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**BULLETIN XXI**

**MECHANISMS CONTROLLING  
MIGRATION OF  
SOCKEYE SALMON FRY**

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## **ABSTRACT**

Field observations in the Fraser River system, combined with field and laboratory experiments, were used to examine the hypothesis that migration of sockeye salmon (*Oncorhynchus nerka*) fry is an inherited response and is characterized, in the presence of certain stimuli, by a deliberate movement to the nursery lake from the incubation area. Distinctly different behavior patterns were displayed by the six native sockeye races examined, and use of hybrid stocks showed these differences to have a genetic basis. Among the variables tested, velocity and odor were shown to be directing factors for the migratory response, whereas temperature and light were found to influence only timing and intensity of migration. Size at emergence and age of fry were found not to be causal mechanisms directing migratory behavior. Directional orientation exhibited by fry suggested light to be a major orientation phenomenon in the absence of current. The relationships of these factors are discussed as mechanisms controlling sockeye fry migration, and the implications that such mechanisms may have in resource development are discussed.

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# MECHANISMS CONTROLLING MIGRATION OF SOCKEYE SALMON FRY

## INTRODUCTION

Migrating behavior of salmonid fishes has long attracted the attention of scientists. Perhaps most spectacular are the long and rigorous migrations of Pacific salmon, genus *Oncorhynchus*, as they course through hundreds of miles of ocean and river, returning to their natal stream, spawning, and finally ending their life cycle. Less well known and often unobserved are the migrations of salmonid fry, emerging from their incubation site and traveling to sea or to the freshwater rearing area of their particular system. The behavior of sockeye salmon fry, *O. nerka*, during migration from the incubation area to the lake nursery area has been part of the continuing investigation undertaken by the International Pacific Salmon Fisheries Commission to understand the life history of the species.

Migration of sockeye fry occurs in a variety of patterns, depending on the relationship of incubation and nursery locations. Most often, emerging fry need only move with the current of the incubation stream to reach their lake. Less frequently, incubation occurs below the nursery area and emerged fry must swim against the current considerable distances to reach the lake. In some instances a more complex route has to be negotiated, down one stream and up another, or from one lake to another, before lake residence begins. And, at the opposite extreme, there are beach incubation sites which require the fry only to emerge to enter the nursery environment. The various relationships of incubation and nursery locations require that sockeye fry possess complex mechanisms for control of migrating behavior.

Hoar (1951) was one of the first to examine salmonid fry migration and pioneered in studies of the factors influencing migration. After his work, and investigations by other scientists, the question of what "controls" migratory behavior of fry was given attention and various hypotheses were developed. Hoar (1954) suggested that downstream movement of sockeye fry occurred by displacement at low light intensities when darkness eliminated rheotactic responses. Similarly, Bams (1969) described downstream movement of sockeye fry as a passive displacement, governed by lack of a cover-seeking response in a light-controlled emergence cycle and a gravity-oriented vertical movement response. A state of night blindness before the eye became fully dark-adapted was suggested by Ali (1959) as causing increased movement downstream of juvenile salmon, and Byrne (1971) added that high nocturnal activity amplitudes in newly emerged sockeye fry, coupled with a semidark-adapted retina, could promote passive displacement downstream.

Upstream migration, however, could not be explained by a passive movement, and thus required a hypothesis incorporating some directing phenomenon. Hoar (1958) observed that behavior of newly emerged sockeye fry, characterized by downstream movement, changed with age; thus with increased size and swimming ability, the fry were considered to acquire the capacity for an upstream migration. As early as 1947, Killick (MS 1949) suggested from observations in the Fraser

River system that delay after emergence and increased size were necessary for upstream migration of sockeye fry. This view was supported by Byrne (1971) who showed a change in sockeye fry locomotory activity periods from nocturnal to day-active, 10 days after emergence. Byrne hypothesized that upstream migrations are facilitated by changes in behavior, and further speculated that downstream migrants might be able to perform upstream migrations if transplanted.

Northcote (1962) was one of the first investigators to propose a system to explain how direction of fry migration was controlled, in at least one stock of fish. In a comprehensive study on behavior of juvenile rainbow trout, *Salmo gairdneri*, entering Loon Lake, British Columbia, from inlet and outlet streams, temperature differences between the streams were considered responsible for regulating fry migration direction. Similarly, stream temperature was suggested important in inducing rheotactic responses of rainbow fry to water current in upper Lardeau River (Northcote 1969a). Stimulation of positive rheotaxis by a sharp rise in temperature has also been entertained as a contributing factor in sockeye fry migration upstream (Hoar 1958).

Genetic differences as a basis for upstream or downstream migration patterns have been given consideration only recently. Genetic control of migratory behavior of sockeye fry was indicated by Brannon (1967) in studies on the Fraser River system, and by Raleigh (1967) on fry from Karluk Lake. Raleigh also postulated an interaction between temperature and heredity in controlling the direction of migration of salmonid fry. Genetic influence on migration of rainbow trout fry has been examined by Kelso (MS 1972) and, with limited numbers of rainbow and cutthroat (*S. clarki*) trout, by Raleigh (1971). Kelso (personal communication) has found that while temperature influences the intensity of response among his trout fry stocks, innate behavior patterns are apparent.

The mechanisms controlling salmonid fry migration, therefore, have been shown by several investigators to be complex and influenced by many factors. Because of the near obligatory requirement of sockeye fry for lake habitation, and the relatively short time they take to reach the nursery lake, the migratory phase of the behavior pattern was considered a period critical in the life history of this species. Since rehabilitation measures in the Fraser River system involve restocking barren areas with introduced populations and extending the use of some rearing lakes, studies on the migratory behavior of sockeye fry were undertaken to determine its potential influence on the success of such operations. In 1962 and 1964, preliminary examination of certain races led to the hypothesis that sockeye fry migration is an inherited response, characterized, in the presence of certain stimuli, by a deliberate movement to the nursery area (Brannon 1967). In this paper, data supporting this hypothesis have been presented, with emphasis on the mechanisms involved and their implication in the management of the resource.

## SCOPE OF STUDY

The existence of different behavior patterns in migration within a species implies that the mechanisms involved are the same for all races, but that the same stimuli elicit different levels of response, resulting in a directed movement. Therefore, since no single race of sockeye could characterize the species, the

comparative approach was used. Six distinct populations were selected for study from the Fraser River system in British Columbia representing a broad spectrum of migratory behavior. Three of these populations were from the upper Fraser watershed and three races were from the lower drainage system (FIGURE 1). Those chosen were Chilko stock, a race which moves from the incubation site upstream to the nursery lake; Stellako stock, a downstream migrating population incubated between lakes; Adams stock, a race which must show both downstream and upstream responses; Weaver stock, a race which moves down its incubation stream and up another stream to the nursery lake; 7-Mile stock, a population that moves down a tributary stream to the lake, and Cultus stock, a race incubated on beaches in its nursery lake.

In advancing the view that fry migration patterns are the manifestation of different levels of response to stimuli, examination of organismic and environmental variables was necessary. The variables selected for study were limited to the influence of 1. fry age, 2. fry size, 3. water velocity, 4. water temperature, 5. water source, and 6. light on the response of stocks to current. By combining field observations and laboratory studies the mechanisms controlling sockeye fry migration were postulated.

To eliminate uncertainty about the meaning of various terms used in this paper, the following definitions are given. "Migration" is considered a directed movement with two components, orientation and locomotion. "Rheotaxis" is reaction to flow and assumes movement with or against current. "Alevin" refers to the stage between hatching and complete yolk absorption, and "fry" refers to the period after yolk is absorbed. However, in field observations once fish emerge from the gravel they are termed "fry" even though some populations migrate with yolk stores remaining. The term "race" means fish from a spatially or temporally distinct spawning population. "Stock" refers to a group of fish removed from a population for study, with "native" meaning stock taken from their natural environment, and "experimental" meaning stock incubated in the laboratory.

## MATERIALS AND METHODS

Observations were made in the natural environment on the migrating behavior of sockeye fry from six races native to the Fraser River watershed. Concurrently, field tests in experimental apparatus were conducted on fry captured from some of these same races to determine migrating response to current, the effect of certain environmental influences on the response, and preferred orientation in the absence of current. To examine the influence of environmental factors on fry migratory behavior more thoroughly, and to elucidate the genetic basis of the migratory response, stocks were acquired from the six races for incubation and subsequent testing at the Sweltzer Creek Salmon Research Laboratory located adjacent to the outlet of Cultus Lake. Hybrid stock, formed by crossing spawners from two populations showing opposite rheotaxis as fry, was examined specifically for influence of heredity on response to current.

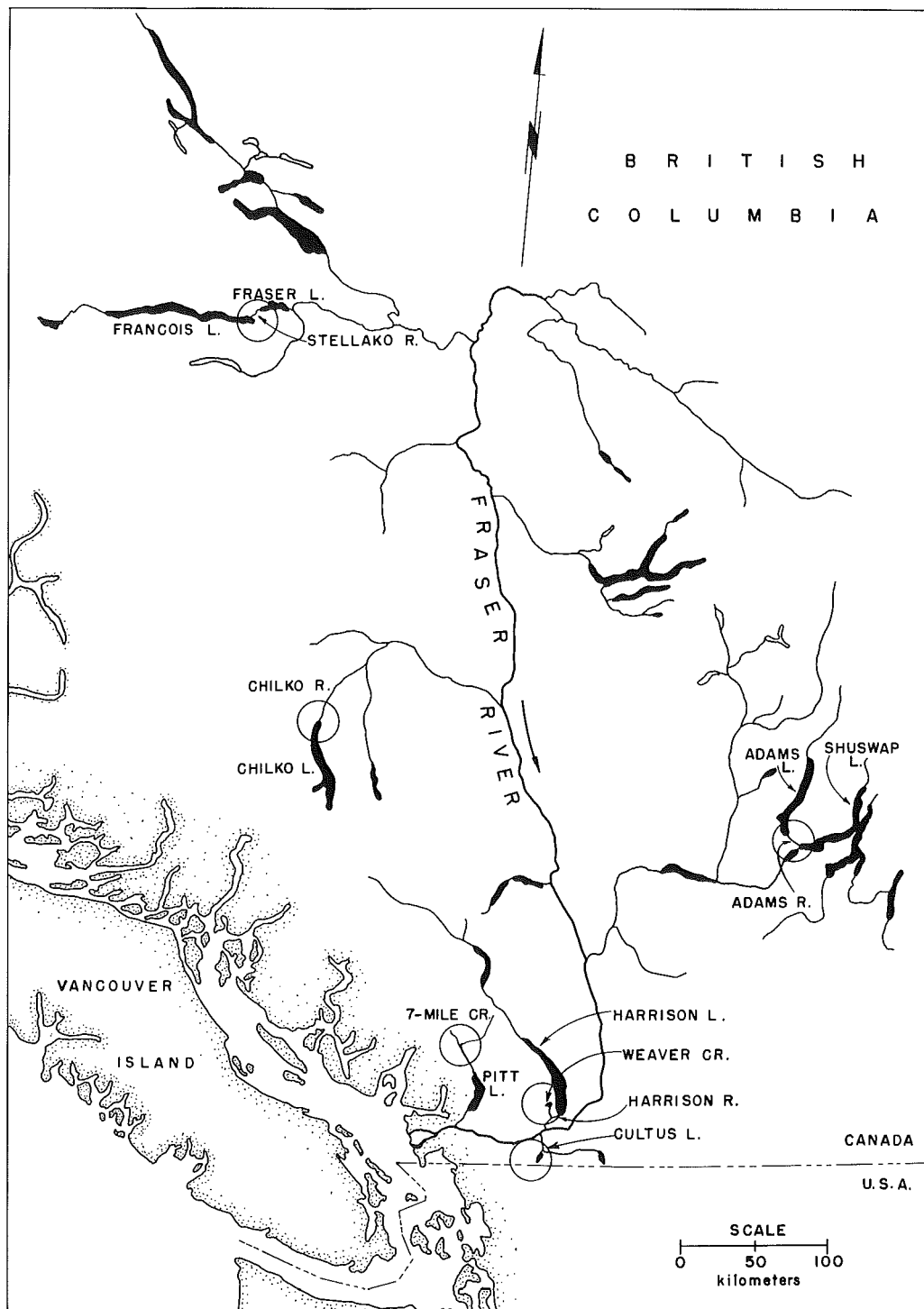


FIGURE 1—Fraser River watershed showing the Chilko, Stellako, Adams, Weaver, 7-Mile and Cultus study areas.



## Field Observations

During spring fry emergence and migration, sockeye fry behavior was observed at each of the six study areas. The data collected included emergence timing, size and stage of advancement of migrating fry, distribution and migration behavior, and the physical characteristics of the particular native environment. To assist observations, scuba gear was used to examine redds and follow fry movements. At night underwater flashlights were shone intermittently to locate and follow fry. Seines and fyke-nets were used to capture samples for length measurements and dry weight determinations. Personal observations for several years and records collected by the Commission personnel were used in describing the specific behavior patterns of migrating fry in each study area.

## Experimental Stocks

In the fall preceding each study year, two or more populations were selected to supply experimental stocks. At each spawning location, eggs removed from 25 females were fertilized with 15 males to provide approximately 10,000 eggs from each race. Since spawning times coincide for two of the races, Stellako and Chilko, females were taken from Stellako in the fall of 1966 and from both races in 1967, killed, packed in moss and ice, and flown to the reciprocal stream where the eggs were artificially spawned and fertilized with native males. After fertilization all eggs were water-hardened, placed in insulated jars, and transported to the Sweltzer Creek Salmon Research Laboratory for incubation.

The eggs and subsequent alevins were incubated in darkness in plastic-screened, wood-framed trays (27.9 by 61.0 cm) without gravel, and in upwelling flow to reduce conditioning to a directional velocity. Once yolk absorption was completed, the fry were removed from the incubation trays and placed in partially covered hatchery troughs (27.9 by 182.9 cm). Fry were fed Cultus Lake zooplankton, supplemented with a dry diet, and the troughs were flushed at a rate of 7.6 liters/min.

The water used for incubation was obtained from two sources, Cultus Lake and from Hatchery Creek, a small tributary stream draining into the outlet of Cultus Lake near the laboratory. In 1966-67 the temperature of the lake water supply was held constant at 5.6°C once the source cooled to that temperature in the fall. In the following years, incubation was carried out in constant temperatures of 5.6°C or allowed to follow the natural annual temperature cycle. When certain temperatures were desired during incubation or testing, refrigerated or heated lake water was mixed with the lake source; the temperature of the creek source was allowed to follow its natural cycle.

In order to relate behavior to size and stage of advancement, samples of eggs, alevins and fry were weighed to determine the rates of yolk absorption and weight gains during incubation of all experimental stocks. Each measurement is the average weight of 20 individuals weighed separately on an analytical balance after oven drying for 24 hr at 98°C. Alevins were dissected from the yolk before weighing, and the subsequent measurements denoted as alevin body weights and

yolk weights. Similarly, fish collected from the field were examined, and any yolk material present was removed before dry body weight was determined.

Each experimental stock studied in 1967, 1968 and 1970 was sampled regularly to monitor development during incubation, thus allowing comparisons of size, dates at complete yolk utilization, and the stage of advancement at which migrating behavior began. The maximum dry weights of fry at yolk utilization showed a considerable range in fish size between the different test stocks. Fry from 7-Mile were largest, followed by Weaver, Adams, Chilko, Stellako and Cultus (TABLE I). Weight differences were the result of different egg sizes characteristic of the populations.

TABLE I—Body weights of experimental stocks at complete yolk utilization.

Stock	1967	1968	1970
	Dry Weight (mg)	Dry Weight (mg)	Dry Weight (mg)
Chilko	24.0	19.3	21.1
Chilko ♀ X Stellako ♂		21.8	
Stellako	19.8	17.9	21.3
Stellako ♀ X Chilko ♂	18.0	14.7	
Cultus	17.6	14.5	
Adams		21.0	
7-Mile		31.9	
Weaver		22.3	

Testing Response to Current

The response of fry to current was tested in an experimental apparatus both in the field and in the laboratory. After measuring response to current under standard test conditions, tests were carried out (mainly on laboratory stocks) to examine the effects of organismic and environmental influences on current response. These included tests on fry of different ages, and tests at four different velocities, three temperatures, two light conditions and using two water sources.

APPARATUS

Tests of response to current were performed in an apparatus representing a convoluted channel 16.0 cm wide and 17.1 m long, termed a migration channel. The apparatus consisted of a 4-ft by 8-ft sheet of 3/4-inch plywood (1.22 m by 2.44 m by 1.9 cm) on which was supported a 10-cm wall around the perimeter with six vertical dividing walls placed parallel to each other inside. The dividing walls, also 10 cm high, were attached to the perimeter wall at alternate ends to form a convoluted channel (FIGURE 2). Over the floor of the apparatus a single layer of gravel was held fast with fiberglass resin, thus simulating the stream bottom and providing hiding or resting areas for the fry. A screen chamber (16.0 by 30.5 cm) was placed in the center of the channel to hold fry prior to testing, and two V-throat traps were installed at the ends of the channel (each 8 m from the central

chamber) to intercept migrating fry. During tests, water flow through the channel was set at a constant velocity, measured by the movement of round floats placed in the flow, and depth was maintained at 2.5 to 5.0 cm.

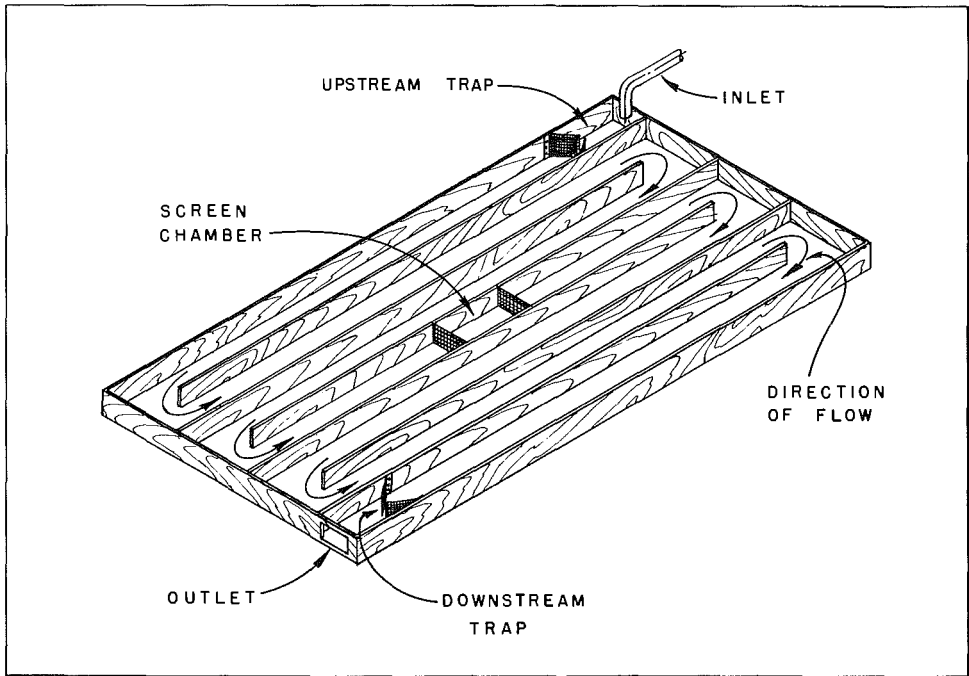


FIGURE 2—Migration channel for testing response to current.

## PROCEDURE

In the field studies, test stock was captured by dip-netting fry holding or migrating along the stream shore. Captured fry were transported to the study sites in buckets and held in 38-liter milk cans overnight for testing the following day.

At the laboratory, as yolk absorption progressed among the alevins, small groups of alevins were removed from the incubation trays and tested in the experimental channel to determine when migrating behavior started. Initially, the alevins responded by hiding in the gravel near the release point, and it was not until the fish had reached the stage where the majority exited the channel that routine tests were begun.

In each routine test, 100 fish from a single stock were removed from the holding container or incubation tray and placed in the central screen chamber of the test apparatus. After an initial adaptation period of 20 min, the velocity was started and fry were exposed to the flow 10 min, for orientation, before the screens inhibiting their migration were removed. After the fry were allowed to move from the central chamber, the numbers appearing at either the upstream or downstream trap were recorded. The duration of each test was determined by how fast the fish exited the apparatus and varied from 48 hr to 30 min depending on the age of the particular group. Each group of fry was released after testing.

Velocity during all routine field and laboratory tests was set at 15.2 cm/sec, a level suggested to be the maximum favorable to continuous upstream migration of sockeye fry (Andrew and Geen 1960). To examine the influence of velocity on current response, tests were run at velocities of 15.2, 7.6, 3.8 or 1.9 cm/sec.

In routine field tests, the water supplied to the test apparatus was obtained from the native stock's incubation stream, and water temperatures were determined by the natural stream temperature (see test results for temperatures at each location). In one field test on the influence of water source, water was also obtained from a tributary stream. All water used in field tests was supplied to the apparatus through polyethylene tubing.

In the laboratory studies, temperatures could be changed in the apparatus by tempering the 5.6°C water from Cultus Lake with water from the same source refrigerated to 2.2°C or heated to 26.7°C. Tests on the effect of temperature were run at 2.2, 5.6 and 8.9°C. A second source of water, used to test the influence of exposure to water other than from Cultus Lake, was obtained from Hatchery Creek, a small tributary drainage stream used as an auxiliary supply for the laboratory. Temperatures of the stream during its use ranged from 2.2 to 6.1°C. Except for tests on the influence of temperature or water source, all laboratory tests were conducted in Cultus Lake water at 5.6°C.

When used outdoors the apparatus was covered with dark plastic which reduced light intensities and other visual stimuli. At the laboratory the apparatus was installed indoors in an enclosure where light could be controlled and constant test conditions provided. Routine laboratory tests on response to current were carried out in near darkness; special tests on effect of light were carried out in daylight conditions.

To test the effect of size and age on current response, experimental stocks of fry were held and fed in standard hatchery troughs under natural light conditions and tested regularly over a period of 60 days. One experimental stock was tested again after an additional 30 days of rearing.

In the laboratory, 8 to 30 replications were carried out for each test. Field tests on response to current were limited in number by the time available, or by the lack of a convenient source of fry, but in all cases at least 10 replicate tests were performed.

In this study the premise was taken that fry migration was a deliberate movement and hence a preferred response was one which differed significantly from a random 50:50 distribution. When describing the current response, the numbers of fry moving upstream and downstream were expressed as proportions trapped of the 100 fry tested. In those instances where some fry remained within the apparatus, the proportion of moving fry totaled less than 100.

### **SUPPLEMENTARY TESTS**

Additional laboratory investigations were conducted to examine the initial current response of fry upon emergence from the gravel environment. Artificial redds were prepared in 15.2 cm of gravel distributed over the length of 0.3-m by 4.9-m troughs outfitted with V-throat traps at both inflow and exit ends. The troughs were set indoors, under natural light and supplied with lake surface water from Cultus Lake at a surface velocity of 20 cm/sec and at temperatures deter-

mined by the natural lake cycle. The gravel mixture used ranged from 0.6 to 1.9 cm in diameter with the exception of the redd location, where a bottom layer of 5.0-cm stones was used as the base material for egg placement. After developing to the eyed stage, eggs were taken from the experimental stocks in incubation trays, described previously, and planted in the redds in late fall. Upon emergence the following spring, the fry could move either upstream or downstream, the choice discerned by counts made from the traps.

### Testing Response to Water Source

Preference exhibited by fry when provided with a choice between two water sources was tested in the field, using one native stock, and with several experimental stocks in the laboratory. Tests were carried out to examine the preference between lake and creek water sources, the response to a diluted water source, and the effect of olfactory occlusion on water source preference. Influence on preference behavior caused by rearing or incubation in a foreign water source was also examined.

### APPARATUS

Olfactory discrimination by sockeye fry was examined in a plywood Y-trough, built with arms 20.3 cm wide, 10.2 cm high and 121.9 cm long, connected to a triangular central section, 45.7 by 45.7 by 55.9 cm in dimension (FIGURE 3). Water was introduced in the two outer arms, flowed to the central section where it mixed and proceeded out the exit arm. A 20.3-cm screen chamber was positioned across the exit arm near the outlet and served as the holding area for fry before release. Two V-throat traps, each placed 30.5 cm from the ends of the outer arms, intercepted migrating fry.

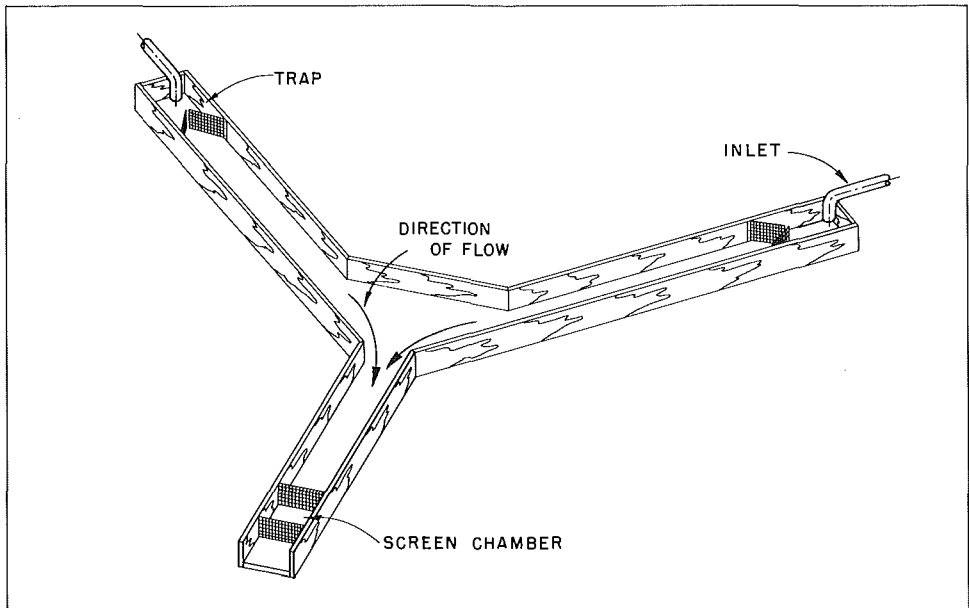


FIGURE 3—Y-trough for testing water source preference.

## PROCEDURE

All tests were executed in daylight in sets of 10 or multiples thereof using 2, 5, 10 or 20 fry in each run, depending on the size of fish and nature of the study. In each test continuous water flow was maintained. Fry were placed in the screen chamber and left for 3 to 5 min to adjust after handling and exposure to new conditions. The upper screen barrier was then raised, manipulated by string from behind a blind, allowing fry to advance and choose either of the water sources.

The velocity of water moving through the apparatus was set at 2.5 or 7.6 cm/sec at a depth of about 5.0 cm. Temperatures during studies in the field were determined by the stream temperatures. At the laboratory, tests were conducted at temperatures available in Hatchery Creek and the temperature of the lake supply was adjusted to coincide. Upon entering one of the two traps, the fry were considered to have shown a choice for the water source supplying that arm. In those instances where fry searched back and forth without entering a trap, or if they remained in the screen chamber area, they were considered to have shown no choice. In each test the numbers of fry entering each trap were recorded as scores.

A distribution of test scores which differed significantly from a random 50:50 distribution was presumed to be evidence that a preference existed.

Laboratory and wild stocks were also tested for water source preference with olfaction denied. Petroleum jelly was profused into the olfactory capsules of anesthetized fry by inserting a No. 26 G hypodermic needle through the anterior nare of each pair of nostrils, and applying sufficient pressure until excess expressed from the posterior nare. When removing the needle, pressure was maintained on the syringe plunger to assure a good jelly seal. The fry were revived immediately and tested the same day.

