BEHAVIOURAL ECOLOGY OF CHUM SALMON (*O. KETA*) AND COHO SALMON (*O. KISUTCH*) ALEVINS IN THE GRAVEL

by

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ABSTRACT

An integrated laboratory and field approach was used to study the behaviour and ecology of Pacific salmon (genus *Oncorhynchus*) alevins in the gravel. The hypothesis tested was that these yolk sac fry move throughout the gravel prior to emergence, that this movement has both lateral and vertical components, and that changes in the physical or biological environment will alter certain parameters of subgravel behaviour.

Eyed chum salmon (*O. keta*) eggs were buried in incubation channels at Robertson Creek, B. C. Eight experimental treatments were chosen, utilizing two gravel sizes, two burial depths and two planting densities. The fry were captured at emergence by means of specially designed traps that allowed determination of degree of lateral movement, pattern of emergence and survival to emergence. The fry were also sampled for condition (weight-length ratio) at the time of emergence. In the larger gravel, survival was greater, lateral movement was increased, and initial emergence was earlier. At the greater burial depth the emergence period was longer. At the greater burial density initial emergence was earlier. Condition at emergence was the same in all treatments.

The behaviour of coho salmon (*O. kisutch*) alevins was examined in specially constructed aquaria, where light and flow conditions were as natural as possible. The same environmental factors were varied as in the field. In addition to a general description of alevin behaviour, detailed analyses were carried out on: vertical and lateral movement, orientation, spatial

distribution, condition, survival and pattern of emergence. In the larger gravel vertical and lateral movements were increased, survival was higher, area utilization was greater and condition at emergence was poorer. At the greater burial depth lateral movement towards the outlet was increased and initial emergence was earlier. Vertical movement was decreased because more fry were trapped within the gravel. At the higher density the alevins moved farther towards the inlet. The mean area occupied per alevin was unchanged by density and suggests competition within the gravel. The orientation of the alevins is discussed in relation to light and current.

The results indicate that larger gravel is better than smaller gravel for the incubation of Pacific salmon. Burial depth seems unimportant, but should be great enough to prevent predation. The question of optimum density requires further study. Emergence patterns may apparently be modified through environmental control.

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INTRODUCTION

Most phases of the life history of Pacific salmon are well understood as a result of the efforts of countless investigators during the past century. The alevin, however, has not received the attention that it deserves. The present study is an attempt to contribute some knowledge of this period of the life-cycle.

The eggs of the Pacific salmon, like those of most salmonids, are laid in an excavation in the stream bed (a redd) and are then covered by gravel from an excavation dug by the female immediately upstream. The eggs are typically covered by many inches of gravel and after hatching the larvae (alevins) must work their way to the surface from this depth, with the yolk sac attached. Once the yolk sac has been absorbed, the young fish is called a fry. The terminology is that of Lagler (1956).

From hatching to emergence, the alevin may spend up to two months within the gravel bed. That this period of the life history has received but scant attention is surprising, since it is well accepted that mortality in the early life of the salmon plays a key role in determining adult population density, and therefore the commercial value of a particular stock of fish (Neave, 1953; Royce, 1959).

Much work has recently been carried out concerning the environmental requirements of salmonid alevins. Wickett (1954), Gangmark and Bakkala (1960), Coble (1961) and McNeil (1962) have

demonstrated that the rate of flow of the water within the gravel, as well as the quality of the water itself, are of great importance to the survival of the eggs, embryos, and alevins within the gravel bed. In the laboratory, Alderdice et al. (1958), Silver et al. (1963), Shumway et al. (1964) and Brannon (1965) demonstrated the effects of different concentrations of dissolved oxygen and water velocities on survival and growth of salmonid alevins.

Gangmark and Bakkala (1960), Sheridan and McNeil (1960), and McNeil (1962) demonstrated that the stability of the redd gravel was an important factor in determining survival to emergence. Harrison (1923), Shapovalov and Berrian (1940), Shaw and Maga (1943), Neave (1947), Stuart (1953), Campbell (1954), Cordone and Kelly (1961), Bianchi (1963), Cooper (1965), Phillips (1965), and Shelton and Pollock (1966) have all demonstrated the detrimental effects of sedimentation on salmonid embryos and alevins which result from reduced flow and oxygen concentrations in the gravel.

Many authors have examined survival to emergence from the gravel. These include Carl (1940), White (1942), Shaw and Maga (1943), Pritchard (1947), Hobbs (1948), Briggs (1953), Foerster and Ricker (1953), Wales and Coots (1955), Hunter (1959), Phillips and Campbell (1961), Coble (1961), McNeil (1962, 1963, and 1966), Merrell (1962), Wickett (1962), McNeil and Ahnell (1964), and Koski (1966). The above studies demonstrated that survival to emergence varies widely, from zero to 100 percent, and that it is higher for coho and chinook salmon than for chum,

pink and sockeye. Survival appears to be largely dependent on the oxygen availability in the gravel, which in turn depends on water velocity and gravel permeability. It may be that different species have different viabilities, in that one can survive conditions which would cause heavy mortality in another.

The behaviour of the alevin has been studied by only a few authors. White (1915), Woodhead (1957) and Heard (1964) examined the responses of salmonid alevins to light before and during emergence. Bishai (1960, 1961a, 1961b, 1962a, 1962b) examined the orientation of salmonid larvae with respect to water currents, salinity, pH, pressure, and oxygen concentrations. Stuart (1953) made observations of migrations through the gravel of the alevins of the Loch trout (*Salmo trutta* L.), while Marr (1963) reported on the influence of surface contour on their behaviour. Roth and Geiger (1963), and Geiger and Roth (1962) examined the responses of brown trout alevins to gravity, light, and current while in the gravel bed. R. Bams, of the Fisheries Research Board of Canada, has conducted similar unpublished experiments on the alevins of the sockeye salmon (*Oncorhynchus nerka*).

Much of the above mentioned work is incomplete and even contradictory, but, *in toto*, suggests that salmonid alevins do indeed move through the gravel prior to emergence. These movements may have a pronounced vertical component, the alevins moving downward prior to their upward migration to the gravel surface (Roth and Geiger, 1963). Stuart (1953) suggested that the movements have an important lateral component as well, which

Roth was unable to observe in his cylindrical experimental observation chambers, since these allowed no lateral movement. Stuart (1953) stated that "migration... was in a lateral direction and never directly upwards. The alevins dispersed into the gravel... radiating upwards and outwards, and a plot of their relative positions took the form of an inverted cone." This has since been corroborated by work done on coho salmon (O. keta) and steelhead trout (S. gairdneri) alevins in Oregon (H. J. Campbell, pers. comm., 1966).

Shelton (1955) demonstrated that such parameters as survival to and condition at emergence may be altered by conditions within the redd. It may be that such alterations are mediated through changes in alevin behaviour.

The hypotheses tested in the present study, then, were that the alevins of the Pacific salmon move throughout the gravel bed prior to emergence, that this movement has both lateral and vertical components, and that changing the environment may affect subgravel behaviour.

The environmental variables chosen for the study were gravel size, egg burial depth, and egg density. Two levels of each were used in a 2x2x2 factorial design. Gravel size and burial depth were chosen because of their importance in the design of incubation and spawning channels. Emphasis in the past has been placed solely on survival to emergence. It is not inconceivable that factors such as burial depth and gravel size affect the area of gravel required by a group of alevins moving towards the surface. If there is competition for food or space

in the gravel then the area occupied by a group of alevins before or at emergence may determine how many eggs may be planted in a channel without affecting subsequent survival.

The density of planting was varied in an attempt to determine whether competition actually occurs. Competition is a distinct possibility if the alevins actively feed before emergence. Pre-emergent feeding has already been indicated by the studies of Dill (1967), Disler (1953), Burrows (pers. comm. 1965), Phillips (pers. comm. 1966), and others.

In the present study, an integrated field and laboratory approach was utilized to provide as complete information as possible on the effects of the factors examined. Since, under field conditions, at least, it was not practical to control such aspects of the environment as oxygen concentration, subgravel flow, and water temperatures, these variables were measured in order to at least be able to account for them in discussing the results of the experiments.

METHODS

FIELD STUDY

Trapping Facilities and Techniques

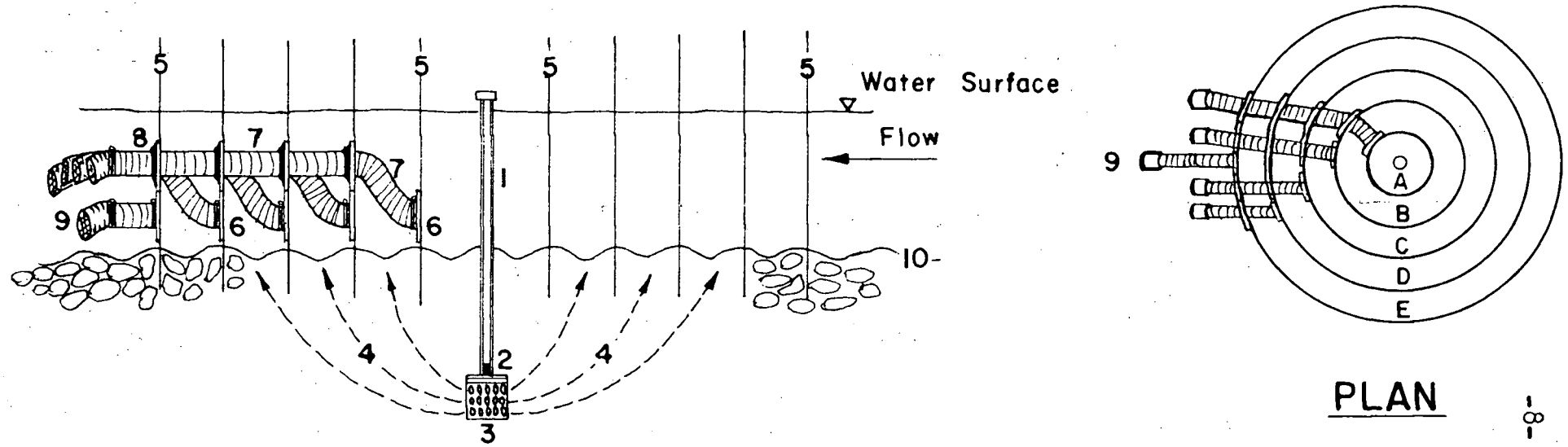
The field portion of the experiment was conducted at the Robertson Creek station of the Department of Fisheries of Canada, located near Alberni, British Columbia. The facilities included a series of small incubation channels, whose flow could be controlled by means of stoplogs at their upstream ends. Fry traps (Figs. 1, 2, and 3) were installed in two of these channels.

The upper fifty feet of two adjacent channels was chosen and eight "concentric-ring traps" were installed in each. The traps were modified from a design used by H. J. Campbell of the Oregon State Game Commission (pers. comm., 1966). They consisted of five concentric rings of 18x16 mesh fiberglass screen, supported by lathes and placed at one-half foot intervals from each other. Each ring, therefore, had a diameter one foot larger than the one inside it, the total diameter of each trap being 5 feet. The screens extended two inches into the gravel and 1-1/2 feet above the water surface (Fig. 3).

Eggs of the chum salmon (*Oncorhynchus keta*) were obtained from several adult spawners in the Big Qualicum River, British Columbia, on December 9, 1966. They were mixed and held to the eyed stage at the Qualicum River Station of the Department of Fisheries. The eyed eggs were transported to Robertson Creek and buried there on February 17, 1967 by gently pouring them down a 3/4 inch PVC standpipe into a plastic Vibert box. The boxes were partially filled with gravel and had been

Figure 1. Concentric ring traps at Robertson Creek.

Figure 2. Another view of the same traps, showing ducts and bags.



ELEVATION

PLAN

LEGEND

1. 3/4 inch P.V.C. standpipe, through which eggs were deposited.
2. Rubber stopper at base of standpipe, to prevent fry exit.
3. Molded plastic Viber box to retain eggs but pass alevins.
4. Routes of alevin migration through the gravel.
5. Concentric rings of 18 x 16 mesh fiberglass screen.
6. Entrance to duct via metal sleeve.
7. Dryerflex hose duct, 4 inches in diameter.
8. Duct passing through 3 inch diameter hole in skirt of 3/16 in neoprene rubber.
9. Cotton bags with mesh ends, one per duct.
10. Gravel level.

FIGURE 3. Schematic representation of the concentric ring traps installed at Robertson Creek, B.C.

buried in the channels the previous day. The slots in the side of each box were small enough to retain the eggs but large enough to allow exit of the alevins. The standpipe was sealed with a number 3 rubber stopper at the point where it entered the box, thus preventing emergence of fry up the standpipe.

A four-inch diameter plastic duct was attached to each screen by means of a tin sleeve projecting from the downstream end. The duct was attached to the sleeve with a clamp and then passed through a three-inch hole in a piece of 3/6-inch neoprene rubber inserted above the metal sleeves in each of the other screens. Thus, the duct leading from the inside ring passed through each of the other four screens. The neoprene skirts fitted tightly around the ducts so no loss of fry could occur between the two. Each trap had five pieces of ducting projecting from its downstream end, and each duct ended in a canvas bag with a marquisette net bottom.

It was intended that the fry emerging in each ring of the trap would find their way into the ducting and be captured in the canvas bags. It proved impossible, however, to capture the fry in this manner, either because the fry could not locate the entrance to the duct or because water velocity in the channels was not marked enough to hold them in the bags. At any rate, the emerged fry remained in the rings rather than moving out. A few may have even vacated the traps by re-entering the gravel and going under the screens. Consequently the only way to assess the distance of subgravel movement and the condition of the emerging fry was to remove them from the rings at night,

using a dipnet. This was done four times nightly (0100, 0300, 0500, and 0700 hours) between May 6 and May 19, and twice nightly (0100 and 0300 hours) between May 20 and June 2. The traps were also checked each morning at 0900 hours between May 6 and June 2. By June 2 there were no fish left in the traps.

