MIGRATORY BEHAVIOUR OF JUVENILE RAINBOW TROUT,
SALMO GAIRDNERI, IN OUTLET AND INLET STREAMS
OF LOON LAKE, BRITISH COLUMBIA

by

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MIGRATORY BEHAVIOUR OF JUVENILE RAINBOW TROUT SALMO GAIRDNERI, IN OUTLET AND INLET STREAMS OF LOON LAKE, BRITISH COLUMBIA

ABSTRACT

The marked differences in response to water current, exhibited by juvenile rainbow trout migrating into Loon Lake from its outlet and inlet streams, were studied both in the field and in experimental laboratory apparatus. All available evidence argued against genetically discrete outlet and inlet stocks, each maintaining innate responses to water current. Difference in water temperature between streams was shown, in field and laboratory experiments, to regulate direction of juvenile trout migration through action on behaviour associated with downstream movement, maintenance of position and upstream movement.

In laboratory experiments with cool (5°, 10°C.) flowing water, recently emerged fry rarely made contact with the stream bottom in darkness and exhibited much more downstream movement than in warm (> 14°C.) water. In cool streams of the Loon Lake system (daily mean consistently < 13°C.) large numbers of recently emerged fry moved downstream in darkness. Laboratory experiments indicated that combination of cool water (10°C.) and long day length (16 hours) induced downstream movement of fingerlings. In the field, fingerlings moved downstream largely in late spring and summer in cool streams of the Loon Lake system.

In laboratory experiments with warm (15°, 20°C.) flowing water, recently emerged fry made frequent contact with the stream bottom in darkness and exhibited much less downstream movement than in cool (10°C.) water. In the warm outlet stream (daily mean in summer usually > 15°C.) recently emerged fry maintained position in darkness. Laboratory experiments suggested that short day length (8 hours) may facilitate maintenance of position exhibited by fingerlings in streams during late autumn and winter.

Upstream movement of fry tested in the field and laboratory was most pronounced in warm water (> 14°C.). Fingerlings subjected to rapid 5 C.° increases in water temperature in an experimental stream exhibited an immediate increase in upstream movement. Upstream movement in summer of large fry and fingerlings occurred only in the warm outlet stream; daily periodicity of upstream movement was positively correlated with sharp rises in water temperature.

Evidence examined from four other widely separated stream systems indicated an environmental control of migration in juvenile rainbow trout similar to that demonstrated in the Loon Lake stream system. Possible mechanisms and interaction of factors controlling migratory patterns between and within streams are discussed. Significance of the predominant role played by temperature is considered.

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In laboratory experiments with cool (5°, 10° C.) flowing water, recently emerged fry rarely made contact with the stream bottom in darkness and exhibited much more downstream movement than in warm (> 14°C.) water. In cool streams of the Loon Lake system (daily mean consistently < 13°C.) large numbers of recently emerged fry moved downstream in darkness. Laboratory experiments indicated that combination of cool water (10°C.) and long day length (sixteen hours) induced downstream movement of fingerlings. In the field, fingerlings moved downstream largely in late spring and summer in cool streams of the Loon Lake system.

In laboratory experiments with warm (15°, 20°C.) flowing water, recently emerged fry made frequent contact with the stream bottom in darkness and exhibited much less downstream movement than in cool (10°C.)

water. In the warm outlet stream (daily mean in summer usually $> 15^{\circ}\text{C}.$) recently emerged fry maintained position in darkness. Laboratory experiments suggested that short day length (eight hours) may facilitate maintenance of position exhibited by fingerlings in streams during late autumn and winter.

Upstream movement of fry tested in the field and laboratory was most pronounced in warm water ($> 14^{\circ}\text{C}.$). Fingerlings subjected to rapid $5^{\circ}\text{C}.$ increases in water temperature in an experimental stream exhibited an immediate increase in upstream movement. Upstream movement in summer of large fry and fingerlings occurred only in the warm outlet stream; daily periodicity of upstream movement was positively correlated with sharp rises in water temperature.

Evidence examined from four other widely separated stream systems indicated an environmental control of migration in juvenile rainbow trout similar to that demonstrated in the Loon Lake stream system. Possible mechanisms and interaction of factors controlling migratory patterns between and within streams are discussed. Significance of the predominant role played by temperature is considered.

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I. INTRODUCTION

The phenomenon of migration--large-scale movement of animals from one place of habitat to another at some reasonably well-defined stage in their life history--has intrigued early naturalists (Bertin, 1956) and claimed attention of zoologists in many fields particularly since the turn of the century. Spectacular, long range migrations exhibited by such diadromous fish as eels and salmon have received a good portion of this interest (Fontaine, 1954). Less attention has been devoted to equally challenging but less dramatic migration of fish strictly within freshwater (Hoar, 1953). Moreover it has been customary to think of many fish migrations, even in freshwater species, as an active upstream movement of maturing adults towards a spawning site and a more or less passive downstream transport of young and surviving adults (Russell, 1937). Few studies have been carried out on a species, some of whose adults in one lake system migrate up inlet streams and others down an outlet stream at spawning time, and whose young in order to take up lake residence must at some stage move downstream from one hatching site and upstream from the other.

Rainbow trout are known to spawn both in the outlet and inlet streams of several lakes in British Columbia. Mottley (1931a) noted the occurrence of inlet and outlet spawning trout at Pinantan Lake near Kamloops. Lindsey, Northcote and Hartman (1959) have studied

homing of trout to inlet and outlet spawning streams at Loon Lake. Spawning trout have been trapped for fish-cultural purposes by the British Columbia Fish and Game Branch on both outlet and inlet streams of several other lakes such as Pennask and Knouff. Rainbow trout spawning runs are known to occur in outlet and inlet streams of Wasilla Lake in Alaska.

The phenomenon of fish spawning both in an outlet and inlet of one lake is not limited to rainbow trout. Such migratory behaviour may occur in brown trout, Salmo trutta (Lake Rensjö¹⁸, and other Swedish lakes--Runnström, 1952), cutthroat-rainbow hybrids and grayling, Thymallus arcticus, (Grebe Lake, Wyoming--Kruse, 1959), sockeye salmon, Oncorhynchus nerka (Owiken Lake--Foskett, 1958; Babine Lake--Johnson, 1958), white suckers, Catostomus commersoni (Cluculz Lake--Geen, 1958) and in longnose suckers, C. catostomus (Bouchie Lake--Geen, 1958).

The mechanism whereby the juveniles move upstream or downstream, as the case may be, to enter the lake has only rarely been considered. Runnström (1952) mentions the upstream and downstream migration of juvenile brown trout in Lake Rensjö¹⁸, Sweden, and notes the behavioural problem created by this phenomenon. Regardless of the details of their migratory behaviour, juveniles in outlet and inlet streams must at some stage exhibit directly opposite responses to water current in order to enter the lake. One of the fundamental problems, then, in a study of migratory behaviour in situations as outlined above, is to determine the mechanism which operates to produce such marked behavioural differences between young of the same species.

Two explanations can be postulated: (1) genetically distinct outlet

and inlet stocks, each maintaining appropriate innate behavioural responses which result in movement of young into the lake;

(2) genetically similar outlet and inlet stocks responding to environmental differences between the streams which produce appropriate current responses and other behavioural characteristics to result in movement of young into the lake.

Maintenance of genetically distinct stocks from each stream would demand an extremely high degree of homing of adults from the lake unless the majority of young resulting from straying individuals were either lost from the system or prevented in some way from reproduction with homing fish. Lindsey, Northcote and Hartman (1959) have reviewed the possibility of genetically distinct groups of trout existing in Loon Lake. As a result of (a) recovery of several marked adult strays spawning in a non-parental stream, (b) calculations of probable fractions of homing and straying fish in inlet and outlet average annual spawning populations, and (c) transfer experiments with adult spawners, they concluded that the available evidence argued against genetically discrete inlet and outlet spawning stocks.

Inlet and outlet spawning populations of rainbow trout have rapidly become established in some formerly barren lakes in British Columbia which probably were stocked with progeny reared from eggs collected at only one type of stream (personal communication, F. Pells, retired hatchery supervisor, British Columbia Fish and Game Branch). As far as it is known, young centered these lakes both from inlet and outlet streams. Spawning populations were maintained in both types of stream for some time after original stocking. If the response to current on the

part of young trout from inlet and outlet spawning stocks was largely innate and distinct in each type, then rapid establishment of both types from planting of one stock would not have been expected.

The alternate postulate is that there are genetically similar inlet and outlet stocks whose current responses are controlled largely by environmental differences between inlet and outlet streams. That no marked genetic differences may exist between inlet and outlet stocks does not, of course, imply that differential response to water current does not involve innate behavioural patterns. As Hoar (1958) has pointed out, fixed innate patterns of behaviour in fish are usually oriented or directed by a variety of environmental factors. At different intensities of a single factor or under combinations of several factors, marked alteration in behavioural response can be expected. For example, reactions of young fish to light and to water current can be greatly changed or reversed at different levels or following sudden changes of temperature (Andrews, 1946; Keenleyside and Hoar, 1954).

A study of juvenile rainbow trout migration was undertaken to obtain data both from field conditions and from controlled experiments in the laboratory which would permit critical examination of environmental control of behavioural differences in migration of young fish from outlet and inlet streams.

II. LOON LAKE STREAM SYSTEM

A. GEOGRAPHY OF THE AREA

Loon Lake is situated in a narrow valley at an elevation of 2820 feet¹ about 12 miles east of Clinton on the southern interior plateau of British Columbia. The lake is approximately 8 miles in length and varies between one quarter and one half mile in width. The shores drop off steeply to a depth exceeding 100 feet along most of the length of the lake; maximum depth is 213 feet.

The principal inlet stream enters the northeast end of the lake, draining Upper Loon Lake, about 6 miles to the northeast, and small lakes and marshes to the southeast (Fig. 1). Other very small inlet streams enter the lake, but most of these do not flow permanently. The outlet, draining the southwest end of Loon Lake, maintains a fairly level gradient to a point about 1000 yards below the lake, where it is joined by Hihium Creek which drains Hihium Lake some 8 miles to the east. Below this junction the outlet gradient increases until it drops over a series of rapids and waterfalls impassable to fish, about 4 miles from the lake.

Rainbow trout, native to Loon Lake and the only species of fish present, spawn in both its inlet and outlet streams. In Loon inlet Creek

¹

English units are used for measurement of distance commonly expressed in these terms in the field; metric units are used to describe field and laboratory apparatus.

Figure 1. Loon Lake stream system showing location of major spawning areas of rainbow trout and situation of traps.

the spawning area begins about one half mile above the lake (Fig.1), near the site of Inlet Trap 1, and extends for over a mile upstream beyond this point. In Loon outlet Creek the majority of spawning takes place in the first 1000 yards below the lake, although some fish spawn in Hihium Creek above its confluence with the outlet, and in the outlet below this junction. Movement of fish between Loon Lake and either Hihium Lake or Upper Loon Lake is probably rare and of negligible importance in this study.

B. PHYSICAL AND CHEMICAL FEATURES

1. Water Temperature

Daily maximum and minimum water temperatures are compared in Figure 2 for Loon outlet, Loon inlet and Hihium Creeks. During most of the spring and throughout summer in 1953 and 1954 Loon outlet temperatures, both maximum and minimum, are consistently higher than those in either Loon inlet or Hihium Creek. In both 1953 and 1954 (Fig. 2), maximum temperature of Loon inlet and Hihium Creek rarely exceeds 15°C. whereas Loon outlet Creek is usually well above 15°C. and frequently higher than 20°C. during most of the late spring and summer. Similar differences in temperature (not shown) are evident between these streams during other periods of study in 1955, 1957 and 1958.

Further inspection of Figure 2 suggests another major difference in temperature characteristics between Loon outlet Creek on one hand and Loon inlet and Hihium Creek on the other. Much more rapid and extensive

fluctuations in temperature (both in daily maximums and minimums) are evident in late spring and summer at Loon outlet Creek than appear either at Loon inlet or Hihium Creeks.

A more detailed comparison of interdiurnal (day to day) variability in maximum temperature between streams in the Loon Lake system was made from data available for summer months (May--August) in 1953 and 1954. Because of short lapses in recording of water temperature at Loon inlet and Hihium Creeks, separate comparisons were made between these streams and Loon outlet Creek to include as many days as possible and still restrict comparisons to days where temperature records were available from each stream. Results shown in Figure 3 confirm differences in temperature variability between streams suggested in Figure 2. A statistical means of comparing variability in frequency distributions of temperature change shown in Figure 3 can be made by examining the ratio of their variances, larger/smaller (Snedecor, 1956). In each comparison, changes in temperature at Loon outlet Creek were significantly more variable than at Loon inlet or Hihium Creeks ($p = < 0.01$). Tests for kurtosis indicate that the frequency distribution of temperature change at Loon outlet Creek departs from normal in a highly significant manner ($p = < 0.01$) while no significant departure was evident at Loon inlet Creek. (The highly significant and positive g_2 value obtained for the outlet curve indicates a preponderance of observations both near the mean and at each tail of the distribution.)

Loon outlet Creek is subject, at least in summer months, to variations in temperature of a greater frequency and magnitude than either Loon inlet Creek or Hihium Creek. Data given by Hofstetter (1953) shows

Figure 2. Comparison of daily maximum and minimum stream temperatures and water level at Loon inlet, Loon outlet, and Hihium Creeks.

Figure 3. Comparison of interdiurnal variability in maximum temperatures of streams in the Loon Lake system during May to August (1953 and 1954 combined).

that interdiurnal variability of water temperature of lake surfaces and outlets is much greater during the period April--September than for October--March. Unfortunately no comparison was made between inlet and outlet streams of these Austrian alpine lakes.

During some summers a decrease in water temperature was noted between the mouth of Loon outlet Creek and Outlet Trap 2 several hundred yards downstream. This decrease was evident in late spring and summer only at relatively low discharge (<10 c.f.s.) and virtually disappeared at medium or high stream levels. Maximum temperature differences between the outlet mouth and Outlet Trap 2 rarely exceeded 2.5°C . Cold springs along the stream above Outlet Trap 2 accounted for much of the temperature change noted in this portion of the outlet stream. Between early spring and late fall the entrance of cold water in Hihium Creek produced a sharp drop in outlet temperature downstream from the confluence of Hihium Creek. Stream temperatures at Inlet Trap 2 occasionally were slightly higher than those recorded at Inlet Trap 1.

2. Water Level and Discharge

Stream water levels and available data on discharge are given for 1954 in Figure 2. Water levels shown cannot be compared directly (cf. discharge and level at Loon outlet Creek and Hihium Creek on May 13), but they do illustrate general seasonal changes between streams. Daily water levels were not recorded during most of the 1953 season. Apart from the absence of excessively high levels in June, the seasonal pattern in 1953 water level was similar to that shown for 1954.

All streams have maximum annual level and discharge in June, the month of maximum rainfall in the section of the central interior plateau around Loon Lake (Chapman, 1952), with minimum discharge during winter and early spring. Hihium Creek showed the most violent fluctuations ranging from flood levels probably slightly below 50 c.f.s. to less than 1 c.f.s. Although water level (and discharge) in Loon outlet Creek is not subject to such rapid and extreme fluctuation as evident both for Loon inlet Creek and Hihium Creek, nevertheless seasonal changes in discharge are similar in the three streams.

3. Water Quality

Several samples of water were taken from Loon outlet, Loon inlet and Hihium Creeks in 1957 and 1958. Specific conductivity measurements (18°C.) were made on all samples with a type RC7 conductivity bridge. Total dissolved solid determinations were made on one lot of samples by the British Columbia Research Council. Results of all analyses are given in Table I.

Appreciable differences are present in the dissolved solid content of water from the three streams. Loon inlet Creek has the highest total dissolved solid content, while Hihium Creek is consistently lowest in this respect.

TABLE I. TOTAL DISSOLVED SOLIDS (PARTS PER MILLION) FOR LOON OUTLET, LOON INLET, AND HIHIUM CREEKS

Date	Loon outlet Creek	Loon inlet Creek	Hihium Creek
3 September, 1957	390*; 293**	> 400*; 420**	131*; 118**
25 June, 1958	365*		156*
25 October, 1959	392*	> 400*	147*

*By correlation with specific conductivity at 18°C.

**By evaporation analysis (British Columbia Research Council).

C. BIOLOGICAL FEATURES

1. Invertebrate Fauna

Although no extensive study was made of the invertebrates of Loon outlet, Loon inlet or Hihium Creeks, certain major qualitative differences in this fraction of their fauna became apparent after cursory examination of the streams and a limited amount of sampling.

In the first few hundred yards below Loon Lake, plankters and gammarids, probably originating from the lake, add substantially to the fauna of the outlet stream. This element has largely disappeared at the point where the outlet is joined by Hihium Creek and is not well represented in the latter nor in Loon inlet Creek. In addition to the

portion of the outlet creek fauna donated by the lake, Loon outlet, at least in the portion between Loon Lake and entrance of Hihium Creek, supports a rich "indigenous" fauna with trichopteran and simuliid larvae being particularly abundant.

Hihium Creek, on the other hand, probably supports a much lower abundance of invertebrates than does Loon outlet Creek. Caddis, simuliid and other larval and nymphal stages of insects are much less abundant than in the outlet stream. Excessive fluctuation in stream level and scouring of the bottom during flash floods characteristic of Hihium Creek may, in part, account for its reduced invertebrate fauna.

Abundance of invertebrates in Loon inlet Creek probably is intermediate between that of Loon outlet and Hihium Creeks. Gammarids were not found in any bottom or stream (floating material) samples nor in any stomachs of 125 trout fry examined from the inlet stream in 1953 (Hartman, 1954).

2. Young Trout Density

The average size of spawning populations of trout is markedly different between Loon outlet, Loon inlet and Hihium Creeks. Each year about 5,000 trout spawn in the outlet, about 22,000 in the inlet and only a few hundred at most in Hihium Creek (Lindsey, Northcote, and Hartman, 1959). Consequently far more fry emerge each year in the inlet creek than in Loon outlet or Hihium Creeks. However since the inlet has a much more extensive spawning area (Fig. 1) it is a moot point whether or not concentrations of fry per unit section of stream are actually higher in the inlet than in the outlet creek. In localized areas of the inlet

creek counts of fry along sections of stream edge were somewhat larger than in similar areas at the outlet creek. Concentrations of fry in Hihium Creek were noticeably lower than either Loon inlet or outlet Creeks.

