

INTERNATIONAL PACIFIC SALMON
FISHERIES COMMISSION

PROGRESS REPORT

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ABSTRACT

Genetic control of migrating behavior in response to current was investigated in newly emerged sockeye salmon fry. Fertilized eggs from three races, representing stocks from outlet streams, inlet streams and lake incubation areas of the Fraser River system, were hatchery incubated under controlled conditions very different from their natural environments. The resulting alevins and fry were tested to determine their preferred direction of migration, and each race responded to current with the same behavior pattern exhibited in its natural environment. Although the innate response to current was not influenced by age of the fry or by temperature, the source of water (lake or creek) was shown to have a marked effect on the response of certain races. The implications of a genetic control of fry migrating behavior are discussed with regard to fisheries management.

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GENETIC CONTROL OF MIGRATING BEHAVIOR OF
NEWLY EMERGED SOCKEYE SALMON FRY

INTRODUCTION

Migrating behavior is a perplexing characteristic of the Pacific salmon, genus Oncorhynchus. Perhaps the most complex migration pattern of the five species represented on the Pacific Coast is found among the sockeye salmon, Oncorhynchus nerka. The adults are able to course through many hundreds of miles of ocean, rivers and lakes, returning to their place of origin each summer and fall to spawn and eventually die. The following spring, the resulting fry enter the lake nursery area shortly after emergence from the gravel and take up pelagic residence for at least a year before migrating to the sea as smolts. Since incubation areas are usually in lake tributary streams, one would expect the lakeward movement of newly emerged fry to occur somewhat passively downstream. Hoar (1954), in discussing the behavior of juvenile Pacific salmon, concluded that the behavior of sockeye fry upon emergence favored a displacement downstream. However, certain races of adult sockeye returning to the Fraser River system are known to spawn below their nursery area (Andrew and Geen, 1960), thus requiring the subsequent fry to make an upstream migration.

Upstream movement of newly emerged fry certainly indicates a directed migration and raises the question as to what evokes the upstream response. One might suggest that such behavior results from one of three alternatives. Firstly, migration upstream could result from a change in behavior with the age of the fry; secondly, various environmental factors might influence migrating behavior; and thirdly, an inherited response to certain stimuli could be responsible.

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 acquired the capacity for an upstream migration. Fry migration in Little River, the outlet of Shuswap Lake, appears to fit this type of behavior pattern. Fry emerging in Little River move two miles downstream to Little Shuswap Lake, remaining there nearly a month before returning upstream to enter Shuswap Lake for the rest of their freshwater residence (Killick, MS).

The direction of fry movement with respect to current has also been attributed to environmental factors. Northcote (1962) found that migration of juvenile trout (Salmo gairdnerii) into Loon Lake from outlet and inlet streams resulted from differences in water temperature between streams. Length of day was also shown to be an influencing factor.

On the other hand, genetic differences have rarely been given serious consideration as the basis for upstream or downstream fry migration within a given species. Genetics, however, determines many behavioral characteristics in fish as described by Baerends (1957). At Babine Lake, the directional preference among migrating sockeye smolts in locating the lake exit was found to be the result of an inherited direction-finding ability. Babine Lake is a complex system utilized by several spawning runs, the offspring of which remain in separate areas of the lake during pre-smolt residence (Johnson, 1956). As smolts, each "apparently distinct stock" exits the lake by an innate ability to traverse its own particular route to the lake outlet (Johnson and Groot, 1963). Thus it is not unreasonable that genetic differences may also be responsible for different patterns of migrating behavior among newly emerged sockeye fry.

In 1962, 1964 and 1965, preliminary studies led to development of 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. This paper presents data from a study relevant to this hypothesis and examines environmental stimuli thought to evoke upstream movement.

MIGRATING BEHAVIOR OF SOCKEYE FRY

The study of genetic control of fry migrating behavior has made it necessary to examine races¹ with different behavior patterns. Of the many races of sockeye raised in the Fraser River system, several are confronted with unique relationships between their incubation areas and lake nursery

¹In this paper, "race" refers to a specific population isolated by time or space from other populations of the species. "Stock" is used to designate the source from which a particular group of test animals originated.

areas. In most cases, emerging fry seemingly need only to move with the current of the incubation stream to reach the lake below. In other instances, however, certain races spawn below the nursery area and fry must move upstream from the incubation site or negotiate a complex of streams. Perhaps of least significance in the Fraser system is beach spawning, where fry need only emerge to enter the lake. The three races chosen for this study were obtained from Chilko River, Stellako River and Cultus Lake (FIGURE 1), since each typifies one of the above-mentioned behavior patterns characteristic of newly emerged fry. A brief description of fry behavior in each race and the conditions experienced during natural migration are presented here as a basis for comparison with experimental results. Much of the information used in describing this portion of sockeye life history has been obtained from the extensive data collected by the International Pacific Salmon Fisheries Commission,

Chilko River Race

The main incubation area of the Chilko race covers about 3.7 miles of river immediately below Chilko Lake. Emergence occurs at night and the current sweeps the fry some distance downstream until they reach shore or lower velocities. Observations have shown that large numbers of newly emerged fry are carried downstream to a wide area of low velocity in the river just below the incubation area. Upon reaching the low velocities of this area the fry form large schools before commencing upstream migration.

The beginning of emergence precedes upstream migration by about 10 days, but as migration continues it is possible that many newly emerged fry are recruited into the migration shortly after leaving the gravel. Movement upstream usually begins when temperatures reach 38°F during the latter part of April and continues into June at temperatures as high as 48° to 50°F. Upstream migration occurs almost entirely during daylight hours which is the opposite of the negatively phototactic behavior during emergence.

The fry move upstream in a thin but almost continuous band within one to four feet from shore. In many places, rocks along the river bank form many small passages where the fish avoid higher velocities. In other

