments, "Data gathered from Sashin Creek show that in six out of seven years the early

Table II. Age composition, and mean hypural length (H.L.) of each age-group,[a] of female sockeye salmon spawning in the Upper and Lower Babine rivers during 1963 and 1964.

		Age 4_2		Age 5_2		Age 5_3	
Location	Year	%	Mean H.L. (*cm*)	%	Mean H.L. (*cm*)	%	Mean H.L. (*cm*)
Upper River	1963	73.9	44.9	26.1	50.6	–	–
	1964	9.4	43.7	90.6	49.6	–	–
Lower River	1963	66.0	44.6	33.0	50.7	1.0	43.2
	1964	18.8	42.9	81.2	49.3	–	–

[a] The subscript indicates the number of years spent at sea.

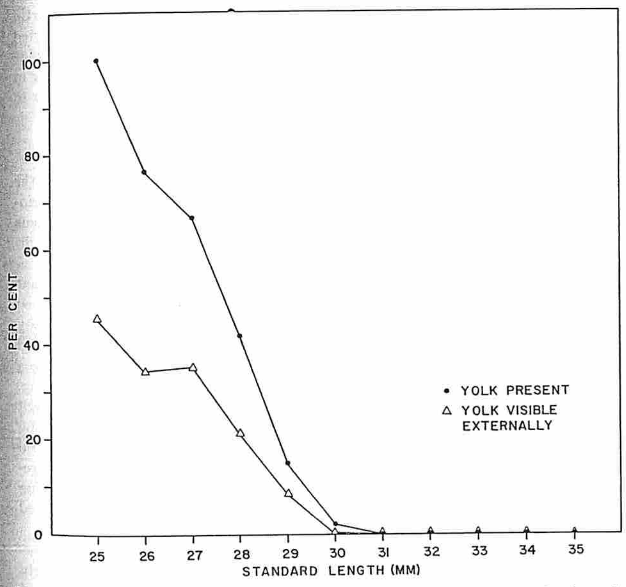

Fig. 18. Relationship of yolk absorption to fish length in a sample of 375 fry from the Upper Babine River, 1965.

spawners were larger than late spawners. The resulting progeny may reflect this adult condition." Possibly the *female size/egg weight* and *egg weight/fry weight* relationship are similar to those indicated for Babine River sockeye salmon.

The factors which govern the increase of weight with length after emergence are also little understood. Parker and Vanstone (1966) give some indication of the complexity of this problem as it applies to pink salmon fry. In the Babine rivers there were differences between year-classes in the same river and differences in the same year-class in different rivers. There is no obvious explanation for the relatively high rate of weight gain in the 1964 fry of both the Upper and Lower Babine rivers. Water temperatures were slightly lower in 1964 (9.4 C — May 25 to July 17, average) than in 1965 (9.8 C). There is no comparative data on plankton abundance during the 2 years but significant annual differences can occur in Babine Lake (Johnson, 1961). The greater rate of weight gain of Upper River fry in comparison with Lower River fry of the same year-class may reflect differences in the energy budget of fry in the two rivers. Martin (1949) suggests that, "changes in the slope of length–weight lines may be effected by such factors as malnutrition." Plankton is less abundant in Lower Babine River and water velocities consistently greater. The balance of energy inflow in the form of food and energy outflow in the form of swimming would appear to favour those fry in the Upper River.

FOOD HABITS

On June 3/4 and June 17/18, 1965, samples of 10 fry were taken at 2-hr intervals over a total period of 24 hr in an attempt to determine the diel periodicity of feeding (Fig. 19). It was assumed that the numbers of intact organisms would be highest when fry were actively feeding and would decrease when digestion exceeded the intake of new material.

Results for the two periods vary considerably but they do agree in that the major peaks occur during the day and the lows during the night. A dotted line illustrates the average tendency. The pattern is similar to one obtained by Northcote and Lorz (1966) for kokanee in Nicola Lake, B.C., and that described by Parker and Vanstone (1966) for pink salmon in Burke Channel, B.C.: a single afternoon peak with a depression during the night and early morning. It contrasts with the apparently bimodal nature of the upstream fry movement in the Babine River. Possibly the periods when fry are not actively swimming are devoted primarily to feeding. Groot (1965) found that under experimental conditions the feeding activity of sockeye smolts was highest when the frequency of behaviour patterns associated with active migration was low; feeding occurred most commonly from 1200 to 2000 hr and was preceded and followed by peaks in fluttering and position change.

The yolk material represents a portable food supply and it was of considerable interest to determine whether fry began feeding before this was completely absorbed. Table III records the results of the examination of two selected samples: 52 fry taken at 1300 hr, June 17, and 48 fry taken at 0100 hr, June 18,

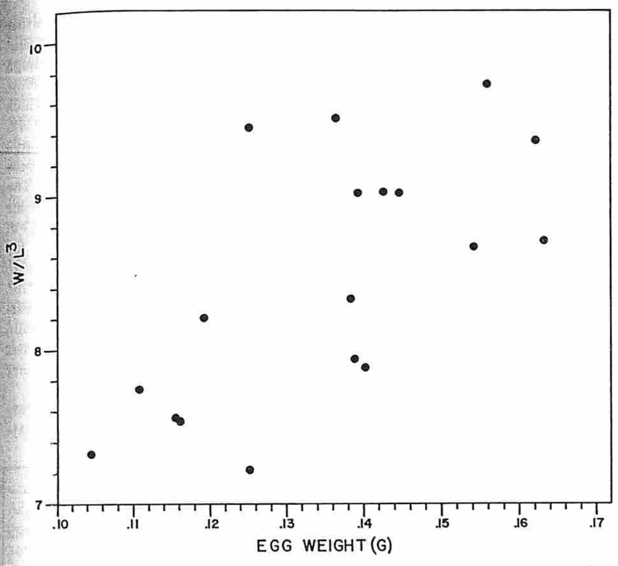

FIG. 19. Relationship of egg weight to the condition factor (W/L^3) of the resultant fry. Data courtesy of T. Bilton.