III. OUTLINE OF MIGRATORY BEHAVIOUR

Any description, however brief, of the migratory behaviour of juvenile rainbow trout in the Loon Lake stream system immediately becomes concerned with three streams, two age groups of young fish, downstream and upstream movement, diel and seasonal patterns of movement, annual changes in some features of migration, as well as maintenance of position in streams by certain ages of young. Nevertheless it is essential to have a general picture of migration before details of young trout behaviour in any one situation may be appreciated. The following section presents in summary fashion major features of the migratory behaviour of young trout in the Loon Lake stream system. Data supporting many of the statements and generalizations will be found in later sections.

Two groups of juvenile rainbow trout were distinguished in outlet and inlet streams of Loon Lake (a) fry or young in their first calendar year of existence and (b) fingerlings or young in their second or later calendar years.

A. FRY

A comparison of migratory behaviour of fry in streams of the Loon Lake system is given in Table II. In both Loon inlet Creek and in Hihium

Creek there occurs each season an extended period of downstream (lake-ward) movement of fry. Many, but by no means all, of these individuals have recently emerged from redds. In Loon outlet Creek, on the other hand, no extensive period of downstream fry movement has been recorded in several years of observation. In some seasons virtually no downstream movement was observed while on others a limited number of fry did move downstream for a short period in June.

Behavioural characteristics of downstream movement of fry in Loon inlet Creek, Hihium Creek, and also in Loon outlet Creek were similar. In all cases movement took place almost entirely at night, involving maximum numbers during the period of maximum darkness and being appreciably affected by natural or artificial variations in nocturnal illumination. At Loon inlet and outlet Creeks fry moving downstream at night usually swam downstream head first in an erratic, disoriented manner near the water surface.

In Loon outlet Creek the majority of fry, after emergence, usually maintained position both day and night within rather restricted locations. A lateral shift in holding positions from more mid-stream areas in daylight hours to the stream margin at night was observed, but this shift did not lead to the downstream displacement of appreciable numbers of fry. Although fry in Loon inlet Creek maintained position during daylight hours, large numbers were apparently unable to do so in darkness. Fry at Loon inlet also exhibited a lateral shift in holding position, moving from more mid-stream areas occupied during the day towards the stream margin at dusk.

After spending several weeks within relatively restricted localities

TABLE II. SUMMARIZED COMPARISON OF MAJOR FEATURES OF MIGRATORY BEHAVIOUR OF RAINBOW TROUT FRY IN LOON OUTLET, LOON INLET AND HIHIUM CREEKS

Loon outlet Creek	Loon inlet Creek	Hihium Creek
No extensive period of downstream movement of fry following emergence.	Extended period of downstream movement following emergence.	Extended period of downstream movement following emergence.
Downstream movement, when occurring, takes place almost entirely at night.	Downstream movement takes place almost entirely at night.	Downstream movement takes place almost entirely at night.
Majority of fry maintain position within restricted areas of stream during both day and night for first few weeks after emergence.	Majority of fry maintain position in streams only during daylight.	Majority of fry maintain position in streams only during daylight.
After spending first few weeks following emergence within restricted locality in stream, many fry begin an active upstream migration towards and into lake during daylight hours. This movement begins in early July and ceases in late September or early October.	No appreciable upstream movement shown by fry at any time.	No appreciable upstream movement shown by fry at any time.
Many fry remain in stream over winter, entering lake as fingerlings the following spring.	Most fry enter lake during first summer and fall; few successfully over-winter in stream.	Most fry leave creek during first summer and fall.

in Loon outlet Creek, fry began an active upstream movement towards the lake, largely during daylight hours. All fry taking part in this movement exceeded 33 mm. in length and the majority were over 40 mm. long. Daily changes in intensity of upstream fry movement were positively correlated with changes in stream temperature. Fry in Loon inlet and Hihium Creeks at no time showed appreciable upstream movement.

Most fry originating from Loon inlet Creek move downstream and enter the lake during their first summer and fall. Only a relatively small number successfully over-winter in the inlet and subsequently may enter the lake the following spring or summer. Similarly, most fry from Hihium Creek move downstream at least as far as its confluence with Loon outlet during their first summer or fall. A few of these fry subsequently may enter the lake in their first fall, or over-winter in Loon outlet Creek until the following spring. Although many fry originating from Loon outlet (up to about 50% of any one year's output of young from the outlet to the lake) may enter the lake in their first summer, others still remain after cessation of upstream movement in the fall. Many of these successfully over-winter in the outlet stream and enter Loon Lake the next spring or summer as fingerlings.

B. FINGERLINGS

Major features of fingerling migratory behaviour in streams of the Loon Lake system are outlined in Table III. No appreciable movement of fingerlings down Loon outlet Creek was recorded at either of the traps above the entrance of Hihium Creek or at the trap near the falls several miles below the lake (Fig. 1). Fingerlings in Loon inlet and Hihium Creeks moved downstream sporadically in mid-summer, however the numbers involved were never large in comparison to those of fingerlings entering Loon Lake from the outlet. In the latter stream, each season, during spring and early summer, a well defined period of upstream fingerling movement was observed. The majority of fingerlings moved upstream during daylight hours with maximum numbers ascending the stream in late afternoon, near or during the period of daily maximum stream temperature. Daily fluctuations in intensity of upstream fingerling movement, similar to that for fry, were positively correlated with changes in daily stream temperature. At Loon inlet Creek, the few fingerlings which were recorded moving upstream did so largely during the day.

As most young trout in Loon inlet and Hihium Creeks move into or towards the lake in their first summer or fall, only a relatively small number of juveniles enter the lake as fingerlings from those streams. In Loon outlet Creek, however, a considerable number of young remain in the stream over winter. Many of these, during the following spring or summer, move upstream into Loon Lake.

TABLE III. SUMMARIZED COMPARISON OF MAJOR FEATURES OF MIGRATORY BEHAVIOUR OF RAINBOW TROUT FINGERLINGS IN LOON OUTLET, LOON INLET AND HIHIUM CREEKS

Loon outlet Creek	Loon inlet Creek	Hihium Creek
Many fingerlings remaining in stream in early spring.	Very few fingerlings remaining in stream in early spring.	Few fingerlings remaining in stream in early spring.
No appreciable downstream fingerling movement recorded at any period of the year.	Sporadic periods of downstream fingerling movement in mid-summer.	Sporadic periods of downstream fingerling movement in mid-summer.
Well-defined period of upstream movement during spring and early summer.	No definite period of upstream movement; occasional days on which a few individuals moved upstream.	No appreciable upstream movement at any time.
Majority of fingerlings move upstream only during hours of daylight.	Few fingerlings which move upstream, do so largely during daylight hours.	

IV. METHODS AND APPARATUS

A. FIELD STUDIES

1. Operation of Traps

Most of the information on movement of young rainbow trout in streams of the Loon Lake system was obtained by operation of traps designed to catch and hold fish of all sizes moving either upstream or downstream. Location of traps in the system is shown in Figure 1; all of these except Outlet Trap 4 retained fish moving in either direction. Inlet and Outlet Traps 1 and 2 were essentially diagonal screen fences with leads and holding boxes at each end, modified from the design of Shetter (1938). Hihium Trap 1 and Outlet Trap 4 were modified Wolf type traps (Wolf, 1951). During most periods of operation, traps were fitted with 8 mesh/lineal inch regalvanized hardware cloth which retained virtually all fry. Occasionally during high stream discharge 3/8 inch square mesh screening was used on traps in order to record movement of fingerlings under freshet conditions.

Traps were attended at least every other day and, during periods of considerable movement, every day. Young trout moving either upstream or downstream were counted and returned to the stream either above or below the fence depending on their direction of movement as indicated

by capture in the two-way traps. Periodically, samples of young trout were preserved in 10% formalin solution for later examination. All fingerlings and some fry moving through each trap were marked by removing portions of either right or left ventral fins. A distinctive fin clip was used at each trap. Although all fry moving upstream through Outlet Traps 1 and 2 were fin clipped, only a small portion of those moving downstream through Inlet Traps 1 and 2 were marked, as the majority of these were too small for effective removal of fins. Lindsey, Northcote and Hartman (1959) have given details of juvenile trout marking in streams of the Loon Lake system.

In addition to use of traps, some information on movement of young trout was obtained by observation of fish crossing standard strips placed in the stream bottom at right angles to the direction of flow.

2. Records of Environmental Conditions

Water temperature was recorded by use of continuous temperature recorders (Negretti & Zambra and Weksler) or maximum-minimum weather thermometers. The standard recording station on Loon outlet Creek was located approximately 810 feet downstream from the lake, between Outlet Traps 1 and 2 (Fig.1). Periodically other records were also obtained at each trap site on the outlet stream. Water temperature was recorded at each of the trap sites on Loon inlet Creek and at the trap on Hihium Creek.

Stream level was recorded on meter sticks firmly anchored into the stream bed at each trap site. Estimation of discharge was obtained by recording water velocity with a Leupold & Stevens Current Meter No. 111 across a stream section.

Measurement of light intensity during the day was made with a Photovolt model 200 photometer calibrated directly in foot-candles. Intensities of nocturnal illumination were determined by use of a Photovolt Model 514 M photometer fitted with phototube C and a scotopic (human eye) correction filter. Divisions on the photometric scale of Model 514 M photometer with and without scotopic filter were calibrated against those on Model 200 photometer in order to express low intensity readings in approximate foot-candle units. Use of such units to express intensity of light whose spectral composition may be different than that of the standard candle is of course open to question.

3. Nocturnal Observation

Nocturnal behaviour of young rainbow trout in streams of the Loon Lake system was observed by use of infra-red viewing apparatus. An infra-red image convertor (AN/SAR--4X) and field power supply, kindly obtained on loan from the U. S. Navy, was used for all field and most laboratory observations in darkness. War surplus infra-red lamps (Model X-264) operated from 6V car batteries were used as a source of infra-red light. The infra-red image converter, flanked on each side with an infra-red lamp, was mounted on a "Star D" swivel head tripod stand to provide a unit convenient for field use.

Experiments conducted by Duncan (1956) yielded no evidence that young coho salmon could detect or were affected by infra-red radiation. No behavioural responses of young rainbow trout were noted, either in streams at Loon Lake or in the laboratory, which suggested that these fish were affected by use of the infra-red viewing apparatus.

4. Experimental Flumes

Two galvanized metal rectangular troughs (20 x 25 x 244 cm.) were used at the confluence of Loon outlet Creek and Hihium Creek to study responses of young trout to water currents at different temperatures.

A small wing dam was constructed across Loon outlet Creek and water was led along a wooden flume to a point on Hihium Creek a few feet upstream from its junction with Loon outlet Creek. In this way a sufficient head was available to operate the two experimental flumes side by side, one supplied from a head tank with Loon outlet Creek water, the other with Hihium Creek water. Both galvanized iron flumes (painted inside with hatchery black asphaltum) were placed at a slight incline to create a flow of water over a series of baffles along their length and into a Wolf-type trap at their downstream end. Baffles divided each flume into five equal sized compartments plus one small compartment screened off at the upper end where water from each head tank was introduced. Height of baffles and incline of flume was adjusted to allow a drop in water level of about 2 cm. between each compartment. Flow into each flume was adjusted by a gate on the head tank supplying its water. Discharge through both flumes was maintained at 57 l./min. during all experiments.

B. LABORATORY STUDIES

Two basic units of apparatus were used in laboratory experiments to hold fry for observation in flowing water. The experimental chamber, constructed at the Department of Zoology, University of Cambridge, England was utilized primarily for studies on activity, vertical distribution, and bottom contact of fry. Current responses of fry and fingerlings were studied largely in the experimental stream, built at the Zoology Department, University of British Columbia.

1. Experimental Chamber

The experimental chamber consisted of a glass-sided tank in which a pumping system maintained a controllable flow of water at velocities up to 10 cm./sec. (Fig. 4A). Water was drawn off at one end of the tank and led into a temperature control basin before going to a pump and recirculating back to the tank. Water temperature was controlled thermostatically with heating and cooling coils immersed in the control basin. Upon entering the glass tank, water passed through baffles which reduced turbulence. A removable section was installed in the tank, forming a chamber 30 cm. in length, 18 cm. in width and 16 cm. in depth (Fig. 4A). The bottom of the chamber was covered with gravel, giving fry the opportunity to avoid direct flow present in the chamber. The glass tank was enclosed in a darkroom where illumination could be maintained at desired intensities. Observation of fish in darkness was accomplished by placing an infra-red light source behind the back wall of the glass tank and viewing from the front with an infra-red image convertor.

Figure 4. Laboratory apparatus used to study movement of juvenile trout in flowing water under various temperature and light conditions. A. Experimental chamber. B. Experimental stream.

Figure 4. Laboratory apparatus used to study movement of juvenile trout in flowing water under various temperature and light conditions. A. Experimental chamber. B. Experimental stream.

2. Experimental Stream

Response of young trout to water current was studied in a continuous flume 50.8 cm. wide, 35.6 cm. deep and 9.7 m. in circumference (measured at middle of channel) which extended around the perimeter of a room (Fig. 4B). Light intensity was controlled either by a Type 116 "Powerstat" in circuit with "Lumiline" incandescent lamps suspended on viewing mirrors overhanging the stream or by an iris diaphragm on an incandescent lamp housing which reflected light off the ceiling. Water temperature was controlled thermostatically by heating and cooling coils in one section of the channel. At a water depth of 15 cm. a current with a maximum velocity approaching 20 cm./sec. (mean cross-sectional velocity of about 8 cm./sec.) could be maintained in the stream channel by a screened double pumping system. Higher or lower water velocities could be maintained by alteration of water level, regulation of valves on the pumping system or operation of only one or both pumping units.

V. DOWNSTREAM MOVEMENT

A. FRY

1. Characteristics of Downstream Movement

a. Seasonal periodicity. Movement of fry down streams of the Loon Lake system is summarized for the 1953 season in Figure 5. Apart from the June period at Loon outlet Creek, no marked annual changes in seasonal periodicity of downstream fry movement in the three streams were evident for years on which data were available (1953, 1954, 1957, 1958). Similar patterns of downstream movement in 1953 were evident at both locations on Loon inlet Creek (Inlet Traps 1 and 2) and at three locations on Loon outlet Creek (Outlet Traps 1, 2, and 4; Outlet Trap 3 was not operated with fine screen during most of the season). As Hihium Trap 1 sampled between 25 to 75% of the stream discharge during most of the 1953 season, the fry total given for that trap in Figure 5 probably represents somewhat more than one quarter of the total number of descending fry.

Downstream movement of fry in Loon outlet Creek is meagre when compared to that evident in the other two streams. However, free-swimming fry are present in Loon outlet Creek by early June each year, the 1953 season being no exception. Outlet Trap 2 was not operating that year

until June 29 so downstream movement of fry prior to that date may have been missed. High discharge of Loon outlet in June and July 1954 prevented operation of traps with screen fine enough to retain all fry. Absence of descending fry at either Outlet Trap 1 or 2 in 1954 therefore cannot negate the possibility of an appreciable amount of downstream movement of fry occurring in June. To examine fry movement in June further, Outlet Trap 2 was operated effectively with fine screen for short periods (2—5 consecutive days) in 1957 and 1958. Pertinent results are included in Figure 5. Considerable numbers of fry (maximum recorded/24 hour period equals 137) moved downstream into Outlet Trap 2 in mid and late June 1957, while very few were taken during a similar period in late June 1958. No obvious difference in abundance of recently emerged fry was evident between the two years.

In both Loon inlet and Hihium Creeks there occurs each summer an extended period within which considerable numbers of young trout fry move downstream. Such movement also occurs, at least during some years, at Loon outlet Creek, but there it is apparently restricted to a few weeks in June even though recently emerged fry are usually present until early August.

b. Diel periodicity. Repeated observation on the three streams studied has shown that nearly all fry which move downstream do so almost exclusively at night. Results from trap operation over typical periods of approximately 24 hours, given in Figures 6 and 7, clearly demonstrate the sharply delineated nocturnal periodicity of downstream fry movement. Except for some data at Loon inlet Creek, no direct readings of nocturnal illumination were taken. Information on degree of darkness from field

Figure 5. Seasonal periodicity of downstream movement of rainbow trout fry in streams of the Loon Lake system. Numbers in brackets indicate total number of fry moving downstream in 1953 during period shown.

Figure 6. Diel periodicity of downstream movement of rainbow trout fry in Loon outlet and Hihium Creeks. Numbers in brackets indicate total numbers of fry moving downstream during period shown. Night hours shaded to indicate degree of darkness (based on field notes).

Figure 7. Diel periodicity of downstream movement of rainbow trout fry in Loon Inlet Creek. Numbers in brackets indicate total numbers of fry moving downstream during period shown. Night hours shaded to indicate degree of darkness (based on field notes).

notes on cloud cover, moonlight and other weather conditions have been indicated by shading within each night period.

At each stream the period of maximum downstream movement usually, but not invariably, occurred between 2300 and 0100 hours which generally included the period of lowest nocturnal illumination. Timing of maximum periods of downstream movement and other minor rises and drops in numbers of descending fry did not appear to be directly related to changes in stream discharge or temperature but instead followed characteristics of intensity of nocturnal illumination. Virtually no changes in water level were recorded during many of the observation periods. A gradual decline in water temperature occurred each night while downstream movement of fry began, reached peak intensity and ceased.

Where a more or less regular cycle in nocturnal illumination occurred between dusk and dawn, the concomitant pattern of downstream fry movement followed a sharply peaked form, without marked skewness.

Such patterns of nocturnal illumination and fry movement were evident early in the season when periods of low illumination were short. Irregular patterns of nocturnal illumination were reflected in the periodicity of downstream fry movement. When dusk was quickly followed by a period of very low illumination and then by a brighter period before dawn (often the result of heavy overcast in early evening which subsequently broke up to expose the moon) a distinct peak in downstream fry movement occurred shortly after dusk, followed by a longer period of reduced downstream movement before cessation at dawn. Examples of such patterns were seen in events of August 3-4, 1953 at both Inlet Trap 1 and 2 (Fig. 7), and to some extent on the night of July 23, 1953 at Hihium Creek

(Fig. 6). The reverse situation was evident at Inlet Trap 1 on the night of August 11--12, 1954 (Fig. 7).