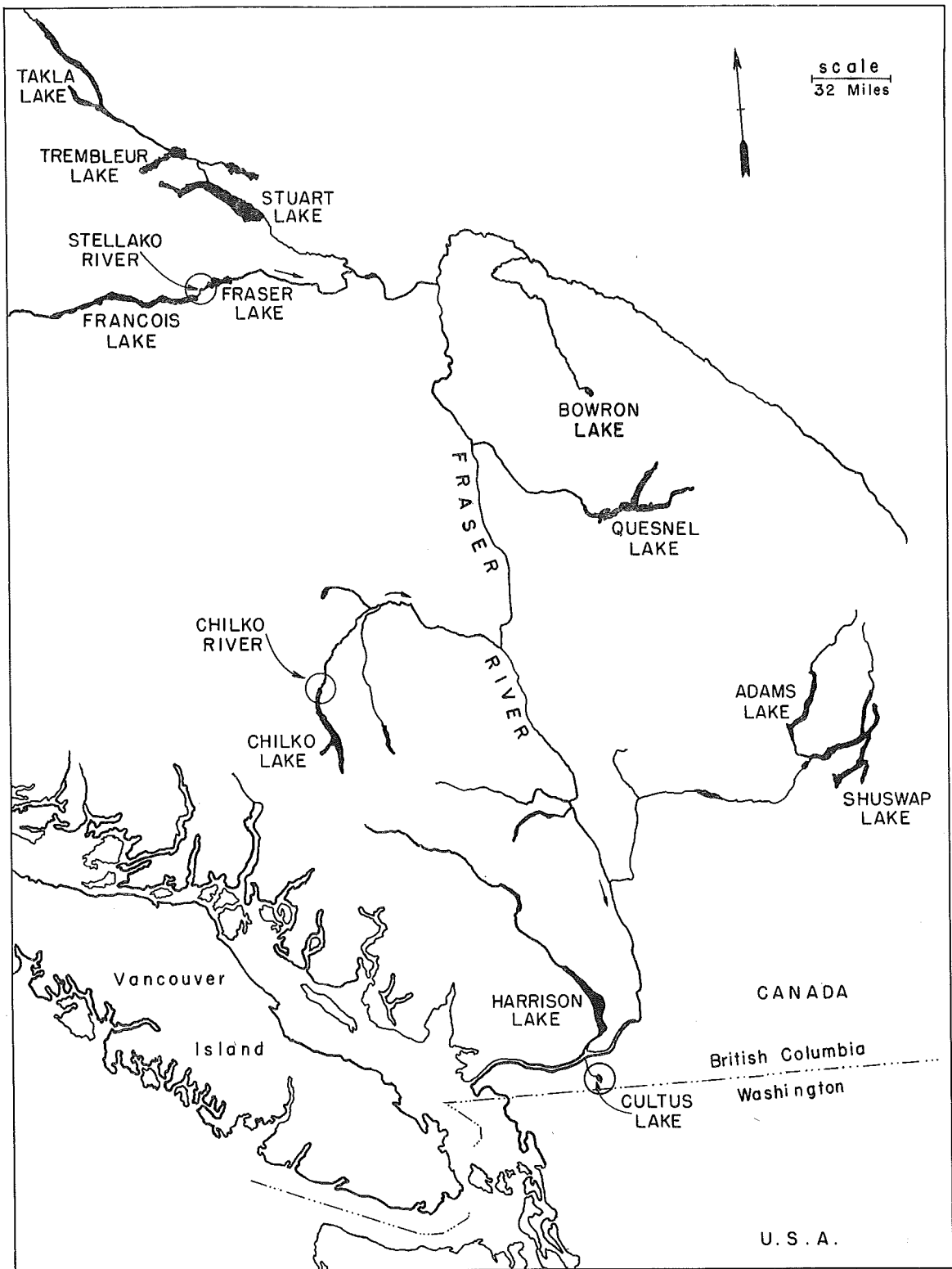


FIGURE 1 - Fraser River watershed showing the incubation and nursery areas of Stellako, Chilko and Cultus sockeye salmon.

places, the fry are exposed to faster water but appear to detect the lowest velocity available, moving along the face of rocks, next to the bottom, or within an inch of the shoreline. Frequently, fry are observed holding or resting between rocks or in larger areas of low velocity along the migratory route.

Fry have been observed as far as 10 miles below Chilko Lake which makes their return and subsequent survival questionable, although schools moving upstream have been observed as far as five miles below the lake. An indication that some fish continue downstream and are lost is apparent from the capture of fry 79 miles below the spawning area.

Stellako River Race

Stellako River, flowing seven miles from Francois Lake to Fraser Lake, 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 smolts from another race reared in that area, 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 one mile below the lake and a small falls occurs 3.5 miles further 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. If upstream tendencies are present among these fry, there has been very limited evidence of such behavior from field observations. No accumulation of fry has ever been observed below the falls or rapids to suggest an attempted upstream migration. Similarly, fry traps located at the rapids have not captured fry moving upstream and those placed just below the outlet of Francois Lake have caught only small numbers.

Further evidence of predominantly downstream migration is provided by freshwater circuli counts from scales of Stellako spawners. Circuli counts of Stellako fish form a unimodal distribution normally averaging 3.0 circuli less than counts from fish of the Nadina race reared in Francois Lake, indicating that few Stellako fry are reared in the larger lake.

Fry emergence in Stellako River begins in mid-April at temperatures near 38°F and continues through the first part of June in temperatures ranging from 44° to 48°F. 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 two weeks prior to entering the nursery lake, but this number is confined to a small portion of the population.

Cultus Lake Race

In Cultus Lake, the sockeye spawning grounds are, for the most part, confined to the southern end of the lake. The incubation area is a weathered shale alluvial beach extending 200 ft from shore and subsequently dropping rapidly into deep water. Spring water percolates through much of the beach at a near constant temperature of 46.5°F year round. 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 20 ft indicate that fry swim close to the bottom as they leave the beach area. The depth to which some newly emerged fry swim in Cultus Lake is also shown by the small numbers drawn into the pipeline supplying Sweltzer Creek Field Station from a depth of 120 ft.

The reluctance of fry to remain near the incubation area may be due to the abundance of predator fish, of which sculpins, Cottus asper, are by far the most numerous. 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.

MATERIALS AND METHODS

Eggs were obtained from the Chilko, Stellako and Cultus races, artificially fertilized, and hatchery incubated until the subsequent fry were tested in an apparatus to determine direction of migration in relation to current. To further elucidate the genetic influence on fry behavior, fish from the Chilko and Stellako races were crossed and the progeny were tested. The four stocks of fry were examined primarily for their response to current, but some data were obtained on the effect of temperature and water source on that response.

Comparisons of the four test stocks involved terms describing various stages of advancement of fish during the study. In this paper, "alevin" refers to that stage between hatching and complete yolk absorption, and "fry" refers to the post-absorption period. However, when reference is made to emergence and migration of wild fry populations, the terminology is less precise and no attempt has been made to differentiate between alevins and fry. Although some of the migrating fish still contained yolk material in the abdominal cavity, all fish once emerged in nature have been classified as fry.

Experimental Stocks

Eggs were obtained from spawners at Stellako and Chilko Rivers on September 28 and from Cultus Lake spawners on November 24, 1966. At each location, eggs removed from 25 females were fertilized with 15 males to provide a total of approximately 10,000 eggs from each race. Since spawning times coincided at Stellako and Chilko, five females and five males from Stellako River were killed, packed in moss and ice, and flown to Chilko River to cross with the Chilko race. Because of the flight duration, however, the Stellako males proved infertile and only the reciprocal cross was successful. All eggs were fertilized, water-hardened, placed in insulated quart jars, and then transported to the Sweltzer Creek Field Station near Cultus Lake for incubation.

