FRI-UW-8414
December 1984

FISHERIES RESEARCH INSTITUTE
University of Washington
Seattle, Washington 98195

Intragravel Behavior of Salmonid Alevins in Response to Environmental Changes

by

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Project Completion Report

July 20, 1983 to September 30, 1984
Project A-0120-WASH, U.S. Department of the Interior Grant No. G-876

with

State of Washington Water Research Center
Washington State University
Pullman, Washington

and

City of Seattle
Department of Lighting
Office of Environmental Affairs
Seattle, Washington

Approved:

Submitted: December 1984

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Director

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ABSTRACT

The purpose of this research was to study the morphological development, survival, and behavior of chum, coho, and chinook salmon, and steelhead trout alevins from hatching through yolk absorption. The ability of alevins to respond adaptively to conditions of environmental stress was determined and a comparison of responses between species was made. Throughout development the chinook salmon were the largest in total weight (body plus yolk). The chum and coho salmon were intermediate and similar in size while the steelhead were the smallest of the four species studied. The alevins of all four species were unable to swim at hatching due to poorly developed fins and large yolk sacs. Swimming ability increased as body and fin development proceeded and yolk sac volume decreased.

The metabolic rates of chum, coho and steelhead alevins were measured with a respirometer. All three species increased the amount of oxygen consumed per gram of total dry weight from hatching through yolk absorption.

The LT_{50}'s of alevins subjected to single, long-term dewaterings were directly related to time in days after hatching. The decrease in survival time was attributed to increased metabolic rate and decreased yolk sac size. The highly vascularized yolk sac surface acted as a secondary respiratory organ when gill respiration was limited due to dewatering.

Downward intragravel movement of alevins of all four species occurred within 48 hours of hatching under conditions of adequate velocity, dissolved oxygen and darkness. Chum, coho, and steelhead alevins made more successful migrations than chinook alevins. The differences in number of alevins moving was attributed to size. Alevins of all four species demonstrated positive rheotaxis by migrating into the current.

Chum salmon alevins were able to migrate downward through smaller

openings than similar sized coho alevins and in greater numbers than the smaller steelhead. Greatest head diameter appeared to limit the size of opening an alevin could move through.

Alevins of all four species were positively rheotactic during the middle and late developmental stages when tested at apparent water velocities of 40 and 120 cm/min. Movement was random at zero velocity for all developmental stages and all species tested.

The alevins of all four species moved toward the water source with higher dissolved oxygen when tested in a two choice tank at 2 vs. 6 mg/L, 4 vs. 8 mg/L and 6 vs. 10 mg/L dissolved oxygen concentrations. The number of alevins responding was greater at later developmental stages.

Photobehavioral studies indicated that negative photoresponses increased as morphological development progressed. A transition from photonegative to photopositive behavior occurred before initiation of emergence from the gravel in each species. The transition to photopositive behavior was most rapid in chinook alevins, intermediate in chum and coho, and slowest in steelhead trout. The earlier transition to photopositive behavior may allow the larger alevins to initiate upward migrations with sufficient remaining yolk supplies to insure successful emergence from the gravel.

ACKNOWLEDGMENTS

The research on which this report is based was financed in part by the United States Department of Interior as authorized by the Water Research and Development Act of 1978 (P.L. 95-467) and made available through the State of Washington Water Research Center. Additional funding was provided by the City of Seattle Department of Lighting. These studies were initiated to gain a better understanding of the potential effects of natural and hydroelectric flow fluctuation on salmonid alevins in the Skagit River, Washington.

We thank the Washington State Departments of Fisheries and Game for providing the salmon and steelhead eggs for this research. Dr. E. L. Brannon, University of Washington School of Fisheries gave advice on salmon egg development, handling, and salmon alevin behavior. Mr. Glen Yokoyama, University of Washington hatchery supplied eggs and technical assistance. Students who assisted in various aspects of this study were William Edwards, Geoffrey Lang, and Bruce Campbell.

DISCLAIMER

1.0 Introduction

The Pacific salmon (Oncorhynchus) are anadromous fish that spawn in their natal streams after one to four years of feeding on the high seas. Salmon have been classified as non-guarding, brood-hiders (Balon 1975). The female digs a nest or redd in the stream gravel and deposits from 1500 to 7000 eggs. Embryonic mortality during the intragravel phase often exceeds 90% (Wicket 1952, Salo and Noble 1954; Semko 1954; Hunter 1959; McNeil 1969, 1980; and Larkin 1977). Kryzhanovsky (in Balon 1975) stated that the two most significant factors which influence mortality during embryonic development are "predators and availability of oxygen. All other factors are associated with these two and create together an extraordinary variety of adaptations associated with early development."

The salmonid strategy of depositing eggs in the gravel has lowered the number of potential predators but increased the problems of obtaining sufficient oxygen for survival and growth. Some of the interrelated factors that affect the embryonic survival are 1) the size of the embryo which can vary between and within species; 2) the metabolic rate; 3) the composition of the stream gravel; 4) the apparent water velocity through the gravel; 5) temperature and 6) dissolved oxygen content of the water; 7) redd dewatering from natural stream fluctuations or those caused by man; and 8) potential dislodgement of embryos and alevins from the gravel by redd superimposition or scouring from floods.

The embryonic phase of salmon development can be divided into two stages, the embryo and the alevin. The embryo stage extends from fertilization to hatching. The response of the embryo to various conditions of stress has been studied extensively. It has been shown that both exposure to light (Brannon 1965) and a reduction in water velocity result in decreased size at hatching

(Silver et al. 1963; Shumway et al. 1964). At the other extreme, high water velocities have been responsible for downstream displacement of eggs (Crisp 1981; Ottaway and Clarke 1981). Studies have demonstrated that oxygen requirements increase throughout embryonic development (Alderdice et al. 1958). Those embryos subjected to chronic low dissolved oxygen concentrations throughout their development hatched later and were smaller than embryos incubated at higher oxygen levels (Alderdice et al. 1958; Garside 1959, 1966; Silver et al. 1963; Shumway et al. 1964). Embryos exposed to low dissolved oxygen just prior to hatching will hatch prematurely at a rate dependent on the degree of hypoxia (Alderdice et al. 1958). Studies of embryos that had been dewatered in natural streams (Hobbs 1937; Hardy 1963 and Hawke 1978) and in the laboratory (Reiser and White 1981; Fast et al. 1982; Becker et al. 1982) have found that embryos are capable of surviving for extensive periods without water.

The alevin stage of development begins at hatching and ends as the fish emerge from the gravel as free swimming fry. Hatching gives the alevin the adaptive advantage of mobility that was previously lacking in the embryo stage. In utilizing this mobility to enhance survival the alevin should demonstrate an adaptive response to environmental stresses such as light, low or high velocity, low dissolved oxygen, and redd dewatering. Very little research has been done on the ability of the alevin to move through the gravel to avoid or reduce these stresses.

At least two distinctly different early life history strategies exist in anadromous salmonids. Chum salmon (Oncorhynchus keta) and pink salmon (O. gorbuscha) migrate to sea shortly after emerging from the gravel. In the second strategy, coho salmon (O. kisutch), chinook salmon (O. tshawytscha), sockeye salmon (O. nerka) and steelhead trout (Salmo gairdneri), remain in freshwater for one to two years before migrating to sea. These differences in post-emergent strategy raise the possibility of the evolution of other adaptive strategy differences between species during the intragravel incubation stages.

The purpose of this study was twofold:

1. to determine the ability of salmonid alevins to respond adaptively to conditions of environmental stress, and
2. to compare these responses between chum, coho, and chinook salmon and steelhead trout.

The specific objectives were:

1. to determine the relative size and morphological development of each species,
2. to determine the oxygen consumption rate of developing alevins,
3. to determine the tolerance of alevins to one time dewatering,
4. to determine if intragravel movement of alevins occurs when adequate conditions of velocity, dissolved oxygen and darkness exist,
5. to determine what limits the downward intragravel migrations of alevins,
6. to determine the movement and rheotactic behavior of alevins at several water velocities,
7. to determine the intragravel movement of alevins in response to changes in dissolved oxygen concentrations,
8. to determine the photobehavior (direction and magnitude)of developing alevins.