The 16 traps were placed in the incubation channels as shown in Fig. 4. Two levels of each of three factors were studied, resulting in a 2^3 factorial design with two replications. The large and small gravel sizes were 2 inches to 4 inches, and 3/8 inches to 1-1/2 inches respectively. The gravel was graded and washed, and put into the two channels, one gravel size per channel, in early January, 1967. The eggs were buried at either 8-inch or 12-inch depths (measured to the middle of the Vibert boxes) and at a density of either 50 or 100 eggs per trap. A total of 1200 eyed eggs was deposited in the two channels.

Campbell (pers. comm., 1966) reported that coho salmon and steelhead trout alevins moved a maximum of 17 inches laterally when buried 10 inches in the gravel. It was assumed, therefore, that the traps at Robertson Creek, being five feet in diameter, would catch all of the emerging fry. To ascertain this, and to assess any possible leakage from the ring traps, v-screens (inclined-plane traps) were placed across each channel fifty feet below the downstream ring trap and lined with polyethylene sheeting on all sides to prevent further leakage (Fig. 5). They were checked daily from April 27 to June 2, usually at 0830 hours in the morning. All of the chum fry captured were recorded and preserved. One hundred chum fry were dyed with Bismarck brown

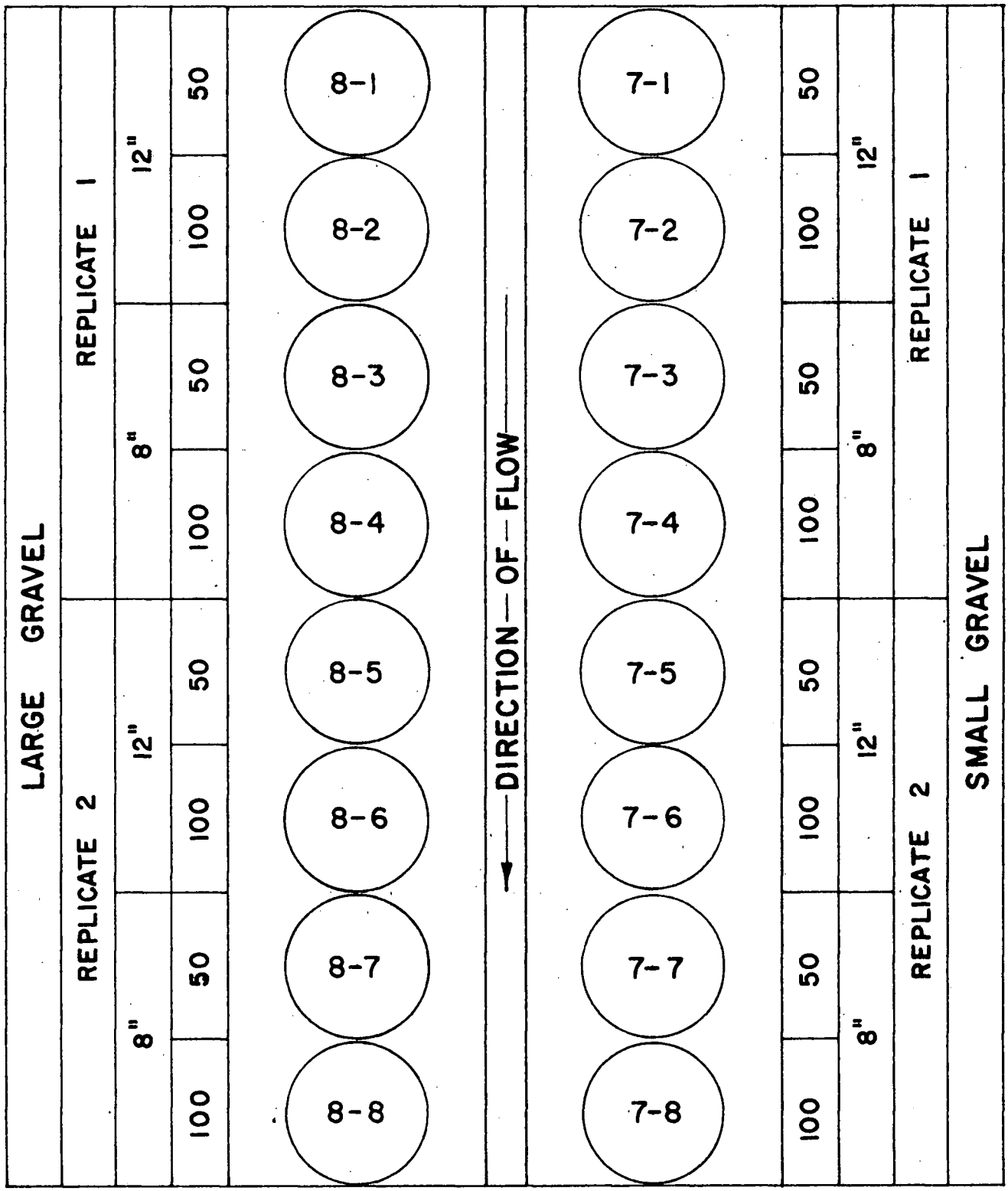


FIGURE 4. Experimental design, Robertson Creek traps.

Figure 5. V-screen in operation
at Robertson Creek.

and placed in each channel on May 4 at 2330 hours. These dyed fry were recorded in the v-screen captures and used to determine the efficiency of the two traps.

Analysis of Results

An appendix giving daily tabulation of all the Robertson Creek data is available. Copies are on file with the Department of Fisheries, Resource Development Branch in Vancouver; Dr. T. G. Northcote at the University of British Columbia; and the author.

(i) distance of migration through the gravel

The fish in each screened area were recorded as noted above. Appearance in rings A, B, C, D, and E (Fig. 3) was taken to reveal movement from the point of deposition of .25, .75, 1.25, 1.75, and 2.25 feet respectively. A mean distance of migration within each trap was calculated for each day and a composite value was determined for the entire emergence period. The latter was then analyzed for differences resulting from treatments, using the Yates tabular method of factorial analysis outline in Davies (1956). If $p < .05$ the data was considered significant. Since replicates of three treatments were lost, no attempt was made to estimate them. If two replicates of a treatment were available they were averaged to provide the values used in the analysis.

(ii) condition at emergence

All fry captured were preserved in ten percent formalin. After a period of at least two weeks they were

measured to the nearest millimeter and then dried in a 37 C oven for 24 hours before being weighed to the nearest milligram on an electric balance. The data for both weight and length were tabulated and summed over the entire period of emergence for each ring and each trap. A condition factor (k) was then determined for each trap by using the following formula (modified from Lagler, 1956):

$$k = \frac{\text{WEIGHT} \times 10^6}{\text{LENGTH}^3}$$

These were analyzed by the Yates tabular method. Replicates of five treatments were lost and no attempt was made to estimate them. If both replicates of a treatment were available, they were averaged as above.

(iii) survival to emergence

Percent survival from each trap was determined solely from the number of fry captured. The number seen in the traps was often greater than this, however, and some fry were obviously being lost, even through the v-screens. At the termination of the experiment, each Vibert box was removed and the contents examined and enumerated.

(iv) pattern of emergence

It was not possible to compare directly emergence patterns between treatments since many fry were left in the traps for days and perhaps weeks before they were finally captured with the dipnet. The only parameters examinable with regard to emergence pattern were: (1) date of first fry observed in trap; (2) date that last fry disappeared from trap;

and (3) length of emergence period. Any differences in these parameters were also analyzed by the Yates tabular method of factorial analysis, summing over two replicates when available.

Due to an inordinately small piece of data (a one day emergence period in one trap compared to an average of 10.8 for the others) the data were also summed over the main effects (for example, the two gravel sizes) and significant differences revealed by means of Student's t-test (Steel and Torrie, 1960).

Physical Factors

Although the surface flows in the two channels were controlled and equal, it was thought possible that dissolved oxygen level differences might influence the parameters studied. Eight water samples, therefore, were taken on April 27, and another four on June 11. These were obtained by means of a stainless steel barrel syringe with a probe end inserted ten inches into the gravel through a 3/4 inch PVC standpipe. The samples were placed in 300 ml BOD bottles and analyzed by the standard, unmodified Winkler technique. Organic material proved troublesome in three of the samples taken on April 27 and these were not considered in the analysis.

Water temperatures were taken in all of the standpipes on April 27 but from May 6 to June 2 the temperature was taken in only one standpipe at each observation time.

Flow through the gravel was not considered in this study, although P. Ryan (pers. comm., 1966) found that it averaged .31 to .38 ft./min. in mixed gravel at Robertson Creek.

In this study, no comparison of flow was made between the two gravel sizes.

LABORATORY STUDY

This portion of the study was conducted in a specially built laboratory at the University of British Columbia. Eggs of the coho salmon (*Oncorhynchus kisutch*) were used. The eyed eggs were obtained from the excavation of a single redd in a sub-channel (Department of Fisheries designation 3B) of the Chehalis River, British Columbia on March 21, and were placed in the experimental aquaria on March 23, 1967.

Experimental Aquaria and Design

Sixteen aquaria, modified from a type previously employed by R. Bams of the Fisheries Research Board of Canada (pers. comm., 1966) were constructed by Calvert Woodworks Ltd., Vancouver, B. C. Each aquarium measured 24-3/4 inches high, 26 inches wide, and 2 inches deep (back to front). The base and end plates were made of solid oak and were slotted to receive the two panes of 3/8 inch plexiglass. Plexiglass has the advantages of high tensile strength and high infrared light transmittance (approx. 90%) and therefore was used in place of glass. Its principal disadvantage was its susceptibility to scratching.

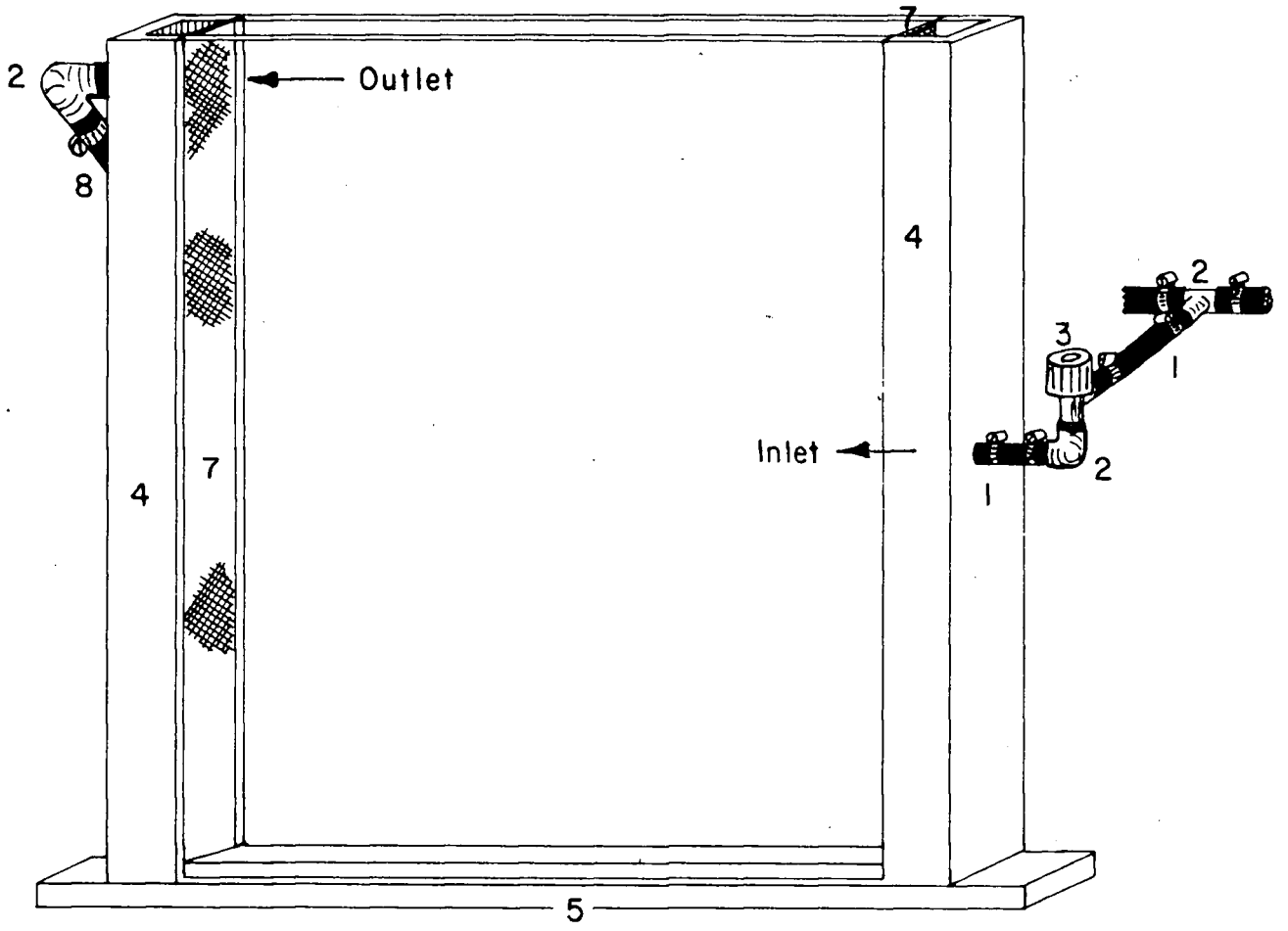
The area of observation, viewed from the front, measured 22 inches by 23 inches. A plastic inlet pipe, 1/2 inch in diameter, was located ten inches from the bottom on the right

side and a 3/4 inch plastic pipe served as the outlet on the left side of each aquarium, one inch from the top. The gravel was retained between two 20 x 20 mesh stainless steel screens, located in slots in each end plate. This permitted an open water area at the end of each aquarium to improve circulation. The amount of water entering each tank was controlled with a Nalgene spigot valve on each inlet. The design of the aquarium is shown schematically in Fig. 6.