During incubation, developing embryos and alevins were preserved and prepared for histological examination to study development of olfactory tissue. Tissues were preserved in formalin, paraffin sectioned, and serial sections stained in hematoxylin and eosin.

## Testing Orientation

Orientation in the absence of current was tested on native stocks in the field and after transfer to the laboratory. Experimental stocks were also tested at the laboratory, involving two year-classes of fry in some cases.

## APPARATUS

Orientation in the absence of velocity was examined in a plywood trough arrangement, consisting of a central polygonal compartment 61.0 cm in diameter and 7.6 cm in depth, with 6 arms, 15.2 cm wide by 121.9 cm long, spaced equally around its circumference (FIGURE 4). At the center, a 25.4-cm cylindrical screen was positioned to hold the fry before testing. A V-throat trap was placed 15.2 cm from the end of each radial arm to retain fry once they moved down the length of the arm.

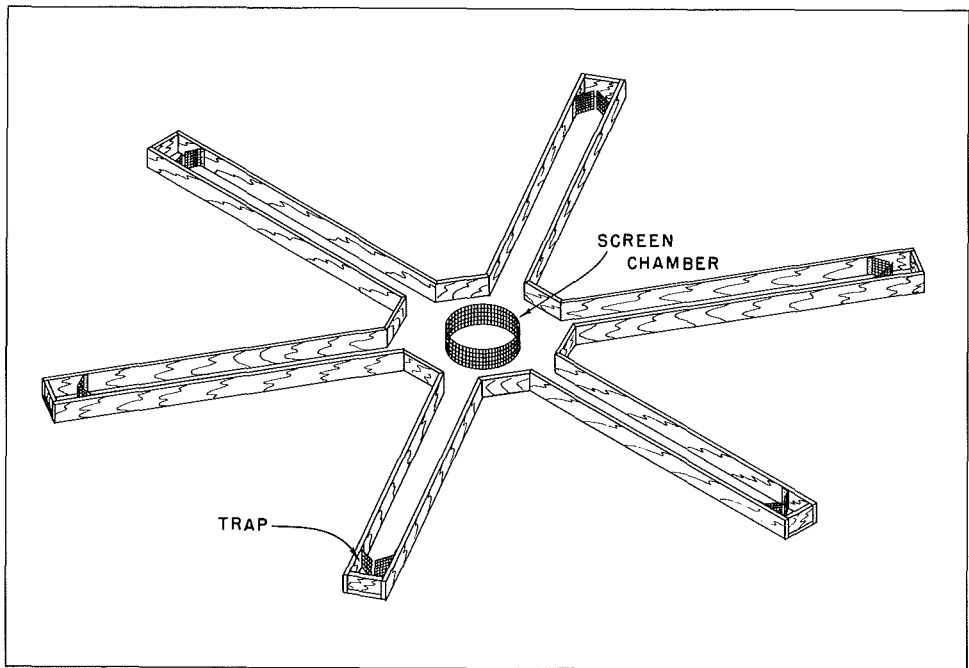


FIGURE 4—Orientation testing apparatus.

## PROCEDURE

For tests in the field and at the laboratory, the apparatus was placed outdoors in an open area with a full view of the sky and rotated at intervals to eliminate bias. Water depth during tests was 5.0 cm and temperatures were determined by the river or lake water used for supply. Water was renewed at intervals to reduce temperature variability.

Fry were removed from holding containers or troughs and placed in the screen chamber for about 20 min to allow for adjustment to the apparatus and initial orientation. After the adjustment period, a string and pulley were used to lift the screen about 4 cm, or nearly out of the water. The pulley system was operated from a distance of several meters, the position of which was rotated around the apparatus between tests. Once the fish were released they were free to move in any direction within the central compartment and choose any of the radial arms. A choice of direction was considered to have been shown when a fish entered a trap, and the score for each arm was the number of fish trapped. Since random movement would show equal distribution in all six traps, preferred direction was assumed if distribution was significantly different from random choice. When direction of fry movement is given, the reference is to magnetic north.

Tests were run in sunlight, heavy overcast or darkness with 25 fry per trial. The number of trial replications in the limited time available depended on length of time required for all fish to trap. During tests, fry behavior was observed from a distance.

## MIGRATORY BEHAVIOR IN THE NATURAL ENVIRONMENT

To form a general thesis on mechanisms of sockeye fry migration, detailed observations were made in the native environments of the six populations chosen for study. A comparative description of their migrating behavior emphasizes the differences found between populations, and is presented as a foundation on which to develop the interpretation of experimental investigations.

### Upstream Response in a Lake Outlet Stream

Upstream migrating behavior is well exemplified by Chilko River sockeye fry. The major incubation area in the system covers about 6 km of Chilko River immediately below Chilko Lake (FIGURE 5) and fry must move upstream to reach the lake. The incubation area is lake-fed except for small periodic tributary creeks which drain the adjacent terrain.

Emergence from the gravel occurs almost entirely at night which is characteristic of the species. After leaving the stream bottom fry become vulnerable to the river velocity and are swept downstream until they reach the shore or lower velocities. An indication that some fish continue downstream is apparent from their capture 127 km below the spawning area.

Many recently emerged fry are found holding in shallow bays along the river bank or in a wide area of the river, called Canoe Cross, at the lower end of the incubation grounds. Into one such bay, Madison Creek empties and forms pools of quiet water protected from high velocity and intrusion of river water. Although Madison Creek is unfamiliar to their incubation experience, the fry emerging from the adjacent river are frequently found holding in the pools of creek water overnight.

Upstream migration is first noticed 5 to 10 days after emergence begins and usually occurs when river temperatures approach 3.3°C during the latter part of April. In contrast to the negatively phototactic emergence behavior, migration upstream occurs primarily in daylight, beginning at or before first light of dawn and showing a bimodal abundance pattern which peaks mid-morning and afternoon. Upstream migration first occurs among fry reaching shore above the increased gradient starting 1.5 km below the lake. Migrating fry are observed swimming along the river shore approaching the lake before fry are seen moving up the steeper gradient, indicating that some fry begin upstream migration without having to drop downstream. Observations at night showed individual fry along the bottom of the river having no apparent difficulty maintaining position in areas of moderate velocity.

Fry move upstream very close to shore, in small groups or, during peak migration, in a thin almost continuous band, progressing at an average rate of 7.92 cm/sec (Andrew and Geen, 1960). The shoreline varies, with areas of turbulence, high velocities, eddies, and calm water. In many places, rocks along the river bank form small passages where the fish avoid higher velocities. In areas where fry are forced to negotiate faster water they do so in the lowest velocity available, moving along the face of rocks, next to the bottom or within 2 to 3 cm of the shoreline.



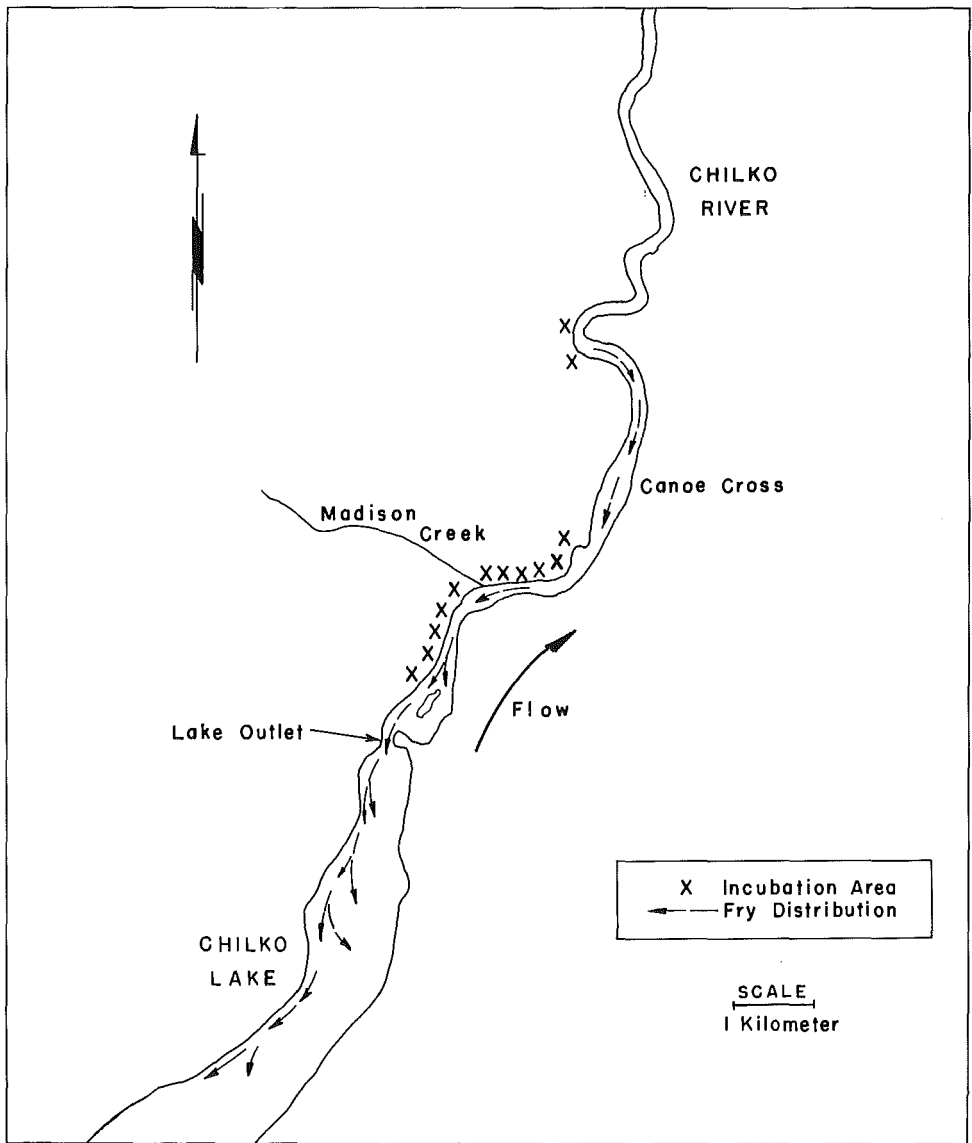


FIGURE 5—Incubation sites and migration distribution of stock native to Chilko River.

where small waves may wash them ashore momentarily. Frequently no choice is available. The fry collect below an obstruction and dart around its perimeter as quickly as possible. In the shallow areas with low velocity the fry have no difficulty migrating and do not appear impeded by changing temperatures; fry are often found moving through temperatures from 3.3°C to over 10.0°C.

Migrating Chilko fry orient primarily to current regardless of changes in river direction. As the river meanders, the change in direction of flow does not affect the apparent persistence of fry to ascend the stream. However, there appear to be other

factors which influence their response to current. In one area of the river a large eddy sweeps against one shore and reverses the current over a distance of several meters upstream. Fry entering the reverse current change their direction of orientation  $180^\circ$ , but slip tail first with the current which carries them in the same direction as their previous movement. Upon approaching the upstream interface of eddy and river currents, the fry reorient  $180^\circ$  again and immediately continue migrating upstream. Their response to reversed currents suggest that fry reference on the shoreline or that drifting back is a general reaction to rapid changes in current direction.

As the migration continues, fry move from the river and enter the north end of Chilko Lake, positioned on a south-north axis, and swim along the shoreline for several kilometers in wide loose bands before they leave the littoral areas. Migration along the lakeshore in the absence of current suggests that shoreline reference still influences the direction of movement once fry leave the influence of the river, or that fry respond to another orientation phenomenon when in the lake environment.

Chilko fry emerge with remnants of yolk still present. Dry body weight of fry at emergence is around 22 mg, which is also the initial weight of upstream migrating fry. However, since migration to the lake continues long after emergence is over, size during movement upstream increases with time, and late in the spring much heavier fry are found migrating.

### **Downstream Response in a Lake Outlet Stream**

Another large lake outlet stream is Stellako River (FIGURE 6), which flows 11.2 km from Francois Lake to Fraser Lake, and serves as the incubation area for Stellako fry. Although the large upper lake provides a good nursery environment for sockeye, based on the size of other smolts reared in Francois Lake, Stellako fry migrate downstream to the smaller rearing area of Fraser Lake.

The entire length of Stellako River is used by spawners, including areas immediately below Francois Lake. A rapids is located 1.6 km below the lake and a small falls occurs 5.6 km farther downstream. The rapids are swift enough to limit the access of fry upstream, and certainly any fry below the falls are prevented from reaching the upper lake. In fact, there has been only limited evidence of any upstream migration from field observations at Stellako River. No accumulation of fry has ever been observed below the falls or rapids to suggest an attempted upstream migration. Similarly, traps located at the rapids have not captured fry moving upstream, and those placed just below the outlet of Francois Lake in an area used by many spawners have caught only small numbers, although velocities next to shore are not severe enough to prevent movement upstream.

Further evidence of predominantly downstream migration to Fraser Lake is provided by freshwater scale growth of Stellako spawners. Circulus counts on scales of Stellako fish form a unimodal distribution, normally averaging 3.0 circuli less than the growth recorded on another sockeye race reared in Francois Lake, indicating that few if any Stellako fry are reared in the upper lake.

Fry emergence in Stellako River begins in mid-April at temperatures near 3.3°C and continues through the first part of June in temperatures ranging from 6.7 to 8.9°C. Newly emerged fry move downstream during hours of darkness and enter Fraser Lake for rearing. Some fry linger in the sheltered areas along the banks of the lower river and feed for approximately 2 wk prior to entering the nursery lake, but this number represents only a small portion of the population.

Fry enter near the western end of Fraser Lake, positioned on a west-east axis, and are found in large numbers along shallow grassy flats around the western margin of the lake. Schools of fry have been observed moving east and west along the beaches of the lake, and have been found displaced from the river mouth far into the limnetic zone. As the spring progresses, distribution proceeds farther down the lake.

Fry emerge from Stellako River with no yolk reserves remaining and have a dry body weight of about 19 mg. Small numbers of fry holding in the river feed for a short time and consequently weigh more when downstream movement finally occurs.

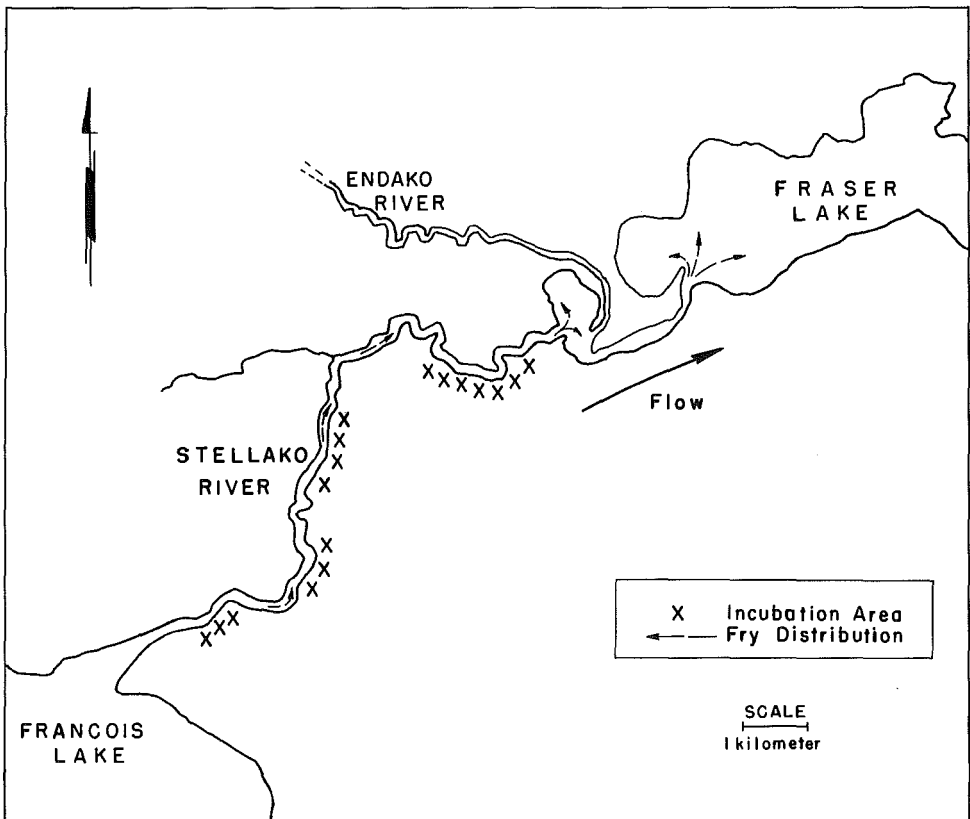


FIGURE 6—Incubation sites and migration distribution of stock native to Stellako River.

## Reversed Responses in Lake Outlet Streams

Upon emergence from their incubation environment, Adams River sockeye fry show a reverse in their response to current during movement to the nursery system of Shuswap Lake. Spawners use primarily the lower third of Adams River (FIGURE 7), a 10-km stream flowing from Adams Lake and entering the west end of Shuswap Lake just above its outlet, Little River. Although Adams Lake is a suitable nursery area for sockeye, very few fry have been observed migrating upstream to the system. Some concentrations of fry have been seen holding in the river, but observations confirm that with few exceptions fry move downstream to Shuswap Lake. The river has numerous turbulent or rapid areas which are believed sufficiently swift to preclude fry migration upstream. Downstream movement to Shuswap Lake is substantiated by freshwater circulus counts of Adams River spawners. When populations are large, freshwater scale growth of Adams River and other Shuswap tributary populations shows a mean of only 11 circuli compared with approximately 16 circuli for sockeye reared in Adams Lake during the same year.

Fry emergence from Adams River begins during the last 2 wk of April and continues through the first part of June at temperatures ranging from 4.4 to 10.0°C. Emergence each night reaches peak abundance near midnight as measured at trap locations near the river mouth. Once the fry leave the incubation sites they are carried downstream into Shuswap Lake, into an area where the river current merges with the lake currents approaching the lake exit. Although the velocity near the lake outlet is not high, unless the fry attempt to swim against the flow they can be displaced into Little River and thus carried another 3 km downstream to Little Shuswap Lake.

Most of the fry, however, appear to cross the throat of the lake exit, reaching the southern shore of Shuswap Lake or the southern bank of Little River above swift water, and start daylight migrations up the shore of the nursery lake. Migration starts with little or no delay, and fry move in continuous bands over a meter in width. During peak densities, moving at rates of 6.0 to 15.2 cm/sec, numbers past any one point can reach over 200,000/hr. The bands of fry often move close to shore in shallow water, but they have been observed in deeper water several meters from shore. Numbers of fry continue migrating along shore over 40 km east from the Adams River.

At emergence, Adams fry may have a mean dry weight of yolk measuring over 2.5 mg, representing about 7% of the original yolk available. Dry body weight at emergence is 25 mg and remains the same during initial migration along the lakeshore, but with less yolk, indicating that little holding behavior occurs among fry reaching the southern shore after emergence.

The extent of Adams River fry displacement to Little Shuswap Lake is unknown, since another spawning area in Little River can account for a large number of fry in the lower lake. However, considering the nocturnal emergence behavior of Adams River fry, the high discharge in the spring, and the fact that Adams River temperatures can be warmer than the recipient lake outlet, some fry are displaced with the surface waters exiting the lake. Those fry carried down or

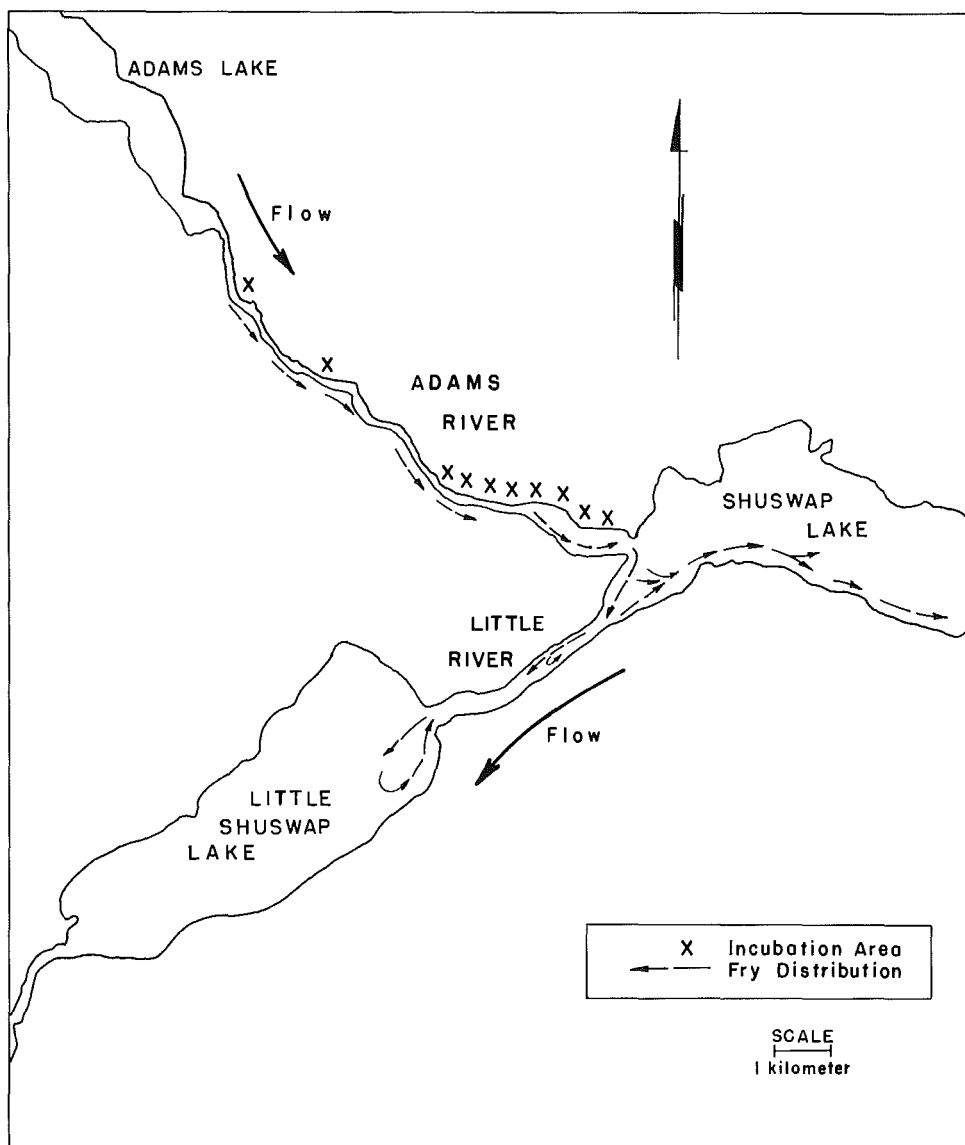


FIGURE 7—Incubation sites and migration distribution of stock native to Adams River.

emerging from Little River initially concentrate along the eastern beaches of Little Shuswap Lake before attempting to migrate back up the river to Shuswap Lake. The time spent in Little Shuswap Lake varies. In some years fry have been observed moving up Little River by the middle of April, coincident with first emergence. In other years, migration has been delayed several weeks. The factor controlling migration timing up Little River appears to be stream velocity. When newly emerged fry are confronted with a discharge in Little River of less than 185 m<sup>3</sup>/sec, movement occurs with little delay. In years when emergence coincides with

higher discharge, migration is delayed until additional growth has occurred. Generally the mean size of fry first attempting to negotiate the current of Little River is larger when discharge is greater. However, although a physical barrier from velocity is possible and no doubt occurs at some discharge levels, even when discharge approaches its maximum of over 1,500 m<sup>3</sup>/sec, the range in size of migrating fry is large. Moreover, in years of low discharge, the variation in size of fry holding in Little Shuswap Lake is also large, indicating that the migrating response is not size specific. Fry moving up Little River have dry weights ranging from 23 to 500 mg during migration which shows the extent that some fry reside in Little Shuswap Lake and feed before proceeding upstream.

Movement up Little River occurs as close to shore as the fry can manage. The river banks are quite steep and have little or no exposed rock in most areas. Brush and grass grow on top of the banks and closer to the river's edge where the shore has more gradual slope. Large concentrations of fry are found in the flood bays or sloughs that occur in the lower river during higher water levels. As discharge increases the thin bands of moving fry take advantage of the lowest velocities available. The path of migration is often among the clumps of grass or in the brush covering the flooded banks. Late in the season, larger fry are seen farther from shore along the river bottom or around small islands in the stream, as migration continues through July, August and September.

### **Reversed Responses in Tributary and Lake Outlet Streams**

Newly emerged fry from Weaver Creek (FIGURE 8), a tributary to the Harrison River system, display a complex migrating behavior pattern to reach their nursery environment in Harrison Lake. Fry move downstream to Harrison River and then reverse their direction of movement and migrate upstream to Harrison Lake.

Weaver Creek receives water from a combination of small streams draining a precipitous watershed, and from Weaver Lake situated a few kilometers above the sockeye incubation area which covers the lower 3 to 5 km of the stream. Weaver Creek empties into Morris Slough, a deeper slower moving body of water flowing generally southward for 1 km to Harrison River. Harrison River, a very wide and deep stream, flows southwest from Harrison Lake to the Fraser River. Morris Slough enters the system about 5 km from Harrison Lake, at a point above the swift moving water, but where currents are still quite marked.

Emergence from Weaver Creek begins near the first of April as temperatures approach 4.4°C, and ends after the middle of May at temperatures over 7.2°C. The newly emerged fry move downstream with the onset of darkness and can reach the slower velocities of Morris Slough from minutes to an hour after leaving the gravel of the incubation stream. Once in Morris Slough, the fry swim downstream to Harrison River, where they reverse their orientation to current and migrate 5 km upstream to Harrison Lake. Concentrations of fry arrive at the lake only 4 or 5 days after emergence from the creek begins, which suggests that upstream migration in Harrison River occurs immediately without holding or displacement downstream. The speed of migration is further verified by the size of fry arriving at the lake. Their weight and length early in the season is the same as that of emerging fry.