2.0 Materials and Methods

2.1 Morphological Development

2.1.1 Experimental Stocks of Fish

Four species of salmonids were studied in the 1983-84 experimental season. Chinook and coho salmon eggs were obtained from the Washington Department of Fisheries Skagit Hatchery. Chum eggs were from the W.D.F. Garrison Springs Hatchery and steelhead trout eggs were obtained from the Washington Department of Game South Tacoma Fish Hatchery. Each lot consisted of eggs that had been stripped from at least three females and fertilized by milt from several males to ensure genetic diversity of the progeny.

2.1.2 Laboratory Description

The eggs were transported to the University of Washington Fisheries Research Institute either immediately after fertilization or after the eggs had reached the eyed stage. This was done to avoid mortality from shock. The eggs were kept in a Heath Techna incubator that was covered with black polyethylene sheeting to maintain darkness. The Heath Incubator and associated experimental apparatus were housed in a 10 x 12 x 8 foot dark room constructed of black polyethylene sheeting. The water supply used for incubation and all experiments was pumped to the wet lab from Lake Washington. The mean daily water temperature was estimated from several readings taken on a standard mercury thermometer. The dissolved oxygen level of the incubation water was monitored on a daily basis using a Yellow Springs Instruments Model 54 oxygen meter. The meter was air calibrated daily. Meter readings were occasionally compared with results of the azide modification of the iodometric winkler method (standard methods) to provide greater accuracy. Infrared lights were used to illuminate the room during the set up of experiments and for recording data.

2.1.3 Alevin size, growth, and development

The size of an alevin can have a great effect on its ability to survive and move through the gravel. Differences in egg size within a species of salmon have been studied by Rounsefell (1957), Bagenal (1966), Kazakov (1981) and others. Bakkala (1970) found that chum eggs ranged in diameter from 4 to 9 mm. Other studies have shown that a direct relationship exists between egg size and the size of the resulting fry (Koski 1975). Fry that emerge from the gravel at a size larger than their siblings are less susceptible to capture by predators (Parker 1971; Beall 1972; Walker 1974). Mason (1976) found that large coho fry established territories and drove their smaller siblings from the experimental tanks. Thus there appears to be an advantage in producing as large a fry as possible. At the same time it has been demonstrated that smaller fry have a higher survival to emergence rate than larger fry (Bjornn 1969; Koski 1975; Phillips et al. 1975). Bjornn (1969) found that steelhead fry had a higher emergence rate than larger coho and chinook fry in the same gravel substrate. Koski (1975) believed that this was due to size selective pressure limiting the movement of the larger fry through the gravel interstices. Thus size also has an effect on the alevins ability to move through the gravel.

The stage of morphological development (fin development, yolk absorbed, etc.) also affects the movements of an alevin. Thomas et al. (1969) have demonstrated that the degree of yolk sac absorption influences an alevins ability to swim.

To record the morphological development of the fish being studied, samples of 30 alevins (for chum and coho) or 10 alevins (for chinook and steelhead) were removed from the Heath incubator at four to eight day intervals from hatching to emergence. The alevins were preserved in 10% neutralized formalin. Parker (1963) determined that fish preserved in formalin shrank to 97% of their original length in 24 hours and 96% after 30 to 40 days. Further shrinkage was not significant. At a later date the alevins were removed from the formalin, rinsed and dried. Measurements of the total length; caudal, dorsal and pectoral fin heights; diameter of left eye; head width and depth and greatest body depth were made using a Bausch & Lomb binocular dissection scope and Enco calipers (Figure 1). The yolk material was then separated from the body and each was dried overnight at 98°C in preweighed aluminum foil cups. The dry yolks and bodies were then weighed on a Mettler H20T analytical balance. These weights yielded accurate information on the size and stage of yolk absorption of the species and stocks of fish studied.

The dry yolk and body weights were converted to percentage of total dry weight and plotted against time from hatching to yolk absorption to determine the amount of yolk that was converted to body tissue and the amount used for metabolism (activity and maintenance). The conversion factor of yolk to body weight was calculated using the formula

$$100 \left[\frac{B_1 - B_0}{Y_0 - Y_1} \right] = \% \text{ conversion efficiency}$$

where $B_1 - B_o$ = dry weight increment of body

and $Y_o - Y_1$ = dry weight decrement of yolk

The morphological indices of development (MI from Carey and Noakes 1981) were determined by dividing each morphological measurement by the largest

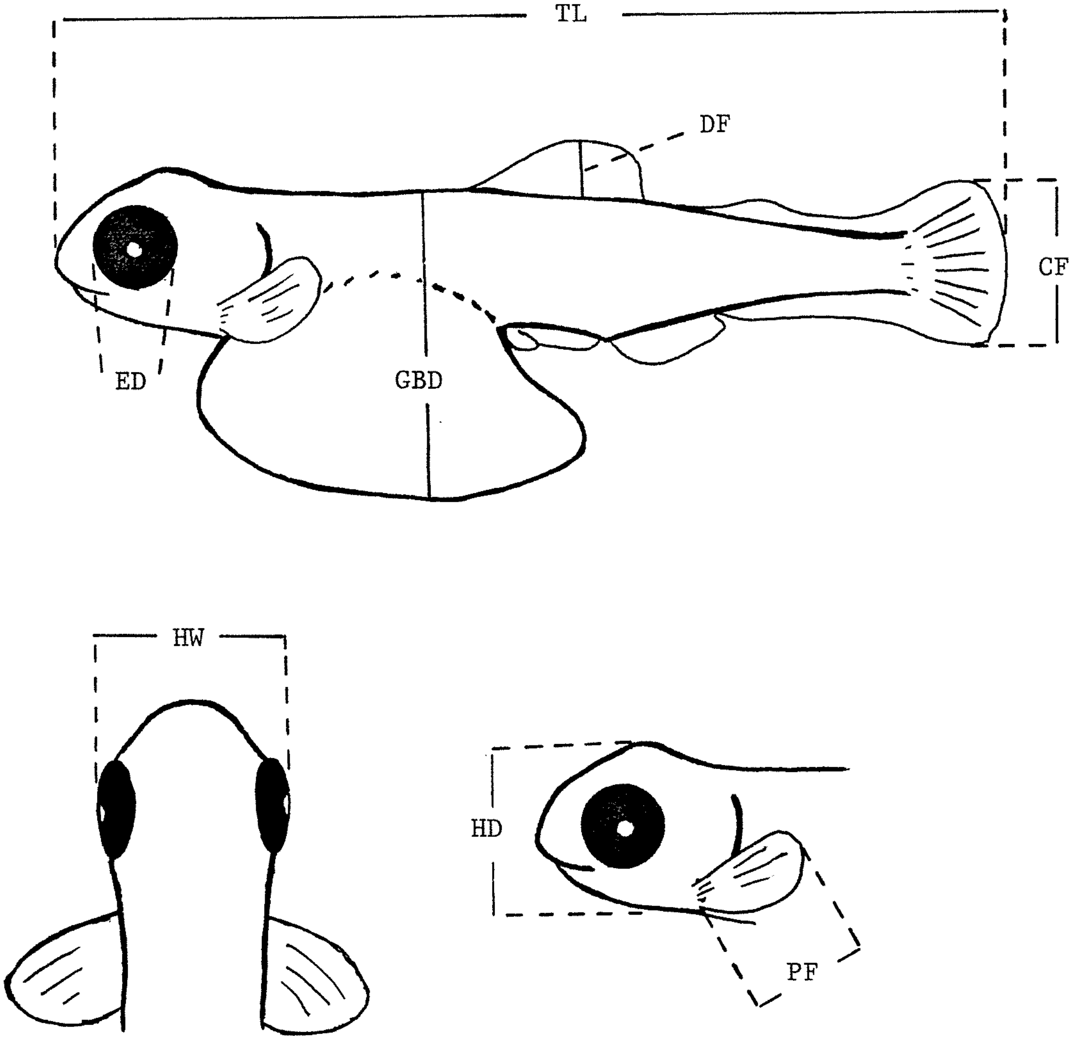

Fig. 1. Schematic drawing of salmonid alevin showing where morphological measurements were made. CF = caudal fin height, DF = dorsal fin height, ED = diameter of left eye, GBD = greatest body depth, HD = head depth, HW = head width, PF = pectoral fin height, TL = total length.

value for that feature and multiplying by 100. Dry yolk weight was divided by initial yolk weight. The MI's were plotted against time (days after hatching) to show the development of the alevin in relation to swimming ability (fin growth and body streamlining).