The tanks were set on dexion framed plywood shelves, connected in two series and designated in the manner shown in Fig. 7. The water was dechlorinated and all piping was polyethylene. Plastic fittings were used throughout, 1/2 inch for the inlet, and 3/4 inch for the outlet piping. PVC (plastic) diaphragm valves, one on each inlet line, provided gross flow control for each bank of aquaria.

As in the field study, gravel size, burial depth, and egg density were each tested at two levels. The egg densities were 50 or 100 eggs per aquarium. The burial depths were again 8 inches and 12 inches. Large and small gravel sizes were 1-1/4 to 2-1/2 inches and 3/4 to 1-1/4 inches, respectively. Eighteen inches of gravel were placed in each aquarium on March 18 and the eggs deposited through PVC pipes on March 23, 1967. The pipes were removed after deposition and this technique usually allowed the localization of the eggs in a single small pocket against the front plate of plexiglass.

The tanks were lighted from 16 inches above the gravel surface by banks of 40 watt "cool white" fluorescent tubes



1. Inlet pipe of 1/2 inch polyethylene pipe.
2. Plastic insert fittings in inlet and outlet lines.
3. Nalgene inlet valve.
4. Oak end frame, painted with Rustoleum enamel.
5. Oak base, painted with Rustoleum enamel.
6. Walls of 3/8 inch plexiglass, inserted into grooves in ends and base and secured with Silastic adhesive.
7. Stainless steel and screens, 20 x 20 mesh.
8. Outlet hose of 3/4 inch polyethylene pipe.

FIGURE 6. Schematic representation of experimental aquarium.

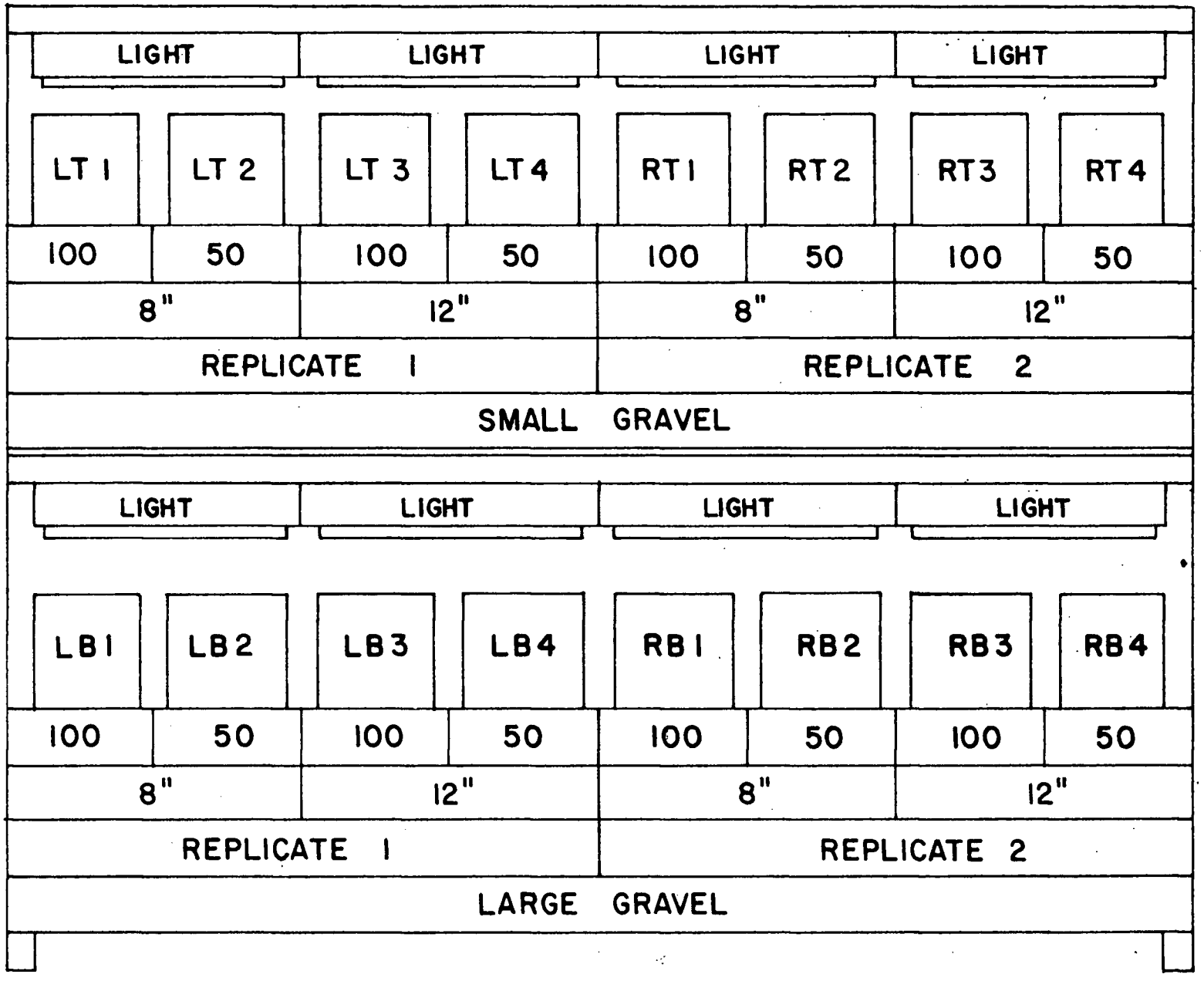


FIGURE 7 Experimental design, aquaria in laboratory.

connected to an Intermatic time switch kept adjusted to the natural day-night rhythm throughout the course of the experiment. Light was largely prevented from striking the front or back of the aquaria by means of black polyethylene curtains. Some light may have been able to reach alevins against the glass because of the light transmittant properties of the plexiglass. At any rate, the light conditions were as close to natural as possible. The entire area was surrounded by walls of black polyethylene to provide complete darkness when the lights were off, as well as to minimize other extraneous stimuli.

Observations

(i) daytime

Daytime observations were begun as soon as hatching started. With a few exceptions these observations were made every day from April 14 to May 18, and every second day from May 18 to June 10 in the large gravel (May 18 to July 10 in the small gravel). The position and orientation of each fish was recorded by placing a grid over the aquarium and copying on to a piece of paper ruled out in the same fashion. Lifting the black plastic curtain allowed enough light to carry out this operation.

(ii) night time

Night observations were made with an infra-red viewer (AN/SAR-4). The infra-red light source consisted of two six volt lamps covered by Kodak Wratten filters #87 and operated from the power mains by means of a transformer. Resolution was

not absolute, and it was often difficult to locate all of the fish known to be in the gravel. For this reason, the results of the night time observations are of a more subjective nature than are their daytime counterparts. Night observations were made on April 18, April 29, May 14, May 19, May 29, May 30, June 1, and July 9.

In addition a series of colour photographs was taken at one hour intervals from 2000 hours on June 7 to 0900 hours on June 8. An electronic flash outfit was used.

Analysis of Results

Appendices giving daily tabulation of all the laboratory data are available. Copies are on file with the Department of Fisheries, Resource Development Branch in Vancouver; Dr. T. G. Northcote at the University of British Columbia; and the author.

(i) movement in the gravel

Both the mean lateral and the mean vertical positions of the alevins in the gravel bed were determined for each observation date. This was done by assigning a number to each grid section, multiplying this number by the number of fish in the section, summing over all sections, and dividing this value by the total number of fish visible. The mean lateral and vertical positions were then plotted against time for each treatment, and differences between the treatments analyzed.

The amount of downward movement in the large gravel treatments was expressed as a percentage of the distance from

the point of burial to the bottom of the tank. In the small gravel treatments, the figure used was a percentage of the distance from the first point of the graph to the bottom of the tank. This modification was necessary because the eggs were not as localized in the small as in the large gravel.

The amount of upward movement was calculated as a percentage of the distance from the lowest point reached to the surface of the gravel.

The parameters chosen to study lateral movement were extent of movement to the left and extent of movement to the right, without any consideration of the time at which these occurred. All of the above data were analyzed by means of the Yates tabular method of factorial analysis. Replicates of four treatments were lost and no attempt was made to estimate them. If both of the replicates of a treatment were available, they were averaged to provide the data used in the analysis.

(ii) <u>orientation in the gravel</u>

All of the fish entirely visible on the front plate were recorded as being orientated either left (L), right (R), up (U), or down (D). These directions were considered as the following angles (α), clockwise from top centre: L=90, D=180, R=270, U=360. Analysis was carried out using the method of Batschelet (1965) to determine the vector resultant ($\mathcal{R}$) for the empirical circular distribution. This is determined by the following set of equations:

$$x = \frac{1}{n}(\cos\alpha_1 + \cos\alpha_2 + \ldots\cos\alpha_n) = \frac{1}{n}\sum_{i=1}^{n} \cos\alpha_i$$

$$y = \frac{1}{n}(\sin\alpha_1 + \sin\alpha_2 + \ldots\sin\alpha_n) = \frac{1}{n}\sum_{i=1}^{n} \sin\alpha_i$$

$$r = \sqrt{x^2 + y^2}$$

$$\cos\lambda = x/r$$

$$\sin\lambda = y/r$$

λ is then determined from tables. A similar method was used by Groot (1965) to study the orientation of young sockeye salmon in Babine Lake.

The mean angle of orientation in the 16 tanks was then compared over the following periods: first hatch - April 30, May 1-May 10, May 11-May 20, May 21-May 31, and June 1-June 10 (June 1-July 10 in the small gravel). Where possible, the data were summed over two replicates as above. The data were also summed over the entire period of observation, and analyzed using the Yates tabular method.

(iii) <u>spatial distribution in the gravel</u>

When three or more alevins were present in the observation area their positions were connected by straight lines, and the area contained within these lines measured to the nearest vernier unit (v.u.) with an area planimeter. This was converted to square inches of gravel by multiplying the value by .01 sq. in./v.u. x 16/1 (the scale of the drawing). The value so obtained was then divided by the total number of alevins observed, to provide a measure of spatial distribution, square inches per

alevin. This was done for each observation day for each aquarium, and the data were tabulated. The only figure to be statistically analyzed was the maximum area utilized per alevin, using the Yates tabular method, as above.

(iv) condition at emergence

Fry were captured with a dipnet in the four inches of open water above the gravel surface. Those emerging in the small gravel were captured immediately, but those emerging in the large gravel often could not be captured because of the ease with which they were able to re-enter the gravel. Those fry remaining in the large gravel aquaria, after emergence was deemed complete, were counted out when the gravel was removed (June 17-June 19). All fry were preserved in 10% formalin and after at least one week were measured to the nearest millimeter, dried 24 hours in a 37 C oven, and weighed to the nearest milligram on an electric balance. The data for both weight and length were tabulated and summed over the entire period of emergence. As with the Robertson Creek data, a condition factor was then calculated from the formula:

$$k = \frac{\text{WEIGHT} \times 10^6}{\text{LENGTH}^3}$$

The data were then analyzed using the Yates tabular method. Two replications, when available, were averaged as above.

(v) survival to emergence

The percent survival was determined solely from the number of samples taken. At the end of the experiment, organic

remains in the aquaria were examined but were usually in such an advanced state of decay as to be beyond enumeration. The figure for survival to emergence is therefore a minimum one, since there is a possibility that some fish may have been lost from the system, even though wire screens in the tanks make this highly unlikely. The figures obtained were analyzed in the usual manner to determine differences arising from treatments.

(vi) pattern of emergence

Due to the ease of re-entry by the fry into the large gravel, the date of first emergence is the only reliable parameter to compare emergence between treatments. The date of last emergence was arbitrarily set as June 10 in the large gravel and July 10 in the small gravel, and the date of maximum emergence was impossible to ascertain in the large gravel. The data for first emergence were analyzed factorially as before.

Physical Factors

(i) water temperatures

Temperatures were recorded at intervals (usually every second observation date) with a hand thermometer in the open water of each aquarium. A continuous temperature record was also obtained for one aquarium from May 9 to July 10 using a Taylor Automatic thermograph. The mean daily temperature, calculated as follows, was plotted.

$$\text{m.d.t.} = \frac{\text{daily maximum} - \text{daily minimum}}{2}$$

(ii) oxygen concentrations

Water samples were taken from the aquaria on June 16, four each from the two different gravel sizes. These samples were taken in the screened area at the outlet end of the aquaria through a piece of surgical rubber tubing. They were placed in 300 ml BOD bottles and analyzed by the standard, unmodified Winkler method. Organic material was negligible.

(iii) subgravel flow

Five aquaria, three containing small gravel (LT4, RT2, and RT4) and two containing large gravel (LB4 and RB1), were chosen to study this environmental factor. The tests were conducted between June 13 and June 16. Approximately 1 ml of Rhodamine B dye was injected into the inlet pipe of each tank, above the inlet control valve, and its distribution pattern in the gravel was recorded at intervals of two minutes to determine both rate of flow and flow characteristics.

RESULTS

FIELD STUDY

Distance of Migration

The Yates method of factorial analysis demonstrated that the only factor to affect significantly the distance of migration in the Robertson Creek traps was gravel size, i.e. in the larger gravel the alevins emerged farther from the point of deposition. The mean values for distance of migration, summed over the entire emergence period, are shown in Table I below. The variance (S^2) is shown in brackets below each treatment mean.