Larger numbers of fry tended to move downstream on dark heavily overcast nights than on bright, moonlight nights (cf. August 11--12, 1954 with August 12--13, 1954, Fig. 7). Where nocturnal light conditions were similar, such as at Inlet Traps 1 and 2 (August 3--4, 1953, Fig. 7), the patterns of downstream fry movement also were similar.

Appreciable changes occurred throughout the season in timing of initiation and cessation of downstream movement of fry each night. In June few fry began to move downstream until 2300 hours in the evening, and the majority had ceased movement by 0300 hours the following morning. By early to mid August considerable numbers of fry began moving downstream by 2200 hours, and continued to do so until at least 0400 hours, next morning. At the end of August downstream movement began before 2000 hours and did not cease until after 0400 hours the following day. Such seasonal changes in diel periodicity of downstream fry movement are probably related to increase in the length of night throughout summer. A similar relation between nocturnal duration of downstream movement in streams and seasonal changes in day length has been suggested for sockeye fry (McDonald, 1956).

A more precise examination of the relation between levels of nocturnal illumination and downstream movement of fry is possible in some data collected at Loon inlet Creek in 1957 and 1958. Data presented in Figures 7 and 8A, B indicate that downstream movement of fry begins when light intensity falls below the 0.01 foot-candle level and ceases when illumination rises above that level with the approach of dawn. Changes in nocturnal illumination within the 0.0001 to 0.001 foot-candle range

Figure 8. Initiation of downstream movement of rainbow trout fry in Loon Inlet Creek. A, B: downstream fry movement into inlet Trap 1. C, D: downstream fry movement as indicated by counts (infra-red viewing) of fry passing over standard counting strips on stream bottom.

are apparently expressed in degree of downstream fry movement as evidenced in Figures 7 and 8A, B.

A separate measure of diel periodicity in downstream fry movement, unaffected by operation of traps, was afforded by counts of fry moving downstream over standard strips placed on the stream bottom. Thin strips of wood or aluminum, 5 x 30 cm., were firmly anchored onto the stream bottom. Observations and counts of fry passing over such strips were made with binoculars until light conditions required use of infra-red viewing apparatus. All counts were made for five minute intervals.

Data for two successive nights are presented in Figure 8 C, D. Strip count data on initiation, rise to maximum and partial decline in numbers of fry moving downstream on the night of August 30, 1958 (Fig. 8C) agree closely with observations on fry movement based on trap operation (Fig. 8B) during the same evening. Light intensity at the start of fry movement across strips is also below the 0.01 foot-candle range.

c. Size relationships. Length--frequency distributions of fry which were taken while moving downstream in Loon inlet, Loon outlet and Hihium Creeks are given in Figure 9. The majority of fry moving downstream in all streams ranged between 20 and 30 mm. in length. Information obtained from redd samples of alevins and lengths of free-swimming fry which still retained vestiges of the yolk sac indicated that the free-swimming stage was not reached in these streams until the young attained a length of at least 20 mm. Thus it is probable that most fry involved in downstream movement have only recently become free-swimming.

Some seasonal changes in length--frequency distribution are evident

Figure 9. Length-frequency distribution of rainbow trout fry moving downstream in Loon inlet, Loon outlet and Hihium Creeks.

in data on downstream movement of fry at Loon inlet Creek (Fig. 9). Although fry in the 20--30 mm. size range still dominate total numbers of those moving downstream in mid-August to early September, considerable numbers of larger fry were also taken. After early September, at the close of fry emergence, a gradual shift took place in length--frequency distribution of fry which moved downstream. By the third week in September the modal group had exceeded 35 mm.

The length distribution of fry moving downstream over a twenty-four hour period was determined from samples collected at frequent intervals at Inlet Traps 1 and 2 during August 3--4, 1953. Respective length--frequency distributions of descending fry were similar for both traps. The few fry which moved downstream during daylight hours were largely in the 30--45 mm. length range. With the onset of darkness, considerable numbers of fry, ranging between 20 and 30 mm. in length, began moving downstream. The contributions from the 20--25 mm. size group was far greater than that from larger groups; in fact numbers of larger fry (30--45 mm.) moving downstream in hours of darkness were not greatly different from numbers in this size group which descended in daylight. The majority of fry moving downstream at night, being less than 25 mm. in length, must have emerged recently from redds.

Comparison was made between length--frequency distributions of fry collected while moving downstream at night and those collected by seining while holding position in the stream during the day. Samples of fry moving downstream in Loon outlet Creek at night contained a somewhat higher proportion of smaller individuals than evident in day samples (Fig. 10). Little difference in length--frequency distribution was

Figure 10. Comparison of length--frequency distributions between rainbow trout fry captured by seining above Loon Outlet Trap 2 during the day and those moving downstream into Outlet Trap 2 at night.

evident between similar night and day samples from Loon inlet Creek. However only small day samples were available for comparison and these may not have been representative of the total size range of fry present.

d. Extent of movement. Information on extent of downstream movement per night was obtained from fry marking experiments conducted on Loon inlet stream in 1957 and 1958.

On the morning of August 31, 1957 six hundred fry were removed from Inlet Trap 1; all these fish had moved downstream into the trap on the night of August 30. Fry were marked by "squaring-off" with fin clippers a small portion of the upper, lower or both lobes of the caudal fin, using a weak urethane solution for anaesthetizing fry. Three lots of 200 fry were marked distinctively and held in screen containers in the stream to recover for one hour. Fry were all swimming actively at the end of an hour and did not show any difficulties in maintaining position in the stream immediately following release. Lots of 200 marked fry were released in small backeddies along the bank 75, 150 and 300 feet (measured stream distance) upstream from Inlet Trap 1 at 1030 hours, August 31, 1957. A similar marking experiment was conducted on the morning of August 30, 1958 releasing two lots of 210 fry each at distances of 100 and 1000 feet upstream from Inlet Trap 1.

Results of recovery of marked fry during the first and subsequent nights following release are presented in Figure 11A. In experiments on both years no marked fry were recovered at the trap until after dusk. Many of the fry placed a short distance (75--300 feet) above the trap moved downstream into it very shortly after the period of downstream movement began. By next dawn, when downstream fry movement ceased,

between 65 and 89 percent of fry in four lots placed up to 300 feet above the trap had been recovered. A few fry from these lots were recovered amongst fry moving downstream on the second and third night following release. Only a small number of marked fry placed 1000 feet above Inlet Trap 1 were recovered there during the first two hours of overnight downstream movement. Less than a third of the fry in this group had been recovered by dawn, although recovery rose to nearly fifty percent by completion of downstream movement on the second night following release. Fry marking and recovery experiments at Inlet Trap 1 indicate that a considerable number of fry move at least several hundred feet downstream each night and that some may move well over 1000 feet downstream. Predation by larger fry and fingerlings upon the marked fry may have accounted, in part, for their reduced recovery when placed 1000 feet upstream from the trap.

Results from similar but less extensive experiments with marked outlet fry are also shown in Figure 11A. Two groups of 106 and 46 marked fry were placed 75 and 300 feet respectively upstream from Outlet Trap 2 at mid-day on June 26, 1957. Only a few of the fry introduced 75 feet upstream and none of those from 300 feet upstream were recovered after two successive nights of trap operation. Apparently extent of downstream movement of fry in Loon outlet Creek is considerably lower than that recorded at the inlet stream. Certainly fry in the outlet stream in June experienced a much shorter period of darkness than did fry in the inlet stream at the end of August and thus may have moved a correspondingly shorter distance downstream.

A field experiment was conducted to assess the effect of fry size

Figure 11. Extent of movement of rainbow trout fry down Loon inlet and outlet Creeks based on marking and recovery experiments.
 A. Recovery of marked fry following release at different distances upstream from traps.
 B. Recovery of different length groups of fry following release 100 feet upstream from Loon Inlet Trap 1.

upon extent of downstream movement in Loon inlet Creek. On the morning of August 30, 1958 a total of 420 fry were measured, marked and released 100 feet upstream from Inlet Trap 1 in a manner similar to that described above. All fry were marked by clipping a small portion off the upper lobe of the caudal fin.

Recovery results are shown in Figure 11B. A very high percentage of fry in the smallest size group had moved downstream within three hours after such movement began. A somewhat lower percentage of intermediate sized fry (26--30 mm.) were recovered, while only about twenty-five percent of the larger sized fry were taken within the same period. At the end of the second night similar differences in extent of downstream movement were maintained between small, intermediate, and large fry.

e. Orientation. As almost all downstream movement of fry occurred at night, observation of various features of fry behaviour at that time were made with infra-red viewing apparatus. The following notes summarize observations at Loon inlet and outlet Creeks during several nights in the summer and fall of both 1957 and 1958.

Observations were made on the orientation and swimming movements of fry in relation to water current as they moved downstream. The majority of fry which moved downstream did not appear to be carried passively along with the current, but rather attempted to continue swimming motions of the body. Orientation of fry in relation to direction of water flow was noted as fry approached 5 x 30 cm. strips of aluminum attached to the stream bottom. Fry were counted as "heading downstream" if they approached the strip head first, even though the angle of approach might be acute, and as "slipping downstream" if they approached tail first either at right

angles or from a relatively acute angle. Orientation counts were made for five minute intervals.

Orientation of fry moving down Loon outlet Creek was observed on three successive nights in June, 1957 for a total of ninety-five minutes. Of 29 fry observed crossing the aluminum strip during that time, 27 were "heading downstream" more or less in the direction of stream flow. At Loon inlet Creek eight counting periods were recorded on the night of August 30, 1958 and seven on the following night. Out of a total of 308 fry observed during these periods, 219 or about 71 percent were "heading downstream".

As fry heading downstream approached stones or sticks protruding from the stream bottom, they usually turned sharply and oriented actively into the current for a few seconds. This orientation often took place before the fry came into contact with the object. Fry rarely maintained position upon orientation when an object was encountered mid-stream, but merely drifted for a short time with head upstream, then turned and headed on downstream. If this orientation occurred near or at the stream edge, fry occasionally held position there for several minutes.

A characteristic feature of downstream movement was the rapid, erratic spurts of swimming in a zig-zag fashion displayed by fry as they headed downstream (Fig. 22). The majority of fry were moving at or near the surface of the stream as evidenced by their white appearance under infra-red illumination and by frequent presence of "bow-wakes" from the dorsal fin. The latter phenomenon, which was regularly observed, indicated that the fry were moving downstream at a higher velocity than the stream surface current.

2. Factors Affecting Downstream Movement

a. Water temperature.

(i) Relationships in field. The fact that fry move downstream in Loon inlet and Hihium Creeks over an extended period during the summer and fall, but do not do so in Loon outlet Creek, represents one of the key problems in an understanding of the migratory behaviour of young trout in the Loon Lake stream system. One of the most striking environmental differences between Loon outlet Creek on one hand, and Loon inlet and Hihium Creeks on the other is to be found in their temperature characteristics. Such a comparison has been made in Figure 2 for two seasons, 1953 and 1954. Observations recorded during several subsequent years have confirmed the general validity of differences shown.

During July, August and part of September when young free-swimming fry are present in all streams, water temperatures at both Loon inlet and Hihium Creeks are considerably lower than those prevalent in Loon outlet Creek. Not only are consistent differences in temperature evident between the two sets but moreover Loon inlet and Hihium Creeks rarely rise to the level of temperature exhibited by the outlet stream throughout this entire period. Thus, as can be seen in Figure 2, during most of the summer, maximum daily temperatures of both Loon inlet and Hihium Creeks, rarely exceed 15°C. At Loon outlet Creek however, even daily minimum water temperatures are usually above 15°C. during the same period. Therefore during that portion of the summer when marked differences were noted in migratory behaviour of young fry between the streams, there was in fact a consistent difference in range of water temperature between these streams (Loon inlet and Hihium Creek vs. Loon outlet). Downstream

movement of fry was associated with the streams characterized by cool water temperatures.

However fry, at least on some years, exhibit downstream movement in Loon outlet Creek during a few weeks in June. Maximum water temperatures of Loon outlet Creek during periods when appreciable downstream movement was observed (June 13--17; June 26--28, 1957) ranged between 10.6° and 16.0°C . and thus were usually well within the temperature range at which downstream movement of fry was known to occur in Loon inlet and Hihium Creeks. In 1958 when Outlet Trap 2 was operated for two consecutive days and nights (June 24--26) relatively few fry were moving downstream (Fig. 5). Water temperature of the outlet stream at that time was much higher than in the comparable period in 1957, ranging between a minimum of 20.6°C . and a maximum of 24.4°C . Thus the occurrence or absence of downstream movement of fry in Loon outlet Creek also may be related to characteristics of its water temperature.

(ii) Fry transfer experiments. The effect on downstream movement exhibited by fry of reciprocal transfer between Loon inlet and Loon outlet Creeks was studied by experiments conducted in 1957 and 1958.

Details of the transfer of fry from Loon inlet Creek to Loon outlet Creek are given in Table IV. All two hundred fry involved in the transfer had moved down Loon inlet Creek into Inlet Trap 1 during the night before and early morning of the transfer day, along with a considerable number of other inlet fry not involved in the transfer. Fry were anaesthetized (weak urethane solution) and marked by clipping a small portion off one lobe of the caudal fin. Following recovery they were moved in covered fry cans to the site of release, 75 feet above Outlet Trap 2.

TABLE IV. RAINBOW TROUT FRY TRANSFER EXPERIMENTS IN LOON INLET AND OUTLET CREEKS, 1957 AND 1958

Particulars on Transfer	Inlet to Outlet Transfer	Outlet to Inlet Transfer
Date on transfer	2 September 1957	25 June 1958
Time of transfer	0900—0930	1100—1130
Place of transfer	Inlet Trap 1 descender fry placed 75 feet upstream from Outlet Trap 2.	Fry collected near Outlet Trap 2 placed 75 feet upstream from Inlet Trap 1.
Number of fry transferred	200	174
Size range, mm.	21--30	21--30
Temperature range of "original"* stream on: (a) day before transfer (b) day of transfer	(a) 7.7°—10.3°C. (b) 8.9°—10.7°C.	(a) 21.1°—24.0°C. (b) 20.7°—22.1°C.
Temperature range of "new"* stream on: (a) day of transfer (b) day after transfer	(a) 15.6°—18.7°C. (b) 15.6°—18.8°C.	(a) 13.3°—15.5°C. (b) 12.8°—15.0°C.
Number of transfer fry moving downstream: (a) 0--24, (b) 24--48 hours following transfer	(a) 1 (b) 0	(a) 9 (b) 14
Total number of fry moving downstream in original stream 0--24 hours before transfer	7194 (Inlet Trap 1)	8 (Outlet Trap 2)

*"Original" stream refers to stream from which fry were taken; "new" stream refers to stream to which fry were transferred.

Here the inlet water in the can was gradually brought up to the temperature of the outlet stream. At this time Loon outlet Creek averaged nearly 8°C. warmer than the inlet stream. Fry were introduced into several relatively slow-flowing small pools where ready access for movement upstream or downstream was available. Fine mesh screen across Outlet Trap 2 prevented downstream movement of fry past this point without recovery in its descender trap. Most fry immediately held position at or near the site of introduction. Many were recognized (inlet fry were appreciably smaller than outlet fry at time of transfer) in the same area twenty-six hours after release and several marked individuals were captured by dip-netting at the introduction site forty-eight hours after release. As can be seen in Table IV only one of the two hundred inlet fry transferred to the outlet moved downstream into Outlet Trap 2 on the night following release, although all two hundred had descended into Inlet Trap 1 the night previously. None were taken on the second night following release. When the same number of inlet fry had received similar marking, retention, release treatment (except for a slightly shorter period in fry cans) and were placed 75 feet above Inlet Trap 1 on August 31, 1957, over eighty percent moved downstream within the first four hours of that night (Fig. 11A). Apparently a marked alteration in current response of the inlet fry had occurred subsequent to their release in the outlet stream. The most striking environmental difference between the two streams at the time of transfer was that of water temperature.

Reciprocal transfer of similar size groups of fry from outlet to inlet could not be made in late summer of 1957 as no small outlet fry

were available at that time. A summary of data relating to an outlet to inlet fry transfer conducted early the next summer is presented in Table IV. As very few outlet fry were moving downstream into outlet traps in June, 1958, individuals for the experiment were collected during the day by dip-netting. Marking and transfer were accomplished in a manner similar to that of 1957 experiments. Of the 174 outlet fry placed above Inlet Trap 1, 9 were recovered there early on the first morning following transfer and 14 others were taken after the second morning. Although large numbers of outlet fry did not move downstream in the first two days after transfer to the inlet, nevertheless this movement was appreciably higher than in the reverse transfer, and much higher, proportionally, than that taking place in the outlet stream where thousands of fry above Outlet Trap 2 were available to move downstream. Transfer of outlet stream fry into the colder waters of Loon inlet Creek apparently resulted in the occurrence of much more downstream movement than was characteristic of these fry in warmer water of the outlet stream.

(iii) Experimental flume studies. A convenient field set-up was available at the confluence of Loon outlet Creek and Hihium Creek to study the effect of their waters, which differed markedly in temperature (Fig. 2), on downstream movement of trout fry in two experimental flumes placed side by side.

Rainbow trout fry were introduced into the centre section of each flume in the early morning and left undisturbed throughout the day. At dusk fry in each compartment of the flumes and in the Wolf traps were counted and returned to the centre compartment where they were left until early the following morning. At that time fry again were counted and

returned to the centre compartment. This procedure was continued for several days on one lot of fry. Approximately fifty fry were used in each flume.

Most experiments were carried out with 1954 Loon outlet stock fry which had been reared at Loon Creek Hatchery (spring water) where summer water temperatures did not vary greatly from 9°C. One experiment utilized fry collected from Loon inlet Creek (Inlet Trap 1). The outlet fry ranged between 23 and 28 mm. in length while those from the inlet were slightly smaller.