The measurements of the head width and depth and the greatest body depth were used in determining the morphological factors limiting the downward intragravel movement of alevins.

2.2 Metabolic rates

In addition to the size of an alevin, the metabolic rate may also influence its survival and/or fitness. The metabolic rate can be measured by the quantity of oxygen an organism consumes over a given period of time. The requirements of embryos and alevins differ during the incubation period. Hayes et al. (1951) have shown that hatched alevins of Atlantic salmon (Salmo salar) could obtain twice as much oxygen as unhatched embryos in the same water. It has been suggested that a higher oxygen requirement per egg at the later prehatching stages creates a local hypoxial micro-environment causing premature hatching (Alderdice et al. 1958). This premature hatching may be an adaptation of the embryo to increase its oxygen uptake.

After hatching the oxygen demand of larval fishes increases markedly with age (Sharmardina 1954, from Davis 1975; Semko 1954). Nikiforou (1952, from Davis 1975) found better growth in yolk sac fry of Atlantic salmon (Salmo salar) reared at 6.8-7.5 mg O_2/liter compared with those reared at 4.5-5.0 mg O_2/liter. The latter group weighed less than one-half of the high oxygen group. Brett and Blackburn (1981) found that a critical oxygen level of 4.0 to 4.5 mg O_2/liter existed for growth of coho fry. Thus metabolic rate and alevin development may be limited by the dissolved oxygen content of the incubation water.

Temperature also affects the survival and fitness of alevins (Hayes et al. 1953; Combs and Burrows 1957; Alderdice et al. 1958; Combs 1965; Garside 1966; Hamor and Garside 1976; Alderdice and Velson 1978; Graybill et al. 1979; Dong 1981; Heming 1982). Increases in temperature will generally cause an increase in the rate of development of the alevin. Temperature increases also lower the oxygen content of the water. Very high temperatures or near freezing temperatures will lower the survival of the alevins.

A Gilson Differential Respirometer was used to measure the alevin metabolic rate in relation to stage of development and water temperature. Three alevins were placed in a respiration flask and water was added to give a total volume of 10 ml. Filter paper was placed in the center well and 0.2 ml of 10% KOH was added to absorb the CO_2 gas given off as a respiratory byproduct. The system was then closed to atmospheric air and the amount of oxygen respired by the alevins was measured hourly for a total of three hours. Five replicate samples were tested simultaneously. Oxygen consumption was measured at 4, 8, and 12°C for each sample. All the alevins were then preserved in 10% formalin and dry yolk and body weights were determined as described in section 2.1.3. The mean of the three hourly readings was divided by the weight of the three alevins in each flask to yield the amount of oxygen consumed per gram alevin dry weight per hour for each of the three temperatures tested. These oxygen consumption rates were plotted against time from hatching to yolk absorption.

2.3 Dewatering Tests

Another cause of mortality in salmonid redds is dewatering. Salmon redds have been subjected to dewatering due to natural river fluctuations and regulated flows downstream from hydropower generating stations. Field observations (Hobbs 1937; Hardy 1963; Hawke 1978) and laboratory experiments (Reiser and White 1981; Becker et al. 1982; Fast et al. 1982) have shown the resiliency of salmonid embryos to dewatering. Dewatered embryos have been shown to survive for periods of one to five weeks with no significant effects on hatching survival, growth rates or fry quality (Reiser and White 1981). Fast et al. (1982) believe that embryos in the dewatered gravel could obtain sufficient moisture from the surrounding gravel to sustain oxygen transfer across the egg membrane.

Upon hatching an alevin loses this method of oxygen transfer and is forced to obtain oxygen across the gill surfaces. Several studies have been conducted to determine the survival of dewatered alevins when downward movement was restricted by smaller gravel sizes. Becker et al. (1982) reported total mortality with repetitive 8 hour dewatering of yolk sac alevins and with repetitive one hour dewatering of emerging fry. Fast et al. (1982) found that newly hatched chinook and coho alevins suffered high mortalities in repetitive dewatering tests except in cases where alevins were able to avoid being dewatered by making downward migrations through larger gravel sizes. Preliminary studies have been performed on the survival of alevins in single, dewatering events (Stober et al. 1982).

The purpose of the dewatering experiment was to determine the survival time of alevins that were subjected to single, long-term dewatering incidents at various stages of development from hatching to yolk absorption. In the dewatering experiment 50 alevins from each species were randomly selected from the incubation trays and placed in polyvinyl chloride cylinders in a water bath. The cylinders had a screen barrier at their midpoint so that the upper half of the cylinder had glass marbles (2.16 cm diameter) and alevins while the lower half was empty (Figure 2). The alevins were placed on the marbles in the upper half of the cylinder and given a 15 minute adjustment period. During this period the alevins would migrate downward through the 15 cm of glass marble substrate. The water bath was then lowered so that the alevins were 5 to 10 cm above the water level. Three replicates of 50 alevins were dewatered for test periods of .5, 1, 2, 4, 8, 16, 24, 36, and 48 hours. The samples were rewatered at the end of the test period and the alevins were given 30 minutes to recover. The number of dead and live alevins was then recorded. The number of surviving alevins was plotted against length of time dewatered on "Log-probability" paper. The LT_{50} (time to 50% mortality) was then estimated for each test series by eye fitting a line to the partial response points. The LT_{50} values were then plotted against days after hatching to yield a survival curve from hatching to emergence.

2.4 Alevin Behavior Experiments

2.4.1 Movement under favorable conditions.

Hatching gives the alevin mobility previously lacking in the embryo stage. Intragravel movement is an adaptation that may be used by alevins to avoid stress. Under optimal conditions one would predict that alevin movement would be limited because utilization of energy for movement would reduce the energy available for growth. There are conflicting results reported in the literature regarding the intragravel movement of alevins under conditions of favorable dissolved oxygen, velocity and darkness.

Bams (1969), found that under favorable conditions there was no intragravel migration of sockeye alevins until emergence. Other studies have reported an immediate posthatching downward movement in coho salmon (Dill and Northcote 1970), brown trout (Roth and Geiger 1963) and rainbow trout (Carey and Noakes 1981). These conflicting results may be due to the different