TABLE III. Percentages of stomachs containing food, in fry with and without remaining yolk material.

Date and time	No. examined	With food (%)	Average length (*mm*)
With yolk			
June 17, 1300 hr	26	34	27.5
June 18, 0100 hr	24	45	27.3
Total	50	40	27.4
Without yolk			
June 17, 1300 hr	26	96	30.5
June 18, 0100 hr	24	95	28.2
Total	50	96	29.4

1965. In both instances half the fry examined contained yolk material, either externally or internally. Both day and night, the proportion of stomachs containing food was far higher among non-yolk than among yolk fry. Thus, although the presence of yolk material within the body cavity did not preclude feeding, fry containing yolk material did not feed to the same extent as fry in which the yolk was entirely absorbed. This difference was not simply the result of a difference in the size of yolk and non-yolk fry. Small (<28 mm) and large (28 mm +) yolk fry did not differ appreciably in the percentage of stomachs containing food: 36% and 44% respectively of two samples of 25 fish. The mean size of the latter group (28.2 mm) was the same as that of the nighttime sample of non-yolk fry (Table III) which had a very high proportion (95%) of stomachs containing food. There are several possible explanations. Yolk fry may be very recent emergents which have not yet had much opportunity to take food, or the presence of yolk may in some way inhibit their appetite.

Foerster (1925) reported marked differences in the food of sockeye yearlings in lakes and those in streams; crustacean plankters in the former and insects, chiefly chironomid larvae and pupae, in the latter. In 1965, numerous stomachs were examined to determine whether there was a similar difference in the food of fry in the river and those in the lake.

Information on the stomach contents of fry taken during June and July 1965 in five areas is given in Fig. 20. Estimated volume was used only to indicate

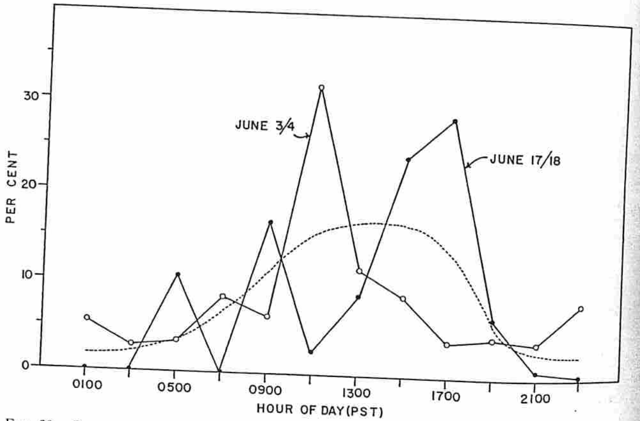

FIG. 20. Percentage of the total identifiable food organisms occurring in each of 12 samples taken at 2-hr intervals from 1300 hr June 3 to 1100 hr June 4 and from 0900 hr June 17 to 0700 hr June 18. The data have been plotted from midnight to midnight, not in the order in which samples were taken. The dotted line indicates the general trend.

the importance of those insects and plankters which were too far digested to be identifiable as individuals and to compare the total volume of insects with the total volume of plankters. The data labelled "Upper River Downstream" included both day and night downstream migrants removed from the trap at the regular morning and evening counting times. These had all had some experience of daylight and were not necessarily representative of fry migrating during the nightly peak of downstream movement. These data might best be viewed as an indication of the food items which constitute the first "meals" of recently emerged fry. That these were predominantly recently emerged fry is indicated by the nearly 50% of the stomachs which were empty, the only samples in which a significant proportion of empty stomachs occurred.

Insects did not exceed 8% of the total number of food items in any samples. However, they appeared in a relatively high percentage of the stomachs. Also, because they were individually large, they constituted a relatively large percentage of the total food volume. Insects were numerically most important in the Upper Babine River. Volumetrically, the Upper and Lower river and the North Arm inshore samples were very similar. Insects were of least importance in samples taken offshore in the North Arm.

In all samples, dipterans of the family Chironomidae were the most important insect food. Among these, pupae occurred more frequently than either larvae or adults.

By every measure, crustacean plankters were the most important food of the young fry. The copepods *Diaptomus* and *Cyclops*, in that order, were the mainstay of the diet of fry in the rivers and, to a lesser extent, in the North Arm of Babine Lake. Immature and partly digested individuals of these two genera were not distinguished and have been grouped as "unassigned *Cyclops* and *Diaptomus*." A third large copepod, *Heterocope*, appeared in only small numbers in stomach samples taken in the rivers but was of considerable importance in offshore townet samples, occurring widely in relation to its numbers. The intake of the cladoceran plankters *Daphnia* and *Bosmina* in the rivers was small in comparison with that of the copepods. However, in North Arm inshore samples, *Bosmina* was taken in fair numbers and occurred in over 40% of the stomachs. Offshore, *Daphnia* was second only to *Diaptomus* in total numbers of identifiable organisms and occurred in more stomachs than any other plankter; *Bosmina*, though not abundant, also occurred widely.

Except for the North Arm offshore samples there was fair agreement between the relative abundance of individual plankters in plankton samples and their relative abundance in fry stomachs. An exception was *Heterocope*, which appeared in small numbers in stomachs taken in the rivers but was not present in any of the plankton samples from these areas.

Offshore in the North Arm, both *Heterocope*, which was not present in the plankton samples, and *Daphnia*, present in very small numbers, formed a considerable part of the stomach contents. However, sockeye fry in Babine Lake are thought to undergo a daily vertical migration from the deeper water, which they occupy during the day, toward the surface (Johnson, 1961). This movement takes place at dusk. It was at this time that the surface townet catches were made. As a result, the plankton samples, taken from 0-5 m, may not be representative of the relative abundance of organisms at the depths at which fry were feeding. There is the additional possibility that the relative abundance of various food items is the result of selective feeding by fry. Ricker (1937) has shown that such selection does occur in sockeye fry.