Movement was expressed as the number of compartments fish had moved downstream or upstream from the centre compartment. A summed score was thereby obtained for movement in either direction over the interval that fry were left undisturbed. Results of flume experiments conducted from August 2--9, 1954 are given in Figure 12.

In nine out of the ten consecutive experiments, more downstream movement was shown by fry in the flume supplied with Hihium Creek water, when compared with that in the flume with Loon outlet Creek water during the same period. In the one experiment utilizing fry from Loon inlet Creek results were similar to the remainder of experiments with fry from Loon outlet Creek.

On August 8, fry which had been held in the flume with Loon outlet Creek water since the evening of August 3 were transferred to the flume supplied with Hihium Creek water and fry from the latter flume were moved to the flume with Loon outlet water. All fry were placed in the centre compartment, as in previous experiments, and were not counted until early the following morning. As can be seen in Figure 12, their

Figure 12. Downstream and upstream movement of rainbow trout fry held in identical experimental flumes, one supplied with Loon outlet Creek water, the other with Hihium Creek water.

current response during the interval was consistent with that for the new environmental situation.

Between August 10 and 11, 1954, fry distribution in the flumes, following the same methods of introduction as used previously, was checked every three hours from early morning to dusk (when fry were again returned to the centre compartments) and then periodically throughout the night. Numbers of fry moving downstream into the Wolf traps at the end of each flume increased gradually throughout the day and night.

b. Light. The effect of alternate periods of lantern light and darkness on periodicity of downstream movement of fry was tested at Hihium Creek (Hihium Trap 1) and Loon inlet Creek (Inlet Trap 1). In each experiment a 300 C.P. Coleman gasoline lantern was suspended over the stream a few feet upstream from the trap and turned off and on for two hour intervals during the night. Fry were removed from the trap and counted at the end of each two hour period. At both streams, numbers of fry moving downstream during intervals with lantern illumination were much lower than those for periods without such illumination (Fig. 13). No marked changes in natural nocturnal illumination, except those associated with setting and rising of the sun and moon, occurred during either experiment. The complicating factor of changing cloud cover was not present on nights when these experiments were performed.

c. Combined effects of water temperature and light. Laboratory studies on downstream movement of rainbow trout fry held at different acclimatization¹ temperatures and under several levels of illumination

¹Acclimatization, as used in this study, refers solely to the temperature at which fish were held and does not connote any special meaning such as that suggested recently by Fry (1958).

Figure 13. Effect of alternate periods with and without lantern illumination on downstream movement of fry in Loon inlet and Hihium Creeks.

were conducted in the experimental stream in 1955, 1957 and 1958.

In one group of experiments a 7.3 m. length of stream was utilized; the rest of the stream containing pumping and temperature control apparatus was blocked by perforated aluminum screens at each end. The bottom of the portion utilized was marked off into thirteen sections of approximately the same length by 5 cm. high baffles placed against the bottom at right angles to the direction of flow. At a total depth of 10 cm. of water in the stream, used for all experiments in this series, water velocity over each baffle averaged about 6 cm./sec.

Eggs collected from the Loon outlet spawning run in May 1955 were reared at Loon Creek Hatchery at about 9°C. until eyed when they were transported to the laboratory. Hatchery water temperature there varied between 9° and 11.5°C. throughout the course of experiments. On July 16, 1955 about 100 fry from this stock were transferred to an aquarium maintained at 15°C. ($\pm 0.5^\circ\text{C}.$); another group of about the same number were changed to 18°C. ($\pm 0.5^\circ\text{C}.$) on July 26. Fry used in experiments ranged from 21 to 26 mm. in fork length.

A series of experiments in the experimental stream were conducted as follows: 30 fry were transferred from holding troughs or aquaria into the middle section of the experimental stream maintained at the same temperature and surface light intensity as fry experienced in the holding facilities. Fry were free to move upstream or downstream into any one of six sections in each direction. After a two hour period following introduction the distribution of fry was noted and light intensity reduced over a fifteen minute interval to the next lower level tested. Distribution of fry was noted after each period of reduction. A shielded penlight with a

red filter was used to make counts at the two lowest light intensities. A method similar to that used in field flume experiments was employed for expression of upstream and downstream movement. The number of fry counted in each successive section away from the centre section was multiplied by a factor increasing by 1. Units of upstream and downstream movement were summed for each observation period.

Results of all experiments conducted in the above manner are shown in Figure 14. Marked differences are evident in amount of downstream movement shown by Loon outlet fry held at different temperatures. Those held in hatchery water at about 10°C. exhibited much more downstream movement, particularly at lower light intensities, than did those held for a period of about a week at temperatures 5° or 8°C. higher. (The units of upstream movement recorded for each lot decreased at lower light intensities as units of downstream movement increased. Upstream units for 18°C. fry were usually more than double those for fry at the lower temperatures.)

In another series of experiments similar groups of fry were introduced to the centre section of the stream as before. This section was provided with a gravel bottom. Perforated aluminum screen barriers, resting on the baffles at the upper and lower ends of the centre section prevented fry from leaving it. Light intensity was gradually reduced over a fifteen minute period, at the end of which the lamps were turned off. Barriers at the ends of the centre section were then removed leaving fry free access for upstream or downstream movement as in the previous series of experiments. Counts were made of fry distribution in sections of the experimental stream after they had remained 15, 30, 45, 60, and 75 minutes in darkness. Results of the seven experiments conducted in this manner

Figure 14. Downstream movement exhibited by rainbow trout fry (Loon outlet stock) in experimental stream at different levels of illumination and different temperatures.

Figure 15. Downstream movement exhibited by rainbow trout fry (Loon outlet stock) in experimental stream at different temperatures and after different periods of time at low light intensity (<0.00001 foot-candles).

are given in Figure 15. As in the previous experiments, fry from Loon outlet Creek held at low temperature (about $10^{\circ}\text{C}.$) showed appreciably more downstream movement in the experimental stream than did similar fry held for several days (fourteen to twenty) at higher temperatures (16° , $18^{\circ}\text{C}.$).

In another series of experiments conducted in the experimental stream the partitions at each end of the temperature control section (Fig. 4B) were removed permitting fry to move continuously either upstream or downstream. A perforated aluminum shield was placed in front of pump intakes to prevent fry from damage in the pumps. At a water depth of 15 cm. used in this series the maximum velocity was about 10 cm./sec. (mean cross-sectional velocity of 4.2 cm./sec.). Twenty fry were introduced into the same section of the stream as in previous experiments and observations started thirty minutes after introduction. Numbers of fry passing upstream and downstream over a 5 cm. wide strip placed across the flume in the centre of the introduction section were counted for ten minute intervals. Counts at low levels of illumination were made with infra-red viewing apparatus. Fry utilized in these experiments ranged between 22 and 26 mm. in length. Reduction to the next lower level of illumination was made gradually (over a five minute interval) by means of an iris diaphragm in a lamp housing. Indirect illumination was provided by reflecting light from the lamp housing off the ceiling of the room containing the experimental stream.

Results of this series of experiments on inlet stock from Loon Lake and Pennask Lake are presented in Figure 16. Particularly at lower levels of illumination, downstream movement was more pronounced in the groups

Figure 16. Downstream movement exhibited by rainbow trout fry in experimental stream at different levels of illumination. 13° and 18°C. fry--Loon 1958 inlet stock held over fourteen days at respective temperature; 10° and 15°C. fry--Pennask Lake 1957 inlet stock held over fourteen days at respective temperature.

of fry held at lower (10° , 13°C.) than at higher (15° , 18°C.) temperatures.

d. Size of fry. Evidence previously presented (Fig. 10) suggests that downstream movement of fry in Loon outlet Creek involves a higher proportion of small fry than would be expected on the basis of the length--frequency distribution of those holding position in the stream during the day. Furthermore it was shown by marking and recapture experiments (Fig. 11B) at Loon inlet Creek that small fry (21--30 mm.) exhibited more downstream movement than did large fry (31--50 mm.). Both observations suggest that size may be of importance in affecting downstream movement of fry.

Throughout autumn and winter, fry in Loon outlet Creek exhibit virtually no downstream movement even though water temperatures at that time drop well within the range at which downstream movement occurs at Loon inlet and Hihium Creeks. Nearly all fry in samples of young trout collected by seining in Loon outlet Creek at the end of August exceeded 40 mm. in length. Apparently downstream movement of these larger fry, even in declining water temperatures is not appreciable at Loon outlet Creek. At Loon inlet Creek, however, some downstream movement of fry larger than 40 mm. did occur in September (Fig. 9).

B. FINGERLINGS

1. Characteristics of Downstream Movement

a. Seasonal periodicity. The amount and seasonal periodicity of

fingerling downstream movement in streams of the Loon Lake system is shown in Figure 17. The total given for Hihium Creek probably represents somewhat more than twenty-five percent of total numbers moving downstream as the trap there did not screen the whole creek volume during most of the season.

Downstream movement of fingerlings in Loon outlet Creek was negligible at Outlet Trap 1 and involved only relatively small numbers at Outlet Trap 2. At Outlet Trap 4, which sampled between 1/10 and 1/3 of the stream depending on discharge, only 18 fingerlings moved downstream during its continuous operation from May 20 to October 14, 1953. Only 1 descending fingerling was taken at this trap during a sampling period from November 4—8, 1953 and only 15 between March 18 and May 14, 1954. Permanent loss of fingerling trout from the Loon Lake system by passing over the falls is apparently negligible. Considerably more fingerlings moved downstream in Hihium Creek and Loon inlet Creek than did in Loon outlet Creek. In all streams the majority of downstream movement of fingerlings occurred in late spring and early summer.

b. Diel periodicity. No marked diel periodicity (such as shown by fry) in downstream movement was evident for fingerlings in any of the streams studied. During most of the periods over which traps were checked at short intervals for twenty-four hours or longer, relatively few fingerlings were taken although on most of these occasions more fingerlings moved downstream at night than during daylight hours.

Figure 17. Seasonal periodicity of downstream movement of rainbow trout fingerlings in streams of the Loon Lake system. Numbers in brackets indicate total number of fingerlings moving downstream during period shown.

2. Factors Affecting Downstream Movement

Field evidence (Fig. 17) suggested that downstream movement of fingerling trout was predominant in streams of the Loon Lake system characterized by cool summer water temperatures, i.e. Loon inlet Creek and Hihium Creek. In addition it was evident that the majority of this movement occurred at a time of the year associated with long days and short nights, but that the marked diel periodicity of downstream movement typical for fry was not so marked for fingerlings.

Response to water current of fingerling rainbow trout held at different temperatures and day length was tested in the experimental stream at the laboratory. Rainbow trout fingerlings were held in six tanks during October, 1957, two tanks held at 10°, two at 15° and two at 20°C. (control $\pm 0.5^\circ\text{C}$.). On November 4, 1957, light hoods were placed on each tank. One set of tanks at 10°, 15° and 20°C. received eight hours' illumination alternating with sixteen hours' darkness, while three others at the same temperatures received sixteen hours' illumination alternating with eight hours' darkness. Incandescent bulbs (7.5 watt) provided illumination varying between 2.4 and 4.8 foot-candles at the water surface during the "day" period.

Fish tested in the experimental stream were free to swim in either direction around the apparatus without interruption, and when doing so were said to "cycle" with or against water current. Illumination from an overhead incandescent lamp varied between 0.5 foot-candles in shade of the stream wall and 7.5 foot-candles in direct light at the water surface. At a water depth of 15 cm. a current with a maximum velocity of 9.7 cm./sec. (mean cross-sectional velocity of 4.2 cm./sec.) was maintained in the

experimental stream. Cover and resting positions were provided for fish by placing stones (15 to 25 cm. in diameter) at intervals along both sides of the stream.

Fish were removed from a holding tank, placed in the stream at their acclimatization temperature (maintained throughout the test) and left for one hour before observation. All observations were made during "day" periods for fish tested.

Groups of five fish were used for each experiment. Reactions to current were measured by counting the number of times fish made a complete cycle around the stream, either upstream or downstream within a five minute period. Number of cycles around the stream made by all fish in the group within a five minute period was taken as a unit measurement of movement. Observations were continued at intervals until responses were recorded for from nine to fifteen separate five minute periods. Replications (three to five) were made with different lots of five fish at each temperature and day length. Experiments were begun forty-one days after fish were first exposed to controlled day length and were completed forty days later.

Fingerling trout used in experiments ranged between 55 and 125 mm. in fork length. No difference was noted in gonadal development between eight and sixteen hour fish either in gonad appearance or in a gonad to total body weight comparison. Gonads appeared to be characteristically immature.

The amount of downstream movement exhibited in the experimental stream by rainbow trout fingerlings held at different combinations of temperature and day length is shown in Figure 18. Fingerlings held at low temperature (10°C.) and long day length showed a greater tendency to move downstream

than did those held at the same day length but at higher temperature (20°C.). These results tend to support the generalizations made from field observations at the Loon Lake stream system where fingerlings at low temperature (Hihium Creek and Loon inlet Creek) during the long day length period (June and July) moved downstream in much greater numbers than did fingerlings at the same period in warm water of Loon outlet stream (Fig. 17). In addition, fingerlings under fall and winter conditions of low temperature and short day length exhibited very little downstream movement in any of the streams studied. Experimental results given in Figure 18 for fingerlings held at 10°C. and eight hour day length again suggest that water temperature—day length combination may be of considerable importance in regulation of migratory patterns of fingerling trout. Apparently the depressant effect of short day length on downstream movement was expressed at all temperatures tested.

In addition to the above experiments, the effect of sudden and prolonged temperature change was tested on downstream movement shown by fingerling trout held at different temperatures and day length. Only one group of five fingerlings which had been held at eight hour day length was studied at each initial temperature (10°, 15°, 20°C.) while two groups of sixteen hour day length fish were used. Responses of fingerlings to water current were recorded on over nine separate five minute periods with each group of fish at each temperature.

Groups of five fingerlings held under the same conditions as in previous experiments were subjected to a relatively rapid increase of 5°C. in the experimental stream. Fingerlings first were introduced to the stream held at their acclimatization temperature and a series of

Figure 18. Downstream movement exhibited in experimental stream by rainbow trout fingerlings held at different combinations of temperature and day length. Average for all eight hour day length lots $\square$, individual lots $\circ$; average for all sixteen hour day length lots $\blacksquare$, individual lots $\bullet$.

observations made on their response to current as before. Then a number of immersion heaters were turned on while fingerlings remained in the experimental stream. In less than two hours the stream temperature was raised 5°C. and another series of observations of current response of fingerlings was started. Fingerlings were then transferred to holding tanks maintained at the appropriate day length and new temperature until their response in the stream was again tested twenty-four and seventy-two hours after the initial temperature increase.

Increases in temperature produced no appreciable change in the slight amount of downstream movement shown by eight hour day length fingerlings. In both lots of 10°C. fish held at sixteen hour day length, under which conditions a considerable amount of downstream movement occurred (Fig. 18), downstream movement decreased immediately following the 5°C. increase. After twenty-four hours downstream movement had further decreased in one lot and had completely ceased in another.

The immediate effect of a 5°C. decrease in temperature was examined only in sixteen hour day length fingerlings. Experimental procedure was the same as in temperature increase tests except for the 5°C. decrease which required about two and a half hours. In the groups of fish held at 10° and 15°C., which exhibited considerable downstream movement at their respective holding temperature, downstream movement was reduced immediately following the temperature decrease. Longer term effects of these sudden decreases in temperature were not examined, however results given in Figure 18 would indicate an eventual increase in downstream movement at lower temperature.

VI. MAINTENANCE OF POSITION

Movement of young trout in streams of the Loon Lake system is undoubtedly essential to their eventual residence in Loon Lake itself. However, maintenance of position is of prime importance to young trout in Loon outlet Creek if they are to remain within the system before entering the lake and indeed is a daily feature even in the behaviour of young trout in Hihium Creek and Loon inlet Creek. An understanding of the migratory behaviour of juvenile trout in the Loon Lake stream system would be far from complete without consideration of their characteristics and mechanisms of position maintenance in flowing water.

A. FRY

1. Characteristics of Position Maintenance

a. Size and specificity of "holding area". In the first few weeks following emergence from redds, fry in Loon outlet, Loon inlet and Hihium Creeks maintain position, at least during the day, without appreciable movement either upstream or downstream. Continuous observation of small groups of fry within local areas for several hours and marking and recapture

experiments showed that fry in both Loon inlet and outlet Creeks maintain position during the day within restricted areas, often less than one foot from where they were initially observed or marked. Groups of young fry at Loon outlet Creek were recovered over a week later in the same small pool or riffle where they had been marked and released. On the other hand, fry moving down Loon inlet and Hihium Creeks at night must occupy new holding areas each day.

b. Change of holding areas between day and night. Observations in both Loon outlet and inlet Creeks during the day and at night with infra-red viewing apparatus suggested that fry changed their holding position in the stream between day and night. Quantification of the shift was accomplished by counting numbers of fry holding position within areas marked off by string boundaries (above the water surface) both along and away from the stream margin. During the day counts were made with 7 x 50 binoculars from a vantage point where fry in counting areas would not be disturbed. At Loon outlet Creek a counting site a short distance upstream from Outlet Trap 2 was chosen, while at Loon inlet Creek counts were made in areas both above and below Inlet Trap 1. Dimensions and physical features of counting areas at Loon inlet and outlet Creeks are shown in Figure 19. Where large numbers of fry were present in counting areas (such as in "edge areas" at Loon inlet Creek on the night of July 22, 1957) counts were only approximate and probably minimal.

Results of fry counts in "edge" and "off-edge" holding areas at Loon outlet Creek are given in Figure 20. Those for an area above (July 22--23) and below (August 30--September 1) Loon Inlet Trap 1 are given in Figure 21. General features of the shift in holding areas are similar at

both streams. During the day few fry held position in edge areas whereas appreciable numbers were dispersed in off-edge areas of the stream at that time. At night, however, the situation was reversed with many fry in edge areas and few fry occupying off-edge areas.