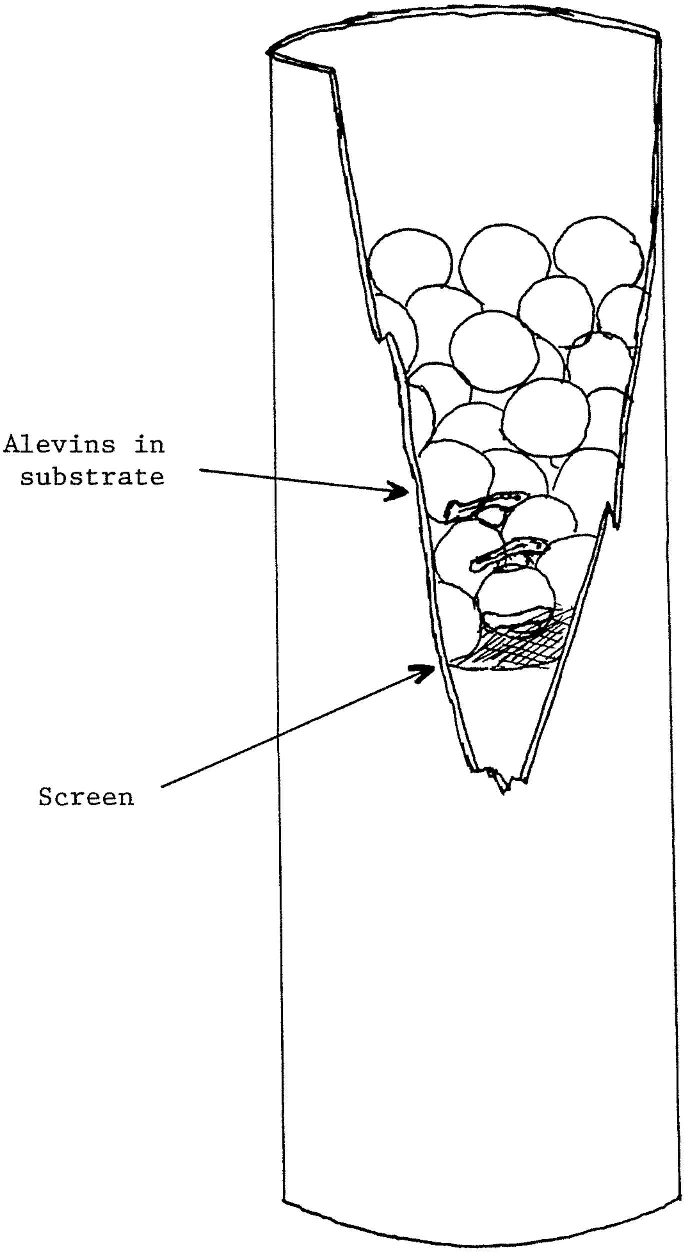

Fig. 2. Dewatering chamber with alevins in substrate in upper section. The screen prevents downward movement of alevins when dewatered.

species that were tested or the different experimental designs. In this study four different species were tested under the same experimental conditions in an attempt to resolve this question.

Three plexiglas aquaria (modified from Dill and Northcote 1970), designed to facilitate observations of alevins in the intragravel environment, were used to determine if intragravel movement occurred under conditions of adequate velocity, dissolved oxygen, and darkness. These aquaria were 7.5, 77 and 62 cm high (Figure 3). The aquaria were filled with gravel substrate. The gravel substrate approximated the gravel composition found in chinook and pink salmon redds sampled with a freeze core apparatus on the Skagit River (Stober et al. 1982). The geometric mean diameter (dg) of the substrate was 31.6 mm. A lateral water flow at an apparent velocity of 30.0 cm/min was supplied to the aquaria. Traps were placed beneath the gravel substrate to collect alevins that had moved. One hundred embryos were placed in the center of the tank, 20 cm above the traps just before hatching. Dissolved oxygen levels of the outflow water were monitered. The aquaria were covered with black polyethylene sheeting to maintain darkness. The covers were removed after 48 hours to observe the position of the alevins.

The alevin traps allowed the rheotactic component of movement to be quantified by the retention of the alevins in each of four separate compartments from upstream (positive rheotaxis) to downstream (negative rheotaxis). For analysis, the numbers of alevins were combined into two groups, upstream (1 and 2) and downstream (3 and 4) and the independent experiments were tested for heterogeneity within each species (Zar 1974). The pooled results were tested for randomness using chi-square analyses with the null hypothesis that 50:50 distribution between upstream and downstream movement would occur (Zar 1974). In addition, the compartments allowed

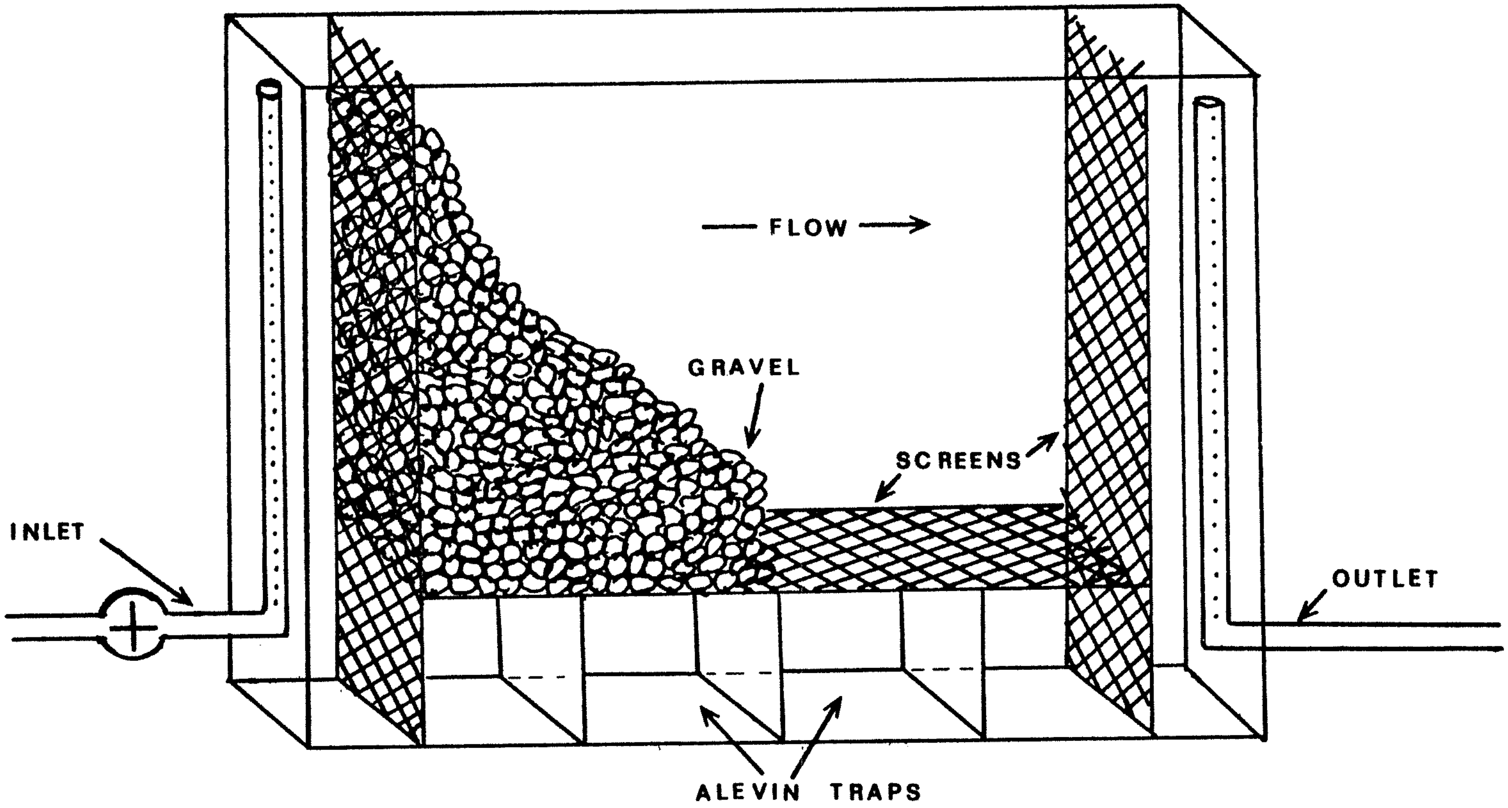

Fig. 3. Alevin behavior aquarium with alevin traps underneath to determine rheotactic movement.

observations on the timing of the onset of emergence of alevins from the substrate. The aquaria were monitored on a daily basis at later yolk absorption stages to determine when the alevins began their upward movement through the gravel.

2.4.2 Downward Intragravel Movement

An important factor regulating the movement of alevins through the substrate is gravel size, or more specifically, interstitial space size. Numerous field and laboratory studies have been conducted on the relationship between emergence of salmonid alevins and the composition of the gravel substrate in the redds (Wickett 1958; Coble 1961; McNeil and Ahnell 1964; Koski 1966, 1975; Hall and Lantz 1969; Bjornn 1969 in Reiser and Bjornn 1979; Hausle and Coble 1976; Phillips et al. 1975; and McCuddin 1977 in Reiser and Bjornn 1979). These studies demonstrate that fine sediment, usually less than 3 mm in diameter, is inversely related to salmonid survival to the point of emergence. Koski (1975) in studies of chum alevins emerging from sand gravel mixtures, found that smaller fry emerged from gravel containing a high percentage of sand. He suggested that there was a selective mortality against the larger fry in high sand substrates.