Condition at Emergence

The analysis of variance revealed that there was no effect on condition at emergence of any of the factors tested. Neither gravel size, burial depth, nor egg density significantly changed the value of the condition factor "k" (Table II). The results may not be valid, however, because of the relatively small size of the samples.

Survival to Emergence

Apparent survival to emergence was extremely variable, ranging from 1 to 98% in the small gravel, and 3 to 22% in the large gravel. In total, 156 fry were captured from the traps located in the small gravel and 49 from the traps located in the large gravel.

TABLE I.

Mean Distance (Ft.) of Alevin Migration from Point of Deposition in Concentric Ring Traps at Robertson Creek

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	1.60 (.1123)	1.47 (.0937)	0.50 (.0569)	0.48 (.0970)
100	1.30 (.0341)	1.58 (.4055)	0.75 (.0000)	0.75 (.0390)

TABLE II.

Condition Factor (k) for Fry Emerging within Concentric Ring Traps. See Text for Calculation of "k".

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	1.29	1.42	1.40	1.43
100	1.48	1.37	0.96	1.41

Besides these captures, 21 fry were captured on the v-screen in the small gravel channel between April 28 and May 16. During the same time period 191 fry were captured from the v-screen in the large gravel channel. The dye mark tests conducted May 5 indicated trapping efficiencies of 71% and 34% from the v-screens in these two channels respectively. From the following calculations:

$$x_{small} = \frac{100 \times 21}{71} = 30$$

$$x_{large} = \frac{100 \times 191}{34} = 562$$

it would appear that 562 fry vacated the concentric ring traps located in the large gravel, while 30 fry did the same in the small gravel. The revised totals for the estimates of survival therefore become:

$$\text{small gravel} = \frac{156 + 30}{600} = 31\%$$

$$\text{large gravel} = \frac{49 + 562}{600} = 102\%$$

The percent survival in the large gravel is clearly an overestimate. The reason for this is not clear, since the weights and lengths of the dyed fry captured on the v-screen were less than the weights and lengths of the fry captured in the concentric ring traps of the same channel (Table III). The effect of the dye on catchability is unknown, however.

It appears obvious, however, that survival was very much greater in the large gravel than in the small gravel. This is substantiated by the fact that although 49 dead eggs and 47

TABLE III.

A Comparison of the Weights and Lengths of the Fry Produced in Channel 8 with Those of the Dyed Fish Introduced to the Channel and Recaptured.

	CHANNEL 8 FRY CAPTURES	
	CONCENTRIC RING TRAPS	DYED FISH CAPTURED
MEAN WEIGHT	.063 gm.	.060 gm.
MEAN LENGTH	35.2 mm.	34.0 mm.

dead alevins were found in the excavated Vibert boxes in the small gravel channel, only two of the boxes from the large gravel channel contained eggs (total of 10). Many fry were still unaccounted for in the small gravel. They presumably died within the gravel after leaving the Vibert boxes.

Despite the low percentage of captures within the rings themselves, the conclusions drawn regarding degree of lateral movement are still felt to be valid. This is because mean distance changed very little from day to day, indicating that fry were not moving from one ring to another. In the large gravel, many fry may have missed the concentric rings althogether and the mean distance moved may be an underestimate.

Pattern of Emergence

The number of days after planting when the first fry appeared in the traps is listed in Table IV below. The analysis revealed that time to first emergence was significantly increased independently by both high density and small gravel; the latter is the most important of the two factors.

It is possible that the significance may be spurious, however, since emergence began very much later in one treatment (91.0 days) than in the others (mean of 77.9 days).

The number of days after planting at which emergence was deemed complete was determined by the date at which the last fry left the trap. These values are summarized in Table V below. The analysis of variance indicates that the 8 inch burial depth significantly decreased and the small gravel size significantly increased the time to last emergence.

The length of the emergence period (Table V value minus Table IV value) is shown in Table VI below. The data is unworkable, however, because of the zero value in the table. Excluding this value and summing over all of the treatments in each channel gives the following data for the mean length of the emergence period.

large gravel - 10.25 days

small gravel - 11.50 days

A t-test (Steele and Torrie, 1960) shows that these are not significantly different at the .05 level. Similar tests were carried out for effects of planting depth (8 inches = 9.50 days; 12 inches = 11.74 days) and planting density (50 eggs = 10.75 days; 100 eggs = 10.83 days). These tests indicated that egg density had no effect on the length of the emergence period, but that increasing the depth of planting significantly increased the length of the emergence period (at the .05 level).

In toto the analysis revealed that the fry both began and completed their emergence earlier in the large gravel, but that the time taken to complete emergence was not significantly shorter than in the smaller gravel. There was evidence that the emergence period was lengthened by an increased in planting depth. The alevins buried at 8 inches began their emergence from the gravel at the same time as their more deeply buried counterparts, but the former completed their emergence earlier. Planting density had no effect on the pattern of emergence.

TABLE IV.

Number of Days after Planting at which the First Fry Appeared in the Concentric Ring Traps.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	77.0	78.0	79.0	79.5
100	74.5	79.0	91.0	78.5

TABLE V.

Number of Days after Planting at which the Last Fry Disappeared from the Concentric Ring Traps.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	86.0	89.0	88.5	93.0
100	84.5	90.0	91.0	90.0

TABLE VI.

Length of the Emergence Period (Days) in the Concentric Ring Traps.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	9.0	11.0	9.5	13.5
100	10.0	11.0	0	11.5

Physical Factors

(i) oxygen concentrations

Of the 8 samples taken from the standpipes on April 27, three were discarded because of excess organic matter. Of the remaining five, three were from channel 7 (small gravel) and two from channel 8 (large gravel). Mean values of milligrams of oxygen per liter were:

small gravel - 19.7 mg O_2/l.

large gravel - 12.1 mg O_2/l.

The value for the small gravel is undoubtedly too high but both situations were saturated or supersaturated at 48.4 F.

Those samples taken on June 11 gave the following values for the two channels:

small gravel - 13.6 mg O_2/l.

large gravel - 11.1 mg O_2/l.

Again supersaturation is indicated. It is clear that oxygen concentrations in both channels were not limiting factors in the environment.

There is also evidence that the small gravel contained more oxygen than the large gravel, but this may be only an artifact of sampling. The standpipes were buried slightly deeper in the large gravel ($\bar{x}$ = 8.5 inches) than in the small gravel ($\bar{x}$ = 7.2 inches) because the shallower ones in the large gravel had to be rejected due to the larger amounts of organic matter in the samples.

(ii) water temperatures

The temperatures recorded in the eight standpipes on April 27 were all identical (48.4 F). Therefore, only one location was subsequently used for temperature recording, a standpipe in channel 8. The temperature was taken manually at each observation time between May 6 and June 2, the period of peak emergence. The mean daily temperatures are graphed in Fig. 8.

LABORATORY STUDY

Of the sixteen tanks in the laboratory, only twelve gave useful data. The eggs in LT 1 died because of a water system failure, while those in LB 1 apparently died because of lack of oxygen. Tanks LT 2 and RT 3 were of no use for most of the parameters studied (with the exception of survival and emergence pattern) since the eggs were inadvertantly buried in the middle of the tank and few alevins could be seen against the front plate. Due to the large amount of lost data, the treatments were considered to have had only one replication, and the two replicates were simply averaged if both were complete.

Behaviour of Alevins in the Experimental Aquaria

Within a day of hatching, the alevins moved downward (Fig. 9a). This downward phase was more marked in the large than in the small gravel due to the difference in ease of

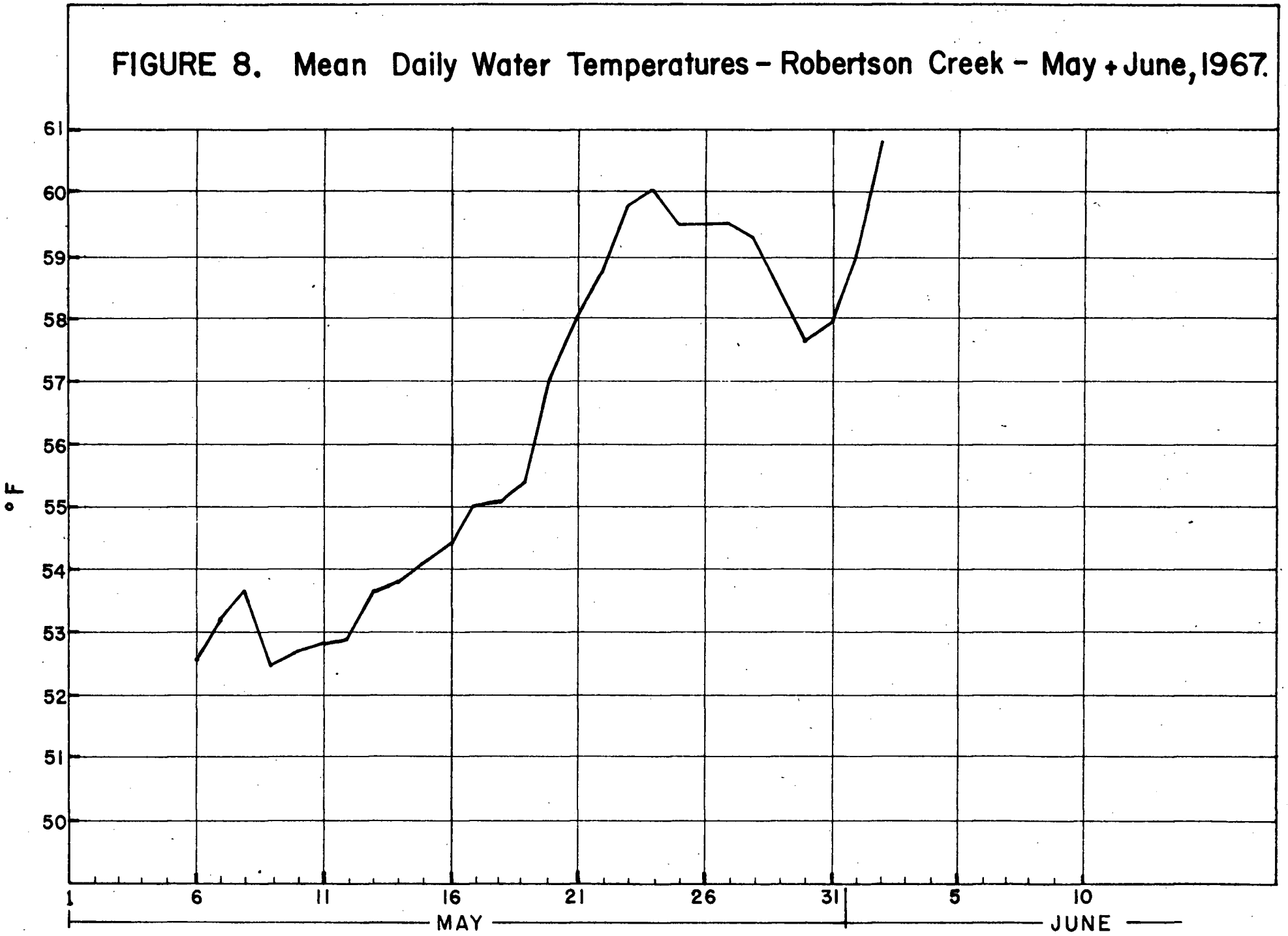


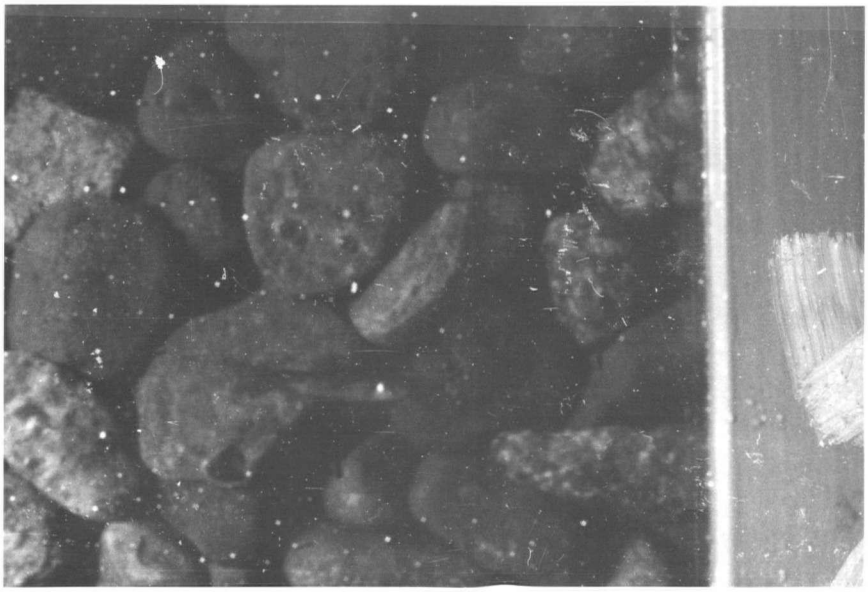
FIGURE 8. Mean Daily Water Temperatures - Robertson Creek - May + June, 1967.

9b. Alevins aggregated on the tank bottom, 5 days after hatching (x 7/16).