The marked shift in position of fry laterally in the stream at dusk and dawn each day appeared to be more directly related to changes in illumination rather than in water temperature or level (Fig. 21). This shift usually took place when illumination dropped (at dusk) or rose (at dawn) beyond the 10 to 0.1 foot-candle range. Differences in timing of the shift evident between June (when it occurred later in the evening and earlier in the morning) and early September (when it occurred earlier in the evening and later in the morning) also may be related to seasonal changes in the daily cycle of illumination.

Movement of fry from midstream areas towards the stream edge in the evening appeared to be a positive movement rather than a slow, irregular shift in position. Detailed observations on the nature of this movement were made on the evening of August 31, 1957 along a short stretch of stream edge below the counting area downstream from Inlet Trap 1. At 1810 hours a group of six fry which had recently moved onto the stream edge from off-edge areas were disturbed by the observer; the fry moved laterally about two feet out towards the stream centre. Within one minute six fry had moved back into the edge area and were holding position. Between 1811 and 1820, six fry were disturbed from the edge area three additional times--on each occasion six fry quickly returned to the stream edge, where they held position. Although it could not be determined positively that the six fry which returned each time were

Figure 19. Sections along Loon outlet and inlet Creeks where counts were made of rainbow trout fry maintaining position in edge and off-edge areas.

A. Counting area at Loon outlet Creek.

B. Counting area at Loon inlet Creek, downstream from Inlet Trap 1.

Figure 19. Sections along Loon outlet and inlet Creeks where counts were made of rainbow trout fry maintaining position in edge and off-edge areas.
A. Counting area at Loon outlet Creek.
B. Counting area at Loon inlet Creek, downstream from Inlet Trap 1.

Figure 20. Diel changes in number of rainbow trout fry maintaining position in edge and off-edge areas of Loon outlet Creek, 1957.

Figure 21. Diel changes in number of rainbow trout fry maintaining position in edge and off-edge areas of Loon inlet Creek, 1957.

the same ones which were there previously, the distinctive marking and size of two fry suggested that at least some were the same individuals.

c. Disturbance of fry holding position. Repeated infra-red observation at Loon inlet Creek showed that sudden intrusion into a dense group of fry near the stream edge by fry moving erratically downstream resulted in violent disturbance of the group. When fry which were erratically heading downstream suddenly turned towards the edge of the stream and almost literally "struck headlong" into a dense group of fry along the margin, the reaction of the group was virtually explosive. Most individuals in the group scattered wildly, many heading away from the edge into the middle of the stream, whereupon they themselves headed downstream. The sequence of events leading to and following such disturbance of a fry cluster along Loon inlet Creek margin is depicted in Figure 22. Similar disturbances of densely packed groups of fry along the stream edge occurred when one fry in a group attempted to nip another, usually following bodily contact by two individuals holding very close together.

2. Factors Affecting Maintenance of Position

a. Combined effects of temperature and light. A series of experiments examining effect of water temperature and light on behaviour associated with maintenance of position in water current by trout fry was conducted in the fall of 1955 and spring of 1956 at Cambridge, England.

Rainbow trout fry used in all experiments were reared from eyed eggs in constant temperature aquaria. Four lots of young were maintained at 5°, 10°, 15°, and 20°C. for at least twenty days before experiments were started. Fry utilized were between 23 and 27 mm. in length. All tests were conducted in the experimental chamber described previously (Fig. 4A).

Figure 22. Diagrammatic representation of disturbance of dense groups of rainbow trout fry maintaining position along margin of Loon inlet Creek in darkness (based on observations with infra-red viewing apparatus).

- A. Fry swimming erratically downstream near surface approaches group of fry maintaining position at stream margin.
- B. Group of fry rapidly disperses when closely approached or contacted by fry swimming downstream.
- C. Several fry from group move out towards centre of stream, others move closer towards stream margin.
- D. Fry leaving edge turn downstream and begin erratic swimming movement; those at edge orient positively to current and continue to maintain position.

(i) Horizontal movement. Groups of five fry were transferred from holding trays in constant temperature aquaria to the experimental chamber which was held at the same respective temperature. Water current in the chamber was maintained at about 2.7 cm./sec. Illumination from an incandescent lamp suspended above a ground glass lid covering the chamber was 2.5 foot-candles on the water surface and 1.0 foot-candles at the bottom of the chamber. This intensity was used for all observations in the light. Light intensity in the dark was probably less than 0.00001 foot-candles, measured by a photomultiplier described by Harden Jones (1955).

All observations in the light were started in the afternoon and extended until early evening. Illumination was then gradually reduced by means of a "variac" in circuit with the incandescent lamp over a fifteen minute period until the room was in darkness. Observations in the dark, utilizing infra-red viewing apparatus were then commenced. The change from light to dark conditions in the experimental chamber occurred at about the same time of day as fry had experienced previously in the aquaria.

As a measure of horizontal movement, counts were made of the number of times within a fifteen minute period each of the five fry crossed a vertical line dividing the chamber into anterior and posterior halves. The first period of observation in the light began one hour after fry were introduced into the chamber. Observations were made at least once an hour for a three--four hour period before the change was made to darkness for a similar series. In addition to these experiments utilizing groups of five fry, another set was conducted in which similar

observations were made on single fry.

Results of observations on fry movement are presented in Figure 23. Averages are based on data obtained using from two to four groups of individuals, each of which was observed at hourly intervals for at least three hours both in light and dark conditions.

Movement of fry in the light, both when measured in groups and by individuals, increased rapidly at higher temperatures. At lower temperatures (5° , $10^{\circ}\text{C}.$) movement of the fry increased in the dark over that shown during the light. However, at $20^{\circ}\text{C}.$ horizontal movement of fry in the dark usually decreased from that in the light, especially in experiments with individual fry. In the latter group, little difference was evident between temperatures in degree of movement in the dark, as those held at 5° and $10^{\circ}\text{C}.$ were more active than in the light while those at 15° and $20^{\circ}\text{C}.$ were less so.

These experiments suggest that at higher temperatures fry shift back and forth more while maintaining position in the day but less so at night, a behavioural characteristic which could lead to greater familiarity with spatial surroundings and thus perhaps greater ability to maintain position when visual contact with the environment is removed or at least greatly reduced. The reverse behaviour, such as shown by fry held at lower temperatures (5° , $10^{\circ}\text{C}.$), would appear to favour loss of position in flowing water at low levels of illumination.

(ii) Depth distribution. Observations on depth distribution of fry in the experimental chamber were made in conjunction with those on activity discussed previously. A horizontal line was drawn across the front and back wall of the chamber half way up from the bottom separating

Figure 23. Activity (expressed as horizontal movement) of rainbow trout fry in experimental chamber at different acclimatization temperatures under light and dark conditions. Circles and lines represent averages and ranges, respectively, of observations.

it into upper and lower sections each 7.5 cm. in depth. The number of fry (using groups of five) in each section was counted at thirty second intervals for a fifteen minute period. Counts were made in light and dark in the same manner as in activity observations.

Percentage of fry counts recorded in the lower half of the chamber (0--7.5 cm. off bottom) is given for different temperatures in Figure 24. Each open or solid circle represents the average of at least five 15 minute observation periods. At all temperatures, both in light and dark, more fry were recorded in the upper than in the lower half of the chamber. However, a marked trend was evident for fry held at 5° and 10°C. to be restricted to the upper half of the chamber, rarely occurring in the section near the bottom. Fry at 15° and 20°C. frequently settled down towards the bottom, accounting for the higher number of counts recorded in the lower half of the chamber. Fry held at 5° and 10°C. usually remained just under the surface for considerable periods of time, particularly during observations made in darkness. Counts in the dark for fry at 5°C. which were recorded in the lower half of the chamber never exceeded two percent of the total during any of the fifteen minute periods of observation.

Young fry which, in darkness and in flowing water, spend most of the time at or near the water surface would appear much more likely to lose spatial orientation and move downstream than would those which frequent regions close to the stream bottom. If such is the case, then fry inhabiting streams characterized by warm temperatures (15°--20°C.) might be expected to be more effective at maintaining position at night than would fry living in relatively cool streams (5°--10°C.).

Figure 24. Depth distribution of rainbow trout fry in experimental chamber at different acclimatization temperatures under light and dark conditions. Circles and lines represent averages and ranges, respectively, of observations.

(iii) Association with bottom. A measure of tactile association which fry had with the bottom in flowing water was obtained by counting the number of times they touched or rested briefly on the bottom of the experimental chamber. Fry were introduced into the chamber held at acclimatization temperature and observations started one hour later in the light and then in the dark, using similar conditions and procedures as described for activity recording. Experiments were made using groups of five fry as well as individuals. Counts, for a fifteen minute period, were made once an hour during at least three hours on each group or individual tested.

Results given in Figure 25 represent series of counts for three hour or longer periods from at least two different groups of individuals. Fry exhibited little contact with the bottom in the light at all temperatures. Those held at 5° , 10° and 15°C . often swam or maintained position for fifteen minutes without touching the bottom of the chamber. In the dark, fry held at 15° and 20°C . exhibited a marked increase in contact with the bottom over that shown in the light. At these temperatures fry frequently settled onto the bottom and remained there for brief intervals, although they usually rose off again into the chamber. Fry held at 5° and 10°C . increased contact with the bottom only slightly in the dark. Experiments with groups and individuals gave similar results.

In addition to observations on bottom contact made by fry at their respective acclimatization temperatures, a few experiments were performed on the effect of sudden and prolonged temperature change. On one day the contacts made by an individual fry were recorded at its acclimatization temperature in the experimental chamber, after which it was

Figure 25. Association with bottom by rainbow trout fry in experimental chamber at different acclimatization temperatures under light and dark conditions. Circles and lines represent averages and ranges, respectively, of observations.

returned again to its appropriate constant temperature aquarium. The next day the same fry was placed in the experimental chamber held 5° above or below the acclimatization temperature of the fry. After an hour, records of bottom association were made as previously over a three--four hour period, whereupon the fry was placed in a constant temperature aquarium at the new higher or lower temperature. After a period of seven--ten days the bottom association of this fry was again recorded at its new temperature. Control experiments, where an individual fry was not subjected to any temperature change, indicated that individual fry maintain a reasonably consistent reaction to the bottom, at least over a ten day period. Only two experiments were conducted at each acclimatization temperature.

Results, shown in Figure 26, are based on the reaction in the dark of individual fry only. Association with the bottom in the light was negligible at all acclimatization temperatures and was not appreciably affected by temperature changes. Where fry experienced an increase of 5°C. from acclimatization temperature an immediate increase in contact with the bottom was noted. This increase was greater in the change from 10° to 15°C. than from 5° to 10°C. After seven to ten days, bottom contact continued to increase in both changes. Where individual fry were subjected to a decrease of 5°C. from their acclimatization level, an immediate drop in bottom contact occurred for the three changes examined, 20° to 15°C. , 15° to 10°C. and 10° to 5°C. The decrease appeared to be somewhat greater in the 15° to 10°C. change than in others. After a period of seven to ten days at the new lower temperature, little further decrease in association with the bottom occurred.

Figure 26. Effect of sudden and prolonged temperature change on association with bottom by rainbow trout fry in experimental chamber in darkness. Circles and lines represent averages and ranges, respectively, of observations.

Contact with solid objects has frequently been put forward as a possible means of position maintenance by stream fishes in the dark (Lyon, 1904; Hoar, 1951; Hoar, 1954). Night observation (infra-red viewing apparatus) at Loon inlet Creek of at least temporary positive reorientation and maintenance of position by fry moving downstream upon touching or approaching solid objects suggests that tactile stimuli may be of importance in this respect. If so, then it seems reasonable to suggest that the increased direct contact with the bottom shown in the dark by fry held at higher water temperatures (15° 20°C.) may, in part at least, account for their increased ability demonstrated in streams of the Loon Lake system to maintain position in the dark at higher water temperatures.

In summary, certain features of horizontal movement, depth distribution and contact with the bottom exhibited by fry in the above experiments all suggest that fry held at relatively warm water temperatures (15° and 20°C.) should have less difficulty in maintaining their position in flowing water at night than should fry held at relatively cool water temperatures (5° and 10°C.). Moreover, the few experiments on rapid and prolonged temperature change suggest that fry transferred to a higher or lower temperature would rapidly take on and retain behavioural features mentioned above which were characteristic of that new temperature.

b. Size and density of fry. Experiments conducted at Loon inlet Creek on downstream movement of different size groups of fry at night (Fig. 11B) suggested that larger fry (31—50 mm.) may be more successful at maintaining position than small fry (21—30 mm.). These experiments considered in conjunction with observations on disturbance of fry along

the stream edge at night suggest that size and density of fry may be of importance in affecting their ability to maintain position. Further laboratory experiments were not conducted in this direction.

B. FINGERLINGS

Considered on a seasonal basis, fingerlings in all streams of the Loon Lake system apparently maintain their position in these waters, without appreciable movements downstream or upstream, throughout most of the late fall, winter and early spring. Diel aspects of position maintenance are not as clear cut as in the case of fry, except in Loon outlet Creek where most fingerlings, even during their migratory period, maintain position in the stream at night. Apart from these general observations little further data has been collected on features of position maintenance by fingerling rainbow trout in streams of the Loon Lake system.

Experimental evidence presented previously (Fig. 18) suggests that short day length may be an important factor in restricting downstream movement of fingerlings and thus favouring maintenance of position during late fall and winter months. Unfortunately, experiments with short day length fingerlings at characteristic winter temperatures ($5^{\circ}\text{C}.$ or less) were not performed. Failure of experimental holding facilities at $5^{\circ}\text{C}.$ eliminated the group of fish slated for that purpose.

VII. UPSTREAM MOVEMENT

A. FRY

1. Characteristics of Upstream Movement

a. Seasonal periodicity. Trapping facilities capable of recording upstream movement of fry were operated for two seasons (1953, 1954) and during shorter periods in other years (1955, 1957, 1958) at Loon inlet, Hihium and Loon outlet Creeks. Upstream movement of fry was confined largely to the latter stream. Of 7,106 fry moving through Inlet Trap 2 between June and November of 1953, only 28 (0.39%) were moving upstream and of 82,684 fry moving through Inlet Trap 1 during the same period, only 309 (0.38%) were moving upstream. Similar amounts of upstream movement of fry were recorded at Hihium Trap 1 during a three month summer period of operation in 1954.

Seasonal periodicity of upstream movement of fry in Loon outlet Creek is shown in Figure 27. Although free-swimming fry were present in Loon outlet by early June in 1953, upstream fry movement did not begin until a month later at either trap location. Difficulty in maintaining traps because of high water in 1954 prevented positive confirmation of this lag in movement on that year, however operation of trapping facilities for periods in June and July of 1957 and 1958 showed it to be a

Figure 27. Seasonal periodicity of upstream movement of rainbow trout fry in Loon outlet Creek. Numbers in brackets indicate total number of fry moving upstream during period shown.

characteristic feature of upstream fry movement in the outlet stream. Upstream movement of fry virtually ceased by early October.

b. Diel periodicity. Fluctuations in number of fry moving upstream over a thirty-six hour period were recorded at Outlet Traps 1 and 2 between July 23 and 24, 1953. Both traps were checked frequently, usually at two hour intervals or less throughout the thirty-six hour period, and fry were counted and put upstream above the trap. Changes in number of fry ascending per hour as well as data on water temperature, weather and light conditions are shown in Figure 28.

Upstream movement of fry in Loon outlet Creek is largely confined to daylight hours, although appreciable upstream movement does not begin until several hours after dawn. The initiation of upstream movement each day appears to follow more directly the diurnal rise in water temperature rather than the rapid changes in light intensity occurring at dawn (Fig. 28). Upstream fry movement reaches a maximum during early afternoon, as do stream temperatures, and gradually decline in late afternoon to virtual cessation at or shortly after dusk. Further observations on diel periodicity of upstream fry movement at Loon outlet Creek made throughout the 1953 season gave essentially the same picture as that recorded in detail between July 23 and 24.

Although very few fry moved upstream at Loon inlet Creek, some information is available for several twenty-four hour periods and is summarized in Table V. As at Loon outlet Creek, the majority of fry moved upstream during the early afternoon and evening.

Figure 28. Diel periodicity of upstream movement of rainbow trout fry in Loon outlet Creek, 1953.

TABLE V. NUMBER OF FRY MOVING UPSTREAM IN SEVERAL TWENTY-FOUR HOUR PERIODS AT TRAPS ON LOON INLET CREEK

Time Period (Standard Time)	Inlet Trap 2 August 3--4 1953	Inlet Trap 1 August 3--4 1953	Inlet Trap 1 August 11--12 1954	Inlet Trap 1 August 12--13 1954	Total
Morning (0400--1200)	2	2	14	4	22
Afternoon (1200--2100)	6	3	25	18	52
Night (2100--0400)	3	0	8	6	17

c. Daily periodicity. Marked day to day fluctuations were evident in numbers of fry moving upstream through Outlet Traps 1 and 2. (Figure 28 shows differences between two consecutive days in July, 1953.) However daily trap catches could not be taken directly as a measure of the total number of fry moving upstream throughout twenty-four hour periods. In the first place, it was not possible to service traps at the time of minimum overlap between runs of successive days (i.e. between 2400 and 0400 hours; see Figure 28). Furthermore traps were not always attended at regular intervals so that catches on some days represented upstream fry movement for more than twenty-four hours, while on other days considerably less.

Recorded "daily" fry catches were adjusted to twenty-four hour (0000--2400 hours) catches by the following method:

1. Diel periodicity of fry catch at Outlet Trap 1, July 24, 1953 was taken as a standard and expressed as hourly percent of total numbers accumulated throughout the twenty-four hour period.
2. Where catches of two or more successive days were confounded, the total catch was apportioned on the basis of accumulated percent catch pertaining to each day in the interval between trap servicing.

This method assumed that diel periodicity of July 24 was representative for the whole season of upstream fry movement, an assumption borne out in general by observation throughout 1953 and during 1954 and 1955. Also in division of a catch between two successive days it must be assumed that total catch was the same on each day. This assumption introduced little error where only a small percentage of the second day's catch would have accumulated, that is in cases where the trap was serviced before noon of the second day (see Fig. 28). Usually both Outlet Traps 1 and 2 were serviced each day in the morning, so appreciable error from this source only occurred on a few days during the season.