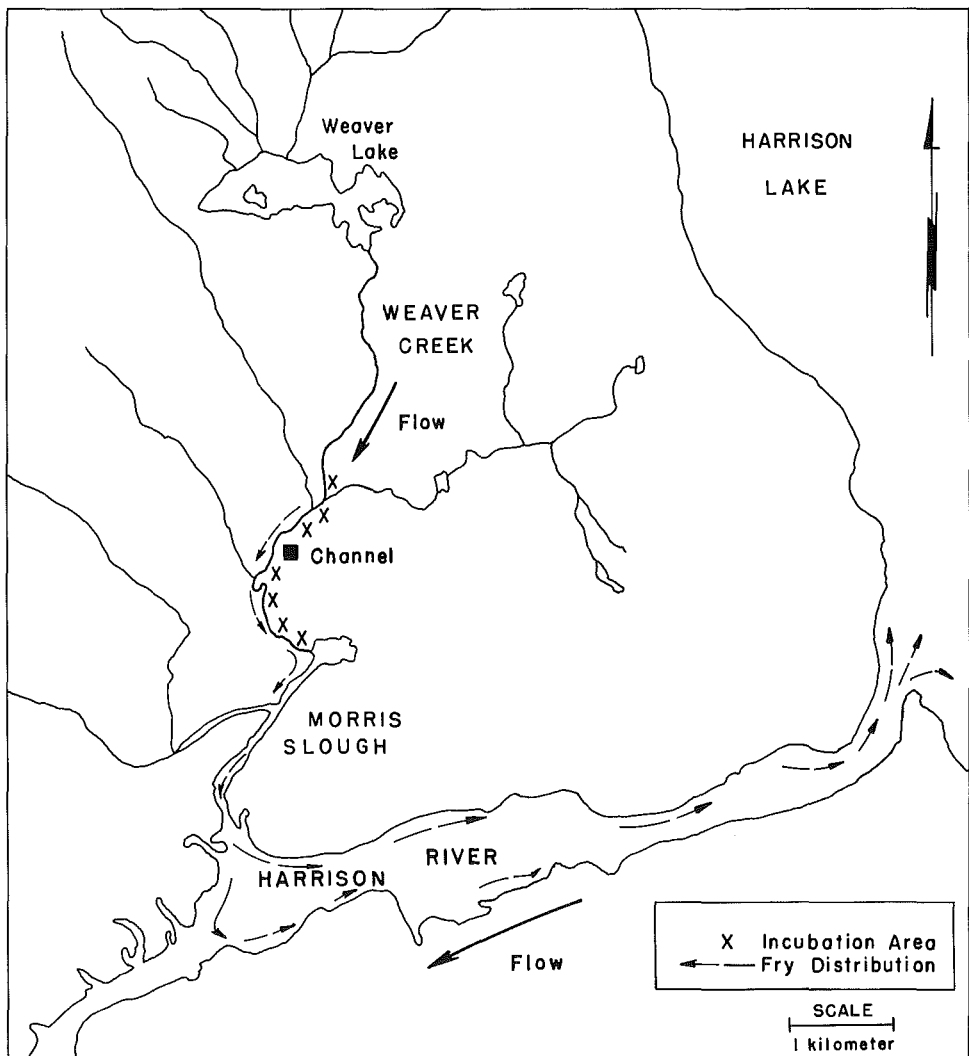


FIGURE 8—Incubation sites and migration distribution of stock native to Weaver Creek.

Migration upstream has not been observed in dense bands along the shorelines, and hence it appears that movement occurs at depth. In some areas, fry hold along shore during daylight hours, but at night a different distribution is noted. With the aid of searchlights, fry have been seen spread across the shallow areas in Harrison River above the mouth of Morris Slough. Fry were in small groups or solitary, with individuals often separated by several meters. All fry thus observed were very close to the bottom and oriented upstream. However, no extensive movement upstream has been seen during darkness.

Distribution in Harrison Lake appears to occur at depth with no concentrated migration occurring adjacent to shore as observed in some lake systems. Fry can be seined along the beaches a few kilometers from the lake outlet, but never in large

numbers. Shortly after the emergence period is over in Weaver Creek, fry are no longer found frequenting the beach areas of Harrison Lake.

The dry weight of fry emerging from Weaver Creek is about 32 mg with little or no yolk remaining. However, with the progress of the spring a number of larger fry can be found in Harrison River, having delayed and grown in the stream.

### Downstream Response in a Tributary Stream

Downstream movement to the lake nursery area is the most common behavior pattern observed among newly emerged sockeye fry. A population characterized by this behavior is a race spawning in 7-Mile Creek (FIGURE 9), a tributary of the Pitt River which ultimately drains into Pitt Lake. Fry incubated in 7-Mile Creek

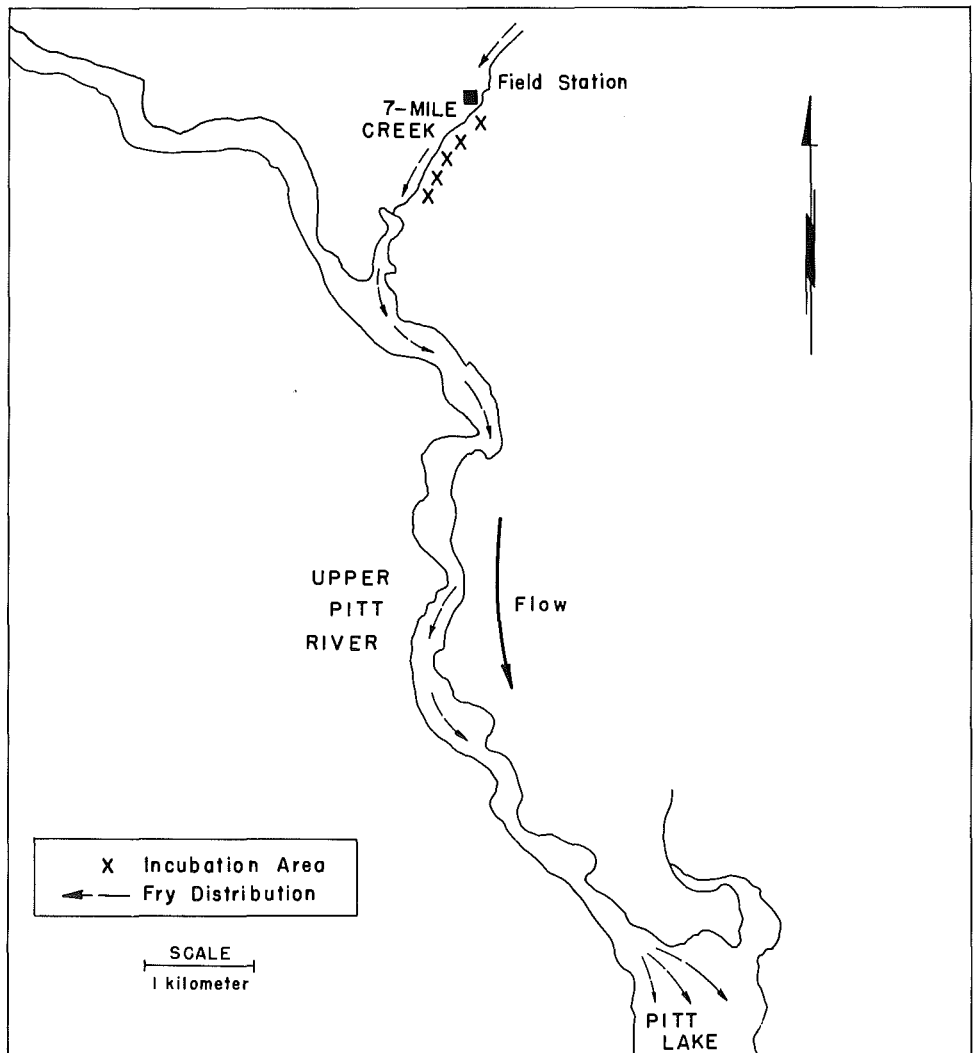


FIGURE 9—Incubation sites and migration distribution of stock native to 7-Mile Creek.



emerge during April and May in temperatures ranging from 3.3 to 7.2°C, and move 11 km downstream to their lake nursery area. Emergence occurs at night and reaches highest intensity just after darkness. The fry can reach Pitt Lake in a few hours after leaving the gravel.

The recipient lake is 27 km long with few beaches and a precipitous rock shoreline leaving little or no littoral zone around the lake perimeter except near the outlet area at the southern end of the system. The lake, positioned on the western slope of the Cascade Mountains and experiencing considerable rainfall, is relatively unproductive in comparison to other lakes in the Fraser River system, and has a tidal influence amounting to 0.6 m.

Sockeye from 7-Mile Creek were the largest fry studied. At emergence the fry have a dry body weight of about 38 mg, and characteristically emerge with about 3.5 mg of yolk material or 5% of the available supply at fertilization. Based on an examination of rate of yolk utilization (Brannon unpublished), this amount of yolk material provides nearly a week of food reserves before an external food source is necessary.

### Response Upon Leaving Lake Incubation Areas

Beach incubation is found in many sockeye systems, but in Cultus Lake (FIGURE 10), a small lake less than 5 km long, it occurs exclusively. The sockeye incubation area is, for the most part, confined to the southern margin of the lake and the fry emerge directly into the lake water.

The incubation area is a weathered shale alluvial beach extending 70 m from shore and subsequently dropping rapidly into deep water. Spring water percolates through much of the beach at a near constant temperature of 8.0°C all year. The periphery of the incubation area has poor percolation which affects oxygen availability (Brannon 1965) and also reduces incubation temperature during the winter, owing to the greater influence of cold lake water.

Fry emergence occurs from the first of April until late July, the duration of which reflects the variation in incubation environment as well as the lengthy spawning period characteristic of the Cultus Lake population. Newly emerged fry do not frequent the shore areas, as observed in many other lakes, but school almost immediately upon emergence and move offshore into deeper water. Observations to a depth of about 7 m indicate that fry swim close to the bottom as they leave the beach area, and trawl catches have shown that newly emerged fry frequent the limnetic area of the lake.

Observations along the littoral areas have not detected any migration or presence of sockeye fry. Seining attempts along the beaches have produced only small numbers of fry adjacent to the incubation grounds. Very few have been caught on the beaches around the eastern and northern perimeter of the lake. Once emergence is over the only sockeye fry observed in the area are a few which join conglomerate schools of stickleback, *Gasterosteus aculeatus*, and lake chub, *Couesius plumbeus greeni*.

Cultus sockeye are among the smallest fry in the Fraser River system. The fry emerge with no yolk reserves and have a dry body weight approaching 20 mg.

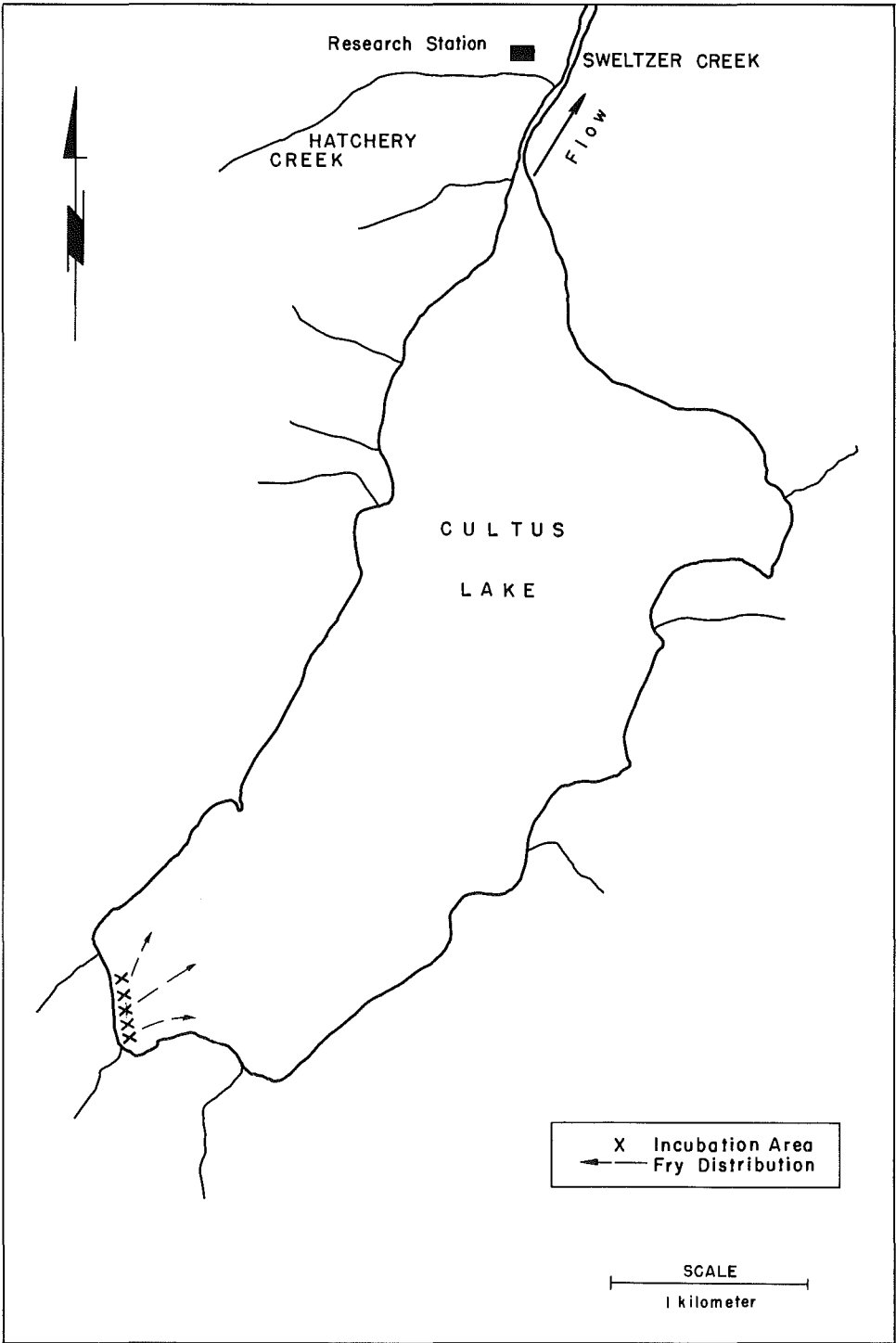


FIGURE 10—Incubation sites and migration distribution of stock native to Cultus Lake.

## CURRENT RESPONSE OF STOCKS

Field observations have established that migrating behavior among the six populations examined followed distinct patterns which demonstrated racial responsiveness to specific circumstances along the migration route to the nursery lake. Native fry from four of these races were tested in the migration channel in the field to determine their response to current when exposed to more standard conditions for evaluation. Additional tests were run in the migration channel on laboratory stocks of all six populations. Results of these tests are presented and compared in the following section.

### Native Stocks

Chilko and Stellako were chosen for study because of their opposite migrating behavior patterns in response to current in lake outlet streams. The stock from Weaver Creek was included as a population that shows a combination of responses to current, and 7-Mile stock exemplified downstream migration in a tributary stream. Test conditions were standardized (but not identical), using water from the respective incubation streams, at the temperatures available, in near darkness (under black plastic cover), and at a constant velocity of 15.2 cm/sec.

### CHILKO FRY TESTS

During the emergence period, concentrations of holding or migrating fry were captured along the river bank and held in 38-liter cans as a source of supply for the studies. Fry were very easily frightened when handled too soon after capture and showed strong escape responses when placed in the migration channel. Although the fry were held for 20 min in the central chamber before they were released, they often dashed into hiding or quickly exited the apparatus once the chamber gates were removed. To overcome this problem, the fry were held in the containers overnight for tests to be run the following day.

Thirty tests were performed in water from Chilko River at temperatures fluctuating between 3.3 and 6.7°C. The fry showed a definite current response, amounting to 79.3% upstream, (TABLE 2).

TABLE 2—Total number and mean response (per cent) of Chilko, Stellako, Weaver and 7-Mile native stocks responding to current in native stream water (U—upstream, D—downstream, NT—not trapped).

Stock	No. Tests	Number of Fry			Mean Response (Per Cent)*			
		U	D	NT	U	(SD)	D	NT
Chilko	30	2,379	619	2	79.3	(12.71)	20.6	0.1
Stellako	10	83	917	0	8.3	( 7.66)	91.7	0.0
Weaver	13	209	1,091	0	16.1	(10.38)	83.9	0.0
7-Mile	30	203	2,743	54	6.8	( 5.50)	91.4	1.8

\*When 100 fry were used in each test mean response is given in the tables for purposes of showing variability, but the value is presented in the text as per cent.

When released from the central chamber, fry movement was initiated as a school. Upon reaching a reverse turn in the channel, the fry often formed a tight group and appeared disoriented. However, most fry soon reoriented into the current and continued up the channel. At each turn, those fry leaving the school either remained in the corner a few seconds before continuing upstream or reversed orientation and moved downstream to the turn below. Once having dropped back, however, the return upstream was persistent, whether as solitary fish or in small groups. Generally, most of the fry reached the upstream trap 5 min after leaving the central chamber, and the remainder trapped within 1 hr. The few fry trapped downstream often slipped tail first with the current the entire length of the channel below the central chamber.

### **STELLAKO FRY TESTS**

Duration of the testing period at Stellako was limited. Access to fry in Stellako River during emergence in May was restricted to a single large eddy where a shallow protected bay provided sufficient fry for testing. Fry were dip-netted from concentrations holding along the shore and were transferred to 38-liter cans as the source of supply for tests the following day.

Ten tests were performed with Stellako fry, in Stellako River water, at temperatures ranging from 3.9 to 6.7°C. Movement downstream was very strong, with an upstream response of only 8.3% (TABLE 2).

Observations in the apparatus showed the fry to slip with the current, tail first, making occasional movements downstream head first. A schooling response was not as evident as with Chilko fish. The fry showed no reluctance to behave as individuals, which resulted in fry spreading out over a large area during their movement downstream. Some fry initially moved upstream, but this usually included less than 20% of the fish and most often ended once the first turn was reached. As individuals dropped away from movement upstream, they often hesitated momentarily and then darted downstream head first as though frightened.

### **WEAVER FRY TESTS**

Weaver Creek fry were captured in a live-trap placed in the spawning channel located on that system adjacent to the natural stream. Newly emerged fry were removed from the trap and placed in covered troughs until tested the following day. The test channel was located outdoors and supplied with Weaver Creek water which remained near 4.4°C during the period of investigation. Limited time allowed only 13 tests, however the fry showed a definite downstream movement. The response upstream was only 16.1% (TABLE 2), but with some variability (SD 10.38).

### **7-MILE FRY TESTS**

Field studies on 7-Mile Creek sockeye were executed with fry emerging from the incubation channel on that stream. Annually, eyed eggs are planted in the gravel medium in upwelling flow for incubation, and emergence occurs naturally.

Newly emerged fry leaving the channel were easily trapped and held in darkened troughs at least 24 hr in the experimental station at the site. The migration channel was placed indoors and exposed to natural light. Water was supplied to the apparatus from 7-Mile Creek and temperatures ranged from 2.5 to 7.5°C during the 37 days of the study. When 7-Mile fry were tested for their response to current they showed a strong downstream response, with only 6.8% of the fry moving upstream (TABLE 2).

## INTERPRETATION

The studies undertaken in the field indicated that each race, when tested in the migration channel as newly emerged fry at a velocity of 15.2 cm/sec, showed a highly significant directional response to current ( $P < 0.005$ ), as opposed to a 50:50 random movement. The specific response of each race corresponded to the initial behavior shown in migrating to the nursery area.

## Experimental Stocks

To determine the factors influencing current responses among the various populations, laboratory studies were conducted on artificially incubated stocks of Chilko, Stellako, Cultus, and hybrid fry in 1967, and on all six stocks plus two hybrid stocks in 1968. All stocks were incubated in water from Cultus Lake and were tested under uniform conditions of temperature (5.6°C), velocity (15.2 cm/sec), in lake water, and under near darkness inside the laboratory to isolate specific responses under controlled conditions.

## CHILKO, STELLAKO, AND HYBRID STOCKS

The most extensive study was made on Chilko, Stellako and hybrid experimental stocks since such a contrast was apparent in the migrating behavior of the natural stocks in their native streams.

Tests on the stocks showed similar results in both years. Chilko alevins and fry showed a very strong positive rheotaxis, migrating against the current with a response of 82.3% in 1967 and 91.7% in 1968 for test lots of 100 fry (TABLE 3). In contrast, Stellako fry primarily slipped or moved with the current, showing a response upstream of only 15.4% in 1967 and 10.1% in 1968. Both stocks showed a highly significant response in their respective choice of current direction ( $P < 0.005$ ).

Although the parental stocks showed distinctly different behavioral responses to current, the hybrid stocks were intermediate in response. In 1967 hybrid fry originating from Stellako female and Chilko male crosses displayed a response upstream of 48.4% with a high degree of variability (SD 31.29). Tests during 1968 agreed closely. Hybrids from Stellako female and Chilko male crosses responded with 46.4% upstream, and the reciprocal cross followed with 47.6% upstream, or no significant difference in response to current direction ( $P > 0.95$ ).

TABLE 3—Total number and mean response (per cent) of Chilko, Stellako and hybrid experimental stocks responding to current in laboratory studies (U—upstream, D—downstream, NT—not trapped).

Stock	No. Tests	Number of Fry			Mean Response (Per Cent)			
		U	D	NT	U	(SD)	D	NT
<u>1967</u>								
Chilko	20	1,646	278	76	82.3	(11.20)	13.9	3.8
Stellako	20	309	1,599	92	15.4	(13.18)	80.0	4.6
Stellako ♀ X Chilko ♂	20	969	955	76	48.4	(31.29)	47.8	3.8
<u>1968</u>								
Chilko	30	2,750	173	77	91.7	( 6.86)	5.8	2.6
Chilko ♀ X Stellako ♂	20	952	994	54	47.6	(23.68)	49.7	2.7
Stellako	30	302	2,681	17	10.1	( 8.69)	89.3	0.6
Stellako ♀ X Chilko ♂	20	928	1,008	64	46.4	(19.68)	50.4	3.2

Observations of fry behavior in the migration channel showed that the same patterns of movement were exhibited by both experimental and native stocks, although Chilko and Stellako showed slightly stronger upstream responses in the laboratory. Experimental stocks showed less reluctance to move in the migration channel and less disorientation when negotiating reverse turns. Stellako fry often displayed an initial upstream movement well beyond the first reverse turn before changing their orientation and slipping or swimming downstream.

#### ADAMS, WEAVER, 7-MILE AND CULTUS STOCKS

Experimental stocks of Adams, Weaver, 7-Mile and Cultus fry responded similarly and all displayed an intermediate response to current (TABLE 4). Adams fry showed a slightly stronger response upstream (56.0%) than downstream in the limited number of tests executed, but also displayed high variability (SD 24.17). In these laboratory studies with Weaver and 7-Mile fry, the strong downstream preference displayed in the field studies was not shown under the laboratory conditions to which the stocks were exposed. Weaver fry, in 2 yr of tests, showed a mean response upstream of 69.3% and 59.9%, and 7-Mile fry responded upstream with a mean of 63.0%. While heterogeneity of responses were excessive, the marked difference in per cent responses between native and laboratory stock suggested that exposure to the free-swimming environment in the trough may influence certain stocks to display more positively rheotactic behavior than would occur upon emergence from the natural incubation environment. Cultus fry examined in 1967 showed a tendency for upstream movement by a response of 57.5%. However, repeating the study in 1968, Cultus stock displayed a response upstream of 48.0%, nearly an equal separation in upstream and downstream movement, and again having a high degree of variability (SD 21.52).

TABLE 4—Total number and mean response (per cent) of Adams, Weaver, 7-Mile and Cultus experimental stocks responding to current in laboratory studies. (U—upstream, D—downstream, NT—not trapped).

Stock	No. Tests	Number of Fry			Mean Response (Per Cent)			
		U	D	NT	U	(SD)	D	NT
<u>1967</u>								
Weaver	11	762	338	0	69.3	(18.55)	30.7	0.0
Cultus	15	862	539	99	57.5	(18.10)	35.9	6.6
<u>1968</u>								
Adams	9	504	357	39	56.0	(24.17)	40.0	4.0
Weaver	11	659	397	44	59.9	(20.76)	36.1	4.0
7-Mile	15	945	555	0	63.0	(24.76)	37.0	0.0
Cultus	30	1,439	1,530	31	48.0	(21.52)	51.0	1.0

Analysis of the tests on these four experimental stocks indicates that Adams and the 1968 Cultus fry displayed random movement ( $P_1 > 0.05$ ) whereas Weaver, 7-Mile, and the 1967 Cultus stock showed slight but significant responses upstream ( $P_1 < 0.05$ ,  $P_1 < 0.01$  and  $P_1 < 0.025$  respectively).

The experimental stock from Cultus and Adams demonstrated indecisive behavior patterns in the test apparatus. Individuals appeared to be influenced strongly by the group, and the initial response of the largest mass of fry appeared to be determined by the type of behavior exhibited by one or two fry at the head of the group. Upstream movement could be evoked among others if a few individuals showed a persistent upstream response, and the reverse was initiated when leading fry hesitated or darted back.

## INTERPRETATION

Laboratory studies showed that among the six racial stocks incubated and tested under identical conditions, differences in current response were displayed, and thus established that response patterns induced by current are racially specific. Moreover, the response of the hybrid stocks, intermediate to that of their parental source, showed that migrating behavior has a strong genetic component. Chilko and Stellako experimental stocks responded in the same way as native stocks, but the differences between responses of native and experimental fry from Weaver and 7-Mile stocks implied that an environmental influence on fry behavior can be substantial. Further clarification of this phenomenon will be more appropriately presented later.

## ORGANISMIC VARIABLES AND CURRENT RESPONSE

After determining the response to current of newly emerged fry from each stock, the effects of two organismic variables, size and age, were tested for their effect on current response. In the following section, the potential roles of these variables are considered and discussed, followed by results and interpretation of the tests performed.

### Influence of Fry Size

The effect of fry size on their response to current involves the question of whether or not size is a causal mechanism in migrating behavior. Since migration as a directed response can be detected only as upstream migration, the problem will be dealt with, at this time, by examining the "degree" of upstream responsiveness in experimental stocks. Related information is forthcoming from three sources. If increased size is involved with evoking an upstream response, it should be evidenced as 1. a difference in size of fry between emergence and migration, or 2. differences in response between fry of different sizes within a population, or 3. differences in response between fry populations of unlike size.

### SIZE AT EMERGENCE AND MIGRATION

As mentioned previously, upstream migrating fry observed at Chilko increase in mean weight as the season progresses. This phenomenon is understandable in that once migration begins, contributing fry represent not only the recently emerged, but also those having held and grown. When emergence has ended, the migration source rests solely with the holding fry. To determine the minimum size at which migration is initiated, therefore, fry were sampled from the first of the season's upstream migration. Similarly, inasmuch as fyke-nets set to trap emerging fry may also capture holding or migrating fry that slip downstream, fry were removed from several advanced redds to represent the minimum size of emerging fry.

Samples from the redds were compared with lengths and dry weights of fry holding or migrating along the river banks and indicated that during the first of May fry were nearly the same size in all locations (TABLE 5). The redd samples were less than 2% smaller than the largest holding or migrating fry. Even by May 25, which was near peak migration and approaching the end of emergence, migrating fry were still the same size as newly emerged fry. Moreover, observations made later in the spring disclosed that although mean size had increased, some migrating fry no larger than the newly emerged were still present. These data, indicate therefore, that apart from any environmental influences that may affect behavior, an increased size is not a prerequisite before movement upstream begins in this population.

TABLE 5—Mean length and dry weight of sockeye fry sampled from Chilko River in 1968.

Date of Capture	Source	No.	Mean Fork Length (mm)	Mean Dry Weight and SD (mg)
May 8	Redd	20	27.7	21.5 ± 2.2
May 2	Holding	20	27.7	20.3 ± 3.5
May 5	Holding	20	28.2	21.9 ± 2.8
May 6	Migrating	20	27.7	21.8 ± 2.4
May 25	Migrating	20	27.5	21.9 ± 2.8



### SIZE AND RESPONSE WITHIN A POPULATION

In nearly every test on current response, at least a few fry segregated and trapped in the opposite current direction from the others. In an attempt to correlate current response and fry size within a stock, samples were taken from both upstream and downstream responding fry in laboratory studies, and a mean dry weight was determined for the fry responding in each direction. Fry moving upstream and downstream upon emergence from gravel incubation troughs were measured, and experimental stocks tested in the migration channel well after emergence were also examined.

The newly emerged fry were sampled from Chilko, Stellako, hybrid and Cultus experimental stocks at least four times during the emergence period. The mean weight of fry responding in each direction after leaving the gravel is shown in TABLE 6.

TABLE 6—Mean dry weights of sockeye fry from four experimental stocks moving upstream and downstream upon emergence from simulated incubation redds.