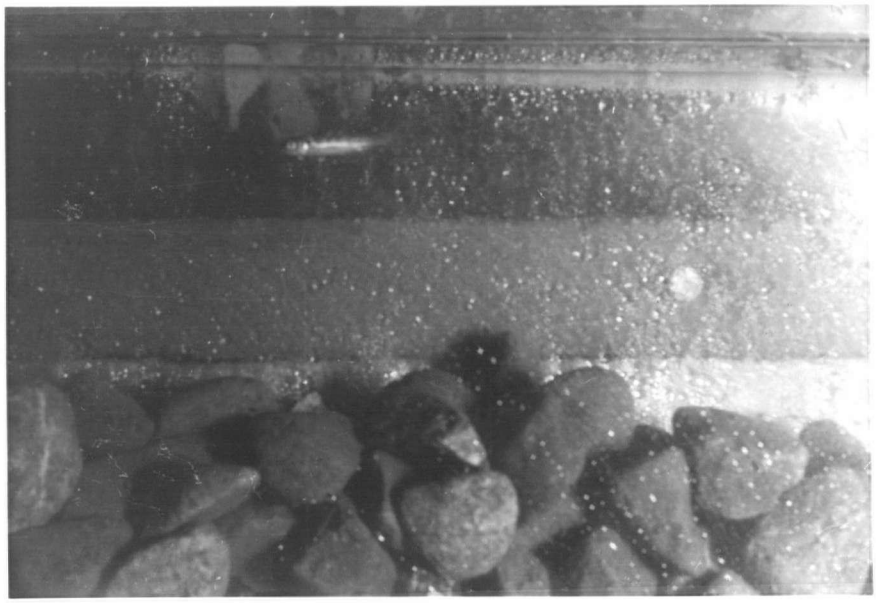
9a. Alevin moving downward 3 days after hatching (x 1/3).

9c. Alevins dispersing along the tank bottom, 31 days after hatching (x 1/3).

Figure 9. Phases in the behaviour of the alevins in the large gravel.



9d. Fry near emergence, 41 days after hatching (x 2/3).



9e. Newly emerged fry, 36 days after hatching (x 1/2).

Figure 9 (cont.). Phases in the behaviour of the alevins in the large gravel.

movement through the two materials. In the large gravel the alevins aggregated on the bottom of the tank (Fig. 9b), but tended to more evident dispersal in the smaller gravel (Fig. 10a). In both situations the alevins demonstrated what could be termed "explosive behaviour" when closely grouped. This was characterized by the rapid scattering of a group of alevins when one member of the aggregation moved. The group of alevins would subsequently reform. Similar behaviour was noted among sockeye salmon alevins by R. Bams (pers. comm., 1966), who suggested that it may be caused by carbon dioxide concentrations reaching a threshold level.

As their yolk sacs were absorbed, the alevins on the bottom of the experimental aquaria containing the large gravel spread out horizontally to the extreme right and left sides (Fig. 9c). From there they made short forays into the upper regions of the gravel (Fig. 9d) and finally emerged (Fig. 9e). This period will be called the upward phase. The snooperscope studies revealed that the alevins (or, more correctly now, fry) were more dispersed through the gravel during the night. However, much dispersion and movement was noted during the day time hours as well. That the fry were able to move extremely easily through the gravel was evidenced by observations on May 31, June 3, and June 5 of fry moving from the bottom of the tank to the top, a total distance of about 36 inches, in a time of about two minutes. Most fry after emergence, however, did not appear to return to any great depth in the gravel. Fry swimming in the open water of the tanks would return to about

10a. Alevins beginning to disperse, 1 day after hatching (x 7/16).

10b. Alevin near the tank bottom, 42 days after hatching (x 2/3).

Figure 10. Phases in the behaviour of the alevins in the small gravel.

10c. Dispersion of the alevins, 42 days after hatching (approx. x 2/3).

Figure 10 (cont.). Phases in the behaviour of the alevins in the small gravel.

the first four inches of the gravel if frightened by a sudden movement. These fry were never seen to return to the bottom of the aquaria.

The downward phase was much less pronounced in the small gravel. In only two instances (RT 2 and RT 4) did alevins reach the bottom of the tank (Fig. 10b). In most instances downward movement was slight, and was associated with dispersion in all directions from the point where hatching occurred (Fig. 10c). Most of the alevins moved upward and out towards the side of the aquaria, although some moved straight up (Fig. 11). This pattern, if rotated through 180 degrees (i.e. three dimensional) would give the form of a rough cone, with the apex slightly below the point of hatching.

There appeared to be considerable day time emergence in the small gravel. This was relatively clear since the fry were unable to re-enter the tightly packed gravel after emergence. The tanks were often cleared twice a day and many fry were captured in the afternoon, indicating emergence since the morning sampling. The hourly photographs taken on June 7 - June 8 (Fig. 11) showed a slow but continuous movement throughout the night, with most of the fry emerging about 0630 hours, about the time that the lights came on.

The behaviour differences noted above were all between the two gravel sizes. No obvious differences were noted between the levels of the other two factors, burial depth and egg density.

Figure 11. Nocturnal movement of coho salmon alevins (53 days after hatching) in the small gravel of the experimental aquaria. Upper: 2100 hours (lights off at 2030 hours); Lower: 2400 hours (x 1/4).

Degree of Vertical Movement

The alevins exhibited significantly greater movement during the downward phase in the large gravel than in the small gravel (Table VII). The mean vertical positions are plotted for each available replicate of each treatment in Fig. 12. The analysis also revealed that the alevins in the small gravel moved downward to a significantly greater degree when planted at lower density.

The analysis of variance showed that large gravel, 8 inch burial depth, and egg density of 50 all acted to increase the extent of movement in the upward phase (Table VIII). The analysis is not particularly revealing, however, since it is biased by the fact that some alevins were undoubtedly trapped within the small gravel, and that they were located deeper in the gravel when the eggs were planted at the deeper location.

Degree of Lateral Movement

It is apparent (Fig. 13) that the predominant lateral movement was towards the inlet in the upward phase of the migration, even though movement began towards the outlet during the downward phase (most evident in the large gravel).

Movement towards the outlet was significantly greater in the larger than in the smaller gravel (Table IX). The degree of this movement was also greater at the higher density and at the deeper burial depth, although these effects were not as great as that of the larger gravel.

TABLE VII.

Percent of Possible Downward Movement in the Experimental Aquaria.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	100.0	100.0	37.0	28.1
100	100.0	100.0	19.0	17.7

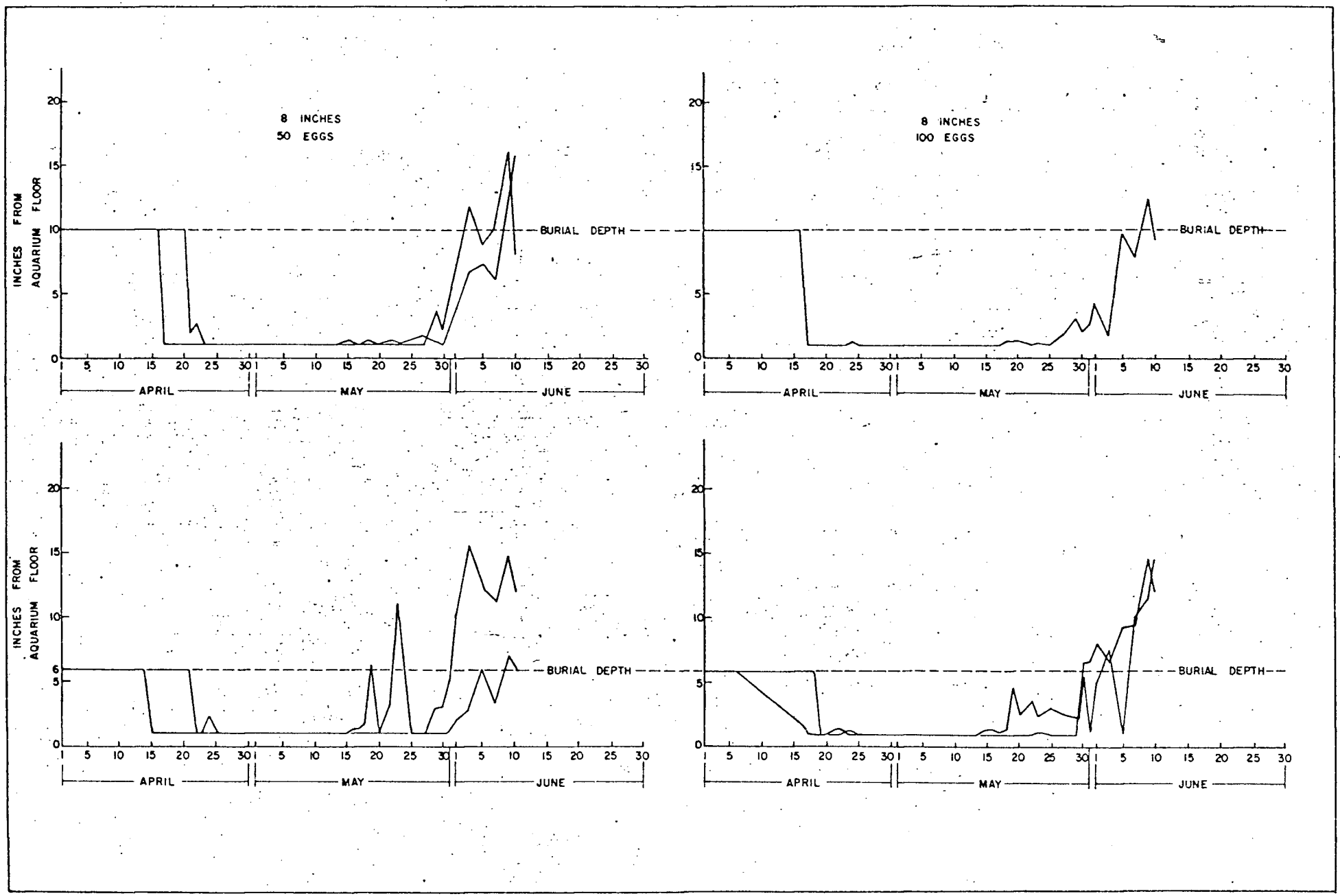


FIGURE 12-1 Mean vertical positions of the alevins in the large gravel. - Upper - 8 inch burial depth, lower- 12 inch burial depth. Left side - egg density 50, right side egg density 100.

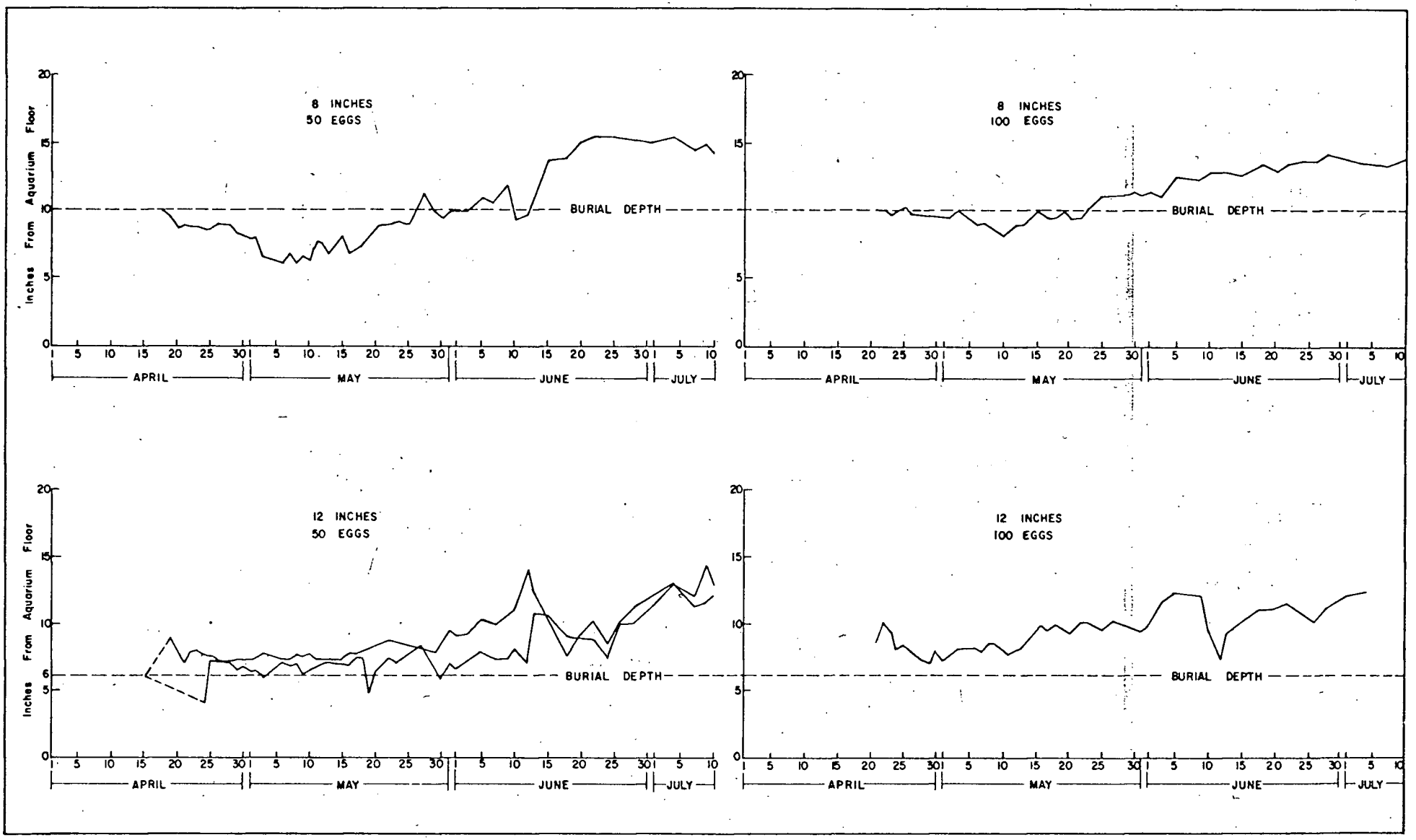


FIGURE 12-2 Mean vertical positions of the alevins in the small gravel.- Upper- 8 inch burial depth, lower- 12 inch burial depth. Left side- egg density 50, right side egg density 100.

TABLE VIII.