The 1965 plankton samples indicate that plankton were most abundant in mid-June (Fig. 21). Throughout June, plankton abundance was considerably greater inshore in the North Arm than elsewhere. Next in order of plankton abundance were the North Arm offshore (0–5 m), Upper Babine River, and Lower River. The tendency for fry to remain inshore after entering the North Arm may be related, in part, to the abundance of plankton there.

PREDATION

From the time fry in the Upper Babine River emerge from the gravel until they leave the river and enter the lake, they are almost entirely confined to a narrow strip along the river bank. The dense populations that accumulate there appear to be very vulnerable to predation. In 1965, regular collections of predatory fishes were made throughout the period of fry migration with both beach seines and gillnets. A few were taken by angling. Collections made in the Upper River near Smokehouse Island and in the North Arm of Babine Lake (primarily in area 1) have been treated separately.

Seven species of fish were found to be preying on sockeye fry: rainbow trout, cutthroat trout, coho salmon, Dolly Varden, lake trout, lake whitefish, and burbot (Table IV). An additional species, the squawfish, contained unidentifiable fish remains some part of which might have been sockeye fry. Of the eight species, only the lake trout was confined to the lake. The others were taken both in the river and in the North Arm. Two predatory sculpins, *Cottus asper* and *C. aleuticus*, are known to inhabit the Babine drainage but neither was taken in the Upper River, where they are apparently not common.

Of the known predators, rainbow trout and juvenile coho were those most frequently captured in the Upper River. Many of the latter were smolts. On the basis of their apparent abundance and the coverage fry content of their stomachs, these two species would appear to be the most important predators on sockeye fry in the Upper River. The stomachs of several other species, the cutthroat, Dolly Varden, lake whitefish, and burbot, contained considerable numbers of fry but these predators seemed to be much less abundant than either rainbow trout or coho. The lake whitefish is ordinarily a bottom feeder and is morphologically ill-adapted for predation, an indication of the vulnerability of sockeye fry while in the river.

Rainbow trout and coho smolts were also the fish most frequently taken in the North Arm. However, they were less important as sockeye predators than in the Upper River. In fact, none of the rainbow trout taken in the lake contained an identifiable sockeye fry. There was also a decline in predation by cutthroat trout and lake whitefish. Although the proportion of burbot stomachs

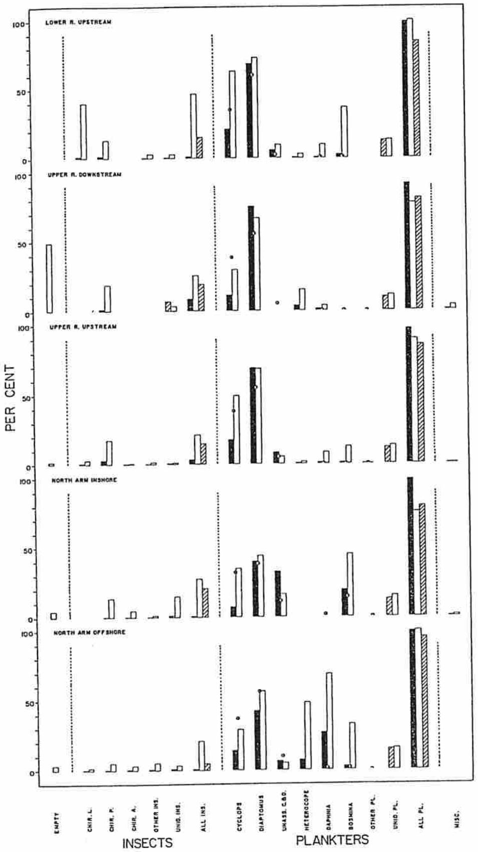

FIG. 21. The stomach contents of fry taken in five areas during 1965. Black bars, percentages of the total number of food organisms; white bars, percentages of the total number of stomach containing food; cross-hatched bars, estimated percentages of total volume of food. The circles indicate the percentages of each plankter in plankton samples from four areas. (The same plankton data are shown with both the upstream and downstream Upper River food data.) Further explanation in text.

TABLE IV. The stomach contents of predatory fishes captured in 1965 in the Upper Babine River and the North Arm of Babine Lake.

Species	Area	Size range (*mm*)	Stomachs: Examined	Stomachs: Empty (%)	Stomachs with Unidentified fish remains: No.	Stomachs with Unidentified fish remains: %	Stomachs with Identified sockeye fry: No.	Stomachs with Identified sockeye fry: %	Number of fry: Total	Number of fry: Avg per stomach
Rainbow trout (*Salmo gairdneri*)	River	94–535	106	4	5	5.	24	23.	860	8.1
	North Arm	106–470	62	2	2	3.	0	0	0	0
Cutthroat trout (*S. clarki*)	River	212–362	9	0	1	11.	7	78.	94	10.4
	North Arm	124–313	12	8	2	17.	2	17.	6	.5
Coho (*Oncorhynchus kisutch*)	River	81–107	29	14	1	3.	20	70.	107	3.7
	North Arm	98–250	63	2	7	11.	6	10.	15	.2
Dolly Varden (*Salvelinus malma*)	River	198–207	2	0	0	0	2	100.	34	17.0
	North Arm	188	1	0	0	0	1	100.	10	10.0
Lake trout (*S. namaycush*)	River	–	0	–	–	–	–	–	–	–
	North Arm	183–458	23	30	7	30.	2	9.	7	.3
Lake whitefish (*Coregonus clupeaformis*)	River	388–505	12	8	4	33.	4	33.	63	5.3
	North Arm	214–380	6	33	0	0	0	0	0	0
Burbot (*Lota lota*)	River	441–737	5	0	1	20.	4	80.	20	4.0
	North Arm	286–610	8	38	0	0	2	25.	49	6.1
Squawfish (*Ptychocheilus oregonense*)	River	223–227	13	38	8	62.	0	0	0	0
	North Arm	183–385	23	52	3	25.	0	0	0	0

containing fry fell from 80% to 25%, the average number of fry per stomach increased. The single Dolly Varden taken in the North Arm contained 10 fry. Obviously, for most of these species, the samples are too small to permit any rigorous comparison of the relative rates of predation in the river and in the lake. However, it does appear that predation on sockeye fry is more intense in the river than in the lake: 6.7 fish per predator stomach in the river and 0.4 in the lake. This is presumably due to the greater availability of fry in the river.