Stock	Upstream		Downstream	
	No.	Mean Dry Weight and Approximate Range (mg)	No.	Mean Dry Weight and Approximate Range (mg)
Chilko	44	25.7 ± 3.0	44	25.6 ± 3.1
Stellako	28	21.6 ± 2.6	32	22.0 ± 2.4
Stellako ♀ X Chilko ♂	33	21.1 ± 2.3	33	20.3 ± 2.3
Cultus	50	22.2 ± 2.7	50	20.6 ± 3.1

Results showed little difference between the weights of upstream and downstream moving elements within stocks. Chilko fry moving upstream during the emergence period averaged the same weight as the downstream element (although at peak emergence, upstream fry were 1.2 mg larger). Stellako fry responding in both directions were nearly the same weight, and the hybrid stock showed a slight but insignificant size difference. Cultus fry, which averaged 1.6 mg smaller in the downstream trap, showed a level of significance for correlated observations with  $t = 2.32$  ( $P_1 < 0.05$  with 4 df). Upon emergence from the gravel, the influence of size on the initial current response therefore appears to have been limited to the Cultus stock which, being lake-incubated, requires no specific pattern of behavior to reach the nursery environment. Since smaller or weaker newly emerged fry presumably have more difficulty negotiating velocity, one might expect to find smaller fry downstream in a population displaying no particular current preference.

In a second experiment, Chilko stock and the hybrid reciprocal crosses were examined 2 wk after the fry reached yolk absorption in an effort to disclose any size-related response differences within stocks beyond the emergence period. Stocks were tested in the migration channel and fry were accumulated from several tests for weight determinations on the composite responding in each direction. Com-

parisons of upstream and downstream moving elements of each stock revealed, however, that response to current was independent of fry size (TABLE 7).

These two studies indicated, therefore, that size difference was not a causal mechanism determining migrating response within a population, either at emergence or in the period immediately thereafter.

TABLE 7—Mean dry weights of sockeye fry from three experimental stocks moving upstream and downstream in the migration channel 2 wk after yolk absorption.

Stock	Upstream		Downstream	
	No.	Mean Dry Weight and Approximate Range (mg)	No.	Mean Dry Weight and Approximate Range (mg)
Chilko	23	24.3 ± 2.1	30	24.0 ± 3.0
Chilko ♀ X Stellako ♂	10	26.8 ± 2.4	10	28.8 ± 2.7
Stellako ♀ X Chilko ♀	10	18.7 ± 1.7	10	18.7 ± 1.5

## SIZE AND RESPONSE DIFFERENCES BETWEEN POPULATIONS

The greatest variations in size at emergence are the differences between populations, which ranged in this study from 31.9 to 14.5 mg in dry body weight (TABLE 1). Since fry size is determined by egg size, which in turn is a population characteristic, size could be a genetic component determining a population's response to current. Magnitude of upstream response relative to fry size at yolk absorption was compared among the various experimental stocks used in the 1967 and 1968 laboratory studies. Since all stocks were treated identically during incubation, their mean response in the migration channel should show a relationship to weight at yolk absorption, if size of fish influences migrating behavior.

When mean fry weight was plotted against mean upstream response, however, it showed a scattered pattern (FIGURE 11). Although weight differences between populations were as great as 17.4 mg, or 120% of the weight of the smallest stock, analysis indicated that the two variables were not significantly correlated  $r = 0.32$ ,  $P_t > 0.05$  with 11 df).

Moreover, the largest (21.8 mg) and smallest (14.7 mg) hybrid stocks were almost identical in upstream response (47.6% and 46.4%, respectively). The larger Cultus and Stellako stocks of 1967 (17.6 mg—57.5% upstream, 19.8 mg—15.4% upstream) did show slightly more positive responses than the smaller respective stocks in 1968 (14.5 mg—48.0% upstream, 17.9 mg—10.1% upstream). However, the larger Chilko stock in 1967 (24.0 mg) showed a less positive response (82.3% upstream) than its smaller (19.3 mg) counterpart in 1968 (91.7% upstream) and was the only stock that showed significantly different responses between year-classes ( $P_t < 0.005$ ). Therefore, comparisons of both spatially distinct and year-class populations revealed that size differences between populations were not responsible for the differences in initial migrating behavior.

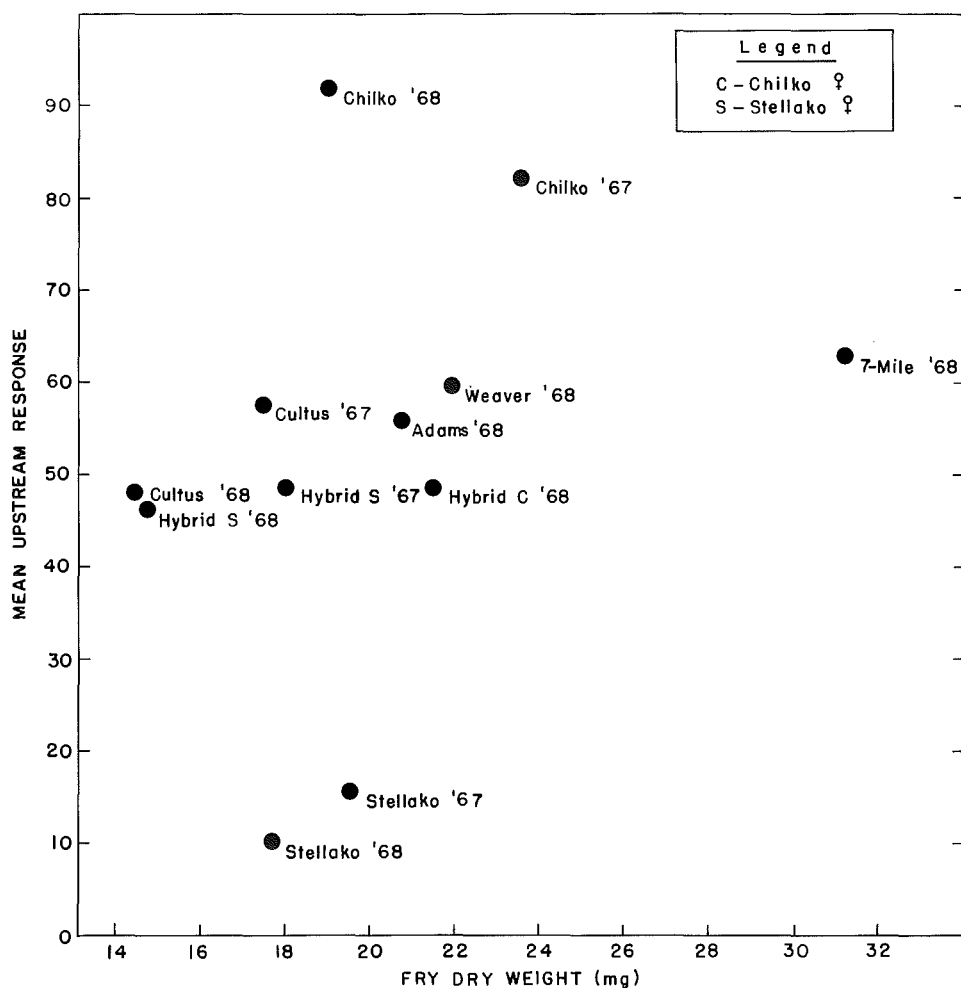


FIGURE 11—Mean upstream response and fry size at yolk absorption of laboratory experimental stocks, 1967 and 1968.

## INTERPRETATION

These three studies on size of fry and their response to current dealt with size variability at or close to emergence. The results indicate that upstream migration can be initiated at the size of emerging fry, that response to current direction is not size-specific within a stock, nor between populations of different initial size. It is thus concluded that size is not a causal mechanism in migratory behavior at the velocities to which stocks were exposed, and thus an upstream response is not the result of having inherited a size-related ability to negotiate velocity.

### Influence of Fry Age

Age as a factor influencing response to current is basically related to the concept that, following emergence, a temporal component exists in the development of migrating behavior. This is a particularly difficult factor to examine because it is intrinsically linked with size and experience. However, since the problem is concerned with the motivational aspect of age or change in the internal state of the fish, the influence of age will be examined primarily for apparent changes in response motivation, with only reference made to size and experience.

Again, without having to resolve whether downstream movement is in fact migration, for the time being the criterion for migrating behavior will be upstream responsiveness.

Observations at Chilko and Adams Rivers have shown that movement upstream can be delayed until several days after emergence first begins. A delay in demonstrating responsiveness to current among upstream migrating fry populations might imply that 1. the appropriate motor patterns are acquired gradually, 2. a transitional phase is necessary between behavior associated with incubation and that of the open stream, or 3. movement is simply inhibited by high velocities which results in a net displacement downstream at emergence. Given that a temporal component exists in migrating behavior then it should be demonstrated by two response patterns. First, upon emergence from the incubation environment, behavior would be displayed as passive displacement or as a holding response. And second, any latent period of transition from emergence behavior to migratory behavior should be detected by a progressive change in responsiveness with time.

### CURRENT RESPONSIVENESS AT EMERGENCE

To demonstrate the first current response shown by fry as they emerged from their incubation environment, fry emerging from prepared redds contained in gravel-filled incubation troughs were studied. In the 2 yr of study, three experimental stocks were examined. The initial current response shown by the emerging fry was evidenced by their presence in traps at the upstream and downstream ends of the troughs, emptied each morning after the night's emergence. The response of each stock as shown in TABLE 8, represents the number of emerged fry recorded from single incubation troughs during the emergence period.

TABLE 8—Number and per cent response of three experimental stocks responding to current upon emergence from prepared redds (U—upstream, D—downstream).

Stock	Number of Fry		Per Cent	
	U	D	U	D
1964				
Chilko	1,351	84	94.1	5.9
Stellako	67	1,287	4.9	95.1
Cultus	382	541	41.6	58.4
1966				
Chilko	526	88	85.7	14.3
Stellako	96	486	16.5	83.5
Cultus	760	486	61.0	39.0

Emerging fry displayed an initial response to current remarkably similar to the behavior of the experimental stocks tested in the migration channel (TABLE 3). The results showed that under simulated natural conditions, with surface velocities not exceeding 20 cm/sec, the initial response to current corresponded to the migratory pattern of the native stocks, and indicated that natural responses in migrating behavior can be displayed at emergence. Moreover, the response to current of an upstream migrating population was shown to be deliberate, without fry first having to be passively displaced downstream and experience a delay before upstream responsiveness could occur. The possibility exists, however, that fry displaying a response downstream did so by passive displacement.

The question naturally follows, therefore, that if the appropriate current responses are shown at emergence, then how much earlier is rheotaxis evoked in the alevin? In the 1967 and 1968 behavior studies, to determine the point at which the preference tests were to begin, fish were exposed to current in the migration channel long before reaching the level of development that characterized emerging fry. Once current responses were displayed, the alevins were considered to have shown migrating behavior, and thus examination of data from the preliminary trial period will establish the time at which such behavior first occurred.

In the earliest trials, the alevins showed a persistent hiding behavior. Most alevins immediately dropped to the bottom of the screen chamber and sought cover among the stones covering the floor of the channel, while others would move downstream a short distance before retreating beneath the gravel. During this phase of the study, most alevins remained without moving from the vicinity of their initial hiding locations until removed from the apparatus 48 hr after placement. This behavior was displayed through diurnal cycles under conditions in the apparatus which offered little cover from currents and lights, and fry often had only their heads hidden beneath the single layer of gravel. Although circumstances provided the opportunity for passive displacement downstream, little or no drift occurred even among the stocks that later showed a downstream response.

The transition from hiding behavior to active swimming occurred quite rapidly. For example, Chilko fish showed no tendency to move in either direction when placed in the apparatus for routine testing on January 17, 1967. In the next test, 4 days later, only 2.0% of this stock remained in the apparatus longer than 16 hr. The number of fish refusing to move during this early phase was not entirely reduced until the yolk stores were nearly exhausted among the individual stocks. The majority of fish, however, were not at all inhibited from migrating by the presence of yolk. When the alevins first began to move, they did so still possessing considerable yolk stores. For instance, in 1967 over 90% of the Chilko fish were migrating when the mean dry weight of yolk within the stock was 10.3 mg, or over 25% of the original yolk available. Similarly, alevins from the other experimental stocks showed initial migrating responses with considerable yolk stores present.

Initiation of migratory behavior among the various stocks of fry is shown in TABLE 9. The dry weight of eggs indicates the amount of yolk originally available. Yolk weight among alevins at first response, when compared with that of native emerging fry, indicates the level of development at which response to current was first shown, and thus the number of days prior to normal emergence could be calculated.

In all instances except Adams, the experimental stocks showed responses to current at least 1 wk before migratory behavior would normally occur in the natural environment. However, Adams and Weaver alevins responded to current during their first trial so the time of earliest migratory response is not known. Chilko and 7-Mile stocks, which naturally emerge with yolk reserves present, showed the earliest migrating behavior, responding about 3 wk before normal emergence timing. For almost all stocks, the degree of upstream responsiveness in their initial tests as alevins (TABLE 9) was similar to their response as fry (see TABLES 3 and 4).

TABLE 9—Initiation of current responses among experimental stocks tested in the migration channel.

Stock	Egg Dry Weight (mg)	Yolk in Native Fry at Emergence (mg)	Initial Current Response of Experimental Stock			Days Remaining to Emergence
			Date	Yolk Dry Wt (mg)	% Upstream	
<u>1967</u>						
Chilko	40.0	1.0	Jan. 21	10.3	81.0	24
Stellako	34.9	0	Jan. 17	4.0	15.0	15
Stellako ♀ X Chilko ♂	34.9	—	Jan. 25	4.0	35.0	15
Cultus	34.7	0	Apr. 17	2.0	32.0	7
<u>1968</u>						
Chilko	37.9	1.0	Feb. 22	8.6	94.0	19
Chilko ♀ X Stellako ♂	41.5	—	Feb. 28	6.1	58.0	13
Stellako	33.2	0	Feb. 20	3.5	6.0	12
Stellako ♀ X Chilko ♂	33.9	—	Feb. 21	4.2	21.0	13
Cultus	31.7	0	Apr. 22	3.1	10.0	11
Adams	39.1	2.5	Apr. 3	3.7	35.0	4
7-Mile	60.2	3.0	Mar. 11	11.8	51.0	20
Weaver	49.9	0	Apr. 1	3.5	65.0	12

The data indicated that the capability to respond in the appropriate current direction was present well before normal emergence. The influence of lack of substrate in the laboratory incubation environments from which these particular stocks were taken is uncertain. Experience as alevins out of substrate could induce an early response to current since motor patterns have had the opportunity to develop in a free-swimming environment.

#### TEMPORAL VARIABILITY IN CURRENT RESPONSIVENESS

Since it was shown that an oriented current responsiveness is evoked at least as soon as emergence in an upstream migrating fry population, it may be postulated that downstream movement in native populations is also the result of an oriented responsiveness. Among populations showing movement downstream, if

initial movement were a passive displacement then one might expect that a change in behavior would occur with time as fry developed more positively rheotactic responses. Variation in response to current as a function of time might be discernible either 1. as a difference in the behavior between the first and last parts of emergence from a single redd, or 2. as a change in behavior of a given number of fry over a post-emergence period of days or weeks. In either case a change in responsiveness should be detected in the degree of upstream or downstream movement with time.

### Emergence Patterns

To characterize the response pattern of fry leaving a redd over the period of emergence, data were used from the study on the initial current responses of the four experimental stocks incubated in gravel-filled troughs in 1966. The response patterns within each stock at 2-day intervals were calculated as percentages of total upstream, and of total downstream movement, *irrespective* of the actual numbers of fry involved in either direction. Interval counts were first smoothed to reduce the irregularity induced by variability in emergence by averaging each count with the two immediately adjacent intervals, and then the data were converted to *percentages of the total moving in that direction*.

Histograms prepared from the data show that while behavior differed between stocks, the rheotaxis-time pattern within each stock was very similar for both upstream and downstream responses (FIGURE 12). Except for slightly greater downstream response displayed at the first of the emergence period, the sequence in magnitude of upstream and downstream movement generally coincided within each stock.

Slightly greater downstream movement of the earliest emerging fry was most noticeable within the Chilko stock. Although only a small proportion of the Chilko fry moved downstream in terms of number, a higher percentage of that number moved downstream early in the emergence period. Many of these early emerging fry possessed very large yolk reserves (13 mg) which at that size may have changed their fusiform shape sufficiently to have affected their swimming ability and in turn influenced the response pattern.

Emergence from a single redd involves fry of advancing absolute age with time. However, because of individual variability and the fact that micro-environments within the redd affect rates of development, the relative development of fry was more similar over the emergence period than one would anticipate based on the time involved. Nevertheless, regardless of the range in development from the first to the last of emergence, the patterns within the upstream and downstream moving components within each stock were complementary. The significant correlation between responses upstream and downstream was indicated by the coefficient which ranged from  $r = 0.48$  to  $r = 0.87$  ( $P_i < 0.05$ ) among the four stocks. Thus on the basis of emerging fry, there appear to be no behavioral differences in the initial responses to current associated with temporal segments, although a physical difference in advancement may tend to influence their ability to respond.

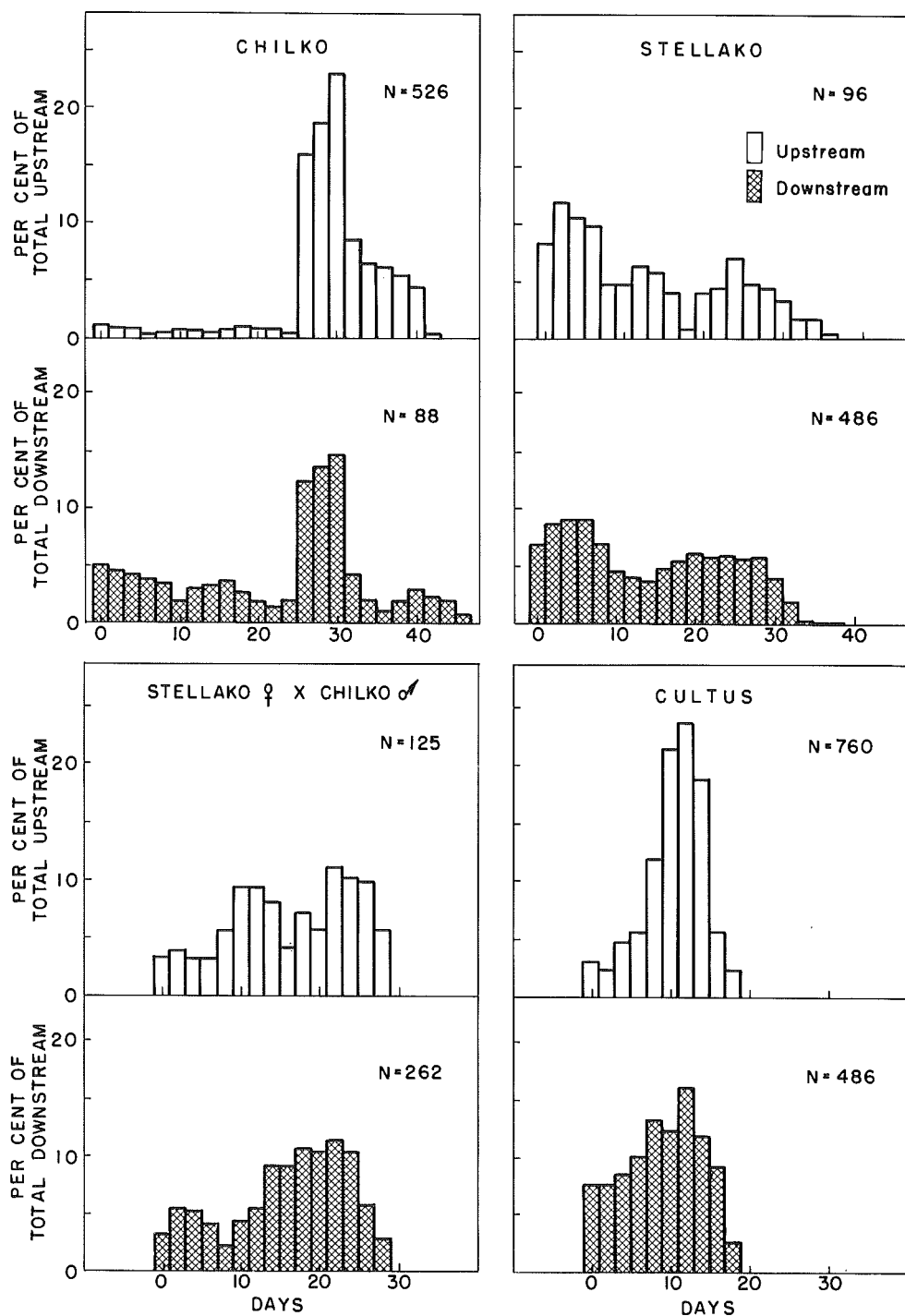


FIGURE 12—Emergence pattern of four experimental stocks of sockeye fry from prepared redds, presented as per cent of total upstream and total downstream movement.



### Post-Emergence Patterns

To establish the temporal response pattern of a given number of fry from their first inclination to move away from substrate until well after feeding had been initiated, the migrating behavior of four experimental stocks was examined over a period of 30 to 36 days. Thus the earliest tests in the migration preference apparatus were with alevins and during the subsequent weeks the test stock became growing fry.

Initially the alevins were slow responding. In fact, an obvious effect of age on the behavior of the fish was its influence on the speed of movement through the apparatus. Advanced alevins took longer than fry to reach the traps, often requiring several hours, and tended to hold between the stones. During the early fry stage the fish moved more readily, the majority being trapped in less than 4 hr. Holding during this stage was less frequent and occurred primarily just above the gravel surface or in corners. Older fish made very deliberate movements in one direction or the other, and often 100% were recaptured 30 min after release. Including a brief period of delay at the trap openings, the first fry entered the outlet trap in 90 sec and the upper trap in 4 min.

Other than speed of migration, influence of age on behavior was not apparent. Although the number of fish reaching the traps and speed of migration increased with age, the response of moving fish remained the same for both alevins and fry within each stock regardless of age (FIGURE 13). Chilko fry maintained a strong preference upstream, Stellako continued a downstream movement, and the hybrid and Cultus stocks responded with an intermediate behavior. Analysis of linear regression showed that age did not significantly change the magnitude of the preferred responses of any of the four stocks during the test period ( $t$  did not exceed 1.74,  $P_t > 0.05$ ).

Since the tests showed that Stellako fry were so responsive downstream, it was a particularly interesting stock to pursue beyond the 2-wk post-absorption period examined in 1967 to explore the possibility that even more time might be necessary to develop a stronger positive rheotaxis. Therefore, in 1968, Stellako fry were reared in hatchery troughs for a period of 3 mo during which time they grew to a size weighing about 1 gm. At the end of this period 10 tests were performed in the migration channel resulting in an upstream response of only 5.0%, even less than that shown the same year by newly emerged fry (10.1%). The study definitely showed a continuing preference downstream and implied that age had no effect on current response for this stock.

Since a genetic component was shown to exist in the migrating behavior of fry, the stocks selected for age-related responsiveness to current were those which in their natural environment are not required to reverse their migratory behavior en route to their nursery lake. In each experimental stock thus far included, selection for a time-related change in behavior should not have occurred. Examination of the two stocks that must show a change in response to current during migration would have provided an interesting comparison, but unfortunately the Adams and Weaver fry were not tested for a long enough period to analyze temporal differences in behavior. However, Weaver fry tested at emergence in field studies showed a consistent downstream response, whereas in laboratory studies Weaver

experimental stock displayed slight upstream preference, suggesting that upstream responsiveness had developed by exposure to the laboratory incubation environment. Similarly, Adams native stock must show an initial strong response downstream as newly emerged fry, but under laboratory incubation conditions an intermediate behavior was displayed in spite of the fact that the experimental stocks were tested well before the stage of development characteristic of natural emergence. In contrast, Chilko, Stellako and Cultus experimental stock incubated without substrate and tested at the laboratory showed the same behavior patterns displayed by these stocks both in field studies and upon emergence from a simulated natural incubation environment. It appears, therefore, that exposure to laboratory incubation conditions without substrate enhanced the early manifestation of the behavior pattern that would otherwise occur sometime after emergence among stocks that must reverse current response during migration. But among stocks such as Chilko and Stellako, that need display only a single current response, incubation without substrate did not influence the initial response normally displayed at emergence among natural fry.

It is curious that the 7-Mile experimental stock showed an intermediate current response when tested after incubation at the laboratory, since downstream movement is required to reach their lake. Unfortunately nothing is known of the fry's lentic behavior in their tidal nursery lake to provide clues to possible causal factors. Fry emerging from the gravel incubation area at 7-Mile Creek continued a strong preference downstream when tested, even after 7 days of holding in hatchery troughs at the field station on 7-Mile Creek. But among fry *incubated* in hatchery troughs at that station a slight upstream responsiveness was shown, similar to 7-Mile experimental stock incubated at the laboratory. This suggests further that the behavior of certain races can be altered to some degree by lengthy exposure to the free-swimming environment during the alevin state.

## INTERPRETATION

The study on temporal variability with age has not shown any evidence that age is a causal mechanism in migrating behavior of fry. The fact that current responsiveness was displayed prematurely by alevins in the migration channel, and that fry made the appropriate response to current immediately upon emergence from gravel incubation, is evidence that delay in responsiveness to current is not required among the stocks examined.

The temporal patterns in migratory behavior of the stocks indicate that oriented responsiveness occurs and persists as an innate pattern in both upstream and downstream movement. Responsiveness downstream, therefore, is an active displacement and hence qualifies to be described as a negative rheotaxis. However, results suggest that a time-experience related phenomenon may be responsible for a change in orientation of migrating fry in populations where reversed responses are necessary to reach their nursery lake, or in populations less rigidly fixed in migratory behavior.

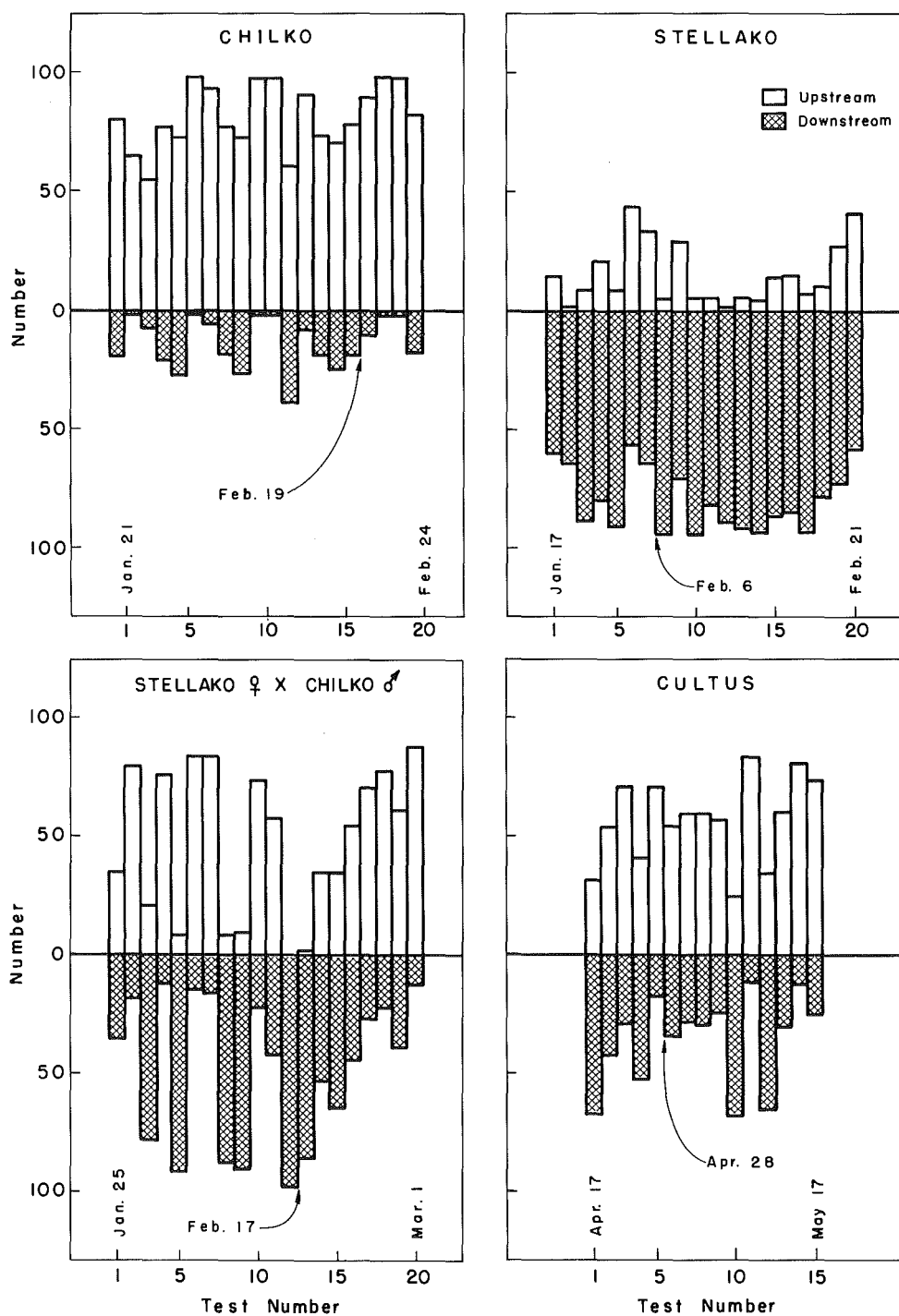


FIGURE 13—Current responses of four experimental stocks in the migration channel during the testing period. (Arrow indicates end of yolk absorption and transition from alevins to fry.)