Calculated daily upstream movement of fry at Outlet Trap 1 is shown in Figure 29. Considered on a day to day basis, upstream movement of fry appears to be characterized by irregular "surges". For periods of several consecutive days numbers moving upstream rapidly increased and then fell off once more to a level below thirty per day. This feature of upstream fry movement is especially evident at Outlet Trap 1 (Fig. 29), but is followed with approximately similar timing at Outlet Trap 2 (data not shown).

Figure 29. Daily periodicity of upstream movement of rainbow trout fry in Loon outlet Creek (Outlet Trap 1), 1953.

d. Size relationships. Periodically, samples of young trout moving upstream through Outlet Traps 1 and 2 were measured during the summer and autumn of 1953. Results of these measurements are given in Figure 30 for Outlet Trap 1. Fry were readily distinguished from young of the previous year class throughout early July, but large fry began to overlap the fingerling size range by late July. The most suitable length separating the two groups was chosen on the basis of these samples and used in the field during periods between sampling to distinguish between ascending fry and fingerlings. The same length division was used at Outlet Traps 1 and 2.

Although fry in Loon outlet Creek emerge free-swimming from the gravel at lengths ranging between 20 and 25 mm., individuals less than 33 mm. were never found to enter either outlet traps in 1953. Water velocity at upstream entrance to Outlet Traps 1 and 2 varied considerably depending upon stream discharge and state of plugging of the screen fence. However even during periods of high stream discharge, average entrance velocities to ascender boxes probably did not often exceed 10 cm./sec. Fry maintaining position or moving upstream for any distance in Loon outlet Creek probably would encounter velocities above this rate at many points along the stream.

Samples of fry were taken by seining from Loon outlet Creek periodically throughout the summer of 1953. Length frequency distributions for these samples indicate that fry less than 30 mm. in length were present in Loon outlet Creek at least until late August, although none moved upstream through outlet traps. Most fry in Loon outlet Creek apparently do not move upstream for any considerable distance towards

Figure 30. Length—frequency distribution of rainbow trout fry and fingerlings moving upstream into Loon Outlet Trap 1 during 1953.

the lake until they attain a length greater than 40 mm.

2. Factors Affecting Upstream Movement

One of the most striking features in the upstream movement of rainbow trout fry in Loon outlet Creek is the occurrence of marked surges in daily numbers ascending the stream, as shown in Figure 29. Consideration of factors which may be responsible for this characteristic of upstream movement could lead not only to a more complete understanding of upstream movement in Loon outlet Creek but also may suggest reasons why such movement does not occur in other streams of the system.

Variations both in supply of fry "available" to move upstream and in favourability of environmental stimulation for upstream movement might contribute to the production of surges. As fry in Loon outlet Creek do not begin to move upstream immediately or shortly after emergence, even a detailed knowledge of numbers of recently emerged fry present in the stream from day to day would not be of great value in determining numbers available to move upstream. However, it does not seem reasonable to postulate that supply alone is responsible for the large, rapid daily fluctuations which occur in numbers of fry ascending the outlet stream. Supply may contribute in large part to seasonal periodicity of upstream movement but probably is of less importance in regulating day to day changes. Considering environmental factors which may be involved, few exhibit fluctuations of a size or rapidity which might reasonably be correlated to surges. Field notes show that water level (and hence roughly discharge) of Loon outlet Creek followed in 1953 a pattern similar to that recorded in 1954 but with a lower maximum level. No marked

day to day changes in level were observed.

a. Water temperature.

(i) Relationships in field. Examination of Figure 2 indicates that marked day to day changes in temperature of Loon outlet Creek do occur and suggests the possibility of a correlation between these changes and surges in upstream movement of fry.

At least five fairly distinct surges in upstream movement of fry through Outlet Trap 1 are evident in Figure 29. Increasing and decreasing phases of these surges have been set out and considered in relation to daily changes in maximum outlet temperatures (Table VI). Only the increasing phase of the last (sixth) surge was well recorded, although numbers of ascending fry had dropped off markedly a few days later (Fig. 29). Five out of six increasing phases were associated with periods of general increase in outlet temperatures, while all five decreasing phases of upstream movement occurred during periods of decrease in outlet temperature. A similar comparison (not shown) was made for three distinct surges in upstream movement of fry at Outlet Trap 1 in 1954. The same relationship between phases of surge and temperature changes was evident as in 1953 data. The highest daily numbers of fry moving upstream into Outlet Trap 1 in 1954 (891) was recorded on August 13, a day of sharp increase in maximum daily outlet temperature following a prior ten day period of consistently lower water temperature (Fig. 2).

The relation between day to day fluctuations in numbers of outlet fry moving upstream and changes in outlet temperature was examined in more detail. Quantitative expression of fluctuation in upstream movement presents a difficult problem, largely because no data were available on

TABLE VI. "SURGES" IN UPSTREAM MOVEMENT OF RAINBOW TROUT FRY AT LOON OUTLET TRAP 1. RELATED TO CHANGES IN OUTLET WATER TEMPERATURE, 1953

"Surge" Number	Time Period	Phase in "Surge" of Upstream Movement	Days with Increasing Maximum Temperature	Days with Decreasing Maximum Temperature	Net* Change in Maximum Temperature
1	5—8 July	Increase	3	1	+ 3.6°C.
	9—12 July	Decrease	1	3	- 1.4°C.
2	13-16 July	Increase	1	1	+ 1.1°C.
	17-20 July	Decrease	2	1	- 0.5°C.
3	22—25 July	Increase	2	2	- 0.6°C.
	28 July— 1 August	Decrease	3	2	- 0.5°C.
4	3—7 August	Increase	3	2	+ 0.8°C.
	14—20 August	Decrease	1	6	- 3.6°C.
5	2—8 September	Increase	4	2	+ 1.9°C.
	16—20 September	Decrease	1	4	- 1.1°C.
6	3—8 October	Increase	3	1	+ 2.7°C.

*

Algebraic sum of daily changes in maximum temperature within period considered.

number of fry present in the stream. Lacking information on supply of fry to move upstream, a method with some merit is obtained by expressing numbers moving on one day as a fraction of those which moved upstream the previous day. Expressions of upstream fry movement in terms of day to day changes, rather than actual numbers, is preferable when data on numbers of fry available to move cannot be obtained. The ratio of numbers moving on day $\frac{N}{N-1}$ may be easily altered where extreme variation in numbers of fry moving upstream occurred. However, throughout a one hundred day period at Outlet Trap 1, there were only fourteen days on which less than ten fry moved upstream. Except for a ten day period of upstream movement in August, numbers of fry ascending into Outlet Trap 1 usually ranged between ten and one hundred.

Various methods of temperature expression which were examined in relation to changes in upstream fry movement included changes in maximum, mean and range over the previous day. These methods were also considered in relation to changes over the previous two days. Change in daily maximum temperature gave a better relation than other ways of expression (2 x 2 contingency tests) when plotted against daily changes in upstream fry movement.

The effectiveness of using changes in daily maximum outlet temperature to predict daily changes in numbers of fry ascending Loon outlet Creek in 1953 was tested by regression analysis. Four units were added to all °C. temperature changes to avoid negative numbers. Daily changes in ascending fry were expressed as the number taken in Outlet Trap 1 on day $\frac{N}{N-1}$. Data for one hundred days between July 1 and October 8 were treated.

A significant positive regression ($p < 0.01$) was obtained between daily changes in maximum outlet water temperature and daily changes in number of ascending fry. The analysis indicates that there is a marked tendency for upstream fry movement to exceed that of the previous day when the maximum daily temperature is above that of the previous day, and likewise to drop below that of the previous day when the maximum daily temperature is lower than that of the previous day.

Comparisons of maximum daily water temperatures in all three streams (Fig. 2) for 1953 and 1954 indicates that Loon outlet Creek, during the period of upstream fry movement (July to mid-September) is not only considerably higher in temperature than Loon inlet or Hihium Creek (usually above $15^{\circ}\text{C}.$, while the latter two streams are generally below $15^{\circ}\text{C}.$) but also is subject to more rapid and extensive daily change in maximum temperature than evident in the other two streams (Figs. 2, 3). Both the lower level of maximum daily stream temperatures and their reduced daily variation may be causal factors in the virtual absence of upstream movement of fry in Loon inlet and Hihium Creeks.

(ii) Experimental flume studies. The use of two experimental flumes at the confluence of Loon outlet Creek and Hihium Creek (each stream supplying water to one of the flumes) to study response of rainbow trout fry to water current of differing temperature characteristics has been described previously in its application to downstream movement (Page 50). Information was also obtained on the effect of these temperature differences on upstream movement under experimental conditions. Although fry used in these experiments were smaller than those moving up Loon outlet Creek, nevertheless consistent differences were evident in positive response to

current between fry held in the two flumes with differing temperatures (Fig. 12). Fry (both Loon inlet and outlet stock) in the flume supplied with warm Loon outlet water in most cases showed appreciably more upstream movement than did fry in cool water from Hihium Creek. Upon transfer (night of August 8) to the Loon outlet flume, fry formerly held in the Hihium flume showed a marked increase in amount of upstream movement.

(iii) Experimental stream studies. A number of experiments were conducted in the stream on upstream movement exhibited by trout fry held at low ($10^{\circ}\text{C}.$) and higher temperatures (15° and $18^{\circ}\text{C}.$). Procedure employed has been outlined previously (Page 55). In the light, units of upstream movement recorded for fry held at higher temperatures were consistently larger than those for fry held at the lower temperature.

b. Light. Field observations (Loon outlet Creek) have shown that upstream movement of fry is largely restricted to daylight hours (Fig. 28). In experiments performed in the experimental stream, upstream movement of fry virtually ceased at light intensities below one foot-candle. Available evidence, although not extensive, does suggest that daily cessation of upstream fry movement is regulated by light intensity.

c. Size of fry. Fry do not ascend Loon outlet Creek in appreciable numbers until they attain a length of about 40 mm., at which time a marked change in response to water current apparently occurs. Laboratory experiments on swimming speeds of fry (see Page 133) indicate that fry smaller than 40 mm. would be physically capable of moving upstream in water velocities present in most of Loon outlet Creek.

B. FINGERLINGS

1. Characteristics of Upstream Movement

a. Seasonal periodicity. Figure 31 summarizes data obtained on seasonal periodicity of fingerling movement up Loon outlet Creek for two consecutive years. A similar pattern (not shown) of upstream movement was obtained on these same years at Outlet Trap 2, although fewer numbers of fingerlings were involved. The majority of fingerlings move up Loon outlet Creek between May and August each year.

Available information on upstream movement of fingerlings in Hihium Creek in 1954 and in 1955 indicates that very few individuals are involved. As known from clip recoveries, the occasional fingerling from Loon outlet Creek moves at least short distances up Hihium Creek.

Throughout the 1953 season very few fingerlings moved up Loon inlet Creek, except during a few days in mid-July when daily number of ascending fingerlings ranged from 14 to 43 individuals. Before and after this period, rarely more than 10 and usually only 1 or 2, if any, fingerlings moved upstream each day.

b. Diel periodicity. Diel changes in numbers of fingerlings moving upstream were recorded in Loon outlet Creek within several twenty-four hour periods when traps were checked at regular intervals, usually about two hours. Data for both Outlet Traps 1 and 2 during a period in July 1953 are shown in Figure 32. Other less complete data on diel periodicity of upstream fingerling movement during 1953, 1954 and 1955 gave essentially the same pattern as that shown in Figure 32.

Figure 31. Seasonal periodicity of upstream movement of rainbow trout fingerlings in Loon outlet Creek (Outlet Trap 1). Numbers in brackets indicate total numbers of fingerlings moving upstream during period shown.

The majority of fingerlings move upstream in mid to late afternoon during the daily rise to maximum stream temperature, however maximum rates of movement do not always occur during the period of daily maximum stream temperature as is evident particularly at Outlet Trap 2. Upstream movement gradually decreases in the late afternoon and evening each day, reaching minimal rates in the early morning after dawn. Periods of minimal upstream movement occur near or during the period of minimal stream temperature.

Diel periodicity of upstream movement of fingerlings at Loon inlet Creek appeared similar to that at the outlet stream on the few days when appreciable upstream movement occurred at the inlet stream.

c. Daily periodicity. Expression of day to day changes in number of rainbow trout fingerlings moving up Loon outlet Creek is subject to similar difficulties outlined previously for daily upstream fry movement. Essentially the same method of adjusting catches as used for fry (Page 93) was also applied to daily catch data for fingerlings. As with fry adjustment, the diel periodicity of upstream fingerling movement on July 23--24, 1953 (Fig. 32) was taken as a standard. The twenty-four hour interval between 0700 hours on one day to 0700 hours on the next was chosen as the most suitable for expression of "a day's run". This division point gave adequate separation between daily catches for other periods. Assumptions and possible errors in adjustment of daily fingerling catches are the same as stated for similar treatment of fry.

Adjusted daily numbers of fingerling trout moving upstream through Outlet Trap 1 are shown in Figure 31. The "surges" in upstream movement found in fry ascending Loon outlet Creek are also evident for ascending fingerlings in 1953 and 1954.

Figure 32. Diel periodicity of upstream movement of rainbow trout fingerlings in Loon outlet Creek, 1953.

d. Size relationships. Seasonal changes in the length--frequency distribution of fingerlings ascending through Outlet Trap 1 are shown in Figure 30. Distinction between fry and fingerlings during mid-summer and fall has been mentioned previously. Comparison of length range between late fall fry and spring fingerlings (Fig. 30), suggests that the majority of fingerlings ascending Loon outlet Creek in late spring and summer are entering into their second year of life. At least some of the larger fingerlings may have spent two or more winters in the outlet stream.

e. Movement between traps. Information on movement of fingerlings ascending Loon outlet Creek was obtained largely from marking at Outlet Trap 2 and recovery at Outlet Trap 1. A total of 100 fingerlings were marked and released above Outlet Trap 2 between 1000 and 1530 hours on July 14, 1953. Fingerlings were marked by insertion of small pieces of red thread into the back immediately posterior of the dorsal fin. Subsequent recovery of 22 red thread fingerlings was made at Outlet Trap 1 (Fig. 33). First recoveries of this group at Outlet Trap 1 occurred between twenty-eight and forty-five hours after release at Outlet Trap 2, but recovery continued up to fifteen days later. None were taken after that date, although Outlet Trap 1 was operated continuously for ninety-two days following initial release of thread-marked fingerlings.

The recovery pattern (Fig. 33) of thread-marked fingerlings at Outlet Trap 1 does not suggest that groups of young trout move upstream in discrete blocks, however the extent to which marking may have altered fingerling behaviour cannot be determined. Days of maximum recovery tend to be associated with days on which considerable upstream movement in general occurred.

Figure 33. Recovery of rainbow trout fingerlings at Loon Outlet Trap 1 following release of one hundred red thread-marked individuals at Outlet Trap 2, 14 July, 1953.

Differential marking of fingerling trout passing through Hihium Trap 1 and Outlet Trap 2, permitted separation of ascending fingerlings at Outlet Trap 1 into three groups; (1) those coming from between Outlet Traps 1 and 2, (2) those coming from below Outlet Trap 2, and (3) those coming from Hihium Creek.

Between mid-July and mid-October, 1953 and throughout April and May, 1954, the majority (usually over eighty percent) of fingerlings moving upstream into Outlet Trap 1 came from the stream section above (upstream from) Outlet Trap 2. The proportion of ascending fingerlings taken at Outlet Trap 1 which could be recognized as having come from Hihium Creek (usually less than five percent) was underestimated because of failure to mark all fingerlings leaving Hihium Creek. Heavy contribution from the upper end of the outlet stream to total numbers of outlet fingerlings entering Loon Lake would be expected as a result of location of spawning areas (Fig. 1) and restricted downstream movement of young.

2. Factors Affecting Upstream Movement

a. Water temperature.

(i) Relationships in field. Surges in upstream movement of fingerlings, as in fry, appeared to be one of the more outstanding features in their upstream migratory behaviour. As pointed out previously for fry, surges in upstream movement could result from variations in "supply" of fingerlings, all moving upstream under more or less constant environmental stimulation, or from a relatively fixed reserve of fingerlings subjected to environmental stimulation which fluctuated between conditions favourable and unfavourable to upstream movement. Stocks of fingerlings in Loon

outlet during the period of upstream movement are not subject to "internal recruitment", such as may occur with numbers of fry as a result of fluctuations in intensity and success of fry emergence. Nevertheless, it might be argued that surges in upstream fingerling movement merely reflect linear changes in fingerling density along the length of the stream, with all fingerlings moving upstream a given distance each day under more or less constant environmental stimulation. However, data on distribution and source of fingerlings moving upstream in Loon outlet Creek, and information on upstream movement of lots marked at one time and location in the outlet tend to negate the above argument.

The most striking fluctuations in environmental conditions in Loon outlet Creek during the period of upstream fingerling movement are those in water temperature. Although marked seasonal changes in stream level and hence discharge occurred these did not fluctuate widely when considered on a day to day basis, as did water temperature (Fig. 2).

The four prominent surges in upstream fingerling movement in 1953, and the only two marked 1954 surges, are considered together in Table VII. Each of the six increasing phases are associated with periods of rising daily maximum stream temperature, while the decreasing phases of the surges in movement occur during periods of little temperature changes or dropping daily maximum temperatures. Similar trends are evident for many of the minor surges in upstream movement shown in Figure 31.

A more detailed examination of the possible relation between water temperature and daily changes in number of fingerlings ascending Loon outlet Creek was made by regression analysis. As in the case of upstream fry movement various methods of expressing changes in stream temperature

TABLE VII. "SURGES" IN UPSTREAM MOVEMENT OF RAINBOW TROUT FINGERLINGS AT LOON OUTLET TRAP 1, 1953 AND 1954, RELATED TO CHANGES IN OUTLET WATER TEMPERATURE

"Surge" Number	Time Period	Phase in "Surge" of Upstream Movement	Days with Increasing Maximum Temperature	Days with Decreasing or Constant Maximum Temperature	Net* Change in Maximum Temperature
1953					
1	11--13 May	Increase	2	1	+ 2.4°C.
	14--16 May	Decrease	2	1	0°C.
2	24--27 May	Increase	4	0	+ 6.1°C.
	29 May-- 1 June	Decrease	1	3	- 3.3°C.
3	9--12 June	Increase	3	1	+ 1.4°C.
	13--15 June	Decrease	2	1	+ 0.9°C.
4	2--8 July	Increase	4	3	+ 3.4°C.
	11--15 July	Decrease	0	5	- 2.0°C.
1954					
5	1--3 June	Increase	3	0	+ 1.4°C.
	4--6 June	Decrease	1	2	- 0.3°C.
6	8--15 July	Increase	4	3	+ 5.3°C.
	16--20 July	Decrease	0	5	- 5.0°C.