Ward and Larkin (1964) found that in the western region of Shuswap Lake juvenile sockeye were an important food of rainbow trout. In years in which juvenile sockeye were scarce, fish as a food item fell below the average volume and the condition of trout was relatively poor. When sockeye were abundant, the fish content of stomachs rose and the condition of trout was above average. At Babine Lake there appear to be differences between river and lake in the availability of sockeye fry and in the average fry content of predator stomachs. The growth of 37 rainbow trout from the Upper Babine River and 31 from the North Arm was backcalculated from scales using the formula:

$$L_n = I + \frac{L_t - I}{S_t} S_n$$

where L_n is the length of the fish at the end of the *n*th year of life, I is the intercept of the body scale relationship, L_t is the length of the fish at capture, S_t is the length of the anterior radius of the scale at capture, and S_n is the length of the anterior radius of the scale within the *n*th annulus. I in this instance was 41 mm. The growth data (Table V and Fig. 22) indicate that trout from the river grow faster than those in the lake although the length–weight relation-

TABLE V. Calculated fork length (mm) at end of each year of life of rainbow trout from the Upper Babine River (U.R.) and the North Arm(N.A.) of Babine Lake.

Age-group	Number of fish: U.R.	Number of fish: N.A.	Calculated length: Mean: U.R.	Calculated length: Mean: N.A.	Calculated length: Range: U.R.	Calculated length: Range: N.A.
I	37	31	75.0	71.3	61.5–92.6	56.8–93.6
II	37	31	115.1	108.5	90.0–140.2	85.1–146.1
III	37	22	194.0	170.8	123.6–245.4	118.5–212.0
IV	36	15	278.3	238.7	179.4–304.6	174.2–300.6
V	10	5	314.4	273.7	268.1–354.0	211.2–333.6
VI	2	0	418.7	–	401.4–436.0	–
VII	1	0	442.8	–	418.7	–

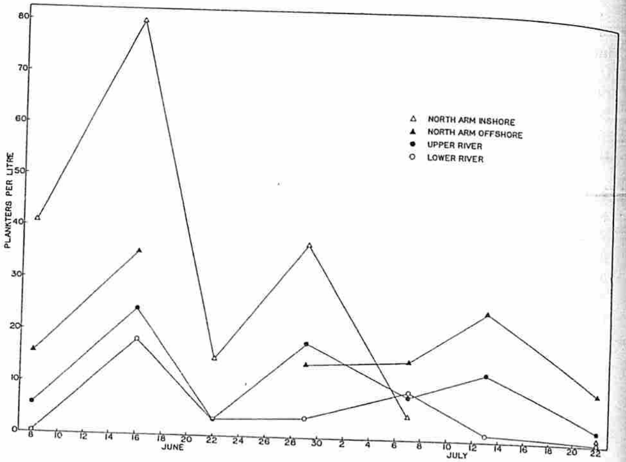

FIG. 22. The abundance of plankton in samples taken in various parts of the Babine River–North Arm area in 1965.

ships are similar (Fig. 22). The length–weight data are from 77 Upper River and 53 North Arm trout and are expressed as the mean weight of fish in each centimeter length class.

Possibly the difference in growth rates results from the greater availability of salmon eggs and salmon fry to the river trout. This hypothesis presumes that the two populations do not mix to any extent and that the two samples are representative of rainbow trout in their respective areas, two assumptions that cannot be justified at present.

Fish were not the only predators on fry in the rivers. The American merganser and Bonaparte gull were frequently observed in the river and in the area around Smokehouse Island, where they appeared to be feeding on sockeye fry. On several occasions the robin, *Turdus migratorius*, was seen pecking at fry at the cutbank in the Lower Babine River. The river at this point was particularly fast and many fry moved upstream within a few inches of the bank. The robin is certainly not a habitually aquatic feeder and its apparent success in capturing sockeye fry again emphasizes the latter's vulnerability to predation while in the river. Aside from these observations no detailed study was made of avian predation during 1964 and 1965. There is, however, some additional

information available on bird predation in the Babine River–Nilkitkwa Lake area during the 1953 and 1954 (V. I. F. Allen, unpublished report at the Biological Station, Nanaimo). This information is summarized in Table VI.

Except for Barrow's goldeneye, each of the species examined was found to be feeding occasionally on fish. In six species, these were highly identifible sockeye fry. Although the stomach analyses indicate a rather high fry consumption in some species, particularly some of the gulls, none was particularly abundant and Allen comments, " . . . it is believed that the information available shows that due to immense numbers of prey available, coupled with a limited bird predator population, it is possible that no serious bird predation problem exists." The author's own observations confirm this. Predation by fishes would appear to be a much more important factor in the mortality of sockeye fry in this area.

COMPARISON WITH FRY MOVEMENTS IN SOME OTHER AREAS

Upstream migrations of sockeye salmon fry occur widely in North America. Sizeable upstream movements have been observed in the Karluk River on Kodiak Island, Alaska, the Wannock River draining Owikeno Lake on the British Columbia coast (Foskett, 1958), the Chilko River in the Fraser system, the Little River below Shuswap Lake, B.C., as well as the Upper and Lower Babine rivers described herein. Each of these upstream fry migrations numbers many millions. Other, smaller upstream populations are known to occur. The upstream movements of sockeye fry in the Karluk and Chilko rivers have been investigated by the Fisheries Research Institute of the College of Fisheries, University of Washington, and the International Pacific Salmon Fisheries Commission respectively. Information relating to the Karluk migration was communicated by C. Walker, formerly of the Institute. The description of the Chilko run is taken from Andrew and Geen (1960) and personal communications from J. Roos of the Salmon Commission.

In general, the upstream migrations in both the Karluk and Chilko are very similar to that in the Babine rivers. There is an initial downstream movement of fry, a period of holding, and an eventual return upstream. In the Chilko, fry emerge at night and move downstream until they reach areas of low velocity along the river edge where they hold. Seven to 10 days elapse between the emergence of fry and their movement upstream. Fry moving upstream average several millimeters longer than downstream migrants.