## ENVIRONMENTAL VARIABLES AND CURRENT RESPONSE

In developing the hypothesis that fry migration was a deliberate movement in the presence of certain stimuli, environmental factors were examined as stimuli that might be involved in evoking or directing fry migration. The four environmental variables selected for examination were velocity, temperature, light and water source. The actual test performances are taken only as indicating a general influence and are not considered as a precise measurement of how a certain race will perform in its native environment.

### Influence of Velocity

Persistent negative rheotaxis in a fry population such as the Stellako stock is not necessarily consistent with the lentic behavior pattern characterizing the species. Since large concentrations of fry frequent the littoral areas of a lake, they can be found very close to or in the influence of the exit stream. In relatively small lakes such as Fraser or Cultus, fry presence in the outlet area is a certainty, and if negative rheotaxis persisted, large numbers would be lost from the nursery area by orientation downstream. Therefore, even in totally downstream migrating populations, a mechanism must be present to reverse fry orientation under certain circumstances. Such a mechanism could also operate in races, or fry populations which reverse their current response en route to the nursery lake. Age- or size-related change in current response was not shown to occur, and "learning", in which experience would produce the appropriate response, could not apply. To fulfill the above requirements, a mechanism reversing fry orientation would 1. be racially specific, 2. depend upon environmental cues to evoke the appropriate behavior, and 3. evoke a response without requiring a lengthy time component.

Field observations on upstream movement of fry have shown that current velocity has marked effects on migration distribution and on the timing of the event. It followed, therefore, that current velocity could be an environmental phenomenon that stimulates the appropriate rheotaxis. Of course, high velocities would be a physical barrier to any population. But a velocity level which is a threshold at which reversed responses are elicited could function as a factor directing rheotactic behavior.

### BEHAVIOR THRESHOLD

If velocity were the eliciting cue on which current responses were dependent, then upstream migratory behavior should increase in magnitude as test velocities decreased. To elucidate the influence of velocity on current response of fry, three experimental stocks were examined, Stellako, Adams and Weaver, each of which showed either negative or reversed rheotaxis in its native system. Fry were exposed to the standard test velocity of 15.2 cm/sec and results compared with trials at velocities decreased arbitrarily to 7.6, 3.8 or 1.9 cm/sec.

The influence of velocity was quite marked (TABLE 10). Stellako fry changed significantly from a response upstream of 9.0% at 15.2 cm/sec, to 52.4% at 7.6 cm/sec and further to 76.0% at 3.8 cm/sec ( $F = 12.7$ ,  $P < 0.01$ ), or a reverse from

negative to positive rheotaxis. Similarly, Adams and Weaver stock changed from an intermediate response at 15.2 cm/sec (53.4% and 55.7%, respectively) to a stronger response upstream at a velocity of 1.9 cm/sec (75.8% and 74.6%, respectively, with  $t$  at least 1.94,  $P_1 < 0.05$ ). The change in response was proportional only between Adams and Weaver stock. The similarity of maximum response magnitudes among the three stocks is of unknown significance and may be coincidental, but even at the lowest velocities, test stocks did not respond as positively upstream as Chilko fry in previous tests at much higher velocity.

TABLE 10—Total number and mean response (per cent) of three experimental stocks of sockeye fry responding to current upon exposure to different current velocities in the migration channel (U—upstream, D—downstream).

Stock	Velocity (cm/sec)	No. Tests	Number of Fry		Mean Response (Per Cent)		
			U	D	U	(SD)	D
Stellako	15.2	5	45	455	9.0	( 2.24)	91.0
	7.6	5	262	238	52.4	(13.57)	47.6
	3.8	5	380	120	76.0	( 2.77)	24.0
Adams	15.2	8	427	334	53.4	(24.97)	41.8*
	1.9	8	606	194	75.8	( 5.60)	24.2
Weaver	15.2	8	446	343	55.7	(21.71)	42.9*
	1.9	8	597	203	74.6	( 9.90)	25.4

\*mean responses  $\div$  100 when some fry remained in apparatus.

Although the responses shown at different velocities are presented as mean scores of several trials, each value is only the sum of individual fry responses. Thus while the mean responses may indicate a gradual influence with decreased velocity, in reality the velocities represent progressive levels at which a greater number of fry were stimulated to react positively. With respect to the individual, therefore, the effect of velocity is specific. As velocity increases the number of fry reaching their velocity threshold increases until the upper limit behaviorally is masked by the physical limit or capability of those remaining.

Observations on Stellako and Weaver fry in the migration channel have shown that at low velocities these stocks behave very much like Chilko fry. Movement upstream occurs in schools or groups instead of more solitary behavior displayed when slipping or swimming downstream. Group behavior, however, apparently can have an influence on the velocity threshold of individuals. As velocity increased the variability in responses also increased among the Adams and Weaver stocks. In part, increased variation was the result of the group responding with or stimulated by the behavior of other members. Erratic responses of a few leading fry often evoked negative rheotaxes while a deliberate movement upstream could stimulate higher numbers of fry to continue positive rheotaxes.

These racial responses to current velocity were not the result of physical inability to negotiate the test velocities. Racial size, by weight, which indicates performance ability, was unrelated to response. Moreover when placed in the central screen chamber of the apparatus, fry seldom were found held against the screen at the routine velocity of 15.2 cm/sec. In fact fry could hold in the chamber

an hour with no evidence of exhaustion. Stellako fry were often observed fighting at the upper screen of the chamber even though negative rheotaxes were evoked shortly after the removal of the same retaining screens.

## INTERPRETATION

Evidence strongly implies that downstream responsiveness is related behaviorally to current velocity. Negative rheotaxes were evoked among the experimental stocks upon reaching a velocity threshold, the level of which is believed to be racially specific. Therefore, one mechanism controlling orientation to current is shown to be velocity dependent, and thus can explain both avoidance behavior of fry when adjacent to a lake outlet stream, and reversed migration responses upon reaching lower velocities en route to their nursery lake. This also suggests that populations demonstrating very positive rheotaxes apparently have a velocity threshold beyond their maximum sustained swimming performance and perhaps equal with their maximum capability, since such tenacity is demonstrated in migrations upstream. Where initial movement occurs downstream in such populations, it probably results from a net displacement because of the inability to negotiate high velocities.

## Influence of Temperature

In most of the sockeye incubation streams of the Fraser River system, as water temperatures approach 3.3 to 4.4°C in the spring, fry emergence begins. Sharp temperature increases often are followed by peak numbers of fry leaving the incubation area, and thus are suggested as the major stimulus evoking locomotory responses. Temperature definitely influences locomotory activity of fry, but is questionable as a stimulus evoking rheotaxes to current direction. If temperatures within the range occurring on any sockeye stream were to influence direction of movement, then a change in rheotactic response should be shown by exposing fry to the temperature extremes recorded in that stream during the migration period.

## EXAMINATION

Influence of temperature on current responses of fry was examined in populations that must swim upstream or change from downstream to upstream migration to reach their nursery areas. Chilko, Adams and Weaver experimental stocks were tested in the migration channel at temperatures of 2.2 and 8.9°C which represented or were slightly beyond the range normally experienced by migrating fry of the races tested. Tests began about a week after yolk absorption. In each test the temperature in the apparatus was maintained at 5.6°C for approximately 20 min after the fry were introduced, then during the following 10 min temperatures were increased or decreased to the test level. The results noted at the two temperature extremes were compared with the "control" test at 5.6°C.

TABLE 11—Per cent response of sockeye fry from three experimental stocks moving upstream (U) and downstream (D) when exposed to temperatures of 2.2, 5.6 and 8.9°C.

Stock	No. Tests	Per Cent					
		2.2°C		5.6°C		8.9°C	
		U	D	U	D	U	D
Chilko	2	79.0	21.0	76.0	24.0	77.5	22.5
Adams	8	26.9	73.1	53.4	41.8*	42.0	58.0
Weaver	8	55.4	44.6	55.7	42.9*	54.1	45.9

\*per cent responses  $\propto$  100 when some fry remained in apparatus.

The results show that temperature had no influence on the responses of Chilko and Weaver fry (TABLE 11). Adams fry showed reduced response upstream at both 2.2 and 8.9°C, but analysis of variance indicated that differences in upstream response were not significant ( $F = 3.24$ ,  $P > 0.05$ ).

A more severe test was executed with alevins. Not too infrequently substantial temperature reductions can occur in outlet streams, caused either by wind action shifting the warmer and cooler waters to opposite ends of the lake, or by their confluence with cold tributary streams. Exploring the influence of such a rapid temperature drop on migrating behavior led to the exposure of alevins to the simulated and somewhat abnormal situation. Chilko, Adams and Weaver alevins incubated in the laboratory at 8.9°C were removed from their compartments as soon as responsiveness to current was first displayed and were tested at 3.9°C after only 20 min of acclimation.

The results indicated that exposure of alevins to a rapid temperature reduction from 8.9 to 3.9°C influenced the intensity of their response markedly. Chilko alevins maintained a positive rheotaxis but at a reduced level (68.3%) whereas Adams and Weaver alevins showed mean responses upstream of only 12.1% and 8.7%, respectively (TABLE 12).

The alevins responded to the lower temperature with greater reluctance to move than with tests run at 5.6°C (TABLES 3 and 4). The greater holding behavior (NT) was attributed to their level of advancement as well as the influence of temperature. Chilko fry were tested with 6.0 mg of dry yolk, Adams with 5.6 mg and Weaver with 8.5 mg.

TABLE 12—Total number and mean response (per cent) of sockeye alevins from three experimental stocks moving upstream (U) and downstream (D) when exposed to 3.9°C after incubation at 8.9°C (NT—not trapped).

Stock	No. Tests	Number of Alevins			Mean Response (Per Cent)			
		U	D	NT	U	(SD)	D	NT
Chilko	12	820	262	118	68.3	(11.85)	21.8	9.8
Adams	8	97	658	46	12.1	( 7.45)	82.2	5.7
Weaver	14	122	1,014	264	8.7	( 6.01)	72.4	18.9

## INTERPRETATION

With a substantial reduction in temperature, the upstream response of alevins was demonstrated as reduced locomotor activity and reduced intensity of positive rheotaxis. In experimental stocks showing an intermediate current response, severe reduction in temperature evoked a negative rheotaxis. But in the upstream migrating stock, the current response persisted at reduced intensity.

Among fry, rheotaxes were not affected nor were intensities of response markedly altered except with Adams stock which showed decreased positive rheotaxis with both increased and decreased temperatures. However, a rapid temperature drop may evoke holding behavior and reduce positive rheotaxis among upstream migrating fry, as observed with alevins. The tests imply that temperature experience of the newly emerged fry immediately prior to a severe temperature change may have a large influence on their subsequent current response.

It is concluded, therefore, that temperature has an effect on locomotor activity and may influence intensity of current response, but there is no evidence that temperature is responsible for controlling orientation during migration.

## Influence of Light

The influence of light on fry behavior is well known. Emergence from the gravel and movement downstream is primarily nocturnal. Even among upstream migrating fry populations, emergence occurs predominantly during the hours of darkness just after dusk. Movement upstream, however, is nearly always undertaken during or very close to daylight, which is a striking deviation from the negatively phototactic behavior pattern characterizing downstream migration. The difference in the two patterns suggests fry need visual orientation to complement a positive rheotaxis in sustaining upstream movement, whereas fry displaying negative rheotaxes may depend primarily on mechano-receptors for orientation.

## EXAMINATION

The diurnal behavior pattern of fry observed in the natural environment was not evident in the migratory behavior of the experimental stocks during routine tests in the migration channel. Stellako fry, both at the laboratory and in the field, and 7-Mile fry emerging from the gravel incubation area, continued to show the strong negative rheotaxes in tests during daylight that were evidenced at night. In contrast, Chilko stock continued their positively rheotactic behavior in tests during darkness, which suggested that light at least did not change migration direction, but of course gave no indication of its influence on response magnitude. Thus special tests were executed on Chilko experimental stock and 7-Mile native stock in the migration channel under conditions of either dark or light exposure, coinciding with 4- to 6-hr time intervals commencing at 8:30 p.m. and 9:30 a.m. daily.

Results of the study showed that mean responses upstream during daylight for Chilko (92.0%) and 7-Mile (22.1%) were higher than during darkness (87.4% and 6.3% respectively), but only 7-Mile fry showed a significant difference in response ( $t = 5.16$ ,  $P_1 < 0.005$ ) (TABLE 13).



TABLE 13—Total number and mean response (per cent) of two experimental stocks of sockeye fry responding to current when exposed to light or dark conditions (U—upstream, D—downstream, NT—not trapped).

Stock	No. Tests	Test Condition	Number of Fry			Mean Response (Per Cent)			
			U	D	NT	U	(SD)	D	NT
Chilko	10	Light	920	54	30	92.0	( 6.16)	5.4	3.0
	10	Dark	874	67	59	87.4	( 8.37)	6.7	5.9
7-Mile	14	Light	309	917	174	22.1	( 9.93)	65.5	12.4
	14	Dark	88	1,270	42	6.3	( 4.78)	90.7	3.0

The fry studied have very different migratory behavior patterns and were from different study sources. Chilko stock incubated at the laboratory may have had sufficient experience as free-swimming fry to manage relatively better against the test velocity (15.2 cm/sec) in darkness than 7-Mile fry, newly emerged from gravel incubation. Moreover, Chilko fry are genetically predisposed to show a strong positive rheotaxis which may preclude downstream movement even during darkness when given little choice regarding exposure to current. Stock from 7-Mile Creek show negative rheotaxis in their native environment and movement normally occurs during darkness. However, in laboratory studies, 7-Mile fry showed an intermediate response to current (TABLE 4), and laboratory tests were executed under conditions of near darkness.

The question arises, therefore, as to what effect the stock's activity pattern has on current responsiveness. Since each of these two stocks normally migrates at different photoperiods, when exposed to current during the opposite photoperiod a greater reluctance to move could be manifested. In this instance the expected response occurred. The number of Chilko fry holding in the apparatus increased by double during darkness, and 7-Mile fry tested in daylight quadrupled their holding response over that of their normal night migration activity pattern. The factor responsible for inducing stronger holding behavior, therefore, may not be that light simply enables visual navigation, but perhaps the stocks also possess or have acquired different activity rhythms and holding is the result of locomotory suppression during the inactive phase.

## INTERPRETATION

Based on the stocks examined, it can be concluded that light does not control the current orientation of sockeye fry. Chilko fry performed remarkably well in darkness and 7-Mile fry continued negative rheotaxis during daylight. Furthermore the study indicated that light is not a requisite for upstream movement. Even field observations have shown that Chilko fry occasionally migrate upstream in slower currents during darkness after dusk or before dawn. This is not to suggest that photoperiod does not regulate migratory behavior, because field evidence is certainly to the contrary. It does imply, however, that when exposed to current, upstream migrating fry will respond positively in the absence of light, which is behaviorally necessary for the fry to reach shore, having emerged during darkness in moving water. The fact that in their native environment many Chilko fry first reach shore only a short distance downstream from their incubation site indicates

that positive rheotaxis is evoked at emergence during darkness, or the relatively high velocities would otherwise displace the fry many kilometers downstream.

Visual orientation is probably necessary for upstream navigation where swifter water requires a degree of maneuverability. And thus during darkness once fry reach the very low velocities adjacent to shore, holding behavior could occur until sufficient light was available for visual contact, corresponding with their diurnal activity pattern in migration. Holding behavior does not mean absence of activity. At Chilko River, many if not all of the major holding sites require a positively rheotactic orientation for the fry to avoid displacement downstream. Although tests in darkness showed reduced intensity of upstream response, the degree of locomotory suppression was not so great as to preclude strong locomotory responses when required.

In contrast, 7-Mile fry have shown no tendency for positive rheotaxis in field observations. Occasionally fry are observed holding close to shore in quiet water during late afternoon, but after darkness they disappear, consistent with their test performance. In downstream migrating populations, therefore, visual orientation during daylight may facilitate holding behavior in response to their activity pattern.

### **Influence of Water Source**

The basic similarity among upstream migrating populations of sockeye fry is that the source of water for this migration always originates from a lake. In contrast, where incubation areas are located in tributary drainage streams from woodlands or forests, downstream migration is mandatory. And thus the topic to be considered in this section is the effect of water source on the fry's orientation to current and hence their migratory behavior.

First, it may be useful to review the circumstances under which the sockeye stocks examined migrate in their native environments. Chilko, Stellako and Adams fry are lake outlet populations and exhibit either downstream or upstream responses to lake water. Weaver and 7-Mile fry are tributary populations responding at least initially downstream in their streams, and Cultus stock is a lake-incubated population which need show no orientation to current to reach their nursery area. Basically, four behavior patterns are displayed; migration upstream in lake outlet water, migration downstream in lake outlet water, migration downstream in tributary streams, and emergence directly into the lake nursery area. To resolve the question of what influence water source has on migratory behavior, three approaches were used; 1. experimental stocks were tested in lake and tributary water sources at the laboratory, 2. native stocks were exposed to similar combinations in the field or were translocated to the laboratory for testing, and 3. experimental stocks were incubated and subsequently tested in both lake and creek water combinations.

### **TRIBUTARY INTRODUCTION**

From 1967 to 1969 a number of experimental stocks incubated in Cultus Lake water were exposed to Hatchery Creek water draining the terrain adjacent to the lake system. In the stocks examined, the responses to creek water were all more negative than their corresponding behavior in lake water (TABLE 14). Chilko, the

most positively rheotactic stock, showed a strong negative rheotaxis in creek water (only 13.9% upstream) which amounted to a completely reversed orientation in the foreign source. In contrast, preliminary studies in 1967 with Chilko fry showed a stronger positive rheotaxis in Hatchery Creek water (Brannon 1967). Thus since the stocks were tested in different years and at different stages of advancement, the significance of the different intensities of response between stocks remains unknown without knowledge of the temporal variability in the components responsible for negative rheotaxis.

The response of the various experimental stocks upon exposure to Hatchery Creek water, however, can be considered generally very similar. And to describe the nature of their behavior, reference is made to Chilko fry which showed the most extreme contrast in response to water source. When Chilko fry were placed in the central screen chamber, an initial rejection of the water was indicated by their swimming position. Fry dropped against the lower retaining screen head first as the water current started, and crowded in the lower quarter of the chamber, often brushing their tails against the screen. Even after 20 min exposure few fry were found fighting against the upper retaining barrier which normally characterized their behavior in lake water.

TABLE 14—Total number and per cent response of five experimental stocks of sockeye fry responding upstream (U) and downstream (D) to Cultus Lake and Hatchery Creek water.

Stock	No. Tests	Water Source	Number of Fry		Per Cent	
			U	D	U	D
Chilko	30	Lake	2,750	173	91.7	5.8*
	20	Creek	277	1,723	13.9	86.1
Cultus	8	Lake	514	286	64.3	35.7
	8	Creek	322	479	40.3	59.7
Adams	7	Lake	296	404	42.3	57.7
	7	Creek	61	639	8.7	91.3
7-Mile	9	Lake	527	373	58.6	41.4
	9	Creek	241	659	26.8	73.2
Weaver	11	Lake	762	338	69.3	30.7
	11	Creek	415	685	37.7	62.3

\*per cent responses  $\approx$  100 when some fry remained in apparatus.

When Chilko fry were released from the chamber they immediately dropped downstream alternating between swimming head first and drifting tail first. As the lower trap was approached some fry would reverse orientation and start upstream, but as they progressed, individuals continually fell away and returned to the trap. In less than 5 min 80% of the fry had entered the downstream trap compartment.

Exposure of the experimental stocks to Hatchery Creek water demonstrated that fry from lake outlet and tributary streams responded in a similar manner to the source. Hatchery Creek water was less favorable than their incubation water when measured by their positive rheotaxis in both sources. Of course increased negative rheotaxis in Hatchery Creek water could be attributed to either 1. some "quality" difference in the water, 2. a general rejection of any tributary stream, or 3. a rejection of any water source foreign to their incubation experience.

## TRANSLOCATION OF STOCKS

To further define the behavior of fry in different water sources two stocks were translocated and their behavior in the apparatus observed. In each instance fry were taken from their native stream at the time of emergence and brought to the laboratory for testing. The same procedure was followed in these trials as with the experimental stocks except the fry were held in lake water at the laboratory and thus had opportunity to experience the trial source before testing. However, since the responses remained the same throughout the test period, it was assumed that prior exposure did not influence behavior.

Fry from the translocated stocks showed intermediate responses to current when tested in Cultus Lake water (TABLE 15) and compared with the responses of the respective experimental stocks incubated in Cultus Lake water and subsequently tested in lake and creek sources (see TABLE 14). Native Chilko fry responded upstream 56.5% when translocated to Cultus Lake, whereas the experimental Chilko stock incubated at Cultus that year responded 91.7% upstream in lake water and 13.9% in creek water. The upstream response of the translocated stock was significantly less than the experimental stock incubated in Cultus Lake water ( $t = 9.36$   $P_t < 0.005$ ) but significantly greater than experimental stock tested in creek water ( $t = 8.91$   $P_t < 0.005$ ). Similarly native fry from 7-Mile responded 42.8% upstream when translocated and tested in Cultus Lake water, whereas the 7-Mile experimental stock incubated in lake water responded 58.6% upstream in lake water and 26.8% in creek water. Again, the upstream response of the translocated stock was significantly greater than the experimental stock tested in creek water ( $t = 1.93$ ,  $P_t < 0.05$ ) and significantly less than experimental stock tested in lake water ( $t = 1.96$ ,  $P_t < 0.05$ ).

TABLE 15--Total number and per cent response of native Chilko and 7-Mile fry responding upstream (U) and downstream (D) when translocated and tested in Cultus Lake water.

Stock	No. Tests	Number of Fry		Per Cent	
		U	D	U	D
Chilko	10	565	381	56.5	38.1*
7-Mile	12	513	687	42.8	57.2

\*per cent response  $\approx 100$  when some fry remain in apparatus.

Chilko fry were also tested in the field at Chilko by exposing them to Madison Creek, a small tributary stream draining from the hillside adjacent to the river, 1.6 km from the lake outlet. Installing the apparatus next to the creek mouth allowed the water source to be alternated between Madison Creek and Chilko Lake to test the fry response in either source. The results of the tests were remarkably similar to the laboratory study (TABLE 16). Upon exposure to Madison Creek water the fry showed strong rejection behavior, rapidly exiting the apparatus, whereas in lake water a strong positive rheotaxis was evoked.

TABLE 16—Total number and per cent response of native Chilko fry responding upstream (U) and downstream (D) in Chilko Lake and Madison Creek water.

Water Source	No. Tests	Number of Fry		Per Cent	
		U	D	U	D
Lake	10	842	158	84.2	15.8
Creek	10	47	953	4.7	95.3

The responses of translocated stocks provided information that began to form the basis for understanding the influence of water source on current response. The combinations of fry stocks and water sources tested suggested that fry detected a "quality" difference existing in the water sources to which they were exposed. Tributary streams of non-lake origin caused the fry to reject the source or evoked more negatively rheotactic behavior than when tested in lake sources, even when the lake source was not previously experienced until just prior to testing.

### INCUBATION EXPERIENCE

The influence of incubation experience on the current response of sockeye fry could not be ascertained from translocation of stocks. Without knowing the components which elicit a particular rheotaxis nor the concentration of such components in specific streams, one cannot assume that in each instance the stocks were not responding positively to the water most similar to their incubation environment, or displaying a behavior pattern evoked by their incubation experience. If migration to the nursery area was controlled by certain properties of the water source, then one would expect a general response to characterize fry behavior if those properties were common to all lake sources or, conversely, a specific response if the incubation environment initiates a spontaneous sequence in rheotaxis or induces a response determined by its similarity to the foreign source.

Elucidation of either phenomenon required that fry be incubated in water sources for which current responses were known from previous testing and which evoked opposite rheotaxes in the experimental stock. Thus experimental stock from Chilko was taken for incubation in Cultus Lake water and Hatchery Creek water and subsequently tested the following spring for current response to both the incubation source, and the reciprocal source in which they had no experience prior to testing.

Results from the trials were strong evidence that lake water in general elicits positively rheotactic behavior (TABLE 17). The upstream response of lake-incubated fry was 84.0% tested in their incubation source. Creek-incubated fry responded upstream in lake water with a mean of 83.5%, indicating that without any previous exposure, lake water would still evoke a very positive rheotaxis in this stock. Lake-incubated fry when tested in the creek source showed a mean response of 11.2% upstream or a highly negative rheotaxis in a creek source previously unexperienced. However, among creek-incubated fry the response to creek water was not negative, but tended to be intermediate in preference. Their behavior shows that for this particular stock, incubation experience in a stream source that otherwise evokes negatively rheotactic behavior can induce a change in that

behavior. Although the creek-incubated fry tended to show a slight preference upstream, it was not significantly different from a 50:50 distribution ( $t = 1.30$ ,  $P_t > 0.05$ ) but greatly different from the lake-incubated stock's response to creek water ( $t = 7.48$ ,  $P_t < 0.005$ ). The results show that incubation experience can alter the response of sockeye fry to stream water of non-lake origin, but when experienced for the first time it will evoke negatively rheotactic behavior. Of greater importance is the suggestion that sockeye fry recognize and show positive response to water of lake origin, regardless of any previous experience with the source during incubation.

TABLE 17—Total number and per cent response of Chilko experimental stocks incubated in creek or lake water and tested in the incubation and reciprocal water sources (U—upstream, D—downstream).

Incubation Source	Test Source	No. Tests	Number of Fry		Per Cent	
			U	D	U	D
Lake	Lake	10	840	160	84.0	16.0
	Creek	10	112	876	11.2	87.6
Creek	Lake	10	835	116	83.5	11.6*
	Creek	10	479	376	47.9	37.6*

\*per cent response  $\approx$  100 when fry remained in apparatus.