All of the aforementioned studies were concerned with upward emergence movement. Dill and Northcote (1970) and Fast et al. (1982) have studied the downward movement of alevins. Both studies concluded that alevins were limited in their downward migrations by smaller gravel sizes. No research on how interstitial space size limits alevin movement has been done.

The purpose of this experiment was to determine the size of interstitial opening that limited the downward movement of alevins. To determine the limiting opening a series of USA Standard Testing Sieves ranging from 4.76 mm to 1.70 mm mesh size were placed in a 5-gallon tank of water. A group of 50 alevins was randomly selected and placed in the water on the top sieve (4.76 mm). The alevins were given one hour to adjust. The water level was then lowered causing the alevins to move downward through the sieve series. The number of alevins on each sieve was recorded and a second group of alevins was tested. Tests were performed every 3 to 7 days for chum and coho and 8 to 12 days for steelhead from hatching to emergence. The morphometric measurements of head depth and width, and greatest body depth were compared to the mesh size the alevins were unable to migrate through.

2.4.3 Movement and Velocity

Apparent water velocity (velocity through a cross section of gravel) is important in transporting oxygen to the incubating embryos and removing metabolic wastes. Coble (1961) reported that higher velocity generally resulted in higher dissolved oxygen content in the water. Several other studies, however, have shown that reductions in water velocity resulted in reduced size of coho and chinook alevins at hatching even when dissolved oxygen levels remained high (Silver et al. 1963; Shumway et al. 1964). Unfortunately these studies were terminated at hatching and gave little information on the requirements of the alevins.

At the other extreme, research has shown that alevins reared at high apparent water velocities generally weighed less than those reared at lower flows (Brannon 1965; Bams and Lam 1983). Very high flows have also been responsible for downstream displacement of embryos and alevins (Crisp 1981; Ottaway and Clarke 1981). Thus both low and high water velocities may be detrimental to the survival and development of alevins.

Intragravel movement of alevins and the positive or negative rheotactic component of that movement may be of considerable importance in locating areas that have not had dissolved oxygen lowered and metabolic wastes increased due to biological oxygen demand of decaying embryos or water reuse by sibling alevins. Bams and Lam (1983) found that pre-emergent fry showed a decrease in length and weight due to deteriorating water quality caused by increased numbers of embryos or alevins upstream. To increase their own fitness one might expect alevins to move forward or off to either side rather than downstream from their siblings.

A 3 x 3 factorial design testing alevin developmental stages at early post-hatching, 50% yolk absorption, and pre-emergence versus water velocities of 0, 40, and 120 cm/min was utilized to study movement and rheotactic behavior. Three wooden tanks 30 x 30 x 90 cm long were constructed with water entering one end of the trough and flowing through an enclosed gravel bed (1.35-5.08 cm) in the center and out a downstream stand pipe (Figure 4). A false bottom 5 cm high was placed in the center of the trough to facilitate trapping alevins moving from the gravel. Alevin traps made of 3/4 round polyvinylchloride pipe were placed up and downstream from the gravel bed to determine the number and direction of alevin movement at each velocity. A lid was placed over the entire box to eliminate light. A group of 50 alevins was placed in the enclosed gravel compound in the center of the trough for each test. After 24 hours the lid was removed and data on movement recorded.

2.4.4 Movement and Dissolved Oxygen

Two levels of oxygen are important to the survival and growth of alevins. The first level is the lethal concentration below which survival decreases rapidly. This level ranges from about 1.5 to 2.0 mg O_2/liter (Shepard 1955; Herrmann et al. 1962; Davis 1975; Koski 1975; Brett and Blackburn 1981). The

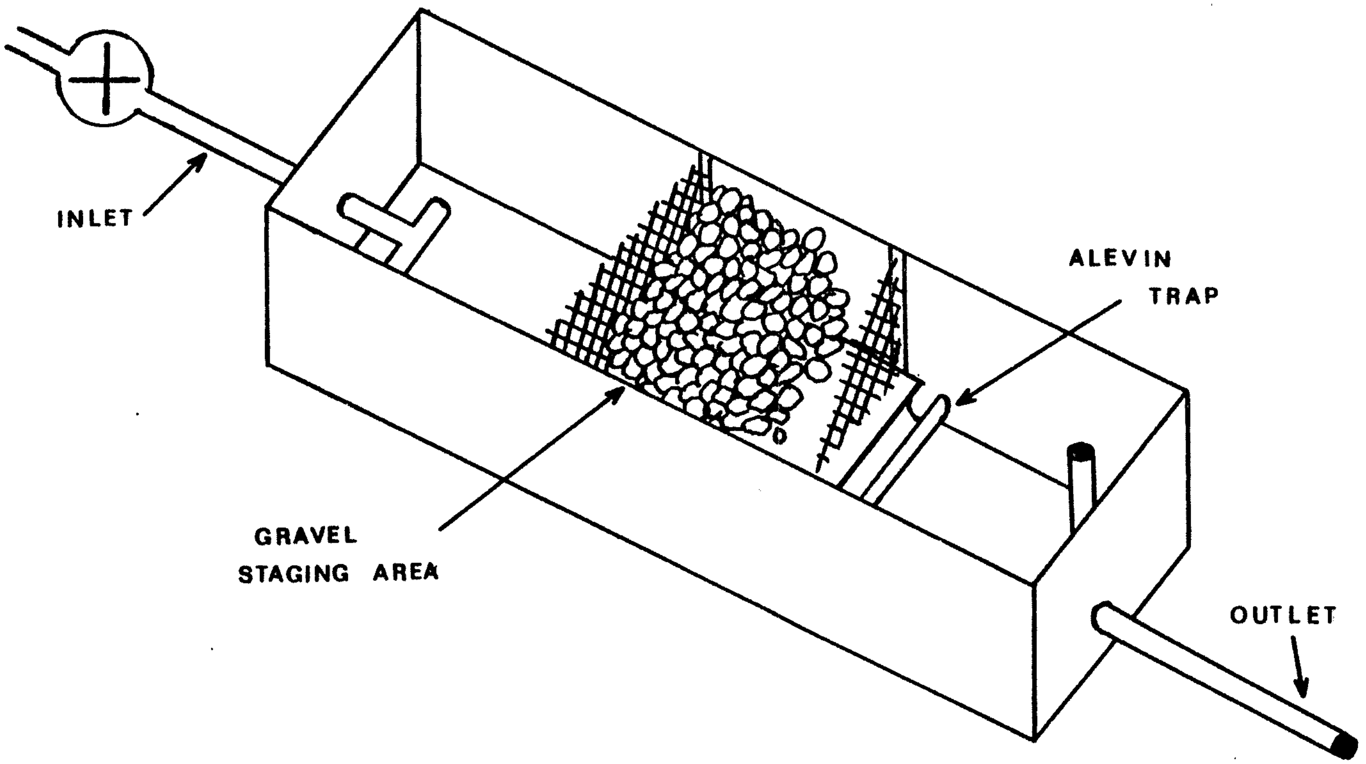

Fig. 4 . Alevin flow box for studies on effect of velocity on movement and behavior.

second level, the incipient sublethal threshold level, is that level that will just support the maximum rate of growth. Different studies have reported this level ranging from about 4.5 to 7.0 mg O_2/liter (Hayes et al. 1951; Wickett 1954; Alderdice et al. 1958; Whitmore et al. 1960; Herrmann et al. 1962; Davis et al. 1963; Randall and Smith 1967; Randall et al. 1967; Holeton 1971; Davis 1975; Brett and Blackburn 1981; Coble 1982; Bams and Lam 1983). Different species and test temperatures may account for a wide range in reported sublethal levels. The sublethal levels generally decreased with increasing water temperature.