The eggs and subsequent alevins were incubated in darkness in plastic-screened, wood-framed trays (11 in. by 24 in.) 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 (12 in. by 72 in.) where they were fed Cultus Lake zooplankton, supplemented with a dry diet.²

The water used for incubation was obtained from Cultus Lake. Temperatures dropped from 47° to 42°F during the 16-week incubation period (September 29 to January 17) of Stellako, Chilko and hybrid stocks and remained at 42°F throughout the testing period. Incubation of the Cultus stock extended from November 24 to April 17, during which time temperatures dropped from 46° to 42°F.

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 material from 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.

Chilko, Stellako and hybrid stocks were exposed to the same temperatures during incubation, thus allowing comparisons of size, number of temperature units to yolk absorption, and the stage of advancement at which migrating behavior began. Measurements indicated that Chilko eggs, fry, and parent females were the largest studied (TABLE 1). At yolk absorption, Chilko fry were significantly larger ($P < .001$) than Stellako fry and experienced more efficient yolk conversion (60 per cent compared with 56.7 per cent), as determined by weight of fish produced compared with weight of eggs at fertilization.

²The dry diet, based on the Abernathy all-meal salmon diet (Fowler, McCormick and Thomas, 1964), was composed of salmon carcass meal, dried skim milk, cottonseed meal, wheat germ meal, carboxymethylcellulose, vitamins and soybean oil.

Chilko fry required 150 more temperature units (Fahrenheit degree-days) after fertilization to complete yolk absorption than Stellako fry. However, Chilko fish started migrating at 1,580 temperature units with considerably more yolk than the other stocks (FIGURE 2). The Chilko-Stellako hybrids, while having the same yolk weight as Stellako eggs at fertilization, required 75 more temperature units to reach yolk absorption and weighed slightly less on reaching the fry stage.

Because of the later spawning date, the Cultus Lake stock was exposed to different temperatures during incubation and thus growth could not be compared with the other stocks. However, it should be noted that Cultus were the smallest eggs and fry to be tested (TABLE 1).

TABLE 1 - Measurement of experimental stocks and accumulated temperature units (TU) to onset of migrating behavior and yolk absorption.

STOCK	PARENT ♀ FORK LENGTH cm	DRY WEIGHT		FIRST TEST SHOWING MIGRATING BEHAVIOR		TU TO YOLK ABSORPTION
		Eggs mg	Fry mg	Date	TU	
Chilko	59.6	40.0	24.0	Jan. 21	1,580	1,900
Hybrid	59.2	34.9	18.0*	Jan. 25	1,620	1,825*
Stellako	58.8	34.9	19.8	Jan. 17	1,540	1,750
Cultus	58.2	34.7	17.6	Apr. 17	1,625	1,725

*Estimated from FIGURE 2.

Throughout the study the fish appeared in excellent condition; no mortality occurred and growth was good. On March 14, near the end of the 60-day test period, the weights of Chilko, hybrid and Stellako stocks averaged 34 mg, 31 mg and 36 mg, with fork lengths of 31.1 mm, 29.9 mm and 31.1 mm, respectively. Cultus fry were tested for only 30 days, and at the termination of the study weighed 25 mg and were 28.6 mm long.

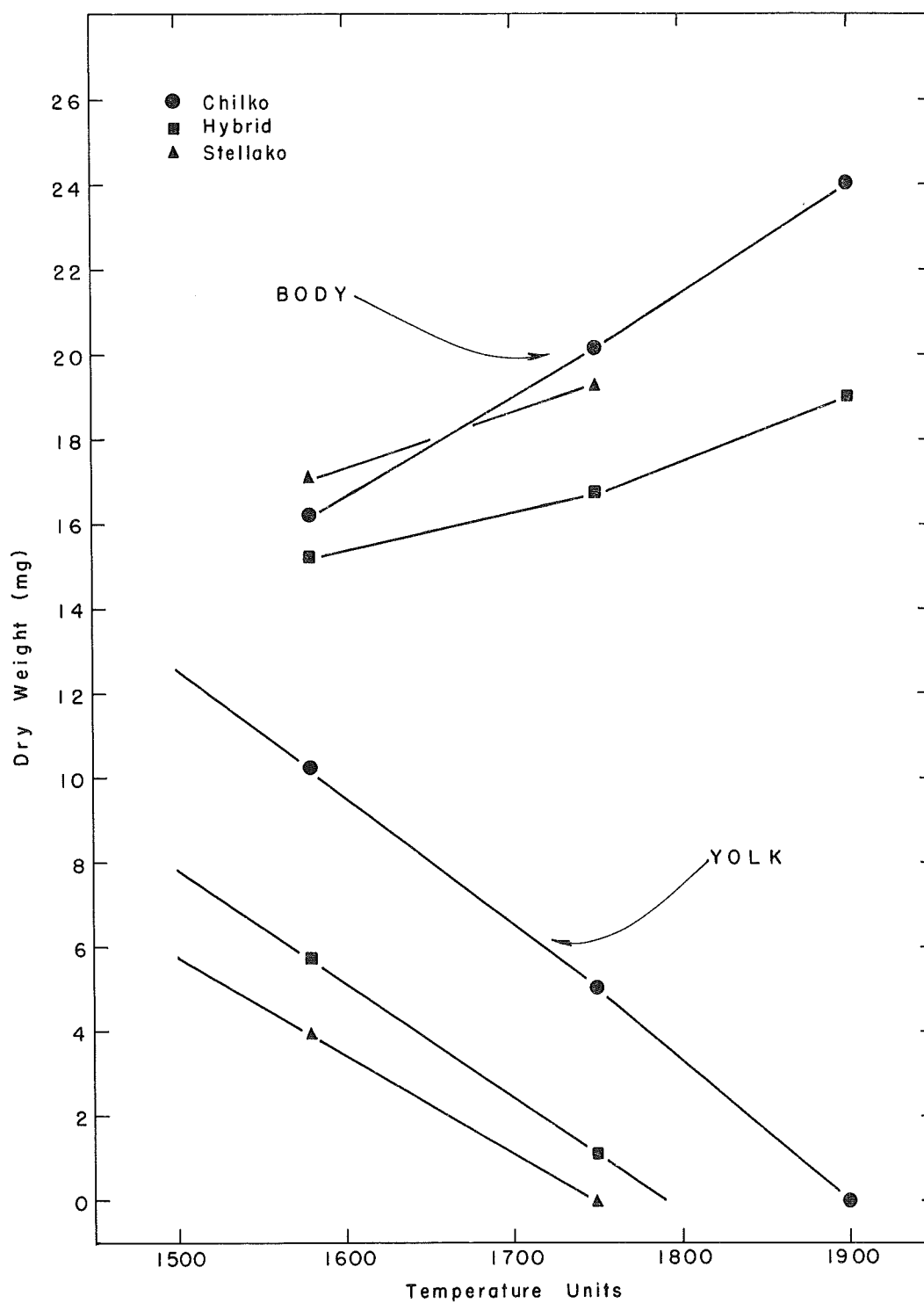


FIGURE 2 - Relationship of body weight and yolk weight to number of temperature units during incubation of Chilko, hybrid and Stellako stocks.