Figure 23 illustrates the mean daily water temperatures and the seasonal periodicity of upstream movement in the Chilko River during 1958, 1959, and 1960, three representative years. Over the years, it has been observed that the upstream movement of fry does not begin in earnest until the mean daily water temperature exceeds 4 C and that in most years the run is over or in decline before the mean temperature exceeds 8 C. Ordinarily, water temperatures increase gradually from late April through June with relatively little day-to-day temperature change. Rarely do temperatures fluctuate over 1 C from one day

TABLE VI. Stomach contents of birds collected by I. V. F. Allen in the Babine River–Nilkitkwa Lake area in 1953 and 1954 with some census information indicating the abundance of each species within the area. The census data indicate first, the maximum number of birds seen on any single day and second, the mean number per day for several censuses made during the months of May, June, and July each year.

Species	No. stomachs examined	No. empty	No. with fish	Stomachs with sockeye fry (%)	Total fry	Average fry per stomach	Census results May–July			
							1953		1954	
							Max.	Mean	Max.	Mean
Common loon (*Gavia immer*)	1	0	1	0	0	0	5	3.3	5	3.0
Red-necked grebe (*Colymbus grisegena*)	7	1	1	0	0	0	6	4.0	14	–
Barrow's goldeneye (*Glaucionetta islandica*)	4	0	0	0	0	0	11	4.4	–	–
American merganser (*Mergus merganser*)	8	1	7	25	6	.7	14	7.0	10	6.4
Herring gull (*Largus argentatus*)	5	3	1	0	0	0	2	1.2	3	2.4
Ring-billed gull (*Larus delawarensis*)	2	0	2	100	19	9.5	1	1.0	5	4.0
Short-billed gull (*Larus canus*)	7	0	5	43	145	20.7	3	1.7	3	2.6
Bonaparte gull (*Larus philadelphia*)	10	1	4	20	78	7.8	16	5.3	27	16.8
Black tern (*Chilidonias nigra*)	6	0	4	17	11	1.8	16	8.3	13	7.3
Belted kingfisher (*Megaceryle alcyon*)	3	0	3	0	0	0	5	1.8	2	1.6
Harlequin duck (*Histrionicus histrionicus*)	2	0	1	50	6	3.0	2	1.5	2	1.7

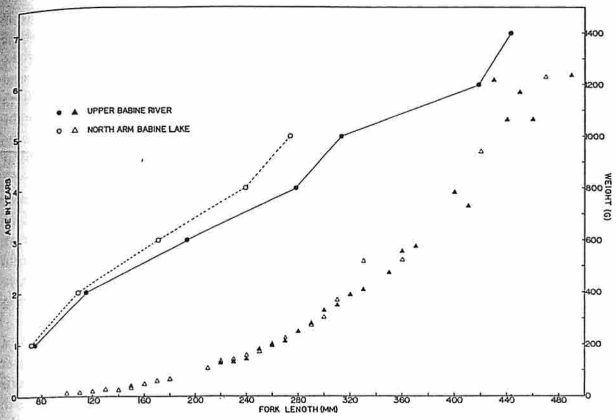

FIG. 23. Length–weight relationships (triangles) and calculated growth (circles) of rainbow trout taken in the Upper Babine River and the North Arm of Babine Lake 1965.

to the next. Small temperature surges do occur, however, and in some years, for instance 1960, there is evidence of a correspondence between water temperature peaks and upstream movement. Aside from such relatively minor fluctuations, the periodicity of upstream movement is broadly peaked and unimodal. Upstream movement generally occurs over about 50 days, from May to mid- or late June. In 1958, when water temperatures were unseasonably high, the upstream migration began April 27 and ended before June 1.

As in the Babine rivers, the upstream movement of fry in the Chilko River appears to be almost entirely confined to the river bank. Andrews and Geen (1960) describe the fry as moving upstream in shallow water not more than 0.46 m from shore at an average rate of 7.9 cm/sec against average water velocities of about 16.5 cm/sec.

The diel pattern of upstream movement in the Chilko is characterized by a sharp peak of activity at about 0500 hr, a mid-morning depression, and a period of moderate activity through the mid- and late afternoon. Fry are active from about 0300 hr to 2300 hr. This pattern is similar in many respects to that of fry in the Upper Babine River. One feature not observed at Babine is the occasional movement downstream along the banks of large numbers of fry known to have recently migrated upstream. The reason for this is unknown.

Fry emergence in the Karluk River is also largely nocturnal. After emergence, fry move downstream some distance before becoming associated with the stream banks where they accumulate in pool areas. During May and June fry move upstream along the banks. These fry are about the same length as newly emerged fry. During this early summer period, traps placed along the banks capture upstream migrants day and night. There is usually a second upstream movement of fry from late July to at least the end of August and, in one year, into October. These fry could be trapped at any point across the width of the stream and were not readily seen. In neither the Babine nor Chilko Rivers is there any significant offshore upstream movement of fry. The traps at Karluk were suspended from a weir which blocked the entire width of the stream and the fry may have been captured while searching along the weir for an easy passage through. Such behaviour was often seen in the Babine River wherever the passage upstream was practically blocked. The Karluk late-run fry had a mean fork length of 50–55 mm in comparison with the 31 mm of the earlier run. These late season migrants are thought to be fry which have remained for some time in the quiet, weedy sections of the stream before moving up.

An interesting variation in upstream migrations occurs in Morris Creek, a tributary of the Harrison River draining Harrison Lake in the lower Fraser River area (Andrews and Geen, 1960: Ricker, 1960). Fry emerging into Morris Creek or entering it from Weaver Creek, a tributary, first move downstream into the Harrison River. Some apparently remain in the sloughs bordering the Harrison River but others move upstream into Harrison Lake where they remain until smolting.