Metabolic waste products (principally un-ionized ammonia) also affect the survival and fitness of alevins. Most recent studies, however, have demonstrated that even high ammonia levels were not detrimental to alevin survival and growth unless combined with low dissolved oxygen (Larmoyeux and Piper 1973; Thurston et al. 1981; Jensen, in Bams and Lam 1983). For this reason ammonia was not included in this study.

It was predicted that salmonid alevins would avoid levels of 2 mg O_2/liter and lower to insure their survival. They should also avoid levels below 7.0 mg O_2/liter to maximize their growth and fitness. The procedures used to study alevin avoidance of low dissolved oxygen levels utilized plywood two-choice tanks (Figure 5). These experiments were designed to test the ability of alevins to select between two water sources varying only in level of dissolved oxygen. It was predicted alevins would migrate toward the source of the less stressful concentration. Three different levels of oxygen choice tests were conducted. The oxygen concentration of the water entering the two arms of the test apparatus were 2 vs. 6, 4 vs. 8, and 6 vs. 10 mg O_2/liter. Dissolved oxygen levels were regulated by using a stripping tower with a counter flow of nitrogen gas bubbled up through the column to deoxygenate the

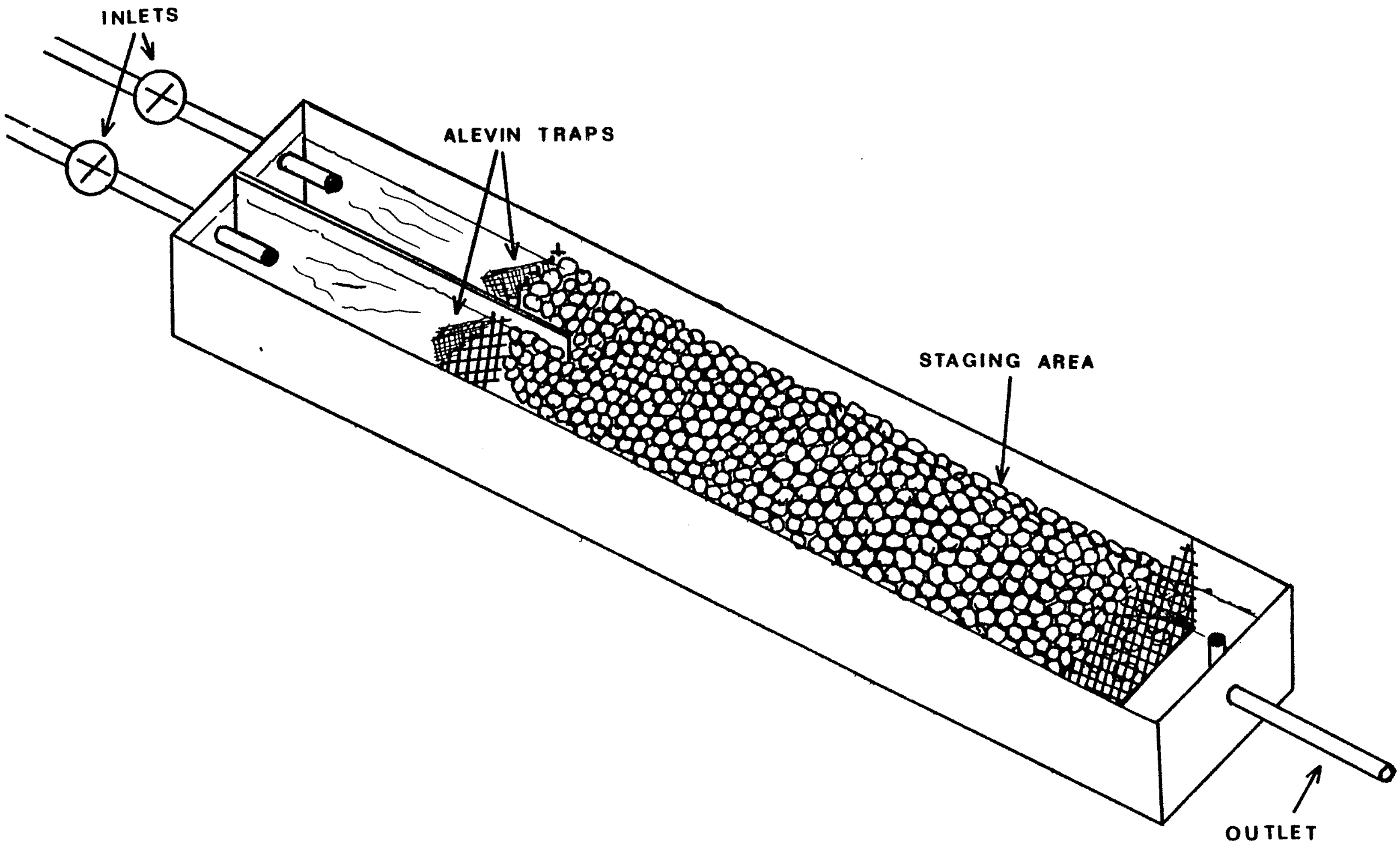

Fig. 5. Y-maze used in studies of alevin movement and behavior related to dissolved oxygen levels.

incoming water. This deoxygenated water was then pumped to two head tanks where oxygen gas was mixed with the water to achieve the desired concentrations. The water then flowed from the head tanks to either arm of the two choice tank.

The testing procedure was to release 50 alevins through a one inch diameter pvc pipe into the glass marble substrate (2.16 cm diameter) in the staging area (Figure 5). Glass marbles were used as substrate in these experiments to create identical interstitial spaces thereby allowing the alevins equal freedom of movement in any direction. Irregular gravel substrate was not used because it may have biased the freedom and direction of alevin movement. The entire tank was then covered for three hours. The number of alevins that had migrated to each arm was recorded. Five replicate experiments were preformed at each oxygen concentration using new alevins and with the water sources reversed to eliminate bias. The results from all independent tests performed during each developmental stage were tested for homogeneity using Chi-square and pooled when allowed (Zar 1974). Pooled results were analyzed and the number of alevins selecting each oxygen level were tested for randomness using Chi-square with expected frequencies of 50:50 (Zar 1974). Avoidance behavior was reported whenever the choice ratio significantly differed from random (*P*0.05).

2.4.5 Movement and Photobehavior

The photobehavior of salmonid alevins has been reported by numerous authors (White 1915; Gray 1928; Stuart 1953; Woodhead 1957; Bams 1969; Dill 1977; Mason 1976; Carey and Noakes 1981; Fast et al. 1982; Godin 1982; Carey, in press). The results of these studies vary considerably, especially in the magnitude of the photoresponse and also in the timing of the transition from photonegative to photopositive behavior as emergence approaches.

Stuart (1953) described both brown trout and Atlantic salmon as unresponsive to light for the first few days after hatching. The alevins then became photonegative until the final stages of yolk sac absorption when they oriented towards the light.

Mason (1976) found coho salmon alevins were strongly photonegative until emergence when 20 to 30 percent became photopositive. Carey and Noakes (1981) reported that rainbow trout were photonegative at hatching but showed a rapid reversal at emergence when 84 percent were photopositive. Field observations by Neave (1955) and Heard (1964) indicate that sockeye, pink and chum salmon emerge from the gravel primarily at night.