Testing Apparatus

The apparatus in which the tests were performed represented a convoluted channel 6.3 in. wide and 56 ft long, termed a migration preference channel. Basically it consisted of a 4 ft by 8 ft sheet of 3/4 in. plywood on which was supported a 4 in. wall around the perimeter with six parallel, 4 in. vertical dividers placed alternately inside (FIGURE 3). 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. Two V-throat traps, each 26 ft from the central chamber, were installed at either end of the channel to intercept migrating fry. A 6.3 in. by 12 in. screen chamber was placed in the center of the channel to hold fry prior to testing. During tests, the water was maintained at a depth of 1 to 2 in., and velocity was set at 0.5 ft per sec, measured by the rate of movement of round floats placed in the flow. This velocity, suggested to be the maximum velocity favorable to continuous upstream migration of sockeye fry (Andrew and Geen, 1960), was used throughout all tests.

The apparatus was installed indoors and enclosed on four sides with black plastic to reduce light intensities and other visual stimuli. Temperatures could be changed in the apparatus by tempering the 42°F water from Cultus Lake with water from the same source refrigerated to 38°F or heated to 80°F. A second source of water, used to test the influence of water other than from a lake, was obtained from Hatchery Creek, a small drainage stream from Vedder Mountain used as an auxiliary supply for the laboratory. Temperatures of the stream during its use ranged from 40° to 43°F.

Testing Procedure

As yolk absorption progressed, 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 (noted in TABLE 1) where the majority exited the channel that routine tests were begun.

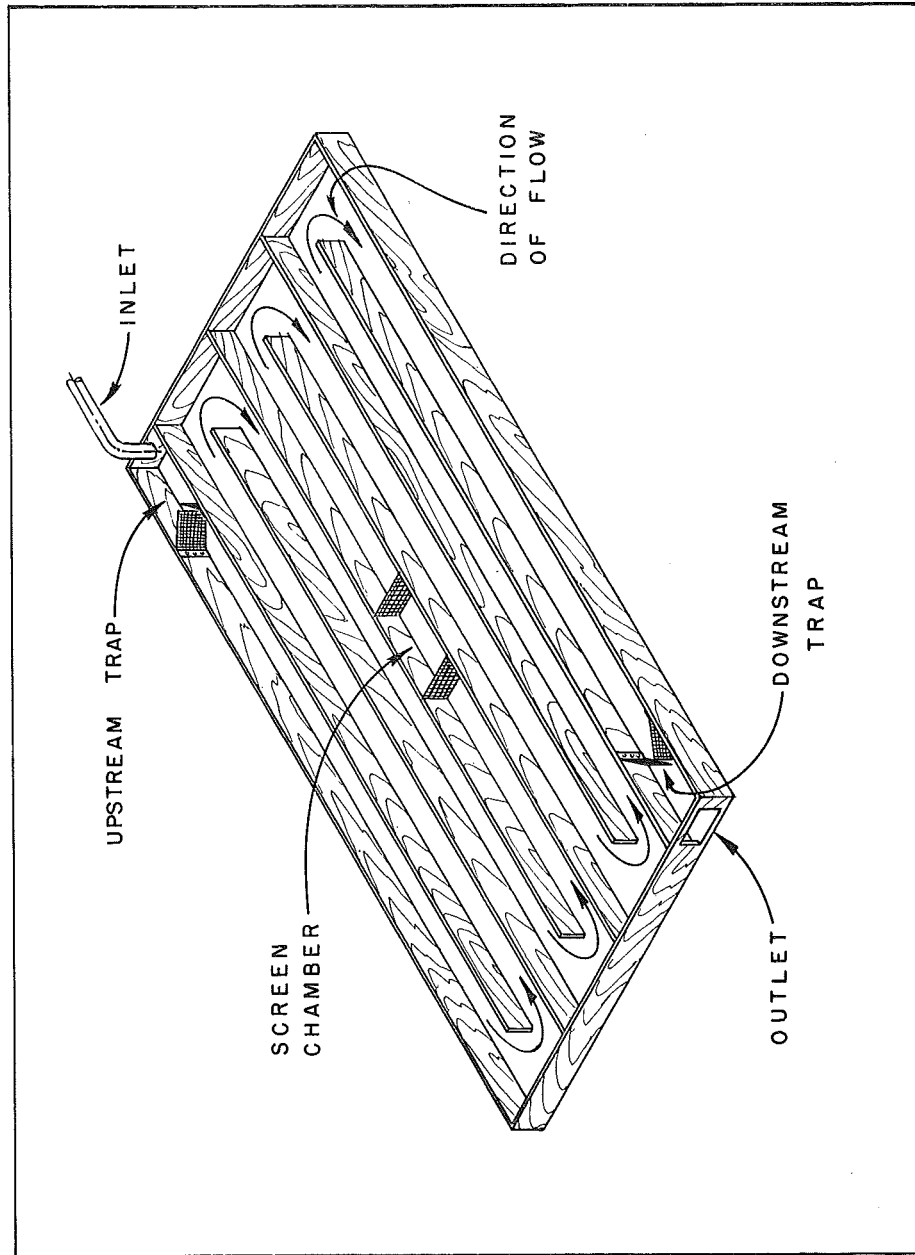


FIGURE 3 - Migration preference channel.

In each routine test of directional preference, 100 normal-appearing fish from one stock were removed from the 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, their appearance at either the upstream or downstream trap was 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 100 individuals was released after testing.

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 directional preference, the numbers of fry moving upstream and downstream were expressed as percentages of the 100 fry tested. In those instances where some fry remained within the apparatus, the percentages of moving fry totalled less than 100 since one could not necessarily assume the same eventual response of non-migrating fry.

Testing covered a period of 60 days on alevins and fry from Chilko, hybrid and Stellako stocks, and 30 days on those from Cultus Lake. These tests included three phases of investigations - preferences in direction, influence of temperature, and effect of water source on migration. Except for brief exposure to diffuse light when counted and placed in the central chamber, all fry were tested in darkness. Additional observations of fry migrating behavior in the channel were carried out using indirect natural daylight.

RESULTS

Migrating Behavior of Different Stocks

During the initial phase of the experiment, the four stocks of fry were tested frequently under uniform conditions (in darkness, at 42°F) to determine whether differences in migrating behavior existed between stocks. In this phase each stock was tested 20 times over a period of 35 days, except that Cultus fry were tested 15 times during a 30-day period.