The upstream movement in the Little River (Andrews and Geen, 1960) is even more complex. Fry emerging in the Little River are borne downstream into Little Shuswap Lake where they remain for several weeks before reentering the river and migrating upstream into Shuswap Lake. Fry from the South Thompson River, below Little Shuswap Lake, pass upstream into Little Shuswap Lake and may continue upstream through the Little River into Shuswap Lake. In addition, there are indications that fry moving downstream from the Adams River, which enters Shuswap Lake near where the Little River flows out, are occasionally swept down into the Little River and must then move upstream to reenter Shuswap Lake. Fry in the Little River, which have lingered for some time in Little Shuswap Lake and are larger at the time of upstream movement than Chilko River fish, have been observed as much as 3 m offshore in water velocities of 30–60 cm/sec.

Some mention should be made of certain streams in which sockeye fry are known to hold along the stream edges for a time although upstream movement apparently does not occur and the fry eventually move downstream into lakes. Hartman et al. (1962) describe fry holding along the edges of Hidden Creek close to where the stream enters Brooks Lake. None of these remained more than a single day and all of them moved on downstream at nightfall to be replaced at dawn. Fry are known to frequent the stream edges for longer periods of time in the Brooks River between Brooks Lake and Naknek Lake (W. Heard, personal communication). Passage upstream into Brooks Lake is blocked by a small falls (not impassable to adult sockeye) and the fry ultimately move downstream. In the Agulowak River in the Woods River system, Alaska, another river between two lakes, sockeye fry often remain for long periods before eventually moving downstream, some 50 mm or larger (Burgner and Green, 1963). Burgner (1962) has also described fry in some of the smaller spawning tributaries of the Wood River system which attain considerable growth before moving downstream. In other downstream situations such behaviour has not been observed. For instance (A. Coburn, personal communication), at Williams Creek, Lakelse Lake, B. C., an intensive search of several miles of stream bank failed to turn up a single fry during the height of the spring outmigration. Holding fry are equally rare in Scully Creek, another tributary of the same lake. In the Fulton River no more than a few isolated individuals have been holding along the stream edges during the day, either upriver or in slower parts of the stream close to where it enters Babine Lake (G. Wilson and J. MacDonald, personal communication).

It is very difficult to identify features which are typical of rivers supporting large upstream migrations. The water may be clear as in the Upper Babine River or somewhat turbid as it is in the Wannock River draining glacial Owikeno Lake. Holding areas may be abundant (Upper Babine River) or sparse (Lower Babine River). Water temperatures during the migration may be relatively high with large day-to-day fluctuations (the Upper Babine River) or low with little day-to-day variability (Chilko). The migration itself may be seasonally very early (Chilko) or very late (the Upper Babine River and the Karluk late run). The most important environmental factor limiting upstream migration would appear to be water velocity. None of the streams with a large upstream migration is particularly swift and where high velocity sections occur, fry seem to experience great difficulty. Andrews and Geen (1960) state, ". . . in any river where sockeye fry are required to migrate upstream to their rearing lake, continuous marginal paths in which the velocity does not exceed 0.5 fps (15.2 cm/sec) for a distance of 1.5 ft (46 cm) should be available." These represent ideal conditions and fry have been observed, in the Babine Rivers and in other areas, passing through short stretches of water in which water velocities considerably exceeded this. However, there is little doubt that prolonged exposure to high velocities would severely limit upstream movement.

COMPARISON WITH FRY MOVEMENTS IN THE FULTON RIVER

The Fulton River flows from Fulton Lake into the main body of Babine Lake (Fig. 1). The upstream movement of spawning sockeye is blocked by an impassable falls immediately below Fulton Lake and the entire fry population of the river moves downstream into Babine Lake. The Resource Development Branch of the Department of Fisheries of Canada has studied the sockeye population of this stream since the fall of 1961. There is thus a considerable body of information available for comparison with what is known of sockeye salmon in the Upper Babine River.

In the Fulton River, the spawning of sockeye salmon occurs over a 6–8 week period from about September 1 to the latter part of October. Spawning ordinarily peaks during the last week in September but may be delayed, as it was in 1963, when water temperatures remained unseasonably high. In the Upper Babine River the spawning period is the latest in the Babine system extending from about October 1 to the last week in November and occasionally into December. Spawning in this river peaks about October 20. The periods of fry emergence in the two rivers correspond in their order to that of spawning: in the Fulton River from May to mid-June with a peak during the last week in May; in the Upper River from early May to at least mid-July with the mid-point about June 15.

As previously indicated, the seasonal periodicity of downstream sockeye fry movements in the Fulton River is closely related to spring discharge patterns. Figure 7 illustrates the seasonal periodicity in 1964 only, but the pattern is typical of that during 1962, 1963, and 1965. In each of these years the downstream run reached its peak during a period of high discharge, declining precipitously thereafter. In the Upper Babine River, water temperatures seem to have the greatest influence on seasonal patterns of emergence and downstream movement.

Northcote (1962) found that water temperature was the single most important factor determining the current responses of juvenile rainbow trout. These fish were able to hold position and move upstream only where water temperatures were relatively high (daily maximum usually 15 C). Northcote (1962) demonstrated first, that there were consistent differences in the seasonal temperature regimes of streams inhabited by upstream and downstream populations and, second, that these were of sufficient magnitude to affect the behaviour of fry. Figure 24 compares the seasonal temperature regimes of the Fulton River and the Upper Babine River during the spring and early summer of 1964 and 1965. The durations and approximate midpoints of the downstream fry runs in the two rivers are indicated.

The most obvious difference in the seasonal temperature patterns of the two streams is the contrast between the smoothly increasing water temperatures of the Fulton River and the fluctuating temperature of the Upper Babine River. However, though water temperatures in the Upper Babine River exceeded those in the Fulton River during peaks, the mean temperature of the Fulton River during the period May 1 to July 15, 1964 was higher than that of the Upper River. The 1965 data do not extend beyond June 21 but a similar pattern was emerging. A simple comparison of seasonal temperature regimes is, however, not entirely satisfactory because of differences in the timing of emergence and downstream movement in the two rivers. In both 1964 and 1965, Fulton River fry emerged and moved downstream in appreciable numbers earlier in the season and at lower temperatures than Upper River fry. If water temperature were a major factor in determining the current responses of sockeye fry in the Fulton River it should be demonstrable that the temperatures prevailing during the period of fry emergence were so low as to preclude holding and upstream movement. The evidence suggests that this is not so.