The photobehavior of alevins and emerging fry may be of extreme importance for survival. In situations where early developmental stages of alevins are displaced from the gravel (e.g. superimposition of redds by later spawning salmon; scouring by floods) photonegative behavior would cause them to return to dark crevices where they would avoid predators. For older alevins, emerging during darkness may reduce the rate of predation. To determine the direction and magnitude of photoresponse of developing alevins a light-dark choice box (modified from Carey and Noakes 1981) was used. The plywood box (50 x 25 x 25 cm) had a 21 cm high center dividing partition (Figure 6) which left a 4 cm space beneath for alevins to move freely between the two sections. A sample of 30 alevins was randomly placed in the compartments and the reversible lid was lowered on one side to create a dark and a light compartment. After a 10-minute adjustment period the alevins in the light compartment were counted after each minute during a 10-minute test period. The lid was then reversed and the same procedure was followed. Two replicates were tested simultaneously and the data from the independent

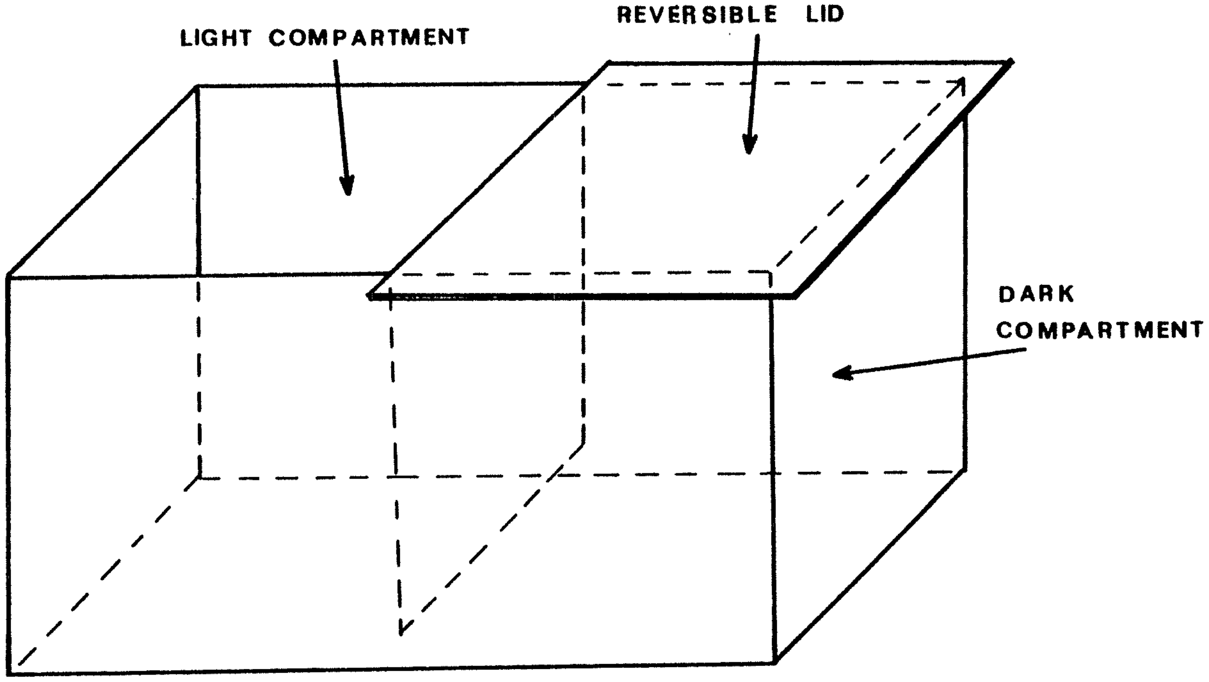

Fig. 6. Light-dark choice box used in studies of photo-behavior.

experiments were tested for homogeneity using chi-square (Zar 1974). When found homogeneous the data were pooled and tested against random (50:50) distribution using chi-square (Zar 1974). A preference was found if x^2 deviated from random (*P*0.05). The mean percentage of alevins in the light compartment was then plotted against time in days after hatching.

3.0 Results

3.1 Morphological Development

The temperature of the Lake Washington water used for incubation is plotted in Figure 7 with the period from hatching to yolk absorption indicated for each species studied. The number of temperature units (TU)[1] accumulated by each species from the day of 50% hatch to mean yolk absorption was:

	T.U.s	
Species	C	F
Chum	435	783
Coho	296	532
Chinook	450	811
Steelhead	296	533

The dissolved oxygen level of the incubation water was monitored throughout the study period and ranged from 10.0 to 12.5 mg O_2/liter (ppm). These oxygen levels were near saturation for the range of water temperatures (6 to 13°C) recorded.

The morphological development of chum, coho and chinook salmon and steelhead trout is reported in Tables 1, 2, 3 and 4. Figures 8, 9, 10 and 11 illustrate the energy budget from hatching to yolk absorption for each species. On day one, the body weight as a percentage of total available energy (body + yolk) ranged from 11% in chinook to 19% in coho. Since no energy had been used for metabolism (activity or maintenance) at hatching the yolk ranged from 89 to 81%, respectively. The amount of yolk used for metabolism appeared to be similar for each of the four species as the percent body weight at complete yolk absorption was 53% in chum, 58% in coho, 59% in chinook and 54% in steelhead. The actual conversion efficiency of yolk to body weight that was calculated for each species indicated, however, that

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[1] TU = the average number of degrees above 32°F or 0°C during each 24-hr period.

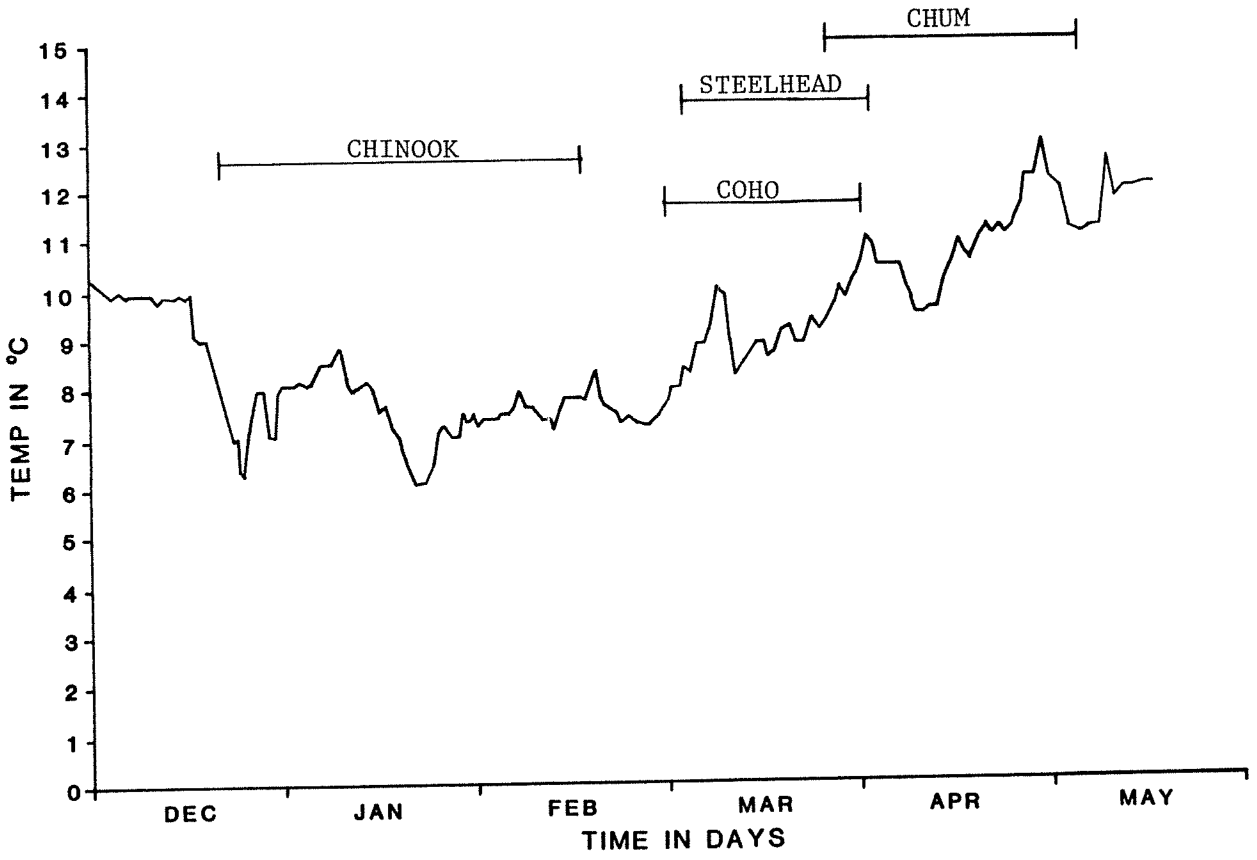


Fig. 7. Temperature of Lake Washington water used in alevin experiments. Period from hatching to yolk absorption is indicated for each species.