Results indicated significant differences in behavior between certain stocks. Chilko advanced alevins and fry showed a very strong upstream response amounting to a mean of 82.3 per cent (SD 11.20) (TABLE 2). In contrast, Stellako alevins and fry preferred downstream movement with a mean response of 80.0 per cent (SD 13.18). Both races showed a highly significant preference for their respective directions, as opposed to a 50:50 random movement, when the data were tested by chi-square ($P < .005$).

TABLE 2 - Total numbers and mean percentage responses of four stocks of sockeye fry migrating upstream (U), downstream (D) and showing no preference (not trapped - NT).

STOCK	NO. TESTS	NUMBER OF FRY				MEAN RESPONSE (Per Cent)		
		U	D	NT	Total	U	D	NT
Chilko	20	1,646	278	76	2,000	82.3	13.9	3.8
Hybrid	20	969	955	76	2,000	48.4	47.8	3.8
Stellako	20	309	1,599	92	2,000	15.4	80.0	4.6
Cultus	15	862	539	99	1,500	57.5	35.9	6.6

While the two parent stocks, Chilko and Stellako, indicated a strong directional preference, the hybrid fry showed an intermediate response. The mean response of the hybrids was 48.4 per cent upstream and 47.8 per cent downstream movement, but varied widely in individual tests as indicated by the standard deviation of 31.29.

Cultus Lake fish showed a tendency to move upstream as shown by the mean of 57.5 per cent and by the statistical analysis with chi-square ($P < .05$). Cultus fry also showed a greater variability in response (SD 17.92) than either Chilko or Stellako fry but not to the extent of the hybrid stock.

Age and Migrating Behavior

Before showing a migrating response, the alevins exhibited a holding behavior. During preliminary tests prior to yolk absorption (at 1,400 to

1,500 temperature units), most alevins immediately dropped to the bottom of the screen chamber and hid among the stones on the floor of the channel. Others moved downstream a short distance and similarly retreated beneath the gravel. During these tests, alevins held in the channel for a 48-hr period (in both daylight and darkness) remained without moving from the vicinity of their initial hiding locations.

The transition from hiding behavior to active swimming occurred quite rapidly. Chilko fish showed no tendency to move in either direction when placed in the apparatus for routine testing (in darkness) on January 17. In the next test, four days later, only 2.0 per cent 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 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, over 90 per cent of the Chilko fish were migrating when the mean dry weight of yolk within the stock was 10.3 mg, or over 25 per cent of the original 40 mg of yolk remaining for absorption. Similarly, the Stellako, hybrid and Cultus alevins were migrating with dry weights of yolk approaching 4.0 mg, 4.0 mg and 2.0 mg, respectively.

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 per cent 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.

However, although the number of fish reaching the traps and the speed of migration increased with age, the direction of migration remained the same for both alevins and fry (FIGURE 4). Analysis of linear regression

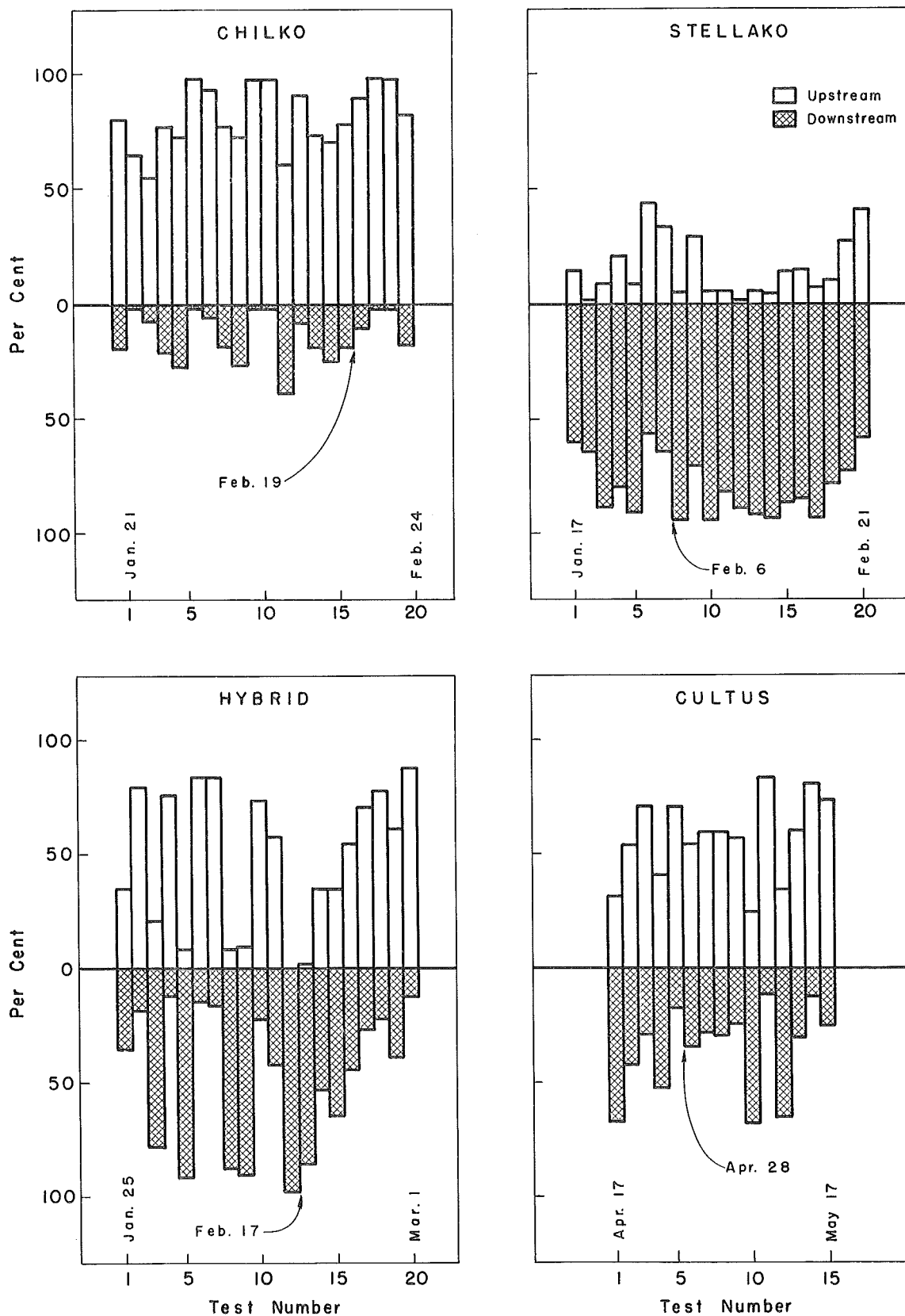


FIGURE 4 - Directional response of four stocks of sockeye throughout the initial testing period. (Arrow indicates end of yolk absorption and transition from alevins to fry.)

also indicated that age did not significantly change the magnitude of the preferred response of any of the four stocks during the 35-day test period ("t" did not exceed 1.74, $P > .05$).