## INTERPRETATION

It is concluded that sockeye fry can detect a "quality" difference between water sources. When fry were incubated in a lake-fed water supply, exposure to tributary stream water during tests evoked rejection behavior. However, exposure to a foreign lake source during tests induced an intermediate response or a positive rheotaxis. When fry were incubated in tributary stream water, exposure to the same source for testing produced an intermediate response rather than rejection behavior, but tests in lake water previously not experienced elicited a strong positive rheotaxis. Therefore evidence suggests that incubation experience can alter behavior, and that some property of water source acts to either repel or attract sockeye fry. In the hierarchy of environmental cues that influence behavior, water source appears to have a strong position. Other factors, however, may subordinate the influence of water source in directing rheotactic responses.

## OLFACTION AND ORIENTATION

Fry migration has thus far been examined as a movement directed by current. Observations of native stocks, however, indicated that migrating fry were also using factors other than current for directed movements. In this section, therefore, other sensory modalities will be examined that appear related to migrating behavior but are either supplementary to, or separate from, current responsiveness.

## Water Source and Preference

Current responses altered by different water sources speak not only of the ability of sockeye fry to detect "quality" differences between sources, but also that fry may have a source "preference" which may or may not be induced by

experience. Of course tests of current responses could only indirectly infer that a preference existed, since at any one time only one source was present in the channel apparatus. Furthermore, with downstream migrating populations, one is uncertain whether a negative rheotaxis in fact represents a preference. However, the evidence that incubation experience could affect response in different water sources suggests the existence of a critical period in development when exposure to environmental variables will result in that experience being incorporated in the fry's behavior. In this particular section, therefore, the study examining "preference" behavior will be presented with evidence relating to the effect of incubation experience on the behavior.

Preference behavior was examined in the Y-trough (FIGURE 3) in which two water sources could be presented to the test stock simultaneously, alternating supplies between sides to overcome left- or right-handed bias. Using this method three studies were undertaken: 1. Native Chilko stock incubated in its natural environment was tested to examine preference between the incubation water source and an alternate source, 2. Two experimental stocks, Chilko and Stellako, which show opposite rheotactic behavior in their native streams, were incubated and later tested in two foreign water sources at the laboratory to determine influence of this incubation experience on preference, and 3. Native Chilko stock was moved to the laboratory after emergence and tested to determine effects of post-incubation experience in two foreign water sources on preference.

### PREFERENCE BEHAVIOR

Chilko fry were captured along the river bank as migration was under way to Chilko Lake and held for trials conducted the same day in a choice of water sources from the original incubation environment, Chilko River (lake source), and from Madison Creek (creek source). Temperature differences between sources varied from 0.3 to 0.6°C with the creek often the colder, and test velocity was set at 7.6 cm/sec.

In each test, 20 fry were placed in the screen chamber in the outlet arm of the "Y" channel and after 3-5 min they were released by raising the upstream barrier. Upon approaching the area where water sources joined, the fry most often made unhesitating choices of lake water. The results from 40 tests combined from 1968 and 1969 indicated that a mean of 14.3 fry (SD 4.68), or 71.5%, chose the lake source (TABLE 18).

TABLE 18—Total number and per cent of native Chilko fry showing preference for Chilko Lake or Madison Creek water (Lk—lake water, Cr—creek water, NP—no preference).

Year	No. Tests	Number of Fry			Per Cent		
		Lk	Cr	NP	Lk	Cr	NP
1968	20	260	122	18	65.0	30.5	4.5
1969	20	312	11	77	78.0	2.8	19.3
Total	40	572	133	95	71.5	16.5	12.0

As fry left the screen chamber they moved as a school, loosely strung out, and generally proceeded to the trap area of the arm supplied with lake water. As the fry approached the trap in the lake source arm, many often reversed downstream and occasionally the whole school would move back to the screen chamber. On return, the route was usually repeated, and with successive trials the fry would become more bold and finally enter the narrow V-throat of the trap. Occasionally, the initial movement up the central arm would be so rapid that fry carried themselves well into the creek water; this elicited a negative response, beginning as hesitation for 1 or 2 sec and followed by reversed migration downstream. Individual fry would sometimes alternate between darts and hesitation before exiting the creek source. Searching behavior sometimes also led fry up the creek arm and infrequently to the trap, or if frightened for some reason the whole school would enter the nearest trap.

An interesting response to water source was observed in the natural environment of Chilko River. As described in the section on migrating behavior of native stocks, Chilko fry often were found holding in pools at the mouth of Madison Creek after having left the main river from the previous night's emergence or earlier migration. Although experiencing an unfamiliar water source, the fry showed normal schooling behavior and were oriented into the current in a manner similar to holding fry elsewhere. On one occasion a school of fry holding in the creek pools was trapped and held there until tested. Results were identical to the tests described above, with the lake water strongly preferred. Thus although the fry entered the pools and held in Madison Creek voluntarily, when asked to make a locomotory response in a choice of both sources the fry did not hesitate to choose lake water. It appeared as though their acceptance of Madison Creek was velocity dependent and hence was satisfactory as temporary refuge but evoked no migrating response.

It is concluded from tests with native Chilko stock that fry can show preferences for water source. Chilko fry incubated in Chilko River prefer water flowing from their nursery lake, although when not migrating they may be content to hold in another water source.

## **INCUBATION EXPERIENCE**

To examine the influence of foreign incubation experience on preference behavior, experimental stocks were incubated in water from two sources, Cultus Lake and Hatchery Creek, and subsequently tested in a combination of the same two sources. Tests were performed on alevins at the stage when current responses first became evident approximately 3 wk before emergence, and later as feeding fry. Test velocity was 7.6 cm/sec unless otherwise specified.

### **Alevin Preferences**

The effect of incubation experience in foreign water sources on alevin behavior was examined in the Chilko stock. Incubation was undertaken in lake and creek sources, but experimental lots were also transferred from one source to the other halfway through yolk absorption, about 5 wk before emergence, or about 2



wk prior to testing. And thus experimental stocks experienced one of four different incubation situations; Lake 100%, Lake to Creek, Creek to Lake, and Creek 100%.

The tests showed that stock incubated entirely in either lake or creek water preferred their incubation water (TABLE 19). Preferences for respective incubation sources were significantly different from random ( $t$  at least = 3.08,  $P_t < 0.01$ ). Stock that had experienced the change in incubation source showed an intermediate choice, but with a tendency to prefer their original incubation source ( $t$  = 1.58,  $P_t > 0.05$ ).

TABLE 19—Total number and per cent of Chilko alevins from experimental stocks showing preference for Cultus Lake or Hatchery Creek water after incubation in each source, or transferred between sources during incubation (Lk—lake, Cr—creek, NP—no preference).

Incubation Source	No. Tests	Total Number			Per Cent		
		Lk	Cr	NP	Lk	Cr	NP
Lake 100%	10	179	0	21	89.5	0.0	10.5
Lake → Creek	10	119	67	14	59.5	33.5	7.0
Creek → Lake	10	67	111	22	33.5	55.5	11.0
Creek 100%	10	25	137	38	12.5	68.5	19.0

Only 10 tests were run on each experimental lot because of the long time required for each test (alevins took up to 1 hr to enter the traps) and the short time available for tests at this specific stage of development, since behavior as alevins was to be compared with that of fry. However, several interesting trends are evident in the data. The lake-incubated alevins completely avoided creek water. In contrast, a few creek-incubated fish selected lake water, which might suggest that lake water, as a source foreign to the alevins' incubation experience, was less repellent than a tributary source at this stage in their development.

Of equal importance were the behavior patterns of the alevins from transferred lots. Although these fish showed an intermediate choice between the two water sources, with stronger preference for the source in which they were first incubated, the fact that they showed any preference for the original incubation source indicates that memory is involved. Although removed from the original source for about 2 wk alevins retained a degree of familiarity with this source and did not completely change their preference. However, only 2 wk exposure to a new source was all that was necessary to induce considerable change in preference behavior. Therefore, during this period of their life history, alevins prefer their incubation water over other introduced sources, but changes in water source cause the fish to incorporate that information into their behavior pattern.

Fry Preferences

The four groups of alevins described previously were maintained at the laboratory and reared in their respective water sources for 90 days, with transferred fry being held in the second water source. Thus fry lots were from the same

experimental environments as the previous alevins. The number of tests run were increased because the time involved at this point was not critical, and the fry responded faster in the apparatus.

Tests showed that behavior of fry had changed from that displayed as alevins. In all instances lake water was the preferred source (TABLE 20). Each experimental lot of fish showed choice for the lake source significantly greater than random ( $t \geq 6.5$ ,  $P_t < 0.005$ ), and the mean responses between lots did not vary significantly from each other ( $t \leq 1.08$ ,  $P_t > 0.05$ ).

TABLE 20—Total number and per cent of Chilko fry from experimental stocks showing preference for Cultus Lake or Hatchery Creek water after incubation in each source, or transferred between sources during incubation (Lk—lake, Cr—creek, NP—no preference).

Incubation Source	No. Tests	Total Number			Per Cent		
		Lk	Cr	NP	Lk	Cr	NP
Lake 100%	30	497	24	79	82.8	4.0	13.2
Lake → Creek	20	352	42	6	88.0	10.5	1.5
Creek → Lake	30	540	24	36	90.0	4.0	6.0
Creek 100%	30	497	69	34	82.8	11.5	5.7

These tests indicated that fry did not maintain a preference for their incubation source, but changed to a lakewater preference regardless of previous experience. This is not to suggest that 90 days made fry lose all memory of their incubation water, but rather that any memory of incubation water was not incorporated into their behavior at this stage of development. Moreover, the stock incubated and later fed in creek water for 90 days showed no less preference for lake water than did lake-incubated fry, indicating that any association between water source and food did not influence preference.

It is concluded, therefore, that experience during incubation has no influence on choice of water source as 90-day-old fry. Also, memory of foreign incubation water is not necessarily lost, but at least is not responded to even after prolonged feeding in the foreign water source.

When the change in preference from creek incubation water to lake water occurred is not known. However, one group incubated entirely in creek water was tested 2 wk after the original alevin tests, which by yolk weight standards (2 mg at 3.3°C) placed these fish 7 days before emergence would have occurred in their native environment. Their preference in the Y-trough was strongly for lake water, 66.2%, with only 15.2% responding to creek water, and the rest showing no preference. This level of preference is less than that shown by fry, but a reverse of that displayed by younger alevins. And thus at the stage corresponding with 7 days before emergence, Chilko alevins incubated in creek water had changed their preference from creek to lake water source.

A second study was conducted using Stellako fry incubated in water from Cultus Lake and Hatchery Creek. No transferred experimental lots were used, but

two velocities were tested since Stellako fry showed such a low velocity threshold in current response studies. The result of exposure to low velocity, 3.6 cm/sec, indicated that the lake-incubated stock preferred lake water (TABLE 21), but the creek-incubated fry showed preference for neither (difference from random,  $t = 0.5$   $P_t > 0.05$ ). When velocity was increased to 7.6 cm/sec, however, a strong lake source preference was displayed by the creek-incubated stock (difference from random,  $t = 7.8$   $P_t < 0.005$ ).

TABLE 21—Total number and per cent of Stellako fry from experimental stocks showing preference for Cultus Lake or Hatchery Creek water after incubation in each source (Lk—lake, Cr—creek, NP—no preference).

Incubation Source	No. Tests	Velocity (cm/sec)	Total Number			Per Cent		
			Lk	Cr	NP	Lk	Cr	NP
Lake 100%	20	3.6	366	31	3	91.5	7.8	0.7
Creek 100%	30	3.6	320	269	11	53.3	44.8	1.8
Creek 100%	20	7.6	310	61	29	77.5	15.3	7.3

The results indicated that Stellako fry incubated in creek water exhibited a preference only at the higher velocity. At low velocity their experience in creek water during incubation and rearing apparently provided sufficient familiarity to cause no preference behavior, or at low velocity tributary water was not repellent when some experience to the source had occurred. As noted previously, Chilko native fry holding during darkness along the banks of Chilko River showed no reluctance to enter and remain in the lower velocities of Madison Creek, which suggests that at very low velocities, even stock without prior experience may not avoid a tributary water source.

The study on Stellako fry showed that lake water was a preferred source at higher velocity, regardless of incubation experience. Since Stellako fry were negatively rheotactic in lake water and still showed preference for a lake source, this suggested that lake water could induce a more positive response than other sources.

## POST-INCUBATION EXPERIENCE

To elucidate the influence of experience in foreign water sources after emergence from the gravel, native fry were removed from Chilko River during their migration and transferred to the laboratory where two separate groups were reared in Cultus Lake water and Hatchery Creek water for a period of 90 days. Thus a race incubated in its native lake water was tested for water source preference after rearing in foreign water sources from another lake and from a tributary stream.

The transferred fish were held at the laboratory during warm summer temperatures which accelerated growth to the fingerling stage during the 90-day rearing period. At the end of this period the fingerlings were exposed to both water sources in test lots of five fish and examined for preference. Behavior was found to

be the same for both groups of fry (TABLE 22). Fingerlings reared in creek water chose the lake source as strongly as did the lake-reared stock, and the response of creek-reared fish apparently was not affected by any association with the water source in which they were fed.

TABLE 22—Total number and per cent of native Chilko fry showing preference for Cultus Lake or Hatchery Creek water after rearing in each source 90 days (Lk—lake, Cr—creek, NP—no preference).

Rearing Source	No. Tests	Number of Fry			Per Cent		
		Lk	Cr	NP	Lk	Cr	NP
Lake	20	86	7	7	86.0	7.0	7.0
Creek	20	96	3	1	96.0	3.0	1.0

The results showed that post-incubation experience in non-lake water did not influence the intensity of an overriding response to a lake water source. Water from a substitute lake evoked the same preference response as the parent lake, even when the stock had a lengthy absence from any lake water and had been reared in a stream foreign to their native experience.

## INTERPRETATION

It is concluded that preference for water source was displayed by sockeye alevins, fry and fingerlings. Prior to emergence, the alevins showed a strong response for their incubation source and incorporated incubation experience in their preference behavior as alevins, indicating that memory was involved. However, as the alevins approached the emergence period a change occurred in their response to water source and they preferred lake water regardless of their incubation experience. Lake water was preferred from then on as fry or fingerlings with neither incubation experience or post-incubation experience influencing their preference. It is suggested that tolerance to tributary water or the particular motor patterns that such a water source evokes is related to some function of velocity.

Tests with a tributary water source were subject to variation from changes in water "quality" of the stream. Since fry were sufficiently sensitive to some properties in the water to prefer or reject a source, then it must be assumed that they could detect various changes that occur during runoff. During rainy periods fine silt was present in the test water and no doubt a higher level of dissolved solids as well. This may or may not have affected fry preference, but it appeared that in tests during turbid conditions, fry showed a more positive response to the tributary source. Attempts were made to test only during sunny weather, but often conditions changed rapidly in the spring, undoubtedly changing the tributary water quality. During the incubation and rearing phase, the creek-incubated fry were subjected to all the variability characteristic of a small stream.

## Preference and Olfaction

In the previous two sections we have seen that fry detect and respond differently to certain water sources. The ability of the small fish tested to detect or differentiate between the "quality" of water sources indicates development of a

very keen sense of perception as newly emerged fry, or even as alevins. This ability to incorporate and respond to changes in water source suggests the cue is chemically mediated. Chemical sensitivity would possibly implicate odor stimulation as the sensory pathway evoking responsiveness. In this section, therefore, evidence will be examined on the role of olfaction in source discrimination, and its importance in current responsiveness.

## SENSORY EPITHELIUM

For the young sockeye to be capable of olfactory discrimination before emergence, sensory epithelium must be present at least by the alevin stage of development. To examine this question, samples of Chilko embryos, preserved 3 wk prior to hatching, and alevins, preserved 1 wk before yolk absorption, were dissected and prepared for histological examination. Following routine dehydration with ethanol, and paraffin embedding, the specimens were serially sectioned at 6 $\mu$  or 10 $\mu$  and stained in Harris hematoxylin and eosin.

Examination of sections revealed that, prior to hatching, the olfactory opening is a single pit appearing as a deep invagination on the dorsal anterior portion of the snout. The olfactory chamber floor has well developed sensory epithelium of ciliated columnar and neurosensory cells (FIGURE 14). The adjacent walls of the chamber show the sensory epithelium merging with polygonal cells and scattered mucous cells. At this stage the sensory epithelium layer appears as well developed as that of the adult, but it is confined to the floor of the chamber.

As the alevin approaches yolk absorption and emergence, a change is apparent in the morphology but not in the sensory tissue. The elevated circular anterior naris is well formed and distinct from the posterior flattened naris, separated from the latter by a slightly elevated septum. The olfactory chamber has widened but the lamellar folds found in adult fish are not yet forming (FIGURE 15). The sensory epithelium looks much as it did in the embryo but has increased in area. Olfactory, ciliated columnar, polygonal, basal and mucous cells are very similar to adult olfactory epithelium, and although lacking the lamellar folds, the tissue appears to be no less functional. The ciliated support cells, shown lightly stained, and the dendritic processes of the more darkly stained elongated olfactory cells (FIGURE 16), line the entire lumen of the olfactory chamber except on the anterior portion adjacent to the naris opening.

The olfactory apparatus of the sockeye advanced embryo and alevin appears very similar to that of the grayling (*Thymallus arcticus*) reported in detail by Watling and Hillemann (1964). The sequence of events, however, appears more accelerated in the grayling, with lamellae development sooner than that observed in the sockeye. However, the apparent formation of sensory epithelium in the embryo, and the well formed nares in the alevin suggest that olfaction is an important sensory phenomenon at this stage of sockeye development.

## OLFACTORY DISCRIMINATION

Behavioral evidence of odor discrimination between water sources was the next phase in the study. The fry's ability to differentiate between odors was examined by comparing water source preference of fry with and without olfaction denied. Treated fry were anesthetized and olfaction prevented by occluding the

nares with petroleum jelly; control fish were anesthetized but not treated. Chilko laboratory stock and native stock were used for tests in the Y-trough. At the laboratory, Chilko fry incubated in Cultus Lake water were exposed to a choice of Cultus Lake water and Hatchery Creek water. At Chilko, native stock incubated in Chilko River were exposed to their incubation source (i.e. Chilko Lake water) and Madison Creek water. Because of the time required for treatment only two fish were used per test.

The control fish responded by showing decisive preference for lake water in both laboratory and field studies (TABLE 23). In contrast, fry with olfaction blocked showed responses that were not significantly different from random ( $t \leq 0.89$ ,  $P_t > 0.05$ ), with considerable numbers showing no preference.

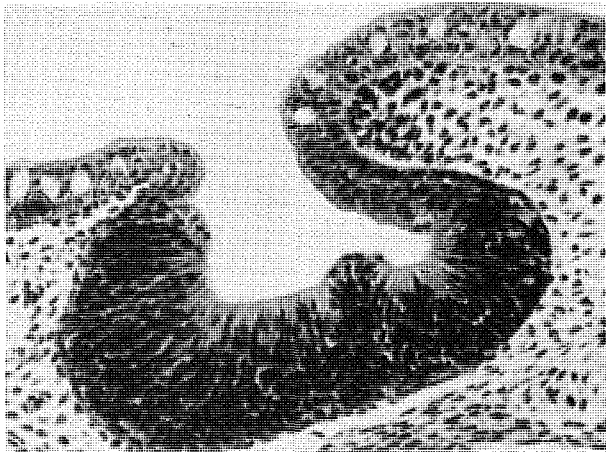
TABLE 23—Total number and per cent response of Chilko fry (native and experimental stock) to lake and creek water sources with and without olfactory occlusion (Lk—lake, Cr—creek, NP—no preference).

Stock	No. Tests	Total Number			Per Cent		
		Lk	Cr	NP	Lk	Cr	NP
Experimental							
Control	10	20	0	0	100	0	0
Treated	20	14	15	11	35.0	37.5	27.5
Native							
Control	10	18	0	2	90.0	0	10.0
Treated	24	14	22	12	29.2	45.8	25.0

Fry with occluded nares showed a marked difference in behavior from the control fish while in the apparatus. Treated fish delayed before leaving the screen chamber and thereafter behaved more independently than control fish. Often the pair of treated fry would separate after reaching the central chamber and proceed as individuals, showing little attention to each other. When both treated fry proceeded up the same arm, one fry often dropped back independently and tried the other arm. Generally the first choice was repeated several times before trying the adjacent arm.

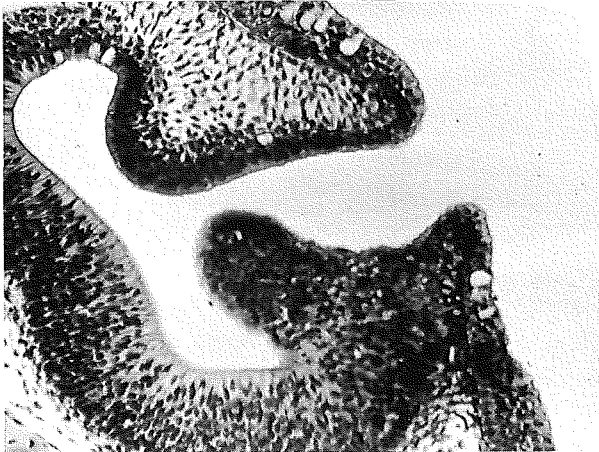
Searching was more apparent among fish with occluded nares than among the controls. Control fry usually selected the appropriate side of the apparatus before arriving at the Y, by moving away from either wall of the main outlet arm and "testing" near the center of the stream. This trial of the other water generally evoked an immediate movement to the appropriate side as they continued upstream. Treated fry also showed similar "testing" behavior, except they swam back and forth across the whole trough width as they continued movement upstream. This behavior was less apparent in the side arms of the apparatus supplied by a single water source, which indicated that while in the main arm, treated fry may have detected some difference between the two water sources. Slight temperature differences between sources could have been a cue that induced greater searching behavior when exposed to the water mixture.

The treated fish appeared more nervous than the controls. Quick movements at angles away from their direction of movement were frequent, and movement up and down the trough or from arm to arm was more prevalent. At certain times the



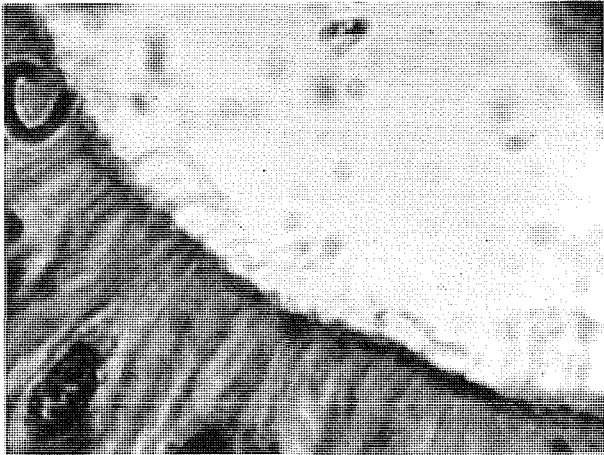
250X

FIGURE 14—Olfactory capsule and sensory epithelium of the sockeye embryo.



170X

FIGURE 15—Olfactory capsule and sensory epithelium of the sockeye alevin.



1500X

FIGURE 16—Sensory epithelium and ciliated columnar cells of the sockeye alevin.

treated fry chose or preferred a side and persisted in that direction as sources were altered from test to test, apparently selecting on the basis of some visual information in the apparatus or external environmental cues.

### SOURCE DILUTION

The ability to detect variations in concentrations of lake water or responsiveness to diluted lake water was the final question examined on the role of olfaction in fry migratory behavior. Chilko experimental stock was exposed to water originating from Hatchery Creek supplied to each arm of the Y-trough, one supply containing either 15 or 5% lake water, and the other 100% creek water. Test results are shown in TABLE 24, and compared with standard (i.e. control) tests in lake and creek sources.

TABLE 24—Total number and per cent of Chilko experimental stock responding to concentrations of lake water diluted with creek water (Lk—lake, Cr—creek, NP—no preference).

Test Water Sources	No. Tests	Total Number			Per Cent		
		Lk	Cr	NP	Lk	Cr	NP
Lk 100%—Cr 100% (control)	10	179	0	21	89.5	0	10.5
Lk 15%—Cr 100%	10	164	20	16	82.0	10.0	8.0
Lk 5%—Cr 100%	20	302	86	12	75.5	21.5	3.0

The data indicate that the experimental stock, incubated in lake water, was able to select the lake water at dilutions down to 5%, with some indication that error in discrimination was starting at that concentration (difference in lake preference from control,  $t = 1.73$ ,  $P < 0.05$ ).

### INTERPRETATION

Examination of the Chilko stock indicated that olfactory epithelium is well developed in the alevin and appears functional even prior to hatching. Discrimination tests in the Y-trough showed that with olfaction prevented, fry cannot select water source. Therefore, stream odor characteristics, as stimulating cues, and olfaction, as the sensory mode of perception, are strongly implicated in source selection. Since fry continued to respond with a positive rheotaxis in the Y-trough when denied olfactory perception, it is concluded that odor is primarily a directing phenomenon and its absence does not markedly influence rheotaxis. However, when the nares were occluded, persistence of response was reduced, group unity was not as evident and individuality in behavior increased. Further, the study shows that fry were capable of detecting lake water odors at concentrations of only 5%.

This information, considered in light of the previous study on water source preference, suggests that lake water may contain an odor component that is recognized by sockeye and acts as a universal attractant for the fry of the species.



### Orientation Without Current

Sockeye fry behavior at Chilko and Adams River is marked by extensive movement along the shoreline of the nursery lake as fry leave the incubation stream and enter the lake. Although moving concentrations of fry have been observed in other lakes on the Fraser River system, they appear characterized by feeding behavior or randomness, and not as intensive nor as directional as those in Chilko and Shuswap Lakes. Fry concentrations in Shuswap Lake can travel for over 40 km in an easterly direction along the shore, with the band of fry often taking short cuts across deep bays that would otherwise divert them from continuing their movement up the lake. Such movements of large numbers of fish were considered to represent definite migrations, and thus were included in this examination of fry migrating behavior. Migration along the lakeshore was suspected to be related to at least one of the following phenomena; 1. location of lake entry and population density, 2. an acquired directional preference, or 3. an innate characteristic of the race.

In an attempt to disclose the nature of lake migrating behavior, two stocks were studied in the orientation testing apparatus (FIGURE 4) without the presence of stream current. The stocks chosen were Chilko, representing a population that displays a strong lakeshore migration, and Stellako, a population that shows more dispersed feeding movement. Native fry were examined in the field and experimental stock were tested at the laboratory. In each case 25 fry were taken from their holding compartments and placed in the screen chamber at the center of the apparatus exposed to a full horizon. When released, fry were free to choose any of the six radial arms projecting from the central compartment, and the number trapped in each arm was recorded. Unfortunately the testing apparatus did not provide the best measure of orientation. Generally the fry showed a definite first choice of one or two arms, but were often hesitant to enter the terminal traps and searched other arms. As a result many fry eventually trapped in arms other than those first selected, reducing the significance of the first choice.

### CHILKO STOCK

Chilko River flows north from Chilko Lake which is positioned on a general north-northwest by south-southeast axis (FIGURE 5). Thus as Chilko fry swim upstream toward the lake they move generally in a southerly direction. Exposure of the native migrating fry in the orientation testing apparatus indicated that native fry in both years tested showed stronger preference for a southerly direction (FIGURE 17-A, B). Analysis of variance showed a significant difference from random movement in both years ( $F \geq 6.58$ ,  $P < 0.005$ ) and Duncan's new multiple range test indicated that the mean preferred direction,  $155^\circ$  (i.e. southerly), among the six arms was significantly different than all others except  $215^\circ$  (southerly) in 1969.