*Algebraic sum of daily changes in maximum temperature within period considered.

were assessed. Again, the best relation between daily numbers of ascenders and temperature appeared when the latter was expressed as changes from daily maximum (2 x 2 contingency tests). Intensity of upstream fingerling movement was measured by daily total adjusted catches at Outlet Trap 1.

Data were available on sixty days between May and August, 1953. Analyses were made for two expressions of change in daily maximum stream temperatures: (a) maximum of one day compared to that of the previous day and (b) maximum of one day compared to the average of the maximums of the two previous days.

A significant positive regression ($p < 0.05$) was obtained for the analysis with (a) temperature expression; that for (b) was highly significant ($p < 0.01$). Daily changes in upstream movement of fingerlings in Loon outlet Creek, as was shown previously for fry (Page 101), can be related to changes in daily maximum water temperature.

In consideration of environmental factors responsible for the marked differences in numbers of fingerlings moving up streams of the Loon Lake system, one must recall that it is only in Loon outlet Creek that fingerlings are abundant. In both Loon inlet and Hihium Creeks the majority of young leave the streams as fry and few apparently successfully overwinter in these streams. Nevertheless, differences in fingerling abundance between the streams may not be the only cause of their differences in amount of upstream movement of fingerlings. Reference to Figure 31 will show that periods of active upstream movement in Loon outlet are generally associated with rises in maximum daily stream temperatures which approach or exceed 15°C . Comparison of temperatures for all three

streams (Fig. 2) shows that only during one period in 1953 did maximum temperatures at Loon inlet Creek exceed 15°C. It was only during these few days in mid-July when an appreciable amount of upstream movement in fingerlings was recorded at Loon inlet Creek.

b. Combined effect of temperature and light. Information on the effect of three different temperatures (10°, 15° and 20°C.) and two day lengths (eight and sixteen hour) on the upstream movement of fingerling rainbow trout was available from observations made in the experimental stream. Experimental procedure and methods of observation were similar to those used for downstream movement of fingerlings described in a previous section. Results are given in Figure 34. Only in the case of fingerlings held at 10°C. were consistent differences evident in amount of upstream movement shown by eight and sixteen hour day length groups. There a positive reaction to current was expressed in at least two of the three groups tested which had been held at eight hour day length. Those held at the low temperature--long day length combination showed less upstream movement than any other group tested in the experimental stream.

The above results indicate that fingerlings held at lower temperature --short day length conditions exhibit a moderately strong rheotaxis--a behavioural feature which might well be of importance to fish attempting to maintain position in a stream during autumn and winter seasons. However, under the higher water temperature--long day length conditions, which characterize late spring and early summer seasons, no marked tendency for increased upstream movement was observed.

The effect of immediate and prolonged temperature change on upstream

movement of fingerlings in the experimental stream was tested for several groups of fish held at different temperature and day length combinations. Only one group of five fingerlings which had been held at eight hour day length was tested at each temperature while a replication was run with sixteen hour day length fish. Responses of fingerlings to current were recorded on over nine separate five minute periods with each group of fish at each temperature and time. The same method of designating units of upstream movement (average number of cycles of experimental stream/five minutes/five fish) as was used in previous experiments was adopted.

Results of experiments in which fingerlings were subjected to a 5°C. increase are given in Figure 35. In eight and sixteen hour day length groups and at both levels of temperature change tested an increase in upstream fingerling movement followed each temperature increase. This increase in upstream movement was greatest after twenty-four hours at the new higher temperature in both groups of eight hour day length fish and one group of sixteen hour day length fish. Upstream movement was lower than maximum in all groups after seventy-two hours at the new temperature.

The immediate effect of a 5°C. decrease in temperature on upstream movement was examined only in sixteen hour day length fingerlings. Experimental procedure was the same as in temperature increase tests except for the 5°C. decrease which required about two and a half hours. In groups of fingerlings showing some upstream movement (those at 20°C.), this movement was reduced markedly following the 5°C. decrease in temperature.

Although laboratory study on effects of rapid temperature change on upstream movement of fingerlings was not extensive, nevertheless in all experiments performed a marked alteration was noted in upstream

Figure 34. Upstream movement exhibited in experimental stream by rainbow trout fingerlings held at different combinations of temperature and day length. Average for all eight hour day length lots $\square$, individual lots $\circ$; averages for all sixteen hour day length lots $\boxtimes$, individual lots $\bullet$.

Figure 35. Effect of sudden and prolonged 5°C. increase in temperature on upstream movement in experimental stream of fingerling rainbow trout held at eight and sixteen hour day length. Circles indicate averages for all lots tested.

movement following both increases and decreases of temperature. Changes in temperature produced greater alterations in positive response of fingerlings to water current than were noted between different combinations of constant holding temperature or day length. The direction of alteration in current response of fingerlings in the experimental stream was the same as noted between temperature change and upstream movement in Loon outlet Creek. In each situation, increases in upstream movement were related to periods of increasing water temperature and declines in upstream movement to decreasing water temperature.

VIII. MIGRATORY PATTERNS IN OTHER STREAM SYSTEMS

A. BAKER LAKE OUTLET

A brief survey was made of available data on migratory patterns shown by juvenile rainbow trout in outlet and inlet streams of lakes other than Loon. The most complete set of data examined were for upstream movement of fingerling trout in the outlet stream of Baker Lake--a small (surface area forty-two acres) lake near Quesnel, B. C. Observations on daily periodicity of upstream fingerling movement, water temperature and level collected by the British Columbia Fish and Game Branch are presented in Figure 36. Some, but probably by no means all of these young trout were progeny of adults inhabiting Baker Lake and spawning in its outlet stream. An unknown fraction may have been progeny of adults either inhabiting the outlet stream or other lakes lower in the system. Diel periodicity of upstream movement on all three years was shown to be very similar to that at Loon Lake where the majority of fingerlings ascended the outlet stream in mid-afternoon and very few during the night and morning.

Movement of fingerling trout in appreciable numbers up Baker Lake outlet stream began, at least in 1956 and 1957, (Fig. 36) after a sharp rise in outlet temperature to levels above 10°C. (daily mean).

Figure 36. Upstream movement of rainbow trout fingerlings at trap on outlet stream of Baker Lake, B. C.

Increase in both daily stream temperature and number of ascending fingerlings appeared to be more gradual in 1958 than in the previous years. Several surges in upstream movement were evident in 1956 and 1957 data (Fig. 36). In most cases increasing and decreasing phases of each surge were associated with periods of general increase and decrease in daily maximum water temperature. In the year (1958) when no marked periods of temperature increase and decrease occurred, little evidence of surges in upstream fingerling movement was found. Fluctuations in water level did not appear to affect numbers of fingerling trout ascending Baker Lake outlet stream. The relation of seasonal, daily and diel periodicity of upstream movement to changes in water temperature at Baker Lake outlet stream was similar to that observed at the outlet of Loon Lake.

B. WASILLA LAKE OUTLET

Data were examined on upstream movement of rainbow trout less than seven inches (18 cm.) at the outlet weir of Cottonwood Creek (outlet stream of Wasilla Lake, Alaska) given in unpublished Job Completion Report Vol. 8, No. 4, U. S. Fish and Wildlife Service Project F-I-R-8, Alaska, 1959. By plotting daily average water temperatures of the outlet stream on the graph showing daily upstream movement of young trout a relation between surges in upstream movement and changes in water temperature similar to that found at outlet streams of Loon and Baker Lakes became apparent. Each of the four major periods of increase and decline in numbers of trout ascending the outlet stream of Wasilla Lake

was associated with respective periods of increase and decrease in stream temperature.

C. PAUL LAKE INLET

Downstream migration of rainbow trout fry in Paul Creek, an inlet to Paul Lake near Kamloops, B. C., has been noted by Mottley (1931b) who estimated that 15,000 fry entered the lake from Paul inlet Creek during the summer of 1931. In 1952 the British Columbia Fish and Game Branch operated a Wolf-type fry trap on Paul Creek a short distance upstream from its entrance into the lake where data on downstream movement of fry and stream temperature were obtained. Downstream movement of fry was recorded throughout most of the period between installation of the trap (July 20) and the end of August at which time low water level prevented its effective operation. During the forty-three day period, mean daily stream temperature was less than 13°C. on twenty-five days and only exceeded 14°C. on four days. Thus throughout most of this summer period the temperature of Paul Creek remained within the range at which downstream movement of fry occurred in Loon Lake streams.

D. LARDEAU RIVER

Some information on migratory behaviour of young rainbow trout resulting from spawning of large adults from Kootenay Lake in the

Lardeau River is available (Larkin, 1951 and unpublished data supplied by J. Cartwright, B. C. Fish and Game Branch). Lardeau River, approximately thirty miles in length, flows from the south-east end of Trout Lake into the north end of Kootenay Lake and thus at its upper end forms the outlet of Trout Lake but at its lower reaches an inlet of Kootenay Lake. Many of the large rainbow trout spawning in the river do so near its upper end a short distance below Trout Lake. Emergence of fry extends from mid-June in the upper reaches to early August in the lower reaches of the river.

Arguing from the effect of water temperature on migratory behaviour of juvenile rainbow trout at Loon Lake, one would predict the following pattern of fry movement from an examination of seasonal changes in temperature (1949, 1958, 1959) of the Lardeau River at several points along its length:

- (a) Most fry emerging in late June to early July would move downstream at night towards Kootenay Lake.
- (b) Most fry emerging in the upper reaches after early July would not move downstream at least during most of July, August and early September.
- (c) Some fry in the upper reaches in late July and August would move upstream towards or into Trout Lake during the day.
- (d) Many fry emerging in the middle and lower reaches throughout the summer would move downstream towards Kootenay Lake.

Although data on movement of juvenile trout in the Lardeau River are not extensive, the following statements can be made on the basis of fyke netting, scoop trap operation and other observations:

- (a) After the beginning of emergence and until early July considerable numbers of fry do move downstream at night.
- (b) Although some downstream movement of fry continues in reduced numbers during later July and August in the upper reaches, many fry apparently maintain position day and night in this section of the river at least until early September.
- (c) Although upstream movement of fry in the upper river towards or into Trout Lake has not been positively recorded, R. McRae, retired hatchery officer for the B. C. Fish and Game Branch, reported (personal communication) that considerable numbers of rainbow trout fry are seen during the summer along the shores of Trout Lake immediately above the mouth of Lardeau River and that in his opinion many fry do move from the uppermost reaches of the river into Trout Lake.
- (d) Downstream movement of fry in lower reaches is known to occur during July and August.

The observed pattern of migratory behaviour of juvenile trout in the Lardeau River is reasonably consistent with predictions based on environmental control of movement at Loon Lake.

In summary, available information has been examined on migratory behaviour of juvenile rainbow trout in four widely separated systems, representing two outlet streams, one inlet stream and a single river which at its upper end forms an outlet stream and at its lower end becomes an inlet stream. In each case, observed migratory behaviour is, in general,

consistent with that which would have been predicted on the basis of the Loon Lake study.

IX. DISCUSSION

A. ENVIRONMENTAL CONTROL OF CURRENT RESPONSES

Three major categories of response to water current have been recognized in the migratory behaviour of juvenile rainbow trout in streams of the Loon Lake system. Each of these, downstream movement, maintenance of position and upstream movement, has been described in some detail in previous sections and various factors which appear to orient responses have been considered. Observations and experiments, both in streams of the Loon Lake system and under controlled laboratory conditions, have indicated that the marked differences in current responses of trout between streams of the system are not different innate responses of genetically discrete stocks, but instead result from consistent environmental differences.

Observations in the field and pertinent field and laboratory experiments are given in Table VIII. This tabular presentation summarizes and assembles in one unit the bulk of field and laboratory data given previously which has bearing on the case for environmental control of juvenile trout migration. All three types of response to water current shown by young trout in the field have been examined experimentally. In general, experimental evidence has corroborated field observations supporting environmental control of current responses.

TABLE VIII. SUMMARIZED INTEGRATION OF FIELD OBSERVATIONS AND EXPERIMENTAL EVIDENCE SUPPORTING ENVIRONMENTAL CONTROL OF CURRENT RESPONSES SHOWN BY JUVENILE RAINBOW TROUT IN STREAMS OF THE LOON LAKE SYSTEM¹

Current Response	Juvenile Stage	Field Observations	Experimental Evidence
<u>Down-</u> <u>stream</u> <u>Move-</u> <u>ment</u>	<u>Fry</u>	<p>1. Occurs consistently each summer in <u>both</u> streams (Loon inlet and Hihium) characterized by daily mean water temperatures $< 13^{\circ}\text{C}$. but different in many other physical, chemical and biological aspects.</p> <p>2. Does not occur in Loon outlet Creek in summers when daily mean water temperatures are usually $> 14^{\circ}\text{C}$.</p> <p>3. Occurs occasionally in early summer in Loon outlet Creek when daily mean water temperatures are considerably $< 14^{\circ}\text{C}$. for several days.</p>	<p>(a) Fry which had moved down Loon inlet Creek (at mean temp. $< 10^{\circ}\text{C}$.) virtually ceased such movement when transferred to Loon outlet Creek (at mean temp. $> 15^{\circ}\text{C}$.), while inlet control fry continued moving down inlet stream. (1, 2, 3)</p> <p>(b) Fry which had exhibited little movement down Loon outlet Creek (at mean temp. $> 20^{\circ}\text{C}$.) moved downstream in relatively greater numbers when transferred to Loon inlet Creek (mean temp. 14.4°C. or less). (1, 2, 3)</p> <p>(c) Fry held in identical experimental flumes usually showed more downstream movement in flume supplied with Hihium Creek water (mean temp. $< 12^{\circ}\text{C}$.)</p>

¹Numbers in brackets behind each item of experimental evidence indicates its pertinence to particular field observations.

TABLE VIII. (CONT'D) SUMMARIZED INTEGRATION OF FIELD OBSERVATIONS AND EXPERIMENTAL EVIDENCE
SUPPORTING ENVIRONMENTAL CONTROL OF CURRENT RESPONSES SHOWN BY JUVENILE
RAINBOW TROUT IN STREAMS OF THE LOON LAKE SYSTEM

Current Response	Juvenile Stage	Field Observations	Experimental Evidence
<u>Down-</u> <u>stream</u>	<u>Fry</u>		than in flume supplied with Loon outlet Creek water (mean temp. $> 15^{\circ}\text{C}.$). (1, 2, 3)
<u>Move-</u> <u>ment</u>		<p>4. Takes place almost entirely at night when illumination falls below 0.01 foot-candles.</p> <p>5. Amount and periodicity on any one night markedly affected by changes in intensity of nocturnal illumination (cloud-cover, moonlight).</p> <p>6. Majority of fry involved range between 20 and 30 mm. in length, although considerable numbers of larger fry may be present in stream.</p>	<p>(d) In several types of tests at low light intensities in the experimental stream, fry reared or held at low temperature ($< 15^{\circ}\text{C}.$) consistently showed more downstream movement than fry reared or held at high temperature ($> 15^{\circ}\text{C}.$). (1, 2, 3)</p> <p>(e) Fry held in experimental stream at $10^{\circ}\text{C}.$ and > 1 foot-candle of illumination show considerable increase in amount of downstream movement when light gradually lowered to levels of and below 0.01 foot-candles. (4)</p> <p>(f) Changes in illumination below 0.01 foot-candles increase amount of downstream movement of fry in experimental stream. (5)</p> <p>(g) Downstream movement of fry at night greatly reduced during periods of lantern illumination over streams. (5)</p>

TABLE VIII. (CONT'D) SUMMARIZED INTEGRATION OF FIELD OBSERVATIONS AND EXPERIMENTAL EVIDENCE SUPPORTING ENVIRONMENTAL CONTROL OF CURRENT RESPONSES SHOWN BY JUVENILE RAINBOW TROUT IN STREAMS OF THE LOON LAKE SYSTEM

Current Response	Juvenile Stage	Field Observations	Experimental Evidence
<u>Down-stream Movement</u>	Fry		(h) Release and recovery of marked small (20--30 mm.) and larger (31--50 mm.) fry at Loon inlet Creek indicates that smaller fry move downstream to a greater extent and more rapidly than larger fry. (6)
<u>Down-stream Movement</u>	<u>Fingerlings</u>	<p>1. Relatively small numbers involved in any of streams studied; largely confined to late spring and early summer (long day length) periods in streams with low daily mean temperature (usually < 13°C.).</p> <p>2. Not evident during autumn, winter or early spring in <u>any</u> of streams studied.</p>	<p>(a) Fingerlings held at low temperature (10°C.) and long day length (16 hours) exhibited much more downstream movement in experimental stream than did those held at high temperature (20°C.) and long day length. (1)</p> <p>(b) Fingerlings held at short day length (8 hours) exhibited virtually no downstream movement in experimental stream. (2)</p>
<u>Maintenance of Position</u>	<u>Fry</u>	<p>1. Above observations (1, 2, 3) on inability of fry to maintain position in streams are pertinent here.</p> <p>2. Fry maintain position at night in Loon outlet Creek when daily mean temperature,</p>	<p>(a) Above experimental evidence (a, b, c, d) on inability of fry to maintain position in flowing water is pertinent.</p> <p>(b) Fry reared at high temperatures (15, 20° C.) show less horizontal movement during night than during day</p>

TABLE VIII. (CONT'D) SUMMARIZED INTEGRATION OF FIELD OBSERVATIONS AND EXPERIMENTAL EVIDENCE SUPPORTING ENVIRONMENTAL CONTROL OF CURRENT RESPONSES SHOWN BY JUVENILE RAINBOW TROUT IN STREAMS OF THE LOON LAKE SYSTEM