Light and Migrating Behavior

As described earlier, stocks were held in incubation trays until yolk absorption was completed and then placed in hatchery troughs. Prior to their removal from the incubation trays, alevins had not been exposed to light except when samples were removed and counted prior to testing. Once in the partially covered feeding troughs, fry behavior was marked by schooling and a decided tendency to avoid exposed areas except during feeding. Although the new environment induced behavior more characteristic of fry in a nursery lake, the response of fry in the migration preference channel remained the same as their previous behavior as alevins. Chilko fry persisted upstream, the hybrids were inconsistent, Stellako fry moved downstream, and Cultus fry continued to show an upstream tendency.

Toward the end of the first phase of the study, fry from the Chilko stock (3 days after yolk absorption) and Stellako stock (18 days after yolk absorption) were tested during daylight hours to observe migrating behavior. Although the fry were very responsive to noise or movement of the observer, if left undisturbed their directional preference appeared similar to that of fish tested at night. Further tests are required to confirm this observation, however.

The daylight movement among both upstream and downstream migrating fry occurred as individuals and small groups. Usually the initial movement was that of the whole group, but some fry would dart ahead or slow down, leaving the group and continuing alone or in two's and three's. Hesitancy in the choice of initial direction of movement normally occurred no further than two or three feet from the screen chamber and once beyond that distance the fry usually maintained their orientation.

Fry moving upstream did not appear to take advantage of slower velocities along the sides of the channel. Often they swam rapidly up the middle of the channel until approaching one of the turns in the apparatus where many would rest momentarily before proceeding.

The response to current among the fry moving downstream was not

always one which would be described as drifting, or negatively rheotactic. Movements sometimes varied between a positive and negative rheotaxis. More rapid movement was accomplished when fry swam with the current headfirst, but often upon approaching a sharp turn, a larger stone or the trap entrance, their swimming behavior changed to an upstream oriented posture. Occasionally the fry would move upstream a short distance, only to turn again and proceed downstream.

Temperature and Migrating Behavior

The second phase of the study, covering the effect of temperature, was confined to the Chilko stock. Since all previous tests were carried out at a temperature of 42°F, further tests were performed to determine the effect of temperature on the directional response. In each test, the temperature in the apparatus was maintained at 42°F for 20 min after the fry were introduced, then during the following 10 min the water temperature was changed to the level selected for the test. The upper and lower temperatures chosen for the study, 48° and 36°F, represented levels slightly beyond the extremes normally experienced by migrating fry of the races tested.

Temperature tests began eight days after the Chilko stock had completed yolk absorption and covered a two-day period. Two tests were performed at each of three temperatures, and in each test all 100 fry reached the traps. Results showed that the great majority of fry moved in an upstream direction in all test temperatures (TABLE 3), and chi-square analysis indicated no significant differences between groups ($P > .80$). These data also showed a similar degree of upstream preference among Chilko fry (average 77.5 per cent upstream), as did tests during the initial phase of the study (82.3 per cent upstream; see TABLE 2).

TABLE 3 - Per cent of Chilko fry moving upstream (U) and downstream (D) when exposed to three different temperatures during migration.

48°F		42°F		36°F	
U	D	U	D	U	D
73	27	84	16	91	9
82	18	68	32	67	33
Mean 77.5	22.5	76.0	24.0	79.0	21.0

Water Source and Migrating Behavior

The tests described thus far were performed in lake water, a situation frequently associated with upstream movement. To study the influence of water from another source on direction of migration, Chilko fry (33 days after yolk absorption) and Cultus fry (0 days after yolk absorption) were tested in water from both Hatchery Creek and Cultus Lake. During the 30 min prior to each test the fry were held in the test water, in the central screen chamber of the experimental channel. As in all previous tests, flow was initiated 10 min prior to fry release. Testing extended over a period of several days but, in each case, each stock was tested in lake and creek water on the same day.

Although the response varied, the number of fry moving upstream in lake water was significantly greater than in creek water among both Chilko and Cultus Lake stocks when tested statistically by the "t" test of significance ($P < .025$). The mean percentage upstream movement of Chilko fry dropped from 88 per cent in lake water to 70 per cent when tested in creek water; Cultus fish showed a similar reduction from 64 per cent to 40 per cent (TABLE 4).

TABLE 4 - Percentage of upstream (U) and downstream (D) migrating fry from Chilko and Cultus Lake stocks when exposed to water from Cultus Lake and Hatchery Creek.

CHILKO STOCK				CULTUS STOCK			
Lake Water		Creek Water		Lake Water		Creek Water	
U	D	U	D	U	D	U	D
94	6	55	45	67	33	80	20
85	15	73	27	70	30	32	68
89	11	86	14	26	74	47	53
86	14	65	35	88	12	14	86
				35	65	14	86
				67	33	39	61
				87	13	49	51
				74	26	47	53
Mean 88.5	11.5	69.8	30.2	64.2	35.8	40.2	59.8

DISCUSSION

The behavior of newly emerged sockeye fry and the subsequent changes occurring with age have been the subject of extensive observation (Hoar, 1954; McDonald, 1960; Hartman, Strickland and Hoopes, 1962; McCart, 1967). The present study investigated the genetic implications of fry migration, and was directed toward the nature and persistence of the innate response evoked by environmental stimuli of the incubation stream.

Genetic Control of Migrating Behavior

If genetic control is responsible for directing migration with respect to current, then certain predictions about the organism's behavior are justified. Firstly, if a response is genetically oriented, then it should be recurrent when the progeny are translocated to a very different environment prior to any experience in the original habitat. Secondly, assuming no extreme interaction, crossing stocks exhibiting opposite behavior patterns should result in progeny showing an intermediate response. And thirdly, in the absence of selectivity within the race's natural environment, the response should be less specific than that of races from more selective environments.

Results of this study have shown that Chilko and Stellako fry, although translocated to a very different environment, responded to current in the migration preference channel in the same direction as they do in their home streams. Beginning shortly after fertilization, both Chilko and Stellako stocks were exposed to incubation temperatures, water quality, and light cycles very different from those of their normal environments and subsequently reached the emergence stage two months prior to normal timing. However, no apparent difference in their normal migrating response was observed. Chilko fry moved upstream, as they do in their natural environment; Stellako fry showed an appropriate downstream response.

The hybrids produced by crossing these two stocks also behaved in the predicted manner. Although the cross of Chilko females with Stellako males was not successful, the reciprocal cross produced hybrids with an intermediate response compared with those of the Chilko and Stellako stocks.