Percent of Possible Upward Movement in the Experimental Aquaria.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	90.0	64.0	80.0	64.0
100	69.0	83.0	63.0	47.0

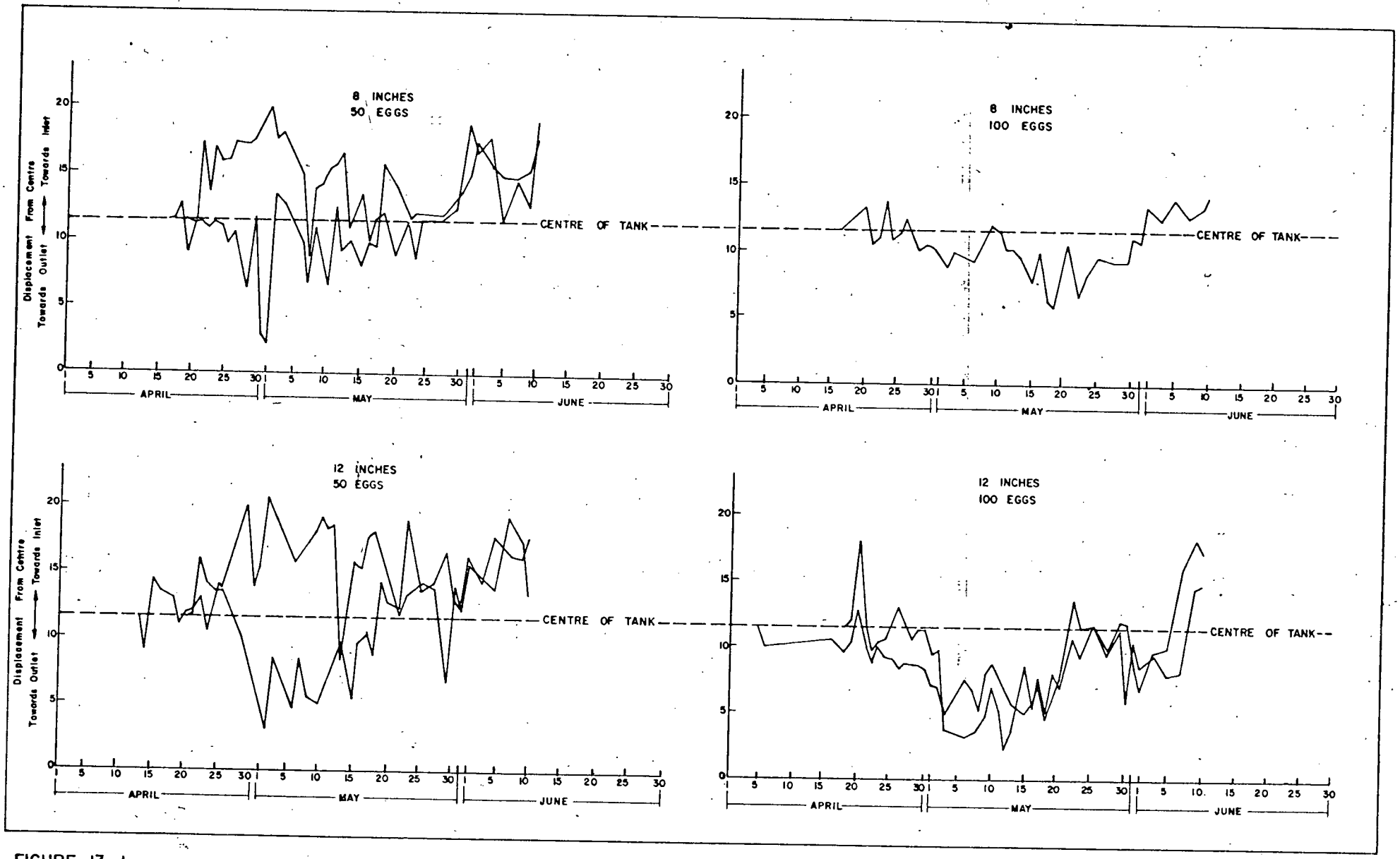


FIGURE 13-1

Mean lateral positions of the alevins in the large gravel. Upper - 8 inch burial depth, lower - 12 inch burial depth. Left side - egg density 50, right side egg density 100.

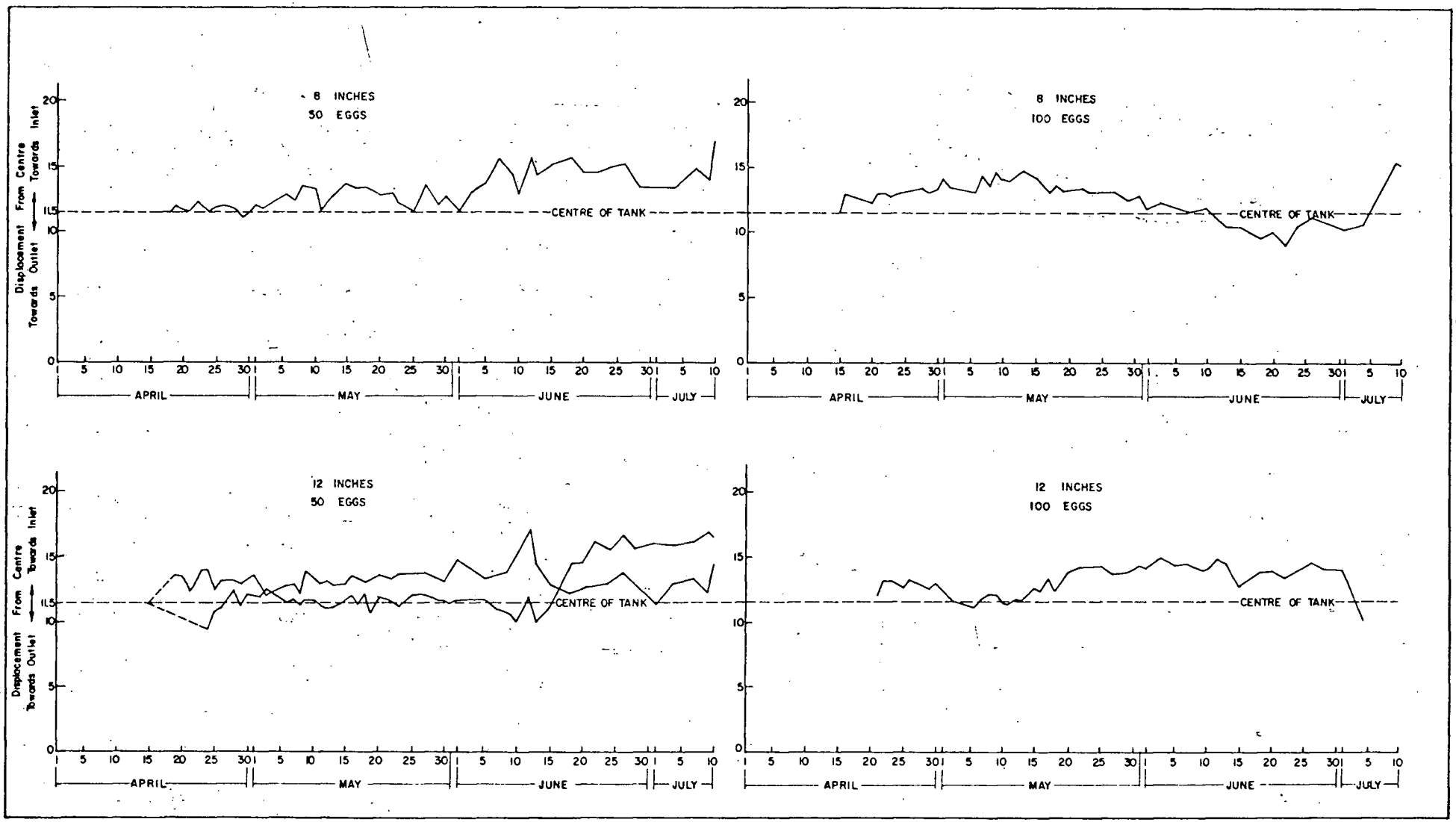


FIGURE 13-2

Mean lateral positions of the alevins in the small gravel. Upper- 8 inch burial depth, lower- 12 inch burial depth. Left side - egg density 50, right side - egg density 100.

The analysis of the data shown in Table IX showed that large gravel and low density significantly increased the extent of movement towards the inlet.

The total range of movement is obtained by adding the figures in Tables IX and X, and is summarized in Table XI. Both large gravel and low density significantly increased the degree of lateral movement. Since these results agree most closely with those of the analysis of movement to the inlet, it is clear that movement towards the inlet was the primary component of lateral movement and was more important than the movement to the outlet which accompanied the downward movement immediately after hatching.

Orientation in the Gravel

The most common direction of orientation ($\vec{\lambda}$) lay between 270 and 360 degrees, i.e. upwards and towards the inlet (Table XII). This agrees well with the data on mean vertical and lateral positions presented above. Downward orientation was noted in only a few instances, all in the small gravel. The fact that it was absent in the large gravel, where downward movement was most evident, is indicative either of a non-orientated mechanical "slipping through" to the bottom of the tanks, or of a rapid orientated movement towards the bottom. Since the alevins in the large gravel appeared on the bottoms very soon after hatching, it is difficult to determine which of these possibilities is correct. No consistent difference appears to exist between the levels of the other factors examined, i.e. burial depth and egg density.

TABLE IX.

Extent of Lateral Movement to the Outlet (Expressed as Inches from Center) in the Experimental Aquaria.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	6.3	6.2	0.2	1.5
100	5.5	7.8	2.5	1.8

TABLE X.

Extent of Lateral Movement to the Inlet (Expressed as Inches from Center) in the Experimental Aquaria.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	8.2	8.3	6.2	4.7
100	2.9	5.1	3.8	2.8

TABLE XI.

Total Lateral Movement (Expressed as Inches from Center) in the Experimental Aquaria.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	14.5	14.5	6.4	6.2
100	8.4	12.9	6.3	4.6

TABLE XII.

Mean Orientation Direction by Time Period, for Each Treatment in the Experimental Aquaria. Directions are Expressed as Angles, Counterclockwise from Top Center.

TREATMENT			DATE				
			HATCH-April 30 DEGREES	May 1 - May 10 DEGREES	May 11-May 20 DEGREES	May 21-May 31 DEGREES	June 1-END DEGREES
SMALL GRAVEL	12"	100	135	338	351	213	270
		50	214	284	328	342	354
	8"	100	46	360	347	343	358
		50	337	333	343	345	356
LARGE GRAVEL	12"	100	352	27	323	347	357
		50	360	88	315	330	334
	8"	100	270	90	50	303	352
		50	5	8	272	277	342

The orientation data were summarized by totalling over the entire period in which alevins or fry were observed in the gravel (Table XIII). The analysis of variance revealed that the angle of orientation was not significantly affected by gravel size, burial depth, or egg density at the .05 level.

Spatial Distribution in the Gravel

The area occupied by each alevin increases with time (Fig. 14). The large fluctuations are caused by the emergence from the gravel of those alevins nearest the surface, resulting in a decrease in the area covered by those still remaining in the gravel. If these fluctuations are ignored the graphs suggest exponential curves, and are all similar except that they cover a greater area in the large gravel treatments. In other words, the alevins were more dispersed in the large gravel. This is also shown by the analysis of variance of the data shown in Table XIV, which showed that dispersion was significantly increased by large gravel size. Other factors had no significant effect.

It is significant that the mean area occupied per alevin was not affected by the number of alevins present, i.e. irregardless of number each alevin occupied the same gravel area. This indicates that the fish were spacing themselves out within the gravel and that competition may have been occurring.

Condition at Emergence

Fry emerging from the small gravel were in significantly better condition than those emerging from the large gravel

TABLE XIII.

Mean Angle of Orientation in the Gravel, Expressed as Degrees, Counterclockwise from Top Center.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	325	349	348	339
100	330	33	357	310