Current Response	Juvenile Stage	Field Observations	Experimental Evidence
<u>Maintenance of Position</u>	<u>Fry</u>	<p>> 14°C. but do not do so there when considerably < 14°C. or in other streams characterized by summer daily mean temperatures < 13°C.</p> <p>3. Many of fry maintaining position at night do so along margin of stream in close proximity or occasional contact with solid objects along stream edge and bottom.</p> <p>4. Most of fry unable to maintain position at night swim erratically in disoriented manner at or near water surface away from stream edge or bottom.</p>	<p>in experimental chamber, while those reared at low temperatures (5°, 10°C.) showed more horizontal movement during night than during day. (2)</p> <p>(c) Fry reared at high temperatures (15°, 20°C.) were more frequently recorded near bottom and made more frequent contact at night with bottom of experimental chamber than did fry reared at low temperatures (5°, 10°C.). Latter group in darkness swam in current near or at surface of experimental chamber. (2, 3, 4)</p> <p>(d) Fry transferred into water 5°C. higher or lower in temperature rapidly assumed response to bottom of experimental chamber characteristic for new temperature. (2, 3, 4)</p>
<u>Maintenance of Position</u>	<u>Fingerlings</u>	<p>1. Maintain position throughout most of winter and early spring in all streams studied.</p>	<p>(a) Fingerlings held at short day length (8 hours) exhibited virtually no downstream movement in experimental stream. (1)</p>

TABLE VIII. (CONT'D) SUMMARIZED INTEGRATION OF FIELD OBSERVATIONS AND EXPERIMENTAL EVIDENCE SUPPORTING ENVIRONMENTAL CONTROL OF CURRENT RESPONSES SHOWN BY JUVENILE RAINBOW TROUT IN STREAMS OF THE LOON LAKE SYSTEM

Current Response	Juvenile Stage	Field Observations	Experimental Evidence
<u>Maintenance of Position</u>	<u>Fingerlings</u>		(b) Fingerlings held at shortest day length (8 hours) and lowest temperature (10°C.) showed strongest positive rheotaxis in experimental streams. (1)
<u>Upstream Movement</u>	<u>Fry</u>	<p>1. Occurs consistently each summer only in Loon outlet Creek where daily maximum water temperatures > 15°C.</p> <p>2. Does not occur in Loon inlet Creek or Hihium Creek where summer daily maximum water temperatures rarely approach or exceed 15°C.</p> <p>3. Fluctuations in daily numbers of fry moving up outlet stream correlated with rapid and extensive fluctuations in daily maximum water temperature, a distinctive feature of Loon outlet Creek.</p>	<p>(a) Fry held in identical experimental flumes usually showed more upstream movement in flume supplied with Loon outlet Creek water (mean temp. > 15°C.) than in flume supplied with Hihium Creek water (mean temp. < 12°C.). (1, 2)</p> <p>(b) Fry held for several days at 18°C. usually exhibited more upstream movement when tested at that temperature in experimental stream than did fry reared and tested at lower temperature (10°C.). (1, 2)</p>

TABLE VIII. (CONT'D) SUMMARIZED INTEGRATION OF FIELD OBSERVATIONS AND EXPERIMENTAL EVIDENCE SUPPORTING ENVIRONMENTAL CONTROL OF CURRENT RESPONSES SHOWN BY JUVENILE RAINBOW TROUT IN STREAMS OF THE LOON LAKE SYSTEM

Current Response	Juvenile Stage	Field Observations	Experimental Evidence
<u>Upstream Move-ment</u>	<u>Fry</u>	4. Most fry in Loon outlet Creek do not begin up-stream movement until they approach 40 mm. in length.	
<u>Upstream Move-ment</u>	<u>Finger-lings</u>	<p>1. Occurs consistently each year only in Loon outlet Creek during late spring and summer when daily maximum water temperatures approach or exceed 15°C.</p> <p>2. Does not occur in Hihium Creek where daily maximum water temperatures never exceed and rarely approach 15°C.</p> <p>3. Occurs to a limited extent in Loon inlet Creek on few days in mid-summer when daily maximum water temperatures approach or slightly exceed 15°C.</p> <p>4. Fluctuations in daily numbers of fingerlings moving up Loon outlet Creek correlated with rapid and extensive fluctuations in daily maximum water temperature.</p>	<p>(a) Fingerlings held under <u>constant</u> day length and <u>temperature</u> conditions, even those at the long day length--high temperature combination, did <u>not</u> exhibit strong positive reactions to water current in the experimental stream. (1, 4)</p> <p>(b) Fingerlings held at moderate temperatures (10°, 15°C.) and either short (8 hour) or long (16 hour) day length showed an immediate increase in upstream movement in experimental stream when subjected to a 5°C. increase in temperature. Decreases of 5°C. resulted in an immediate decrease in amount of upstream movement shown previously. (4)</p>

B. FACTORS INVOLVED IN CONTROL

In the case of juvenile trout during their first summer and autumn, three factors (water temperature, light intensity and size of fry) appear to be largely responsible for their different patterns of movement shown in streams of the Loon Lake system.

Water temperature is responsible, in large part, for differences in migratory pattern of fry between streams of the Loon Lake system and is involved in control of both seasonal and diel periodicity of movement within any one stream. Thus, water temperature is concerned not only in differences of response to current shown between fry in Loon outlet and inlet Creeks, but also in diel and daily changes in upstream movement of fry in Loon outlet Creek itself. Water temperature in Table VIII has been expressed as daily mean with reference to downstream movement and maintenance of position but as daily maximum with respect to upstream movement. In the former two types of behaviour a more general expression of temperature level seemed to be involved while in the case of upstream movement both diel and daily periodicity of movement had shown the best relationship with daily maximum temperatures.

Light intensity, in contrast to water temperature, does not bring about differences in response of fry to water current between streams but instead regulates diel periodicity of these responses within particular streams. Thus, in streams which do have daily mean water temperatures consistently below 13°C. in the summer (such as Loon inlet or Hihium Creeks), timing of downstream movement each night is controlled largely by fall and rise of light intensity in the 0.01 foot-candle level.

The marked decline in numbers of fry moving upstream with approach of dusk suggests that light intensity may regulate cessation of upstream movement each day.

Several marked changes and differences in migratory behaviour were associated with size of fry, both in outlet and inlet streams. The fact that most fry involved in downstream movement were less than 30 mm. in length whereas numerous larger fry were present indicated operation of a "size factor" in downstream movement and maintenance of position. Experiments at Loon inlet Creek (Fig. 11B) clearly demonstrated an effect of fry size on downstream movement. Moreover, a marked change (onset of upstream movement) in current response of fry was noted at Loon outlet Creek as fry approached 40 mm. in length. That fry less than 40 mm. were physically incapable of moving up Loon outlet Creek does not seem probable in consideration of experiments performed on the swimming speeds of 40 mm. rainbow trout fry acclimated to 10° and 20°C. Some data from these experiments were given in Bainbridge (1958) which showed that 40 mm. fry could swim, for several seconds at least, at speeds well in excess of 30 cm./sec. Smaller fry demonstrated swimming speeds approaching the above which would permit them to move up most stretches of Loon outlet Creek. Exclusion of age or other phenomena associated with size which may operate in a "size factor" has not been possible in the study.

Some factors, such as water temperature, which are of importance in control of migratory patterns of rainbow trout fry in streams also appear to have similar effects on movements of fingerlings. Differences in migratory behaviour between streams as well as certain aspects of

seasonal and diel periodicity of movement (particularly upstream) probably are controlled in fingerlings, as in fry, by differences in water temperature. Discrete diel periodicity in both upstream and downstream movement associated with changes in light intensity below or above a reasonably distinct level was not so apparent in migratory behaviour of fingerlings as in fry. Laboratory experiments showed that day length had a marked effect on current response of fingerlings. Downstream movement was greatest at long day length and low temperature, agreeing well with field conditions under which downstream movement of fingerlings was most pronounced. Positive rheotaxis under experimental conditions was highest at short day length and low temperature--a response which possibly would be of importance in maintenance of position in streams from late fall to early spring.

C. MECHANISM AND INTERACTION OF FACTORS

Virtually all fry and many fingerling trout which do move down streams of the Loon Lake system do so during nocturnal periods of low light intensity. Direct observation in the field and experimental evidence both in the field and laboratory indicate that downstream movement of juvenile rainbow trout in water current results from inability or difficulty in maintaining sensory reference to spatial surroundings at low light intensities. Reduction in visual association and actual contact with the bottom is brought about when fry move towards or to the stream surface, a behaviour which in young trout is markedly affected by

temperature. A similar mechanism has been proposed (Hoar 1953, 1954, 1958) for nocturnal migrations of several species of juvenile salmon down streams. In these cases no marked temperature effect on association of fry with stream bottom was noted.

The sudden onset of downstream movement of trout fry each evening (Figs. 6, 7, 8) may be a result of a slow rate of dark adaption of the trout eye in relation to the concomitant rapid decrease in light intensity. Information on cone and rod threshold at low light intensity or on rate of dark adaption of the rainbow trout eye is not available. However, these values may be in the same order as those for several species of Oncorhynchus determined by Ali (1958). In salmon fry cone thresholds in the 1 to 0.1 foot-candle range were reported, with complete dark adaption requiring about forty minutes. Rod thresholds, below which little or no visual orientation would be possible even after complete dark adaption, were given as 0.0001 foot-candles for four species of salmon (sockeye, coho, pink and chum). Hoar (1953) and more recently Ali (1958) suggested that "the marked peak in the downstream migration of the juveniles at dusk" may be due to the "state of partial night-blindness" occurring between the time when light intensities fall below the cone threshold and when the eye is fully dark adapted. Reduction or cessation of downstream movement may occur after complete dark adaption of the eye, provided illumination does not fall below 0.0001 foot-candles. Coincidence of timing in rapid onset of downstream movement of sockeye smolts in Lakelse river with rapid decrease in light intensity and features of dark adaption of the sockeye smolt eye has been noted by Brett and Ali (1958). Ali and Hoar (1959) have demonstrated

a similar relationship for young pink salmon in both field and laboratory experiments. Field readings taken at the surface of Loon inlet Creek (Figs. 7 and 8) and data presented by Dice (1945) show that intensities of nocturnal illumination do fluctuate below and above the 0.0001 foot-candle level on a single night. Such fluctuations may be responsible for abrupt increases and decreases in numbers of trout fry moving downstream on any one night as evident in Figures 6, 7 and 8.

Although loss of visual contact with stream bottom at low water temperature is paramount in the mechanism of downstream migration, other factors may be involved. Lateral movement of fry into shallow water along the stream margin each evening prior to downstream migration results in a pronounced concentration of fry in a narrow band at edges of the stream. Density and size of fry competing for suitable holding areas may affect the extent of downstream movement exhibited by these young fish.

Maintenance of position in daylight by juvenile trout is probably accomplished largely by visual reference points along the stream bottom or side. Classic experiments of Lyon (1904) and those of Schiemenz (1927) have demonstrated the importance of visual orientation in rheotactic responses of fish. Lowenstein (1957), reviewing the work of Dijkgraaf (1933) and others on function of the lateral line system in fishes considers that the chief mechanism of control of rheotactic orientation in darkness appears to be tactile stimulation. In summary Lowenstein (1957) states that

a fairly accurate three-dimensional sensory representation of the topographic features of the immediate environment, as well as the localization of moving objects in the vicinity, may thus be assumed to be mediated by this sense organ in

the absence of visual orientation either in darkness or in a turbid medium.

Mechanisms of position maintenance by stream fishes in the dark, however, have not been carefully worked out in detail.

Hoar (1953) emphasizes the importance of territorial behaviour in prolonged residence of salmonids in streams and notes movement into shallow water, settling to the bottom and inactivity at night as behavioural characteristics associated with territoriality. Nocturnal observations in streams of the Loon Lake system show that lateral movement into shallow water in itself, does not lead necessarily to maintenance of position by juvenile trout. Large numbers of fry lost position at Loon inlet Creek each evening following movement into shallow water along the stream margin. Laboratory observations on behaviour of fry in the dark under simulated stream conditions indicated that movement towards and repeated contact with the stream bottom may well be essential to maintenance of position. In no case, however, either in the field or in the laboratory, were juvenile trout seen to settle more or less permanently onto the stream bottom and remain inactive at low levels of illumination. Rapid re-orientation and temporary maintenance of position observed when fry moving downstream struck or closely approached solid objects again emphasized the role played by tactile or pressure stimuli in the ability of young trout to hold position at night in flowing water.

Upstream migration of rainbow trout fry and fingerlings in streams of the Loon Lake system clearly seems to be regulated by water temperature. In this regard, temperature apparently has a two-fold action,

- (a) setting limits within which upstream movement may occur and
- (b) affecting intensity and timing of the response when it does occur.

The mechanism involved has yet to be determined. Acceleration of metabolism and activity at higher temperatures may be involved in setting the temperature level above which upstream movement occurs, whereas sudden rises in temperature may act as a directing factor (Hoar, 1958) which brings about the reaction of swimming more strongly into water currents. A simple increase in activity coincident with rises in temperature, in itself, will not necessarily explain upstream movement, for this increased activity must be oriented in a specific direction.

Upstream migration of juvenile brown trout in the outlet stream of Lake Rensjön in Sweden (Runnström, 1957) apparently has a relation to water temperature similar to that in upstream movement of juvenile rainbow trout at Loon outlet Creek. Young brown trout only moved up Rensjön's outlet stream when its temperature exceeded 5--6°C. Furthermore sharp increases in temperature above this level markedly increased daily numbers moving upstream while periods of constant or declining temperature were generally associated with reduction in numbers moving upstream. No statistical examination of correlation was made in this study. Limitation of upstream movement to water temperatures above a certain level was evident in the work of Sörensen (1951) on migrating elvers. Both in an experimental flume and in a number of Swedish rivers, elvers did not move upstream until the water temperature reached or slightly exceeded 15°C.

Operation of water temperature as a factor directing or orienting movement with respect to water current was evident in the experimental studies of Keenleyside and Hoar (1954) on young salmon and those of Beauchamp (1937) on Planaria alpina. In the former study sudden rises in temperature of 4--5°C. brought about marked downstream swimming (negative rheotaxis) in both chum and coho fry but no alteration in

current response of sockeye fry. Beauchamp's studies showed that introduction of planarians into water 5°C. higher than that in which they were living caused a positive rheotactic response in the animals. Hoar (1958) suggests that difference in response of sockeye fry to sharp rises in temperature, compared to that shown by chum and coho fry, may be of significance in explaining the spectacular upstream migrations shown by large numbers of sockeye underyearlings which emerged in outlet streams of some lakes.

D. GENERAL CONSIDERATIONS

Considerable evidence has been presented for certain environmental factors, particularly temperature, playing a predominant role in control of migration of juvenile rainbow trout in outlet and inlet streams of Loon Lake. A similar control was suggested in several other stream systems examined. That temperature, of the gamut of factors which could conceivably act to direct or orient movement of fish in water current (Hoar, 1958; Collins, 1952), should claim such eminence appears more reasonable when control of movement both upstream from an outlet and downstream from an inlet is considered. The one environmental factor which might be expected to differ consistently between inlet and outlet streams of most lakes, during observed migratory periods, is water temperature. Outlet streams, draining at most times water warmed at the lake surface, are probably warmer than their respective inlet streams throughout much of the year. However they may be, at the same time,

subject to rapid and extensive changes in temperature resulting from either sudden turbulent mixing by wind action of relatively thin layers of warmed water or by tilting and surfacing of deeper, cool layers of the lake in wind-induced thermal seiches so dramatically demonstrated by Mortimer (1952 a, b). Such sudden changes in temperature would not be characteristic of most inlet streams, except where the outlet of one lake became the inlet of another in a relatively short distance. The importance of rapid changes in water temperature in affecting upstream movement of juvenile trout has been demonstrated both in the field and in controlled laboratory experiments. Thus it seems probable that evolution of appropriate behavioural responses to water current by rainbow trout in order to ensure successful maintenance of lake populations, while exploiting all possible spawning facilities (both of inlet and outlet streams), has involved selection of a set of responses which are altered markedly by the single most consistent environmental difference between these types of streams in the majority of lakes, namely their temperature characteristics.

X. CONCLUSIONS

1. Marked differences in water current responses of juvenile trout migrating into Loon Lake from outlet and inlet streams result from environmental differences between streams, rather than genetic differences between spawning stocks.
2. Differences in water temperature between Loon outlet and inlet Creeks regulate differences in direction of migration through action on behaviour associated with downstream movement, maintenance of position and upstream movement.
3. At cool water temperatures (daily mean consistently $< 13^{\circ}\text{C}.$) recently emerged fry exhibit little tactile association with the stream bottom; consequently, in darkness, they lose visual orientation and move downstream.
4. Maintenance of position in darkness by fry at warm water temperatures ($> 15^{\circ}\text{C}.$) is facilitated by their frequent contact with the stream bottom exhibited under such conditions.
5. Warm water temperatures (daily maximum usually $> 15^{\circ}\text{C}.$) in conjunction with sharp rises in water temperature is associated with upstream movement of large fry (> 40 mm. in length); a similar relationship is evident in fingerlings.
6. Laboratory experiments suggest that combination of cool water temperature and long day length induces downstream movement of fingerlings; in the field, fingerlings move downstream under similar

conditions (late spring and summer).

7. That combination of cool water temperature and short day length may facilitate maintenance of position by fingerlings is suggested by marked lack of downstream movement and slight positive rheotaxis shown by fingerlings tested in laboratory experiments under such conditions; in the field fingerlings maintain position in streams under similar conditions (late fall to early spring).
8. Evidence examined from four other widely separated stream systems indicates an environmental control of migration in juvenile rainbow trout similar to that demonstrated in the Loon Lake stream system.
9. Development of a behavioural response to water current which would permit exploitation of both major types of spawning streams (outlet and inlet) by lake dwelling rainbow trout has involved selection of responses markedly altered by water temperature, which is probably the single most consistent environmental difference between outlet and inlet streams of most lakes.

XI. LITERATURE CITED

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