Further evidence of genetic control was shown by the response of Cultus Lake fry in the migration preference channel. While it is incorrect to describe the environment of Cultus Lake as non-selective, it can be assumed to require a less selective migrating response to current than the environments confronting newly emerged fry from the other two locations. Results indicated that Cultus Lake fry responded upstream, but not nearly as positively as did Chilko fry. Thus the stock from a less selective environment exhibited a less specific migrating behavior, further implicating a genetic mechanism controlling fry migration.

Inherited Characteristics Related to Migrating Behavior

Certain inherent physical differences were noted between the races which may be related to further evolution of specialized behavior. Chilko eggs possessed the largest quantity of yolk material (40.0 mg) and hence the alevins required 150 more temperature units for yolk absorption than Stellako alevins (eggs with 34.9 mg) when exposed to the same temperatures. Proportionally more yolk extends the incubation period for Chilko alevins and allows them to attain a larger size before leaving the gravel. The advantage of this would be realized during upstream migration where greater size increases swimming performance (Bams, 1967).

Furthermore, in situations similar to Chilko River where large numbers of fry make long treks upstream close to shore, food is probably at a premium. If yolk stores were available during the migration it could greatly enhance survival. Field data collected at Chilko River in 1950 indicated that newly emerged fry averaged 26.9 mm in length, holding fry averaged 27.5 mm and migrating fry averaged 28.1 mm. These data showed considerable growth occurring from emergence through migration, a fact difficult to attribute to feeding when fry were in such concentrated numbers close to the river shore. Subsequent analysis of fry sampled throughout the 1961 migration showed that a small quantity of yolk material

was still present in the abdominal cavity of nearly all the fry entering Chilko Lake, and indicated the reason for continued growth.

This supply of yolk material was not common to fry emerging in Stellako River or Cultus Lake. At Stellako River, only about 20 per cent of the emerging fry possessed very small quantities of yolk. Similarly, Cultus Lake fry contained relatively small amounts of yolk at emergence. These observations suggest that, in the case of Chilko fry, the presence of yolk material during migration is of biological significance to the organism, and that a combination of factors related to behavior have been selected for, during the course of evolution.

It should be noted that although Chilko fry were largest (24.0 mg) of those tested, size could not be considered a mechanism directing the preference for upstream migration. Chilko alevins (16.2 mg) were smaller than Stellako alevins (17.1 mg) when migration started at 1,580 temperature units. Also it should be recalled that Cultus Lake fry (17.6 mg) showed a more positive upstream response than the larger Stellako fry (19.8 mg).

Evidence for a Deliberate Migration

Extensive investigations of sockeye fry behavior (Hoar, 1954 and 1958) originally implied that fry migration was a displacement downstream upon emergence. This explanation for migration was most reasonable when one considers that emergence usually occurs at night and often in large rivers. However, genetic determination of a preferred direction of fry movement would strongly suggest that migration is deliberate, except where upstream migrating fry are temporarily swept downstream before they can reach lower velocities. A deliberate movement, as opposed to displacement, is certainly demonstrated by upstream migration.

Other evidence of a directed migration has been furnished in field observations by Hartman et al. (1962) and McCart (1967). These investigators have observed fry actively swimming downstream headfirst. Distribution of sockeye fry during downstream migration in Weaver Creek, a tributary of the Harrison River, also supports this contention. Studies

by the Commission showed a consistent pattern in the cross-sectional distribution of fry which differed from the discharge distribution, further suggesting an oriented fry movement. Similarly, observations during fry emergence in Chilko River revealed that fry among the surface stones showed no difficulty darting away and re-entering the gravel when disturbed, and even in moderately high velocities were only slightly displaced downstream.

Additional observations relevant to a deliberate movement were forthcoming from the studies in the migration preference channel. When Chilko alevins were first placed in the channel they immediately sought cover and even after 48 hr were not displaced downstream more than a few feet. As older alevins, response to current was a persistent upstream movement. Similarly, when Stellako alevins first began migrating behavior, it sometimes took 16 hr before most of the fish covered the 26 ft separating them from the downstream trap. In later tests, Stellako fry were observed actively swimming with the current.

Initiation and Persistence of Response

Concerning the survival value of a strong upstream response, Hartman et al. (1962) concluded that this response, among others, had to dominate the behavior pattern of fry shortly after leaving the redd site. McCart (1967), commenting on upstream migration, states, "there is apparently a precocious development of behavioral responses which, in fry from typical downstream situations, are acquired only after the fry have left the stream and entered the lake." The experimental evidence shows that the response to current does occur very early in the organism's behavior pattern. However, it appears that in both upstream and downstream situations, the taxis is released when the fish reaches the migrating stage, the response elicited being dependent upon the innate predisposition of the race.

When an innate behavior pattern must correspond to a specific cycle in the environment, stimuli are generally necessary for its release. However,

it is apparent that the migrating response of young sockeye can be stimulated before migrating behavior normally occurs. As noted previously, yolk material is enclosed within the abdominal cavities of migrating fry in Chilko River but is seldom observed as external yolk. However, the experimental studies have shown Chilko fish to respond upstream in the apparatus when considerable yolk was still evident externally. Mean dry yolk weight was over 10 mg and represented 25 per cent of the total amount originally available at fertilization, or about 30 days supply at 42°F. Similarly, the experimental Stellako stock of fish responded to current prior to the stage at which emergence occurs in the Stellako River. Thus it would appear that the ability to respond to flow and begin migrating is not necessarily associated with the near absence of yolk.

Age had no apparent effect on the directional response to current when fry were tested in the present experiments. On the other hand, Hoar (1958) has shown experimental evidence of a change in sockeye fry behavior with an increase in age. Fry became more positively phototactic, schooling occurred and a marked positive rheotaxis developed. Field observations (Killick, MS; McDonald, 1960; Hartman et al., 1962; McCart, 1967) have further established that this latter behavior pattern is characteristic of sockeye fry. Consequently, the results obtained from the present study are rather curious, especially the response of Stellako fry. Since Chilko fry responded upstream initially, one might expect a persistent response, but Stellako fry might have been expected to change their behavior after the initial downstream response. However, even when Stellako fry were removed from their incubation trays and placed in a lighted environment where they schooled and were fed, the downstream movement continued. The persistent downstream response suggests that the change reported in fry behavior, with respect to their migrating tendencies, is a response induced by some aspect of the lake environment rather than an age-associated behavior.