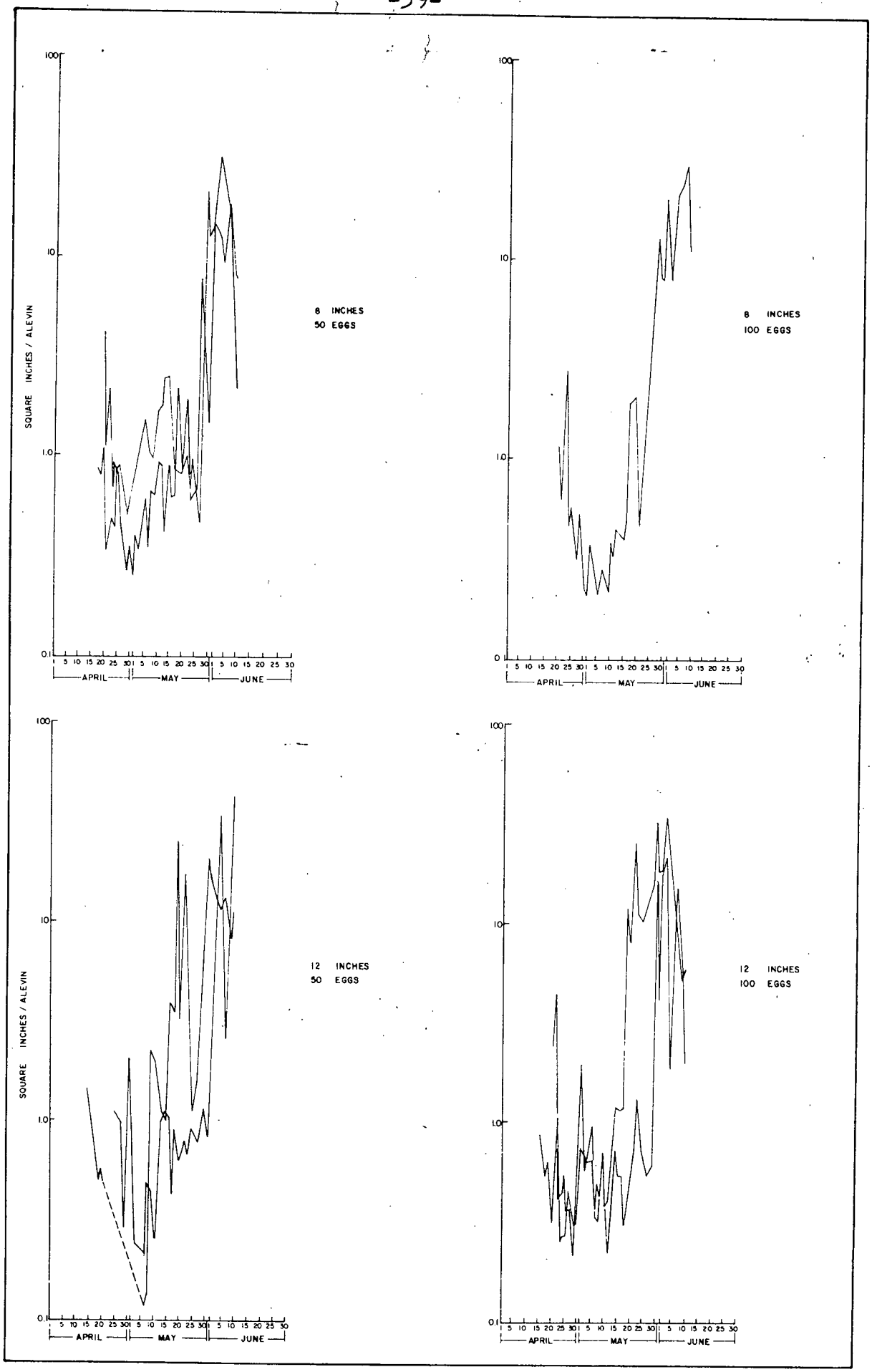


FIGURE 14.-1 Graph of the area occupied by the alevins in the large gravel. Upper - 8 inch burial depth, lower - 12 inch burial depth. Left side - egg density 50, right side - egg density 100.

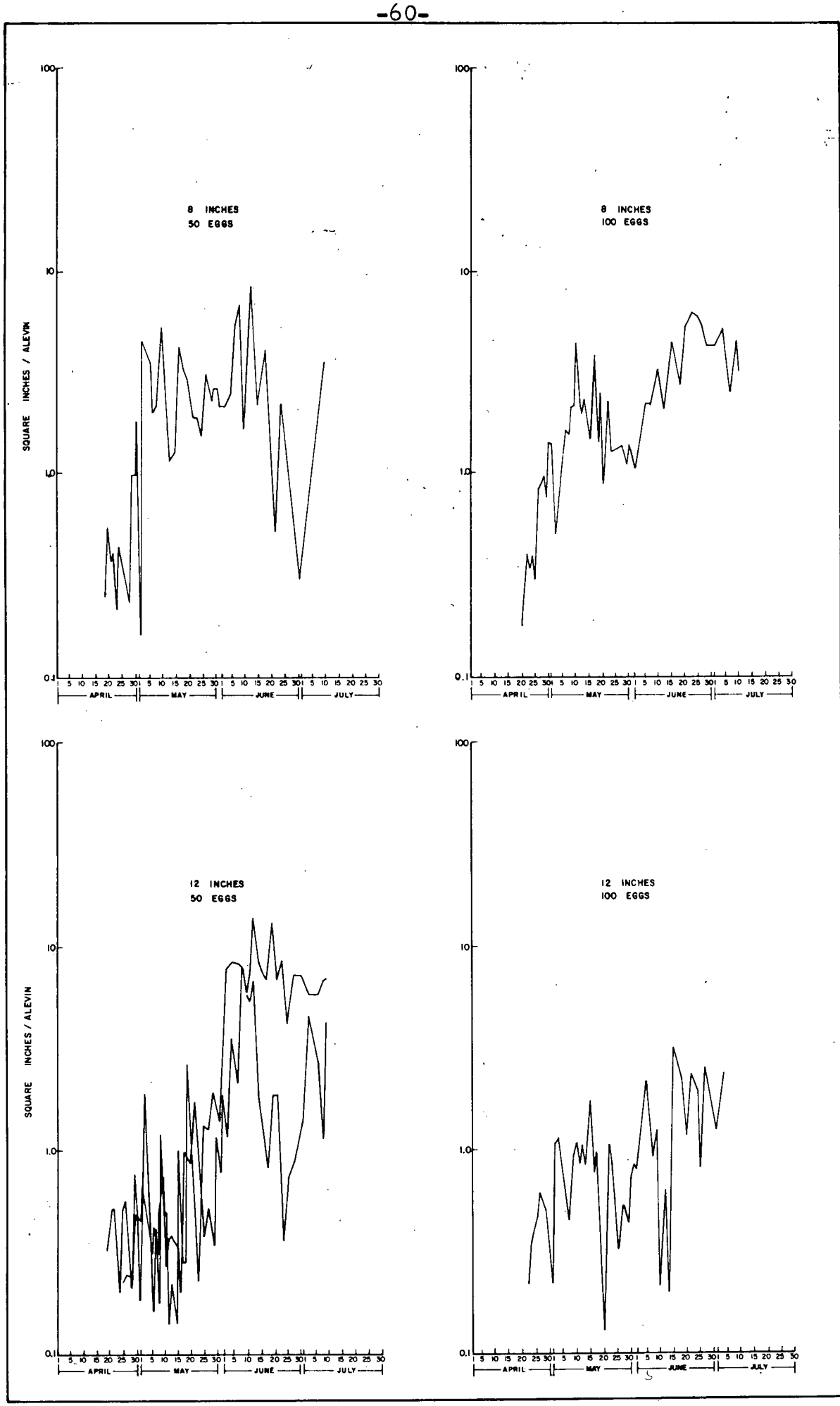


FIGURE 14.-2 Graph of the area occupied by the alevins in the small gravel. Upper - 8 inch burial depth, lower - 12 inch burial depth.

TABLE XIV.

The Maximum Area Utilized Per Alevin in the Experimental Aquaria. Expressed as Square Inches Per Alevin Visible.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	28.06	27.38	8.64	11.14
100	30.79	28.43	6.40	3.23

(Table XV). Burial depth and egg density had no effect on the condition index of the emerging fry.

Survival to Emergence

Survival (expressed as a percentage of emergent fry in relation to the number of eggs deposited) is summarized in Table XVI. The analysis of variance showed that survival was significantly lower in the smaller gravel. The difference may not be as marked as it appears, however, since even after July 12 there were still many fry in the small gravel which may or may not have emerged at a later date.

Pattern of Emergence

The nature of the experimental aquaria allowed only analysis of the number of days to first emergence (Table XVII). Only burial depth significantly affected the time taken to first emergence, i.e. deeper burial depth resulted in increased time.

It is obvious that the small gravel greatly lengthened the period of emergence, since some fry were still emerging up to July 10. It is suggested that future studies of this type would do well to equip the aquaria with traps to capture any fry immediately after emergence. The failure to provide such facilities made it impossible to determine the pattern of emergence, particularly in the large gravel, which the fry readily re-entered. Further, time of emergence may be an important factor in any consideration of subsequent survival.

TABLE XV.

Condition Indices (k) of the Fry Emerging from the Experimental Aquaria.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	1.55	1.37	1.72	1.89
100	1.67	1.47	1.71	1.93

TABLE XVI.

Percent Survival to Emergence in the Experimental Aquaria.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	94	92	46	45
100	52	86	76	30

TABLE XVII.

Number of Days after Planting to First Emergence in the Experimental Aquaria.

EGG DENSITY	BURIAL DEPTH IN LARGE GRAVEL		BURIAL DEPTH IN SMALL GRAVEL	
	8"	12"	8"	12"
50	67	71	67	68
100	67	67	67	73

Physical Factors

(i) temperature

The temperature varied little from one aquarium to another, one degree F being the maximum variance encountered. The thermograph record, therefore, gives the approximate mean daily temperatures for all of the aquaria (Fig. 15). The mean daily water temperature varied only 4.4 C (8 F) over a period of two and one half months, and averaged approximately 5.6 C (10 F) less than in the Robertson Creek channels.

(ii) oxygen concentrations

The mean oxygen concentrations of the water in the two gravel sizes were found to be:

small gravel - 12.3 mg O_2/l.

large gravel - 12.1 mg O_2/l.

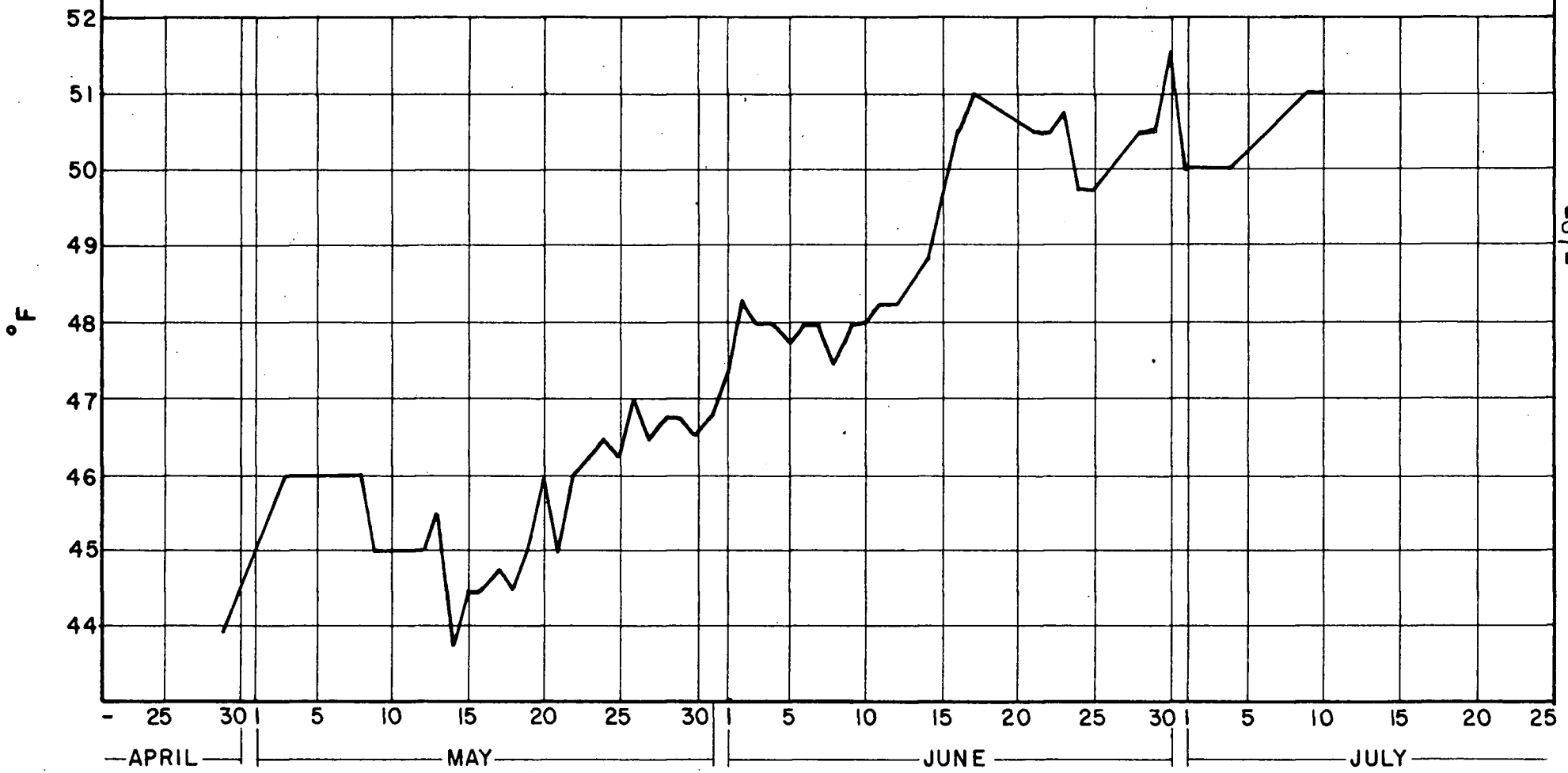
Both situations, then, were well supplied with oxygen and this environmental variable was not a limiting one in either of them.

(iii) subgravel flow

The flow characteristics observed in the gravel are shown in Fig. 16. In the small gravel, the flow was linear in the middle of the tank, but tended to upwell at the edges. Flow through the large gravel was similar but more rapid. Flow rates through the gravel, calculated from the time required for the dye to traverse the aquaria, were approximately .08 and .20 feet per minute in the small and large gravel respectively. These values are considerably less than the flow rates previously observed in the Robertson Creek channel gravel.

FIGURE 15.

Mean Daily Temperatures
Laboratory — April to July, 1967.