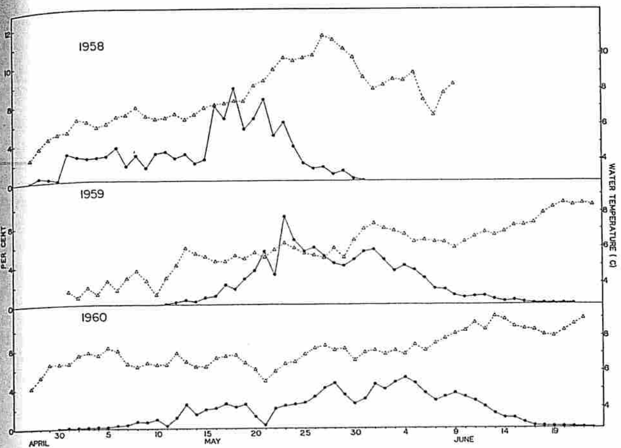

FIG. 24. The seasonal temperature regimes (triangles) and the seasonal periodicities of upstream fry movements (circles) in the Chilko River, 1958 through 1960. Data supplied by J. Roos of the International Pacific Salmon Fisheries Commission.

In the Upper and Lower Babine rivers fry have been observed holding position throughout the night at water temperatures as low as 5 C. Active upstream migrations occurred at the same temperatures. In the Chilko River, major daily upstream runs occur at temperatures of 4 C. Under experimental conditions, the current response of sockeye fry has been found to be remarkably consistent over a wide range of temperatures. Keenleyside and Hoar (1954) observed a marked, positive rheotaxis over a temperature range of 4 to 24 C. Brett et al. (1958) found that fry would orient to, and swim with, a moving background at temperatures from 1 to 24 C, almost the entire range of temperature tolerance of the species.

For purposes of argument, 8 C would seem to be a temperature at which most sockeye fry could either maintain position along the stream edge or move actively upstream. In the Upper Babine River large numbers of fish have been observed holding and moving upstream at temperatures less than this and in the Chilko River, in some years, mean water temperatures during the upstream fry migration never reach 8 C. At this temperature, the maximum sustainable cruising speed of juvenile sockeye is approximately 75% of the maximum sustainable effort at any temperature (Brett et al., 1958). An analysis of the Fulton River fry catches for 1964 and 1965 reveals that respectively 28.1%

and 59.9% of the total fry output passed downstream on days when the mean daily water temperature exceeded 8 C. The estimated runs were about 39 million in 1964 and 25 million in 1965. If a significant proportion of these fry were holding along the banks they would have been readily apparent. In spite of this, none were seen and very few could have been present.

It might be argued that it is not simply the absolute water temperature but the occurrence of sharp fluctuations which effects the holding response and upstream migration in sockeye fry. Northcote (1962) suggest that sudden rises in temperature may act as a directing factor for rainbow trout fry, orienting their movements in an upstream direction. If this kind of mechanism is operative then we should expect a much higher degree of holding and upstream migration in streams like the Upper Babine River where sharp rises in temperature do occur, than in streams such as the Fulton in which temperature changes are more regular. The evidence suggests, however, that large upstream movements of sockeye fry can occur in the absence of extreme temperature surges. In the Upper River, for instance, fry moved upstream during periods of stable and even falling water temperatures. In the Chilko River, which has a large upstream movement, there are in many years, only relatively minor fluctuations in temperature during the course of the upstream migration.

GENERAL DISCUSSION

The published descriptions (Hoar, 1958; McDonald, 1960; Hartman et al., 1962; Heard, 1965) of the behaviour of sockeye salmon fry during emergence and downstream migration can be summarized as follows. (1) The fry are negatively phototactic and during the day most remain either buried in the gravel or hidden in shaded holding areas along the stream banks; (2) with the coming of darkness those fry which are ready to migrate emerge from their hiding places and exhibit a marked negative rheotaxis, swimming downstream; (3) downstream migrants act as individuals while migrating and do not school. As a result of this pattern of behaviour, newly emerged fry very rapidly leave the spawning stream and enter the lake nursery. In most instances, the journey is probably completed in a single night.

Once in the lake, the behaviour of juvenile sockeye salmon changes radically. The fish abandon their previously solitary habits and form schools. Fry in schools show less cover response and remain, swimming and feeding, in brightly lit areas. They are positively rheotactic and are able to maintain position in strong currents (Keenleyside and Hoar, 1954).

Hoar (1958) suggests that these changes in the behaviour of older fry, coupled with an increase in size and swimming ability, might explain upstream migration. The behaviour of upstream migrants in the Babine rivers is, in fact, very similar to that of downstream migrants after they enter lakes: they form schools, they move and feed in the open, they react positively to current and hold position during the night. In addition, fry moving upstream are generally larger than those moving down. However, it is difficult to see how fry emerging in a situation such as that in the Lower Babine River could survive unless they were immediately possessed of these behavioural characteristics. If, as Hoar (1958) suggests, they were subject to progressive development and if fry were borne downstream before these characteristics appeared, catastrophic mortalities would occur. In the Lower Babine River the major spawning beds are only a short distance above the adult enumeration weir, an easy night's journey even if fry were being borne passively downstream. Some fry are swept through the weir but millions more reach the river banks and survive to move upstream into Nilkitkwa Lake. The Babine River studies support Hartman et al. (1962) who, commenting on the upstream movement of sockeye fry in the Karluk River, states, "Apparently schooling and the adaptive changes to positive rheotaxis and loss of negative rheotaxis associated with it take place before the emerging fry reach the sea, or perhaps before they move very far from the redd sites." There is apparently a precocious development of behavioural responses which, in fry from typical downstream situations, are acquired only after the fry have left the stream and entered the lake.