Similarly, native fry transferred to the laboratory at Cultus Lake and held indoors except during tests continued to show a southerly preference (FIGURE 17-C). In these tests the apparatus was rotated  $30^\circ$  so that arms were intermediate in position to that used in field studies. The preferred arm,  $125^\circ$ , was significantly different from all others ( $F = 3.46$ ,  $P < 0.01$ ) except  $185^\circ$  and  $245^\circ$ .

## CHILKO NATIVE STOCKS

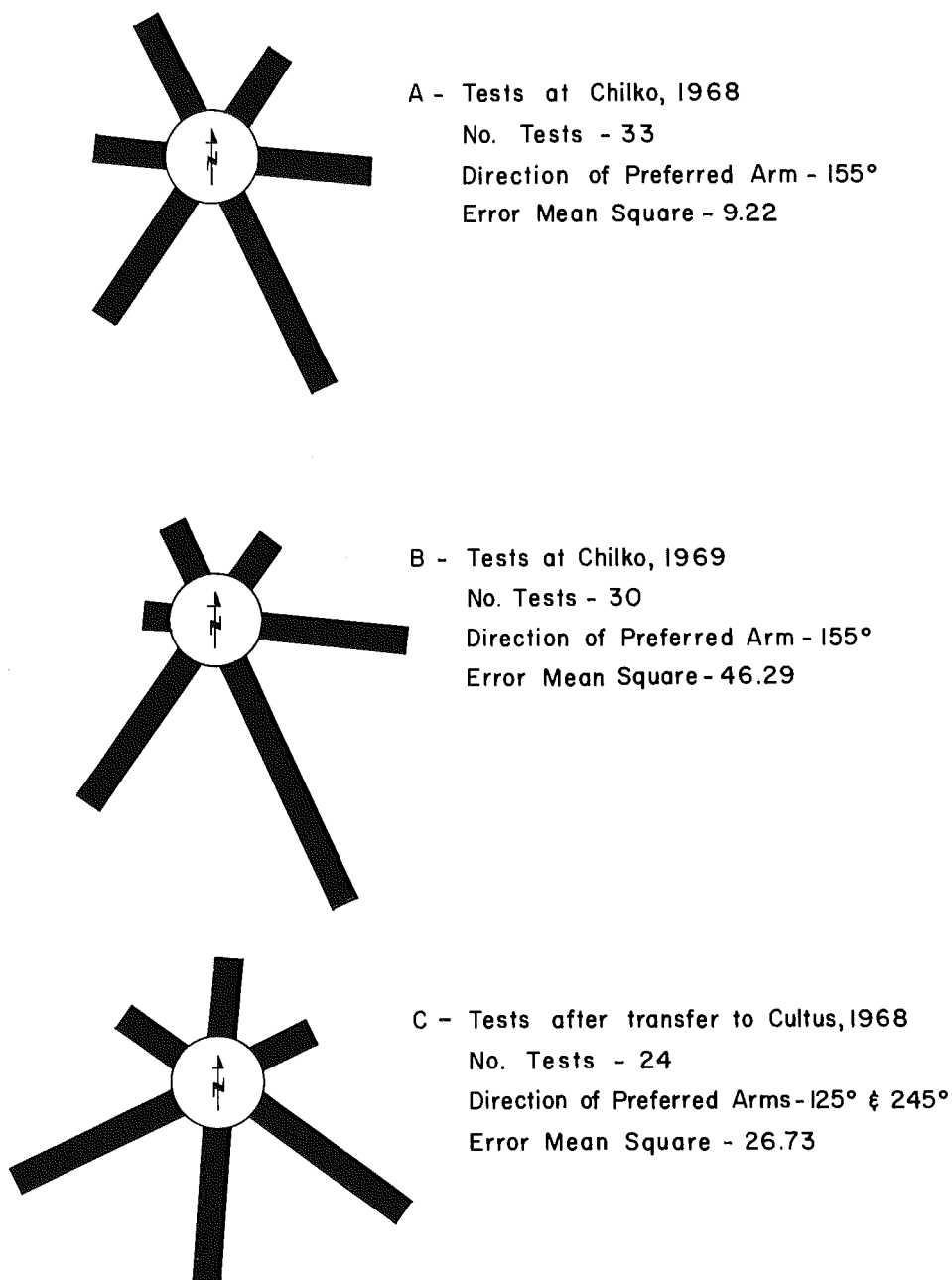
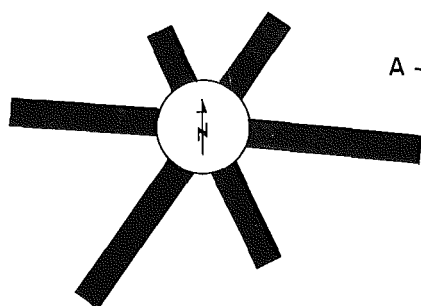


FIGURE 17—Orientation of native Chilko fry tested in apparatus without current (arm lengths indicate mean response from all tests).

## CHILKO EXPERIMENTAL STOCKS

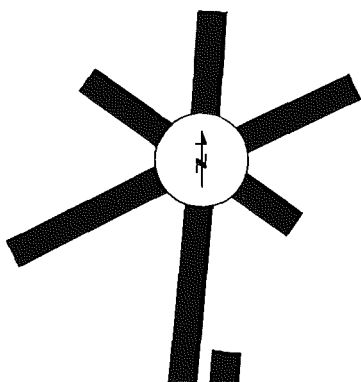


A - Tests at Cultus, 1969

No. Tests - 21

Direction of Preferred Arm -  $95^{\circ}$

Error Mean Square - 23.68

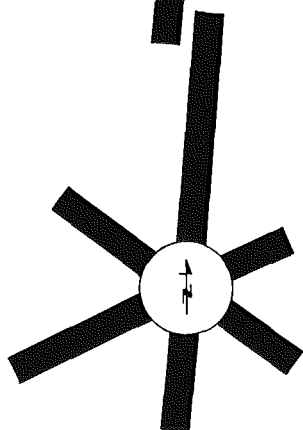


B - Tests at Cultus, 1971

No. Tests - 20

Direction of Preferred Arm -  $185^{\circ}$

Error Mean Square - 20.73



C - Tests at Cultus, 1971, on cloudy days

No. Tests - 11

Direction of Preferred Arm -  $5^{\circ}$

Error Mean Square - 16.23

FIGURE 18—Orientation of experimental stocks of Chilko fry tested in apparatus without current (arm lengths indicate mean response from all tests).

Experimental Chilko stock incubated indoors at the laboratory and tested under the same conditions to which the transferred stock were exposed showed weaker directional preferences than the native stocks ( $F = 2.08$  and  $2.10$ ,  $P > 0.05$ ), but maintained an orientation away from the north (FIGURE 18-A, B). In 1969, the number of fry moving into arms oriented to  $95^\circ$ ,  $215^\circ$  and  $275^\circ$  was significantly greater than the  $35^\circ$  arm, but in 1971, the number of fry in arms at  $185^\circ$  and  $245^\circ$  showed only a tendency for south or westerly preference without scores reaching significant levels.

On cloudy days with no visible reference to the sun, fry tended to show reversed orientation in the limited number of tests executed (FIGURE 18-C). In all daylight tests the fry moved as a school or divided in two groups and searched the apparatus separately. Most often the first arm chosen was the arm in which they were eventually trapped. However, trapping usually took several minutes, during which time the fry searched other arms. Generally the searching carried the fry directly opposite their first choice and back again before trying an adjacent arm. Once the fry persisted in one direction, they would enter the trap and frequently the whole school (25 fish) would follow the leader.

Trials attempted at night were unsuccessful in trapping fry. Observations during darkness were made without any light and were possible only because the grey floor of the apparatus provided contrast over which the fry silhouettes were visible. During late evening, when visibility was reduced for the human eye to the level of only shadow discrimination, the fry became disoriented and randomly distributed in the apparatus. Fry moved as individuals, often in circles, with little attention given to other fry, and many would remain nearly motionless, unresponsive to overhead movement.

The tests with Chilko fry indicated that this particular stock showed a general south-southeasterly directional preference or a northerly avoidance as native fry, and similar behavior as experimental stock. Thus the data showed that fry oriented to some phenomenon in the absence of current during daylight, that orientation corresponded to the migrating direction of fry in the river and the lake, and that the behavior pattern may be innate or acquired.

## STELLAKO STOCK

Stellako River flows northeasterly and enters Fraser Lake near its western end. The lake is positioned on a west-east axis, with the outlet flowing from the eastern end (FIGURE 6).

As fry emerge from Stellako River and migrate downstream during darkness, they can reach Fraser Lake within a single night from any part of the stream. Thus little opportunity would be available when fry could obtain visual information on direction of movement and hence acquire a directional preference from experience during migration. Furthermore, since Chilko fry showed no orientation behavior at night, darkness may prevent fry from acquiring experience at night.

In the 2 yr of study, field tests with native Stellako fry showed that this stock preferred a westerly or northwesterly direction, in the absence of current, completely contrary to the flow direction of the incubation stream (FIGURE 19-A, B). Analysis of variance showed behavior differed significantly from random

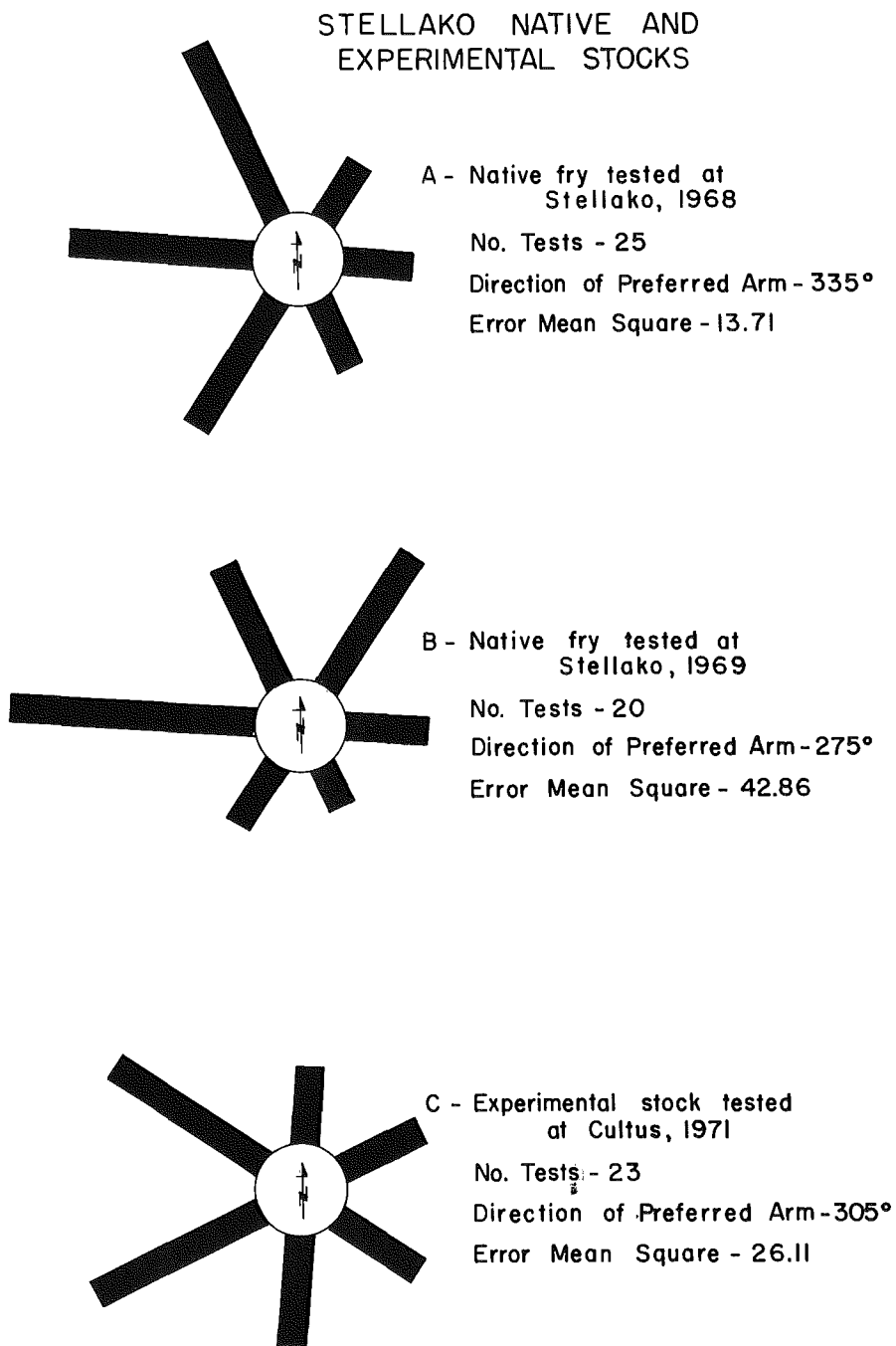


FIGURE 19—Orientation of native and experimental stocks of Stellako fry tested in apparatus without current (arm lengths indicate mean response from all tests).

distribution in both years ( $F \geq 3.07$ ,  $P < 0.05$ ), and Duncan's new multiple range test indicated that arms at either  $215^\circ$ ,  $275^\circ$  or  $335^\circ$  were preferred significantly more than the others.

Experimental Stellako stock incubated indoors at the laboratory was tested in only 1 yr, but analysis of variance applied to these tests still showed a significant difference between scores in arms oriented in different directions. A similar trend to that of native stock was evident, with a general preference for a northwesterly direction (FIGURE 19-C,  $F = 2.40$ ,  $P < 0.05$ ) and with arms at  $245^\circ$  and  $305^\circ$  significantly different from arms at  $5^\circ$  and  $65^\circ$ .

The northwesterly orientation of Stellako fry appears unlikely to be an acquired behavior pattern, since it does not correspond to any directional experience that the native fry are known to have had prior to reaching the lake. This suggestion, plus the fact that Chilko and Stellako stocks displayed different orientation, would suggest that the behavior is racially specific. And since Stellako fry do not show the lakeshore migration behavior displayed by Chilko fry, it appears that an innate pattern of uplake movement along the shore will not necessarily occur as observed at Chilko and Shuswap Lakes.

Furthermore, in Fraser Lake the direction apparently preferred by fry would carry them to some of the only shallow flats on the lake. And thus while the behavior pattern of Chilko fish would tend to provide good distribution in their system, at Stellako the westerly preference would concentrate the fry over shallows where warm temperatures, plentiful diptera larvae and protection by the grass covering the area make it potentially a good initial feeding location for the fry.

Another aspect of the directional tendencies of both stocks is that their preferred orientations are opposite to their respective lake outlets. An innate orientation pattern inducing avoidance of the outlet might function to assure against loss of fry from the system. However, this behavior hardly seems economical, nor as functional as aiding in the distribution of fry for more effective utilization of lake food resources.

## INTERPRETATION

Lake migrating patterns of sockeye fry prompted an examination of orientation without current stimuli, to determine if directional preferences were present. Examination of Chilko and Stellako fry indicated that directional patterns are present, racially specific, and perhaps innate. Functionally, it appears that such behavior assists in feeding distribution and, if so, orientation in the lake may change with time. Both Chilko and Stellako fry showed directional preference behavior, but the concentrated migration along the lakeshore found at Chilko Lake is not characteristic of Stellako fry in Fraser Lake. Thus if prolonged lakeshore migrations such as those observed at Chilko and at Shuswap involve innate directional phenomena, the manifestation of that pattern may be associated with other factors also.

## DISCUSSION

Migrations of the Pacific salmon involve a basic genetic phenomenon which has the capacity to incorporate environmental information or learned responses as directing factors. Craig (1918) recognized two components in instinctive behavior

which he identified as "appetitive behavior", or that which constitutes searching to satisfy an internal drive, and "consummatory action" or performance of that behavior which satisfies the drive. Fish migration has thus been classified as appetitive behavior (Hoar 1953), which provides a very useful concept for examining the various components of fry migration. Appetitive behavior assumes that the basis of the response is innate, and thus consists of a fixed behavior component and its associated directing factors (Baerends 1971).

In 1953, with his work on the control and timing of fish migration, Hoar established the foundation on which a most profitable continuing study could have been based. By comparative ethological analysis he was able to show distinct differences in appetitive behavior in *Oncorhynchus*, at the species level. Unfortunately, in studies on fry migration over the following decade or more, this lead was not pursued by others in the analysis of behavior differences within a species. Instead, it was assumed that such differences could be explained by the different environmental backgrounds confronting the fry, and the possibility of racial differences was not examined.

In the present study, racial behavioral patterns have been shown to exist, not as discrete as those between species, but still quite distinct between those populations that require different migratory behavior in order to reach their nursery areas. Thus, before looking at the mechanisms involved in migrating behavior, the nature of racial differences will first be examined and then the directing phenomena in migration clarified.

### Racial Differences

Racial differences in migratory behavior imply that different levels of expression of a motor pattern occur in response to common stimuli. If the nature of the display has a genetic basis, the motor pattern would continue to the completion of the action, and hence should not be subject to variation under a given set or level of stimuli. In this regard, it is proposed that genetic based differences in expression of motor patterns result in different directions of fry migration.

Genetic differences in sockeye fry migration were well established following the preliminary work in 1964 (Brannon 1967). Sockeye fry from populations that display very different behavior patterns in their natural environment, when isolated under controlled and identical incubation conditions in the laboratory, continued to display behavior patterns characteristic of the current response appropriate to reach their nursery lake in the native system. Moreover, hybrid stock, formed by reciprocal crosses of races showing opposite responses to current direction, displayed behavior intermediate to that of donor stocks. Genetic differences in migratory responses of sockeye were also verified by Raleigh (1967) using stocks from Karluk Lake, and later with part of the 1967 experimental stock from the studies in the present paper (Raleigh 1971).

In the present study, differences in current responses resulting from different degrees of expression of motor patterns were evident in the response of various stocks to water velocity. Chilko fry showed a very strong positive rheotaxis to current at the highest velocity tested. In contrast, Stellako fry showed strong

negative rheotaxis at high velocities, but in reduced currents their response could be reversed. Similarly, the Adams and Weaver races, which require a reversed response to current some time during migration to their nursery lake, changed their response to current at very low velocities. Response differences between stocks at a given velocity, and different responses of a single stock at different velocities, indicated that the genetic control of migrating behavior was exerted as velocity dependent motor activity, that levels of response indicated existence of a threshold, and that the threshold was racially specific.

Another racial characteristic noted in the several years of this study, as well as in other investigations (Mead and Woodall 1968), is timing of fry emergence relative to the amount of yolk reserve. Large yolk reserves in emerging fry are usually found in races undergoing longer migrations. In situations where fry migrate upstream, or for long distances along the lakeshore, they emerge with a measure of yolk material still remaining, as observed with Chilko and Adams stock (TABLE 9). The presence of food reserves among fry showing this migrating behavior is understandable since the fish are concentrated in narrow zones with relatively limited food supplies. Examining fry from upstream migrating races has shown that little feeding takes place en route to the lake, although fry are observed to strike at small materials or bubbles floating in the water, and even at dark specks on the surface of rocks. Comparatively, in this regard, a large quantity of yolk material in 7-Mile fry, moving downstream only a short distance, is a curious phenomenon. Sockeye fry have not been observed migrating along the shore of Pitt Lake, nor concentrating at the lake entrance, but the size of their yolk reserve suggests that a distribution migration may take place down the lake before feeding can sufficiently sustain them.

Weaver fry, which migrate 5 km up Harrison River to reach the nursery lake, emerge with very little yolk reserve. However, Weaver fry are not observed concentrated along the river bank or lakeshore during this migration: instead, their distribution pattern carries them over the whole river. Evidently the velocities are so slow that directed onshore movement is not required, and thus is not displayed. Since Weaver fry can disperse to obtain food and can move rapidly to the lake, racial adaptation to retain yolk reserves at emergence appears to have been unnecessary.

The racial characteristics that apply to sockeye fry migratory behavior, therefore, are the timing of emergence relative to the remaining yolk stores and the motor patterns displayed in response to water velocity. Differences in yolk reserves at the time of emergence among different races are believed to have evolved to compensate for differences in migration time between emergence and lake residence. The velocity threshold of each race is the result of its selective advantage under the circumstances dictated by the migration route.

Behavior patterns related to movement during residence in the nursery lake or to interlake migration could also be racially specific and perhaps innate, but information on this part of the rearing period was not available from the experimental design. Orientation during lake entrance was suggested to involve light. However, response to light as a racial characteristic could not be definitely isolated as an inherited response.



### Directing Factors

The racial behavior pattern in fry migration, considered as a genetically based response, is stimulated and subsequently directed by environmental factors which direct or regulate the expression of the motor responses. Some environmental factors may have indirect influences on the behavior which may be detected only in the intensity of response. However, other factors are cues which the fry integrate as information, perhaps from several sensory modalities, to direct the particular response pattern. In this study four environmental factors were examined that could act as directing phenomena for migratory behavior and each will be discussed briefly, based on the present study and other investigations.

### VELOCITY

The influence of velocity on the responsiveness of sockeye fry to current has received little previous attention. The present laboratory studies with experimental stock have shown that velocity is not only the basic environmental factor responsible for differences in migration direction between sockeye populations, but also a very important directing factor within a population. As velocity changes, it can reverse the rheotactic response of the fry. Even downstream migrating populations can be induced to reverse direction to current at very low velocities. Thus velocity is a phenomenon that directs movement to the lake, and secondarily acts to keep fry from exiting the lake basin.

Velocity, through its directing influence, has a major effect on the initiation and length of holding behavior of fry, and hence on the age and size of migrating fry. Holding behavior in Chilko River and Little Shuswap Lake is well known (Andrew and Geen 1960) and similar behavior has been described on the Upper Babine River (McCart 1967). Earlier observations of fry migrating from Little Shuswap Lake up Little River (Killick MS 1949) indicated that increased age or size was required for movement upstream, and holding behavior was induced until movement in higher velocities was possible. Keenleyside and Hoar (1954) showed that older sockeye fry responded more strongly to current than newly emerged fry, and it was suggested that such behavior in older sockeye fry could account for upstream movement (Hoar 1958). Thus it was generally accepted that holding behavior was an age or size related phenomenon through which upstream migrating characteristics were acquired.

The present laboratory studies of the influence of age or size on fry response to current, however, indicated that neither were causal mechanisms in current responsiveness. Response to current did not change with time when stocks were tested in the migration channel. Tests with Chilko experimental stock showed that upstream responsiveness occurred immediately upon emergence from prepared redds, or among alevins exposed to current 3 wk prior to emergence timing. Field observations at Chilko and Shuswap Lakes indicate that at both systems many fry move upstream shortly after emergence. In fact in Chilko River, fry reaching shore above the swift water show little evidence of holding, but are observed moving upstream to the lake long before fry carried below the swift water return. Moreover, the weights and lengths of emerging, holding, and migrating fry were

found to be identical at the onset of movement up Chilko River which suggests that newly emerged fry can begin migration immediately.

Similarly, at Shuswap Lake, Adams fry have been observed migrating upstream in the low velocities near the outlet of Shuswap Lake coincident with the emergence from Adams River. Examination of fry weight and length also shows that early in the season no difference exists between the fry emerging from Adams River and those migrating up Shuswap Lake.

The evidence from this study on current responsiveness as an immediate and directed behavior upon emergence appears contradictory to observations by other investigators until examined as a velocity dependent behavior. The question of whether or not fry hold is not relevant, but rather the fact that they hold is evidence of current responsiveness, the manifestation of which depends on the nature of the holding area.

At Chilko the size of river holding areas is limited and the opportunity for feeding is restricted. Thus movement upstream, particularly for a large population, cannot be delayed long. Moreover, the holding areas at Chilko show current patterns and thus even when holding, fry must show a level of positive rheotaxis to keep from moving downstream. Most of the holding fry are found at Canoe Cross (FIGURE 5) below the swift water, which suggests that the behavior is velocity dependent. With delay in this location some growth occurs and, as shown by Bams (1967), swimming performance will increase with increased size which would make subsequent migration easier.

At Shuswap, holding occurs primarily among those fry that are carried down Little River to Little Shuswap Lake. This lake is a suitable nursery area (FIGURE 7), and fry can remain there and feed with little difficulty, some rearing there the entire year.

Among these fry, migration up Little River coincides with emergence in some years. However, as discharge increases severely, movement of fry is usually delayed until more growth allows them to negotiate increased velocity, and thus timing of migration up Little River appears closely related to discharge. Similar to Chilko, holding behavior occurs among fry below the swift section of the migration route.

In contrast to Chilko and Adams stocks, Weaver fry show little evidence of holding. Weaver fry emerge from Weaver Creek and immediately show a negative rheotaxis which carries them to the slower velocity of Morris Slough (FIGURE 8). However upon entering reduced velocity conditions, no reversed current response is evoked. Fry are observed along the sides of the stream, but no large concentrations of fry are evident. The apparent reluctance of fry to hold in Morris Slough is attributed to the negative response of fry to a tributary water source. Negative rheotaxis would be the expected behavior in this slough fed largely by tributary streams.

As the fry move downstream, they reach Harrison River 5 km from the nursery lake. In this area, conditions exist where one might expect to find holding fry. The velocity is further reduced from that of Morris Slough and the fry change from negative to positive rheotaxis. However instead of concentrating along the shoreline of the river, they distribute themselves over much of the stream width. No large numbers of fry are seen in the area, and fry are found moving into Harrison Lake within 4 or 5 days after emerging from the incubation stream.

Although fry might be expected to hold or migrate along the shore of Harrison River, as they do in Chilko and Little Rivers, the different behavior in Harrison River can be explained by differences in stream gradient.

In addition to the attracting characteristic of lake water, Harrison River is generally a slow moving stream in this area above the rapids. Fry move upstream with no difficulty and thus apparently have no reason to hold along shore. The behavior pattern of Weaver fry, therefore, suggests that since velocities are not strong and holding does not occur, then holding behavior in other populations must be the result of higher velocities.

It is suggested that fry show holding behavior for two reasons. The first is that velocity creates a barrier. At Chilko, since the velocity threshold apparently is above the fry's sustained swimming ability, the barrier appears to be a physical one and can prevent movement upstream. At Little River, however, there is some evidence that migration upstream is inhibited by a behavioral barrier, imposed when discharge levels exceed the velocity threshold of the fry, apart from any physical barrier that may occur. Response to current in Adams River, the incubation stream, must be negatively rheotactic for fry to exit the system, and thus the velocity threshold is below that of a strictly upstream migrating population as was also apparent in the laboratory studies. If discharge in Little River is too great, the velocity threshold of the fry could inhibit their movement.

Further suggestion of a behavioral barrier is the size of fry migrating up Little River. Large size variability occurs among those leaving the holding area below Little River, which implies that movement upstream at high discharge levels is not only the result of swimming ability being facilitated by growth incurred through delay, but that with time, appetitive migrating behavior is probably increasingly stimulated which could raise the velocity threshold among old fry and hence by their movement induce smaller fry to join the migration.

The second reason for holding behavior is the influence of quiet water on the appetitive migrating behavior of fry. Once fry emerge from incubation and start a directed movement, if that movement takes them to an area of quiet water, a consummatory response may be evoked and the migration drive temporarily subdued. The locomotory activity patterns of newly emerged sockeye fry shown by Byrne (1971) could increase the tendency for holding to occur during the phase of suppressed activity.

## ODOR

Olfactory perception of stream odors has been shown to play an important role in the homing of salmonid fishes (White and Huntsman 1938; Hasler and Wisby 1951; Donaldson and Allen 1957; McCleave 1967; Groves et al. 1968; DeLacy et al. 1969). Little is known of the nature of the chemical cue except that the active component is volatile (Idler et al. 1961), and that it produces the greatest bulbar electroencephalographic response when from water of the home stream origin (Hara et al. 1965). Bulbar responses were also shown, however, when water from the freshwater migratory route was infused into the nostrils of adult salmon that had returned to their home stream (Oshima et al. 1969a).