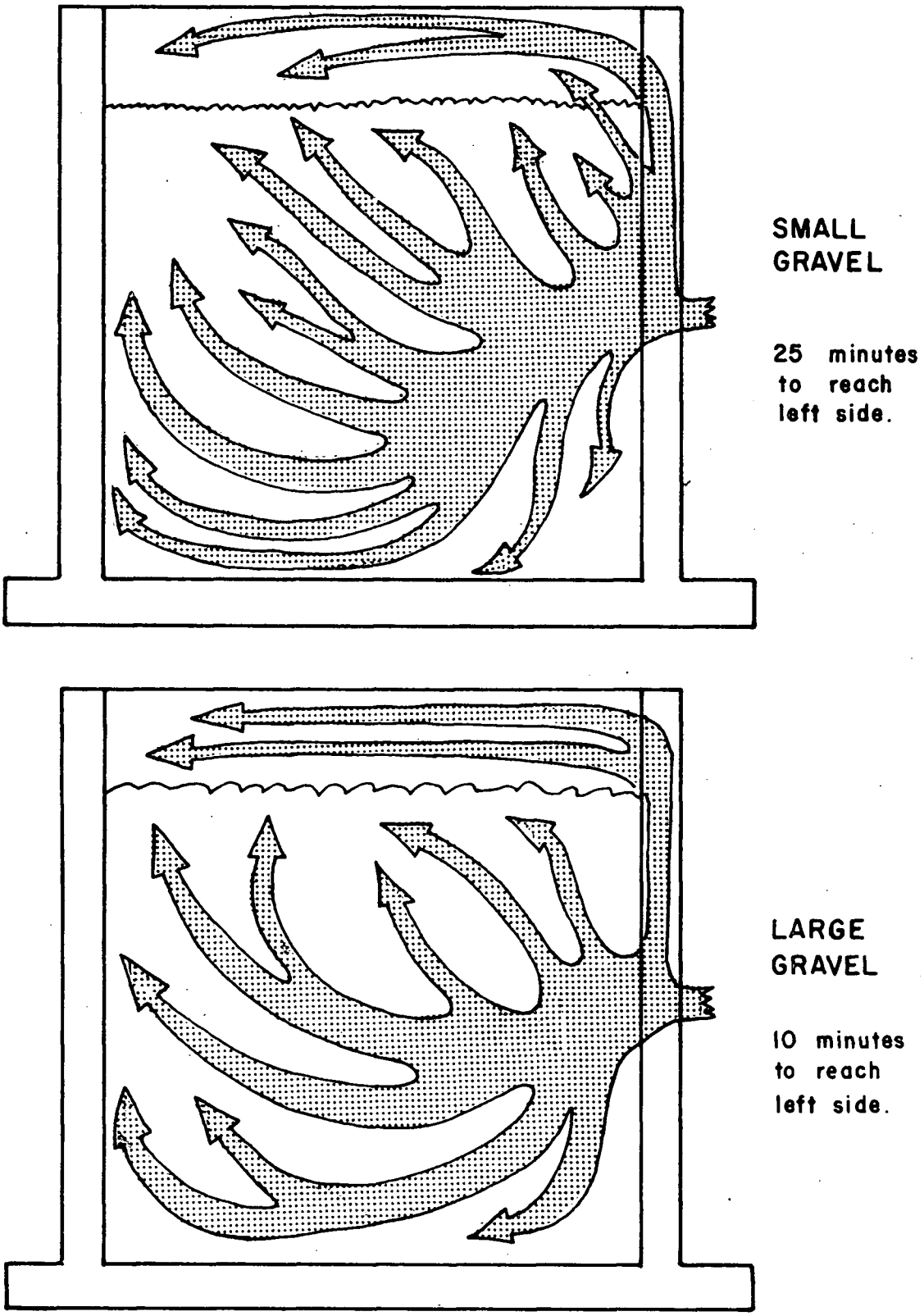


Figure 16. Subgravel flow through the experimental aquaria.

DISCUSSION

Several considerations must be borne in mind throughout the discussion of the above results.

First, because of unavoidable complications, different species of salmon were used in the two phases of the project. Coho salmon were used in the laboratory and chum salmon in the field. It may not be logical to assume that the behaviour patterns of the two species are going to be the same, because their life histories are quite different after emergence from the gravel. On the other hand, however, the work of Roth and Geiger (1963) on *Salmo trutta*; Stuart (1953) on *S. trutta*; Woodhead (1957) on *S. trutta*, *S. irideus*, and *S. salar*; and White (1915) on *Salvelinus fontinalis* indicate that all of these species studied to date have similar behaviour in the early stages. Further, Campbell's unpublished study of coho and steelhead alevins indicate that these species behave in the same manner as the Loch trout studied by Stuart. Comparative studies of salmonid fry have indicated, however, that although behaviour may show gross similarities, detailed observations reveal a great many differences between species. Further studies may show that this is true for the alevin as well.

Secondly, in the laboratory study, the assumption is made that the behaviour of the alevins along the glass is the same as those deeper in the gravel. This may not be a valid assumption, particularly in the small gravel, where those alevins on the plexiglass would be exposed to much more light

than those deeper in the gravel. The alevins in one aquarium however, were not visible but showed similar emergence patterns, condition at emergence, and survival to emergence to those alevins exposed to light, suggesting that the effect of the plexiglass on behaviour was minimal.

Thirdly, it is assumed that differences in temperature, oxygen and flow conditions have not affected the results. Oxygen was never found to be in short supply in the laboratory or the field. Therefore, flow rates must have been adequate in both situations, even though slower in the smaller gravel. Temperature conditions were much lower in the laboratory, but varied little from tank to tank.

The effects of the three variables tested are summarized in Table XVIII and will now be discussed in turn.

Effect of Gravel Size

In the larger gravel the alevins moved farther laterally (both towards the inlet and the outlet), towards the bottom, and towards the surface. They therefore covered a greater area of gravel in the laboratory. For the same reason the alevins emerged farther from the point of deposition in the field. In the field, but not in the laboratory they began their emergence earlier, and, in both situations, completed it earlier in the large gravel. Survival was much higher in the large gravel in both situations, but the fry were in poorer condition at emergence from the large gravel, at least in the laboratory.

TABLE XVIII.

The Effects of Increasing Gravel Size, Burial Depth and Egg Density on the Parameters Measured in the Study.
+, Increase; -, Decrease; 0, No Effect; N.E., Not Examined

EFFECTS OF		LABORATORY STUDY			FIELD STUDY		
		INCREASING GRAVEL SIZE	INCREASING BURIAL DEPTH	INCREASING BURIAL DENSITY	INCREASING GRAVEL SIZE	INCREASING BURIAL DEPTH	INCREASING BURIAL DENSITY
PATTERN OF EMERGENCE	LENGTH	N.E.	N.E.	N.E.	0	+	0
	FINAL	N.E.	N.E.	N.E.	-	+	0
	INITIAL	0	+	0	-	0	+
SURVIVAL TO EMERGENCE		+	0	0	+	0	0
CONDITION AT EMERGENCE		-	0	0	0	0	0
SPATIAL DISTRIBUTION		+	0	0	N.E.	N.E.	N.E.
ORIENTATION IN THE GRAVEL		0	0	0	N.E.	N.E.	N.E.
LATERAL MOVEMENT	TOTAL	+	0	-	N.E.	N.E.	N.E.
	INLET	+	0	-	N.E.	N.E.	N.E.
	OUTLET	+	+	+	N.E.	N.E.	N.E.
VERTICAL MOVEMENT	DOWN	+	0	-	N.E.	N.E.	N.E.
	UP	+	-	-	N.E.	N.E.	N.E.
DISTANCE OF MIGRATION		N.E.	N.E.	N.E.	+	0	0

The greater movement, earlier emergence and better survival were probably the result of more freedom of movement through the larger gravel. The poorer condition at emergence in the laboratory may have been the result of more frequent activity in the large gravel, where there was less support for the alevins with their large yolk sacs. The alevins, constantly having to right themselves, may utilize more energy for maintenance and thus be smaller at emergence than their counterparts in the smaller gravel. Such a relationship has been noted previously by both Marr (1963, 1965) and Bams (pers. comm., 1966). The latter investigator suggests that the alevins in the absence of support have a greater tendency to aggregate, to support each other in a sense. Such aggregation was indeed noted in the present study during the period when the alevins were on the bottom of the aquaria, at which time they would have little support from the gravel.

Effect of Burial Depth

The time to first emergence (in the laboratory) and to last emergence (in the field) was increased by burying the eggs at 12 inches. The net effect, therefore, was to increase the total length of the emergence period, as noted in the field. This may have been simply because the alevins had a greater distance to move to the surface when buried at a greater depth, or because less light was able to penetrate to that depth.

In the laboratory, increasing burial depth increased the amount of movement to the outlet and decreased the amount of

upward movement. The reason for these results cannot presently be ascertained. Burial depth had no effect on survival to emergence, condition at emergence, or distance moved from the point of deposition in the field.

Another factor in any consideration of optimum burial depth should be predation. The work of Phillips and Claire (1966) indicated that the sculpin, Cottus perplexus, could be a significant predator on salmonid alevins, when the gravel is large enough to allow access to them. In one inch gravel sculpins were able to penetrate approximately seven inches to consume alevins. Small sculpins (1.5 inches) were able to penetrate 14 inches into the 1 inch gravel. Obviously, gravel size and burial depth interact, and since burial depth has few if any detrimental effects, and large gravel many beneficial ones, it would appear best to bury eggs at greater depth in larger gravel, and not near the surface in finer material.

Effect of Egg Density

High egg density decreased the degree of vertical movement and of lateral movement, with the exception of movement towards the left. There was also some evidence that fry began their emergence earlier when present at the higher density.

The area utilization on a per alevin basis was not affected by the burial density. This may be evidence of competition in the gravel either for oxygen or for food (Dill, 1967). On the other hand, the alevins may be spacing themselves

out in response to carbon dioxide or nitrogenous waste concentrations. Further work on this subject would certainly appear warranted.

Responses of the Alevins to Light

Roth and Geiger (1963) found that alevins of brown trout were initially photonegative and moved downward after hatching. After spending some time on the bottom of the containers they then became positively phototactic, moved back towards the surface and emerged. That this was not a response to gravity was determined by turning the cylindrical containers sideways. The authors concluded that light was the single most important factor in allowing alevins to find their way up and out of the gravel bed. Bams (pers. comm., 1967), on the other hand, found that light actually retarded emergence and that gravity was a more important factor in subgravel orientation. The latter view seems a more realistic one, since it has been demonstrated by Heard (1964), as well as by Roth and Geiger themselves, that light can penetrate only into the upper few centimeters of the gravel.

In the present experiment, the alevins in the large gravel, i.e. where light penetrated the farthest, showed more downward movement and more activity at night than did the alevins in the smaller gravel. The explanation for such behaviour comes from the studies of Woodhead (1957), Stuart (1953) and White (1915) who found that newly hatched Salmo larvae were negatively phototactic. Stuart found that the alevins during the period of

final yolk absorption became either positively phototactic or neutral to light.

Light may not be of any importance in nature until the alevins have entered the upper few inches of gravel. It is uncertain, therefore, why the young larvae are negatively phototactic but it may prevent them from premature emergence if by chance they are buried too near the surface, or reach there too early in their upward migration.

The alevins' response to light probably accounts for the large proportion of daylight emergence noted, particularly in the smaller gravel, where the alevins (with the exception of those against the glass) had no experience with the day-night cycle until very near the surface. Movement through the gravel to the surface may be the result of gravity orientation or the result of internal physiological factors, i.e. motivation. Both of these need to be examined in future investigations.

Heard (1964) also suggests that daytime emergence may exceed daytime migration downstream, since, once the fish have emerged into high light intensities and filled their air bladders they seek cover until nighttime (Neave, 1955; Hartman et al, 1962). In turbid rivers, migrations of pink and chum salmon fry have also been recorded during daylight hours (Neave, 1955).

It should be noted, however, that the species of Oncorhynchus vary in their response to light (Hoar, 1958). The significance of this finding to the present study is uncertain, although it indicates that we should avoid inferring the

behaviour of an entire genus from studies conducted on one or two species. A comparative study of alevin behaviour should be carried out.

Responses of the Alevins to Current

White (1915) found that brook trout alevins were positively rheotropic (=rheotactic) at the time of hatching, although both Bishai (1960) and Stuart (1953) found that brown trout alevins were negatively rheotropic until yolk absorption, at which time their response became a positive one. Roth and Geiger (1963) found that brown trout alevins were positively rheotactic throughout the entire alevin stage. The present experiments indicate that coho salmon alevins are definitely positively rheotactic in later stages, but show no consistent orientation to current for the first few weeks after hatching, distributing themselves in a fairly random manner with respect to current.

Optimal Conditions of Planting

The present experiments offer conclusive evidence that large gravel is the preferred material for artificial incubation and spawning channels, since it results in earlier emergence and better survival rates. Several factors suggest, however, that the gravel should be of a more mixed grade than that utilized in these experiments. These factors include the poorer condition at emergence, the possibility of higher predation in the gravel, and wider spatial distribution.

Burial depth should be great enough to prevent predation but not so deep as to seriously retard emergence, since fry which emerge over a short period of time and at higher water levels probably suffer less predation during their downstream migration. Further, early emerging fry of such species as coho and chinook salmon stand a better chance of finding suitable habitats in the stream channel and subsequently have higher growth rates (Mason and Chapman, 1965).

Briggs (1953) found that coho buried their eggs at an average depth of 9.8 inches. Burner (1951) found that the average depths of chum and coho salmon eggs in the Columbia River were 8.5 and 8.0 inches respectively, while Kusnetzov (1928) found chum salmon eggs to be buried 9 to 10 inches. This depth, in view of the effects of gravel size noted in the present study, is probably optimum.

There is no evidence that either of the densities utilized in this study were high enough to make competition an important consideration. Egg pockets in natural redds, however, may contain eggs at higher densities than those studied here. The maximum density utilized in the laboratory was 150 eggs per cubic foot.

This study, being one of the first conducted on the subgravel behavioural ecology of the Pacific salmon, may provide useful background information for future investigators, suggest testable hypotheses for them, and stimulate them to concentrate at least some of their efforts on this rewarding field of research.

Several future studies have been suggested by the present work. These include modification of emergence timing through manipulation of environmental conditions, comparative ethological studies of the salmonid alevin, particularly in response to light, and studies of interaction or competition between alevins within the gravel bed. Such studies should be conducted in the immediate future, both because of their theoretical and their practical implications.

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