Northcote (1962), in his study of the migratory behaviour of juvenile rainbow trout at Loon Lake, B.C., concluded that the differential responses

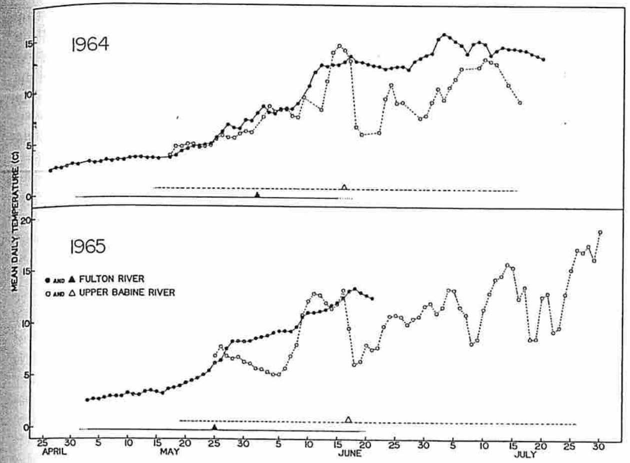

FIG. 25. Mean daily water temperatures of the Upper Babine and Fulton Rivers during the period of fry movements in 1964 and 1965 with the duration and approximate midpoints of emergence and downstream movements.

of upstream and downstream migrants to current were primarily regulated by water temperature. Temperature had a twofold action: it set limits within which upstream migration could occur and it affected the timing and intensity of the responses when it did occur. There is no doubt that in the Upper Babine River water temperatures did affect the timing and intensity of upstream movement, at least seasonally though apparently not diurnally. However, there is no indication that water temperatures were so low as to absolutely preclude holding or upstream migration and fry were seen doing so at temperatures ranging from 5 C to 17 C. During the course of the downstream migration in the Fulton River, water temperatures frequently exceeded those at which large numbers of fry are able to reach the banks and hold position or even move upstream in other systems and yet this type of behaviour has never been observed. From this it would appear that water temperature differences, in themselves, do not determine the ultimate direction of migration.

Northcote was led to reject the hypothesis that there were "... genetically distinct inlet and outlet stocks, each maintaining appropriate innate behaviour responses which result in movement of young into the lake ...." In the case of sockeye fry, however, this does appear to be the most likely explanation. There are no consistently observed differences in water temperature or any other environmental factor which will explain the observed differences in the behaviour of downstream and upstream sockeye stocks. There is, in fact, evidence that under experimental conditions newly emerged sockeye fry from outlet populations have a greater tendency to move upstream than those from inlet populations (E. Brannon, personal communication).

The existence of an intermediate type of fry behaviour in which fry hold for a time along the stream edge but eventually move downstream has been noted. Possibly the development of upstream migratory habits involves selection for behavioural tendencies which exist to some degree in all stream-spawning sockeye populations.

In what situations are outlet spawning and the upstream fry migration which it entails likely to develop? In the first place an upstream migration must be a physical possibility. This appears to be primarily a question of water velocity. Second, and possibly most important, at the termination of their upstream movement the fry must enter a favourable lacustrine environment. The mortality to fry between the time of emergence and the time that they take up lake residence must be very much greater in upstream than in downstream migratory stocks due to downstream loss, to intensive predation, and, possibly, to the effects of intraspecific competition for food during the time when the fry are confined to a very limited area along the stream edge. These severe mortalities must be balanced at some period of the life cycle. Outlet streams are generally more stable than inlet streams and this probably enhances the egg-to-fry survival of outlet stocks. Even so, in highly competitive lacustrine environments already adequately supplied by spawning in inlet streams, the particular behaviour patterns which facilitate upstream migration may be at a selective disadvantage.

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NOTES

Lethal Endrin Concentration in the Blood of Gizzard Shad

One of the persistent problems facing pollution biologists is the identification of the materials that cause fish kills throughout the country. These situations are especially troublesome in areas of concentrated populations and/or industries that compound the possible sources of pollution. In many cases the actual cause is a slug release of a toxicant that has been diluted and passed beyond the location where dead fish and water samples would be collected at least several hours after mortality occurred. Autopsy methods based on analyses of fish tissues can provide the information necessary to identify the specific toxicant. Previous techniques for zinc-caused fish mortality (Mount, 1964) and endrin toxicity to channel catfish (Mount et al., 1966) have been established at the Newtown Laboratory, Federal Water Pollution Control Administration.

In the studies being reported, additional information was sought on autopsy techniques and the feasibility of using gizzard shad, *Dorosoma cepedianum* (LeSueur), as a test species was explored. This species has an extensive range and is very common in the eastern half of the United States. It is also frequently involved in fish kills, apparently being relatively more sensitive than other species to many toxicants. Irwin (1965) determined that of 57 species of fish, gizzard shad is the least resistant to petroleum refinery effluent, and he considered them to be undesirable as a test animal.

Adult gizzard shad, 8–12 inches in length, were collected in April 1965 from Rocky Fork Lake in southern Ohio by means of a fish trap utilized by the Ohio Division of Wildlife for fish population estimates. The shad were in these traps for up to 24 hr before being placed in holding tanks for the 50-mile trip to the laboratory. These fish were observed and treated with antibiotic for 2 weeks before experimentation began. During this time and the additional 2 weeks of exposures, mortality due to causes other than endrin was less than 10%.

The test water was carbon-filtered tap water that was held in a 100,000-gallon outdoor concrete reservoir for about 2 months before use. This water, maintained at about 16 C, was passed to a constant-head box connected to a serial dilution apparatus (Mount and Warner, 1965) that established five endrin concentrations and a control. The chemical characteristics of this test water were 5.4 mg/liter dissolved oxygen, *p*H of 7.5, alkalinity of 45 mg/liter as $CaCO_3$, acidity of 3 mg/liter as $CaCO_3$, and hardness of 128 mg/liter as $CaCO_3$. Results were obtained by previously described procedures (American Public Health Association, 1960).

A total of 31 blood samples from 39 laboratory-exposed fish were analyzed for endrin. When more than one fish died in a test chamber and there was in-

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