The odor of the stream water acts not only as an attractant to returning spawners, but also evokes rejection behavior. General rejection of other streams has been shown by spawning pink salmon, *O. gorbuscha* (Helle 1966) and sockeye (Hartman and Raleigh 1964) when displaced from the stream of their first choice.

The results of the present study with sockeye fry indicated that olfaction also plays an important role in fry orientation. Fry responded to the olfactory cue in water sources, and water source affected their migratory behavior. Four important points were brought out in the study. First, incubating alevins can detect and show a preference for their incubation water regardless of its origin. Although olfaction is not suggested to have an orientation role at this stage of development, the response of alevins indicates that olfaction is functional and that odor can elicit behavioral responses long before emergence occurs. Furthermore, the alevins' preference for incubation water suggests that at least 3 wk before emergence appetitive behavior specifically for lake water is not displayed.

The second point was that alevins transferred between water sources for incubation showed by their intermediate responses that memory is involved. The alevins were able to associate water source with their initial incubation experience, 2 wk after transfer to the new source. It was further enlightening that the new water source had also been incorporated in their experience as an acceptable alternative to the original source, and thus, as part of the odor impression, elicited no particular rejection or preference behavior. The type of memory involved may be short-term, but it could be related to the imprinting phenomenon that occurs on home stream odor. Since sockeye adults home to their incubation stream, imprinting would have to occur during the incubation or emergence period, and histological studies showing development of olfactory epithelium indicate it could occur as early as hatching. However, the need for imprinting so early to satisfy homing requirements seems unnecessary, since it has been shown that less than 48-hr exposure of juvenile chinook salmon to a water source was sufficient to attract them as returning adults (Jensen and Duncan 1971). The point at which imprinting takes place is suspected to occur at or prior to emergence nevertheless, because transplants of sockeye eggs to the Upper Adams River, a barren stream in the Fraser River system, have induced adults to return to the location of the planting site (Internat. Pacific Salmon Fish. Comm. 1956).

The third point concerns the change in preference to a lake water source that took place at some time before emergence. As advanced migrating alevins or fry, definite appetitive behavior was shown for water of lake origin, regardless of the water source experienced during incubation. Thus an apparent preference exists for some odor associated with the lake water that acts as a general attractant to sockeye fry. Positive rheotaxis was elicited by the lake source, and depending on their incubation experience, negative or intermediate responses were evoked by tributary water. This information, when considered with the fact that positive rheotaxis was displayed by fry with olfactory occlusion, also suggests that the nature of the stream odor, rather than the absence of a particular olfactory stimulus, is responsible for evoking negatively rheotactic behavior.

The same preference for lake water was not shown at very low velocities. At Chilko, native fry were found holding in tributary water, but avoided the same

water when tested at the higher velocities experienced by migrating fish. Similarly, Stellako experimental stock showed no apparent preference for water source when tested in low velocities, but exposure to higher velocities evoked a lakewater preference which implies that responsiveness to odor is dependent on velocity feed-back information.

Although studies by McBride et al. (1964) showed no "cross-reaction" of sockeye smolts to water of another lake source, regardless of origin experimental stocks of fry exhibited a more positive response to tested lake sources. This suggests that responsiveness to lake water is particularly related to the fry phase of the life history when lake residence is sought. Fry responsiveness to lake water is further demonstrated by their preference for the lake source over the tributary source in which they were fed and reared for 90 days, since it has been shown that sockeye smolts can be conditioned to a water source by feeding (McBride et al. 1964).

Fourth, the behavior of fry exposed to diluted lake water shows that recognition of preferred natural water sources can be demonstrated at least at concentrations as low as 5%, which presents behavioral evidence that fry respond to dilutions below that demonstrated to evoke bulbar responses in adult coho salmon, *O. kisutch*, (Oshima et al. 1969b).

Olfaction as a directing factor, therefore, plays a very important role in sockeye fry behavior. Not only are fry able to choose between streams of lake and non-lake origin, but odor also appears to induce the particular rheotaxis when exposed to various velocity levels. Evidence that olfactory information is sought by migrating fry was shown in the searching or testing behavior of fry with occluded nares, and by the rapid change in behavior of normal fry after making a wrong choice in source.

## TEMPERATURE

The importance of temperature in the life of sockeye is unquestioned. It has caused a narrow temporal range in emergence to evolve which appears critical enough to have dictated adult migration and spawning time, and to have induced compensatory systems in development rate during incubation to assure correct emergence timing (Internat. Pacific Salmon Fish. Comm. 1971). Temperature has been shown to influence the onset of sockeye fry migration which usually is initiated around 3.5°C, and to markedly affect the intensity of fry migration upstream (Internat. Pacific Salmon Fish. Comm. unpublished).

Temperature has been proposed as the controlling factor in rainbow trout migration in Loon Lake and similarly considered as a possible control for trout migration in the upper Lardeau River (Northcote 1962). Temperature selection by rainbow fingerlings has shown that definite preferences are displayed for temperatures in the range of 17 to 20°C (McCauley and Pond 1971), which is in the range at which Northcote (1962) found recently emerged fry to show reduced movement downstream. Similarly, Brett (1967) showed that swimming performance of fingerling sockeye was greatest at 15°C which might imply, as suggested by Hoar (1958), that greater upstream movement could occur as spring temperatures increased.

Temperature as a directing phenomenon in sockeye fry migration, however, is problematical. Temperatures usually vary from 2.8 to 10.0°C during fry emergence in most locations and if orientation to current were to be influenced by temperature, evidence should be available from field studies. However, the only evidence forthcoming from field data indicates that reduced temperatures may retard emergence and increase holding behavior among early emerging fry. Experimental evidence from this study indicated that locomotory activity, and thus intensity of response to current, can be influenced by temperatures. This corresponds with data from Chilko River showing that once initiated, intensity of migration follows the general pattern of fluctuations in stream temperature (Roos MS 1962).

The mechanism causing reduced intensity of fry migration rests with the general response of poikilotherms to reduced temperatures in the range experienced by emerging fry (Hochachka and Somero 1971). Young sockeye may be thermally independent during brief burst speeds (Brett 1964), but optimum sustained performance is reduced with decreased temperature (Brett 1967).

On the other hand, the mechanism through which temperature would control orientation is uncertain. With regard to rainbow trout fry orientation, Northcote (1962) stated that "a simple increase in activity coincident with rise in temperature, in itself, will not necessarily explain upstream movement, for this increased activity must be oriented in a specific direction". Although Northcote (1969b) showed field evidence for temperature control of trout fry orientation to current, his experimental design involved both lake water and tributary water as sources for temperature control.

In the trout studies by Northcote (1969b), some changes in fry orientation were considered related to temperature differences of 4 to 6°C. This range of temperature occurs regularly at Chilko River during sockeye fry migration with no observed effects on the direction of migration. The alternative to upstream movement at Chilko is simply elimination. Downstream from the spawning area there exists no lake or suitable nursery area where fry could rear if temperature induced negative rheotaxis. Thus in view of temperature variability in sockeye incubation areas, temperature is not considered to be a factor directing orientation of migrating sockeye fry.

## LIGHT

Light, or visual stimulation, has been shown to have an important role in orientation of fish, recently reviewed by Hasler (1971). The influence of photoperiod on regulating the periodicity of sockeye fry emergence has been shown by Heard (1965) and Hartman et al. (1967), and light's inhibitory influence on fry migration activity has been discussed by Bams (1969). The photonegative behavior of sockeye has been reported to be strongest among the newly emerged fry and, with growth, the response to light becomes less intensive (Hoar 1954). In this respect, therefore, downstream migration of fry has generally been looked upon as passive displacement after dark as fry lost rheotactic responses (Hoar 1954; Ali 1959; Bams 1969; Byrne 1971).

Passive displacement suggests that in the absence of light the fry are inadvertently carried with the current once having been stimulated to leave the incubation

gravel. There are several observations that would refute such a hypothesis. Byrne's (1971) own work shows that fry are night-active during this emergence period, which appears contradictory to passiveness. Hartman et al. (1962) have described nocturnal fry movements as a migration in which individuals were headed downstream and usually actively swimming. Studies with stained fry at Weaver Creek showed that distribution of fry migrating downstream was not random (Internat. Pacific Salmon Fish. Comm. unpublished data), thus suggesting an oriented movement and a negative rheotaxis. If nocturnal migration of fry is a negative rheotaxis or "active" rather than passive displacement, then it represents appetitive behavior and can be termed a migration.

Similarly, upstream movement of fry has been considered to result partly from a change in phototaxis of older fry. In line with the idea of passive displacement, it was thought that movement must first occur downstream before fry gained the behavior pattern necessary for upstream movement. Once in the lake environment, fry behavior was considered to change from that believed characteristic of displacement, the fry schooled, became positively rheotactic and were able to sustain themselves in currents (Keenleyside and Hoar 1954). Therefore it was proposed that, with age, an increased size and swimming ability accompanied by the change in phototaxis might form the basis for an upstream migration (Hoar 1958). Recently, Byrne (1971) supported this hypothesis from his study on activity patterns of newly emerged fry. Locomotory activity periods changed about 10 days after emergence, from nocturnal to a day-active rhythm.

Timing of fry migrating behavior is undoubtedly regulated by photoperiod. Opposite to downstream photonegative behavior, upstream movement occurs primarily during daylight. Upstream migrations of sockeye fry are not uncommon, and have been reported in the Babine Lake system (McCart 1967) and Karluk Lake (Hartman et al. 1962), as well as in the Fraser River system. Although observed in several areas by various biologists, few examined the phenomenon as a behavior pattern distinct from that of downstream migrating populations.

Observations at Chilko during hours of darkness have indicated that fry can maintain themselves along the river bottom in moderate currents with no apparent difficulty. Furthermore, fry captured some time after emergence, stained, and released at night in mid-stream showed little evidence of having drifted downstream. Stained fry were observed in onshore areas adjacent to the release site the following morning (J. Roos personal communication). Observations during fry enumeration have also shown that movement upstream occasionally occurs during hours of darkness.

Laboratory tests conducted during darkness have shown that upstream responsiveness continues, regardless of light conditions, which indicates that rheotaxis is not eliminated when visual contact is lost, but persists by use of other sensory means. It appears, therefore, that if movement occurs downstream initially at emergence, it is not because of loss of orientation. Since Chilko fry showed strong positive rheotaxes in darkness when exposed to current in the migration channel, it is assumed that native Chilko stock will also show positive rheotaxis sufficiently strong at night to at least reach shore. Net movement may occur downstream because of high velocity, but unless a positive rheotaxis was shown by emerging fry,

there could be no explanation for the concentrations of fry observed in the shallows along the river bank adjacent to the incubation areas during the emergence period.

Therefore, during nocturnal emergence and subsequent movement downstream or to shore, fry appear to have an oriented rheotaxis using means other than visual stimuli. In commenting on orientation, Lowenstein (1957) suggests that during darkness tactile stimulation is the major rheotactic orientation mechanism in fish. Thus although emerging fry are photonegative, orientation in their natural stream environment may be possible through mechanoreceptors allowing directed movements without visual perception.

Since movement occurs upstream primarily during daylight hours, the behavior of newly emerged upstream migrating fry appears to change from a negative phototaxis almost immediately upon concentrating onshore. And the characteristic day-active period of upstream migrating fry would suggest that their locomotory rhythm pattern also undergoes a rapid change from that shown during emergence.

Once out of the stream velocities and within the relatively quiet waters of the lake, light is believed to supplant current as the primary orientation stimulus. Groot (1965) has shown evidence that both the sun and polarized light can be used in directed migrations of sockeye smolts from lake systems. Groot also presented evidence of landmark orientation, indicating the complexity of the visual orientation system of young sockeye.

Present studies with sockeye fry showed that directional orientation was displayed in the absence of current and under clear skies. Native fry from two populations showed different directional tendencies from one another that were consistent in two consecutive years of study. Laboratory studies on experimental stock incubated indoors and tested upon first exposure to a full horizon showed directional tendencies very similar to the behavior demonstrated by the respective native stocks. The basis of the orientation was uncertain. Innate or acquired directional responsiveness could be implied from the behavior. However, the nature of the cue was light-related. During darkness disorientation occurred, and fish were unresponsive to overhead movement and to other fish. On cloudy days the Chilko stock were tested and a reversed orientation was displayed which was attributed to poor visual stimuli. Reversed orientation has also been shown to occur frequently with sockeye smolts (Groot 1965).

Orientation to light in the absence of current may assist fry in dispersal from the lake entry point or in migration through a sequence of nursery lakes during freshwater residence to maximize use of food resources. In addition, the two populations studied exhibited orientation patterns in the opposite direction from the lake outlet, which along with velocity responsiveness, could reduce the possibility of their leaving the lake basin prematurely.

On the basis of laboratory studies and field observations, therefore, light has been shown to influence the diurnal timing of fry migration, and thus influences the intensity of migration. In the presence of water currents, light is not considered as a directing factor in fry movement. However, in the absence of current, light is viewed as a major directing phenomenon in fry orientation.



### Mechanisms Controlling Migration

Different behavior patterns have been shown to exist among racially distinct populations of sockeye fry. To explain the nature of fry migration, the behavior has been examined as a manifestation of different levels of expression within a common system, involving sensory input and motor responses, rather than the result of different systems functioning for separate races. Since environmental factors are usually components used as evoking cues, the distinctions between "genetic", "acquired", and "environmental" influences tend to merge. In discussing the mechanisms controlling fry migration, therefore, an attempt will be made to show their relationships by considering migratory behavior to be an integrated system made up of fixed patterns and directing phenomena, under the influence of a strong appetitiveness or internal readiness of the fry to perform migration over all other forms of behavior at that phase of their life history.

Baerends (1971) points out that appetitive behavior does not necessarily lead directly to the consummatory action, but might proceed through a hierarchy of appetitive behavior to the ultimate completion of the act. Thus when a sequence exists, each subsequent state in motivation supplants its forerunner. The sequence of behavior during fry migration has been presented as an ethogram in FIGURE 20 to depict the interrelationship of events that occurs, and the factors that direct migratory behavior.

The sequence in appetitive migrating behavior starts with the change in fry disposition, from an incubation oriented state to a migratory state. The basis of the change is unknown, but temperature has both a long-range control of the timing of the event and an immediate inhibitory or stimulatory influence. A genetic component appears to be present on the racial level that influences the timing of the event as well, since variability in the yolk reserves of emerging fry occur among different populations.

During the transition in motivation, a major change in the appetitive behavior is olfactory. An odor component enters the repertoire and the species becomes lake water oriented. A taxis component also enters the motivational state and the species becomes positively rheotactic. Sockeye fry are generally positively rheotactic (Hoar 1954), and even prior to emergence they show positive rheotaxis in preparing to exit their incubation environment (Bams 1969; Goodlad and Brannon MS 1972).

Upon initiation of the appetitive behavior the first transition in the sequence appears at emergence, and the transition is racially specific. Stream velocity, the cue which evokes different responses in different races, stimulates the appetitive behavior transition as the fry leave the incubation substrate. In downstream moving populations the transition is from positive rheotaxis in the gravel to negative rheotaxis in the stream or an active displacement elicited by the velocity threshold of the race, which is genetically based. Such transition is characteristic of Stellako and 7-Mile stocks.

Stellako fry tested in the migration channel indicated that reverse orientation in posture was a regular phenomenon as fry slipped and swam downstream. Frequent brief reversal of orientation is likely characteristic of downstream migrating fry and it may represent successive transitions in appetitive behavior that

might be mistakenly interpreted as random movement. As fry head downstream the velocity threshold is the directing element in orientation to current. In swimming with the current in the absence of light, the relative velocity experienced by fry would be reduced, which may encourage them to show a positive orientation in posture, or "velocity testing" behavior, as they migrate.

In populations such as Adams and Weaver where reversed direction of migration occurs, fry move downstream in high velocities, but the velocity threshold eliciting upstream response is above that of strictly downstream moving populations. Upon emergence, negative rheotaxis is elicited by high stream velocity. However, when the stream enters areas of reduced velocity the next transition in appetitive behavior appears. Fry show positive rheotaxis, which will either tend to place them next to shore in quieter water if mid-stream velocities are relatively strong, such as above Little River at Shuswap Lake, or allow some fry to continue upstream during darkness if velocities are slow, as in Harrison River above the entrance of Morris Slough. Populations such as Weaver fry, moving from a tributary stream to a lake-fed stream, would undergo another transition increasing appetitive behavior since the odor characteristic of lake water would then act as a further inducement for upstream movement.

In upstream migrating populations, because of a very high velocity threshold, emergence into the stream velocity evokes a strong positive rheotaxis which tends to carry fry to the low velocities next to shore and places them in a position to ascend the stream. Where velocities are strong the same motivation maintains the fry in holding position along shore until movement upstream can occur. In areas where velocities along shore are only moderately strong, as in the uppermost section of Chilko River or Little River, an immediate daylight migration results from their positive responsiveness to current.

In upstream migrating populations, another transition in appetitive behavior occurs regarding light; fry become photopositive and movement during daylight is initiated. Where velocities require visual navigation, daylight migration occurs almost entirely, and even where velocities are low, such as the Harrison River, nocturnal migration appears limited.

In Chilko River, many of the holding areas where newly emerged fry await daylight contain slow currents which require the holding fry to maintain positive rheotaxis. In other locations, however, and especially in Little Shuswap Lake, holding areas are in quiet water and when fry reach such areas motor activity is reduced from absence of current, and holding may become consummatory action, temporarily arresting the appetitive migrating behavior. Even among downstream migrating populations holding can occur if movement carries the fish into quiet areas along the stream where negative rheotaxis can be compromised. The migrating drive is strongly motivated, however, and holding in areas typically unlike the lake environment apparently only delays rather than terminates the appetitive behavior.

It is suggested that lakeshore migrations are mainly characteristic of those populations showing strong positive rheotaxis adjacent to shore in upstream movements and are prolonged extensions of the appetitive behavior that has associated the fry with the river bank as they migrated to the lake. The directional

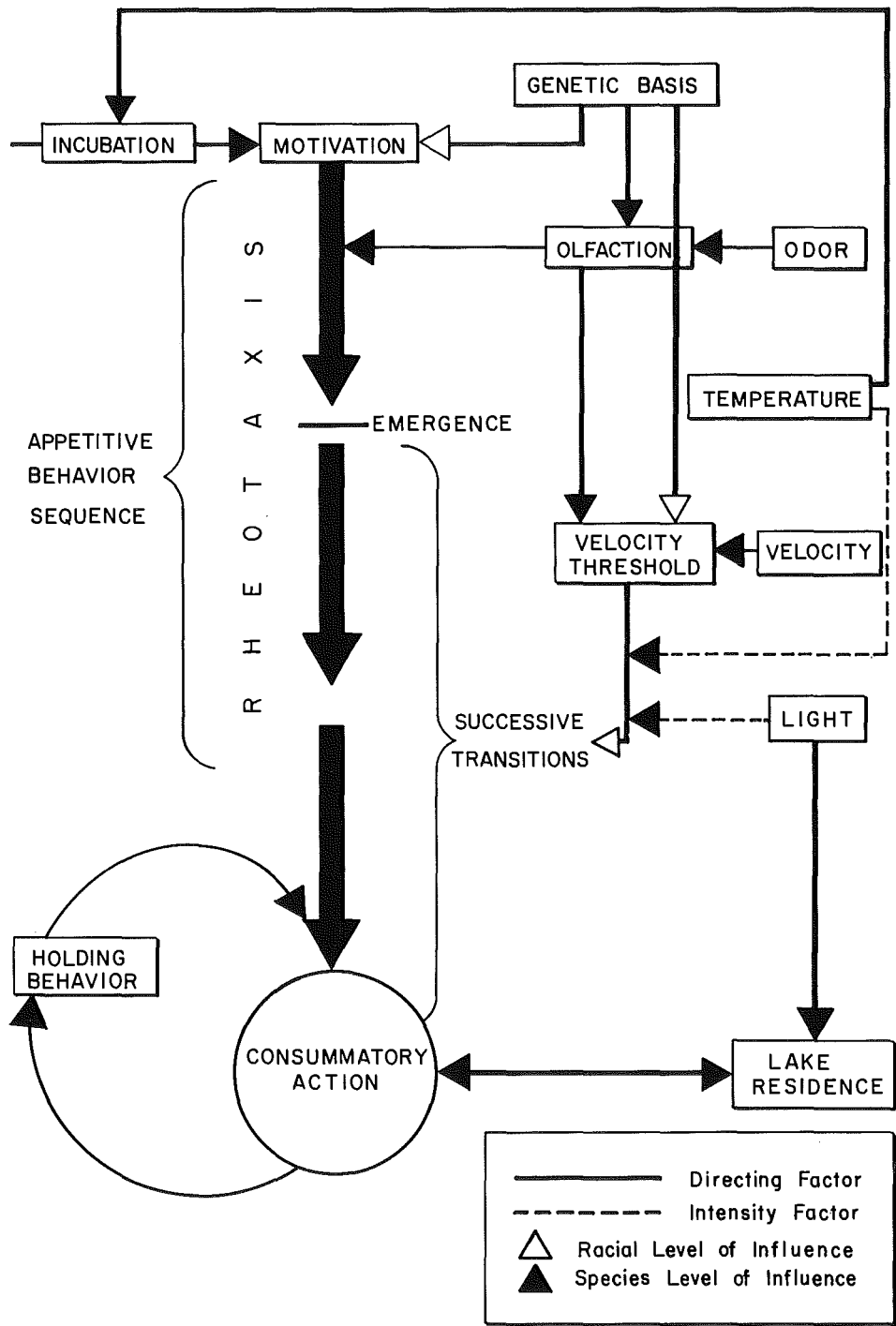


FIGURE 20—Ethogram showing the behavioral sequence during fry migration and the factors directing the behavior.

orientation of fry in the lake, innate or acquired, when combined with a strong migrating drive, appears to manifest itself as a lengthy migration along the lakeshore. In contrast, observations suggest that downstream migrating populations, which display much less intense lakeshore movement, may also show directional orientation, but travel through the limnetic areas predominately.

Regardless of the responsiveness of fry to current and even when migration has consisted only of emergence from lake incubation sites, once in the lake environment the appetitive migrating behavior wanes and terminates with the consummatory action, most probably related to the motor responses in a no current situation. When this has occurred light supplants current as the orientation phenomenon and pelagic residence begins.

It is concluded from this study that mechanisms controlling sockeye fry migration are genetically based, and involve racially specific velocity response patterns, with olfactory stimulation having a directing influence on rheotactic behavior. In the presence of current, light and temperature influence only timing and intensity of responsiveness. Once sockeye fry enter the lake environment, in the absence of current, light appears to become the major phenomenon directing orientation.

### **Implications on Resource Development**

The sockeye rehabilitation program on the Fraser River has been established on the premise that careful assessment must be given to the genetic or racial characteristics of natural populations, and that in initiating runs to barren areas the characteristics of the introduced stock must be appropriate for the receiving environment. The basic concept relates to the fitness of a fish for its particular habitat which must ultimately be measured only in the rate of return of the next generation. Fitness embodies an environmental component, including acquired characteristics, and a genetic component that provides the background on which selection works. An operation that changes the environment or displaces a particular genetic background to a different environment, therefore, can affect survival of the fish involved. Factors such as migration distance of returning fish, time of spawning and incubation temperatures have been considered as critical events to complement in current rehabilitation programs. The study on sockeye fry migration has shown this behavior as another critical event. Both environmental and genetic factors control fry migratory behavior, and thus operations which cause a change in either can be expected to reduce survival.

For rehabilitation programs, therefore, not all races are equally suitable donor stock for initiating new runs. A population with strong negatively rheotactic fry behavior, for example, would be a poor source from which to rehabilitate a lake outlet stream. Innate behavior patterns in rheotaxis or orientation are critical factors which could be decisive in the success or failure of stock introduction.

Changes in the environment of native populations can have an equally significant impact. Any installation in the path of upstream migrating fry that causes the water velocity to exceed the velocity threshold of the fry will effectively create a barrier to upstream movement and reduce survival. Similarly, downstream migration can be inhibited or even halted if impoundments on the migratory route

sufficiently reduce velocity to evoke positive rheotactic behavior and induce residence. Knowledge of the velocity responsiveness of a race, however, will also allow the design of facilities to enhance fry passage in streams that have areas of difficulty for migrating fry.

In addition to discrete racial characteristics in the behavior of fry, consideration must also be given to behavioral attributes of the species. Olfactory sensitivity of alevins and fry, and their response to water source, suggest that a change in water chemistry affecting olfactory cues could result in disorientation and loss of fry. The role of olfaction in the behavior of fry, and the influence of changes in water chemistry on imprinting or subsequent homing of adults is not understood. The value of such information, however, is apparent and points to the need for continuing examination of sockeye biology for effective protection and development of the resource.

## SUMMARY

1. Migratory behavior of sockeye salmon fry from six different areas in the Fraser River watershed was studied by field observations, and field and laboratory experiments, over a period of 8 years.
2. Distinctly different migratory behavior patterns were exhibited by the six sockeye fry populations in the natural environment.
3. When tested in an experimental channel, the responses of native fry to the direction of water current were shown to be racially distinct and corresponded to the response pattern that the respective native fry displayed during migration to the nursery lake.
4. A strong genetic component was displayed in responses to current by laboratory stocks incubated under controlled conditions. Stocks maintained distinctly different behavior patterns which corresponded to the responses of the respective native stock. Hybrid fry from reciprocal crosses showed responses intermediate to those of the parental stocks.
5. In laboratory studies and field observations the size of fry at emergence was not shown to be a causal mechanism directing orientation to current.
6. Similarly, age was shown to have no directing influence on orientation to current. Fry and fingerlings continued to show the same level of responsiveness to current as that first displayed by alevins of the same race.
7. Responsiveness to current was shown to be dependent on velocity, and racially specific responses were interpreted as evidence that velocity thresholds existed above which negative rheotaxis was elicited. Current responsiveness was considered to be directed active movement upstream or downstream, and thus qualified as a directed migration.
8. Temperature and light were shown to influence intensity of response, but in the presence of current were not directing factors. In laboratory studies migratory behavior was displayed regardless of temperature and light conditions.
9. Histological examination of the olfactory capsule of sockeye embryos and alevins showed that the sensory epithelium was well developed at these stages. Sockeye fry were shown to detect differences between water sources by olfactory stimulation, and to show a decided preference for lake water. With olfaction denied fry displayed random behavior and no preference. Diluted lake water elicited a preference at concentrations as low as 5%.
10. Odor was shown to act as a directing factor in rheotactic behavior and experience during incubation altered the behavior. Water source preference was also altered by incubation experience and memory was implicated.
11. Three weeks before emergence timing alevins preferred their incubation water source. At emergence a decided preference was shown for lake water, suggesting that a universal preference for lake water exists in the species during the fry migration period.

12. In the absence of current, an innate or acquired directional preference was displayed by sockeye fry. Directional orientation differed between the two races studied and was considered related to a distribution pattern followed by each race during initial lake residence.
13. In the absence of current in the lake environment, light appears to be a major orientation phenomenon for distribution migrations of fry.
14. Fry migration is proposed as a genetically based behavior pattern, directed by racially specific velocity responses with rheotaxis influenced by olfactory stimulation.
15. Fry migration is described as a racial behavior pattern controlled by directing factors, and is manifested by a strong appetitive behavior toward the consummatory activity associated with lake residence.
16. Migratory behavior of sockeye fry is a factor that must be given consideration in proposals to rehabilitate barren areas, and in the assessment of changes in the aquatic environment.

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