Fluctuations in temperature have been shown to influence the onset and intensity of sockeye fry migration. For example, emergence in Chilko and Stellako Rivers does not usually occur until temperatures approach 38°F. However, reversed movements due to temperature variation, as noted among juvenile rainbow trout (Northcote, 1962), have not been evident among migrating sockeye. In the present tests, different temperatures covering the extremes encountered in the natural environments (of the races studied) were shown to have no effect on directional preference. Chilko fry exposed to water of 36°F responded with the same behavior as that at 42° and 48°F. Tests with other races of sockeye not presented in this paper showed the same preferences irrespective of temperature, although holding tendencies were more evident among alevins when tested in the coldest (36°F) temperature.

Response to Water from Different Sources

A perceptible difference in the natural environments experienced by upstream and downstream migrating fry is the water in which the behavior takes place. Extended upstream migration occurs only when the nursery lake is above the incubation area, and hence the liquid environment of the stream represents that of the lake. A quite different environment may exist in the tributary streams where newly emerged fry migrate downstream. When Chilko and Cultus fry were tested in creek water, they showed significant differences from their responses to lake water. The upstream response of Chilko fry was reduced in magnitude and Cultus fry reversed their upstream tendency to a downstream tendency. It appears that the cue eliciting the more positive upstream response is contained in the lake water.

One must be cautious, however, in making generalizations about the type of water evoking a particular behavior pattern. The characteristics on which fry depend to differentiate lake water from creek water are not known. Thus the only criteria available at present are the different behavior patterns of fry in water from Cultus Lake and Hatchery Creek, and

the strong positive rheotaxis of Chilko fish in water from both Chilko Lake and Cultus Lake. These observations suggest that some characteristic common to lake water is not present in creek or tributary stream water. To emphasize the specific nature of the racial response, however, one need only recall that Stellako fry showed a very negative rheotaxis to Cultus Lake water, a response similar to that evoked in the river by water flowing from Francois Lake. Thus, if lake water furnishes the cue for upstream movement in certain stocks, it also provides for the opposite behavior of others.

With the completion of further studies now in progress, a more thorough understanding of the influence of water source on fry migration will be possible. A study relevant to this subject, and one particularly worthy of mention here, is the behavior pattern of Weaver Creek fry. Fry emerging from Weaver Creek migrate downstream through Morris Slough to enter the Harrison River. Once in the river, which is essentially a flowing extension of Harrison Lake, the majority of the fry reverse their orientation and migrate upstream to Harrison Lake. Fry from Weaver stock were tested repeatedly and found to respond downstream to water from either Weaver Creek or Hatchery Creek, but upstream to Cultus Lake water, and the magnitude of each response was about 80 per cent. Thus their behavior conformed to that which would be necessary for negotiation of the route from their incubation area to the nursery lake.

The behavior of Weaver fry accentuates the effect of the environment in directing the migrating response. Responses so different and so marked as those of Weaver fry suggest that variations in water chemistry are the eliciting cues. It has been demonstrated (Hara, Ueda and Gorbman, 1965) that the infusion of home water onto the olfactory receptors of adult salmon produced a clear stimulation apparent in the electroencephalographic patterns from the olfactory bulb. Presumably imprinting of these odors occurs very early in the life history of the fry. Histological examination of the olfactory epithelium of sockeye fry has shown the sensory tissue to be well developed and thus apparently capable of perception. Therefore, the behavior of a particular race may be associated with its ability to differentiate between certain odors.

The behavior of the various races in response to water source has thus far appeared to fit into two patterns. The first is that which results in a very strong rheotactic response and is related to a particular direction of migration which, in each race, corresponds to the response it must show in its natural environment to reach the nursery area. In this situation, exemplified by Chilko and Stellako stocks, the selective forces of the environment are rather severe toward the evolution of the specialized behavior.

The second behavior pattern, typified by Cultus Lake fry, is a more general response common to all races studied. Sockeye fry appear to be predisposed to respond more positively upstream in lake water than in creek water, regardless of the preferred orientation. This behavior pattern might explain the change in response of older sockeye fry upon entering the lake environment (Hoar, 1958). Young sockeye have also been observed to avoid the lake outlet and a strong rheotactic response has been suggested (Hartman et al., 1962). Perhaps the response to lake water shown in the present study provides the reason for this rheotactic response and hence provides the mechanism to confine sub-yearling sockeye to their lake.

IMPLICATIONS FOR FISHERIES MANAGEMENT

Efforts to replenish small sockeye salmon runs or rehabilitate barren areas have frequently been unsuccessful since the close dependence of the species on its environment has not been thoroughly understood. On the other hand, it is apparent that, over the years, existing populations of sockeye have become adapted to many different environments, and that in some aspects the species is quite plastic.

In transplanting stocks, many characteristics of the receiving environment can be complementary to the donor race if care is taken in selecting a parallel system from which to supply the new area. Therefore, not only should the requirements of adult energy reserves, spawning time, and incubation temperatures be considered, but attention should also be given to the more subtle genetic differences manifest only in the fish's behavior.

In some situations, however, because of the many genetic attributes involved, the donor race may not fit all of the requirements the new environment might impose. Thus in the more extreme situation, only a small percentage of the donor fish may possess those genetic characteristics necessary for success.

Many transplants previously thought to be failures because of very low returns may thus benefit from careful reassessment. Even though the donor and receiving environments may appear to have been parallel, the incubation requirements, fry migrating behavior, or a host of other factors including the innate orientation of smolts (Groot, 1965) may have differed. Under these circumstances perhaps the small number of variants from the normal behavior pattern provide the only opportunity for success, and upon returning to their new environment should be nurtured as selected stock regardless of their seemingly insignificant number.

SUMMARY AND CONCLUSIONS

1. Sockeye salmon fry migration from the incubation area to the nursery lake is generally characterized by one of three behavior patterns. Upon emergence from the incubation area the fry either migrate upstream, move downstream, or emerge directly into the nursery lake from the incubation beach. Different races exhibiting the above-mentioned behavior patterns were examined to test the hypothesis that genetic characteristics control migrating behavior of newly emerged fry.

2. Three races from the Fraser watershed and one hybrid stock were tested in the present study. Eggs were hatchery incubated under controlled conditions and the subsequent alevins and fry were tested in an experimental channel to determine their preferred direction of migration in response to current.

3. Results of this investigation into the factors orienting fry movement indicated that migration appears to be a deliberate, genetically-controlled movement from the incubation area to the nursery lake. Emerging

fry responded to current with an innate behavior pattern evoked by stimuli specific to each race. Hybrid fry responded in a manner consistent with the hypothesis and exhibited an intermediate behavior pattern compared with the two parent stocks.

4. Response to current did not change with age, nor did temperature influence the directional preference of migrating fry. However, the source of water had a marked and sometimes opposite effect on the response of different races to current.

5. The species, in general, appears to possess traits necessary for either upstream or downstream movement and, in the presence of strong selective force, the evolution of a specialized behavior pattern results.

6. Genetic control of fry migrating behavior suggests another parameter to be considered before supplementing small sockeye salmon runs or rehabilitating barren areas.

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