Table 1. Morphological development of chum salmon alevins from hatching to yolk absorption. Values are means and ranges for groups of 30 fish.

Days after hatching	Percent yolk absorbed	Total length (mm)	Dry body weight (mg)	Dry yolk weight (mg)	Caudal fin height (mm)	Dorsal fin height (mm)	Pectoral fin height (mm)	Eye diameter (mm)
1		21.2 (19.0-22.0)	10.7 (8.4-15.97)	60.8 (52.68-72.65)	3.09 (3.0-3.4)	0.49 (0.3-0.7)	1.28 (1.1-1.5)	1.56 (1.4-1.7)
3	4	22.3 (21.5-24.5)	11.9 (9.79-16.65)	58.2 (50.1-67.83)	3.35 (3.0-3.9)	0.71 (0.5-0.9)	1.31 (1.0-1.5)	1.80 (1.7-1.9)
10	18	25.3 (22.0-27.0)	18.5 (14.18-24.38)	50 (39.99-62)	4.15 (3.7-5.0)	1.0 (0.9-1.1)	1.73 (1.5-2.0)	1.98 (1.8-2.0)
13	25	26.6 (25.0-28.0)	18.9 (13.96-27.3)	45.4 (35.36-52.31)	4.25 (3.5-5)	0.94 (0.8-1.2)	1.97 (1.8-2.0)	1.99 (1.9-2.0)
17	36	27.6 (26.0-29.5)	22.7 (16.52-29.82)	39.7 (27.57-51.54)	4.98 (4.0-5.8)	1.16 (1.0-1.5)	2.11 (1.9-2.3)	2.03 (2.0-2.1)
21	48	28.3 (26.0-31.0)	25.6 (18.68-37.23)	31.5 (17.98-41.22)	5.46 (4.5-6.0)	1.30 (1.0-1.7)	2.42 (2.0-3.0)	2.09 (2.0-2.3)
25	58	29.8 (20.0-32.0)	29.9 (22.9-40.7)	25.6 (17.0-37.9)	5.52 (4.5-6.9)	1.54 (1.1-2.0)	2.71 (2.2-3.0)	2.22 (2.1-2.4)
28	65	31.6 (29.0-34.5)	31.2 (19.2-46.3)	21.4 (9.8-33.2)	6.17 (5.3-7.0)	1.90 (1.2-2.8)	2.89 (2.4-3.3)	2.26 (2.0-2.4)
36	92	32.7 (31.0-36.0)	40.1 (32.7-47.9)	4.8 (0.00-14.3)	6.63 (6.0-7.5)	2.02 (1.2-2.3)	3.62 (3.0-4.3)	2.50 (2.3-2.8)
40	97	32.8 (32.0-35.0)	38.18 (30.9-44.6)	1.67 (0.00-5.7)	7.38 (6.3-8.0)	2.21 (2.0-2.5)	3.66 (3.0-4.0)	2.51 (2.5-2.8)

Table 2. Morphological development of coho salmon alevins from hatching to yolk absorption. Values are means and ranges for groups of 30 fish.

Days after hatching	Percent yolk absorbed	Total length (mm)	Dry body weight (mg)	Dry yolk weight (mg)	Caudal fin height (mm)	Dorsal fin height (mm)	Pectoral fin height (mm)	Eye diameter (mm)
1	0	21.5 (20.0-23.0)	12.9 (9.9-16.18)	56.4 (42.04-70.12)	3.73 (3.0-4.0)	0.71 (0.5-0.9)	1.08 (1.0-1.3)	2.0 (1.9-2.0)
5	17	24.1 (22.0-26.0)	15.3 (12.2-20.2)	46.6 (36.2-60.4)	3.93 (3.5-4.2)	0.84 (0.7-1.0)	1.57 (1.2-1.7)	2.0 (2.0)
9	36	24.6 (20.0-26.5)	19.9 (10.85-24.17)	39.6 (22.9-56.31)	4.57 (4.0-5.0)	1.0 (0.8-1.2)	1.86 (1.5-2.0)	2.02 (1.6-2.1)
12	43	26.9 (24.0-28.5)	25.0 (18.67-29.4)	32.1 (13.4-58.64)	4.94 (4.0-5.6)	1.26 (1.0-1.8)	2.07 (1.9-2.5)	2.09 (2.0-2.2)
16	54	28.4 (26.0-31.0)	29.7 (20.0-38.27)	25.7 (10.02-34.2)	5.74 (4.5-6.5)	1.69 (1.3-2.0)	2.46 (2.0-2.9)	2.27 (2.0-2.5)
19	61	30.7 (29.0-32.5)	34.9 (26.3-41.4)	22.0 (9.18-41.76)	5.99 (5.0-7.0)	1.92 (1.5-2.0)	3.16 (2.8-4.0)	2.47 (2.2-2.7)
21	68	30.1 (27.0-32.0)	33.8 (19.14-44.92)	18.0 (4.51-3.74)	6.59 (6.0-7.2)	2.07 (1.6-2.5)	3.0 (2.5-3.5)	2.38 (2.1-2.6)
28	94	32.0 (29.0-35.0)	43.1 (30.2-54.7)	3.6 (0.4-9.7)	6.84 (6.0-8.0)	2.54 (2.0-3.0)	3.42 (3.0-4.0)	2.53 (2.3-2.8)
32	99	32.8 (30.0-35.0)	40.4 (26.5-55.6)	0.5 (0.95-3.5)	6.593 (6.0-7.9)	2.71 (2.4-3.0)	3.59 (3.1-4.0)	2.64 (2.5-2.9)

Table 3. Morphological development of chinook salmon alevins from hatching to yolk absorption. Values are means and ranges for groups of 10 fish.

Days after hatching	Percent yolk absorbed	Total length (mm)	Dry body weight (mg)	Dry yolk weight (mg)	Caudal fin height (mm)	Dorsal fin height (mm)	Pectoral fin height (mm)	Eye diameter (mm)
1	0	21.7 (21.0-23.0)	13.28 (11.01-19.45)	105.2 (79.45-134.92)	3.8 (3.3-4.0)	0.48 (0.3-0.5)	1.2 (1.0-1.3)	1.85 (1.5-1.9)
7	11	24.2 (23.0-25.0)	19.84 (17.46-23.06)	93.72 (72.2-126.41)	4.3 (4.0-5.0)	0.8 (0.6-0.9)	1.61 (1.4-1.8)	2.0 (2.0-2.1)
14	27	26.1 (22.0-27.5)	24.14 (17.98-28.31)	76.29 (46.3-117.93)	4.92 (4.9-5.3)	0.92 (0.6-1.1)	1.92 (1.6-2.1)	2.06 (1.7-2.2)
20	31	30.0 (29.5-31.0)	34.37 (30.84-39.5)	72.76 (33.72-102.55)	5.88 (5.0-6.5)	1.41 (1.3-1.6)	2.31 (2.0-2.5)	2.45 (2.3-2.5)
27	51	32.5 (30.0-38.0)	40.78 (35.94-48.62)	52.00 (24.01-64.25)	6.56 (6.0-7.0)	1.87 (1.6-2.1)	2.85 (2.4-3.0)	2.35 (2.5-2.7)
35	65	33.5 (32.0-35.0)	50.00 (43.71-66.91)	37.1 (10.81-54.45)	7.14 (7.0-7.9)	2.17 (1.9-2.7)	3.01 (2.6-3.3)	2.87 (2.7-3.0)
43	81	35.6 (34.0-37.0)	61.8 (49.65-74.75)	19.8 (26.8-37.59)	7.98 (7.0-9.0)	3.01 (2.8-3.3)	3.52 (3.0-4.0)	3.01 (3.0-3.1)
51	87	37.2 (35.0-39.0)	65.6 (51.2-86.4)	13.4 (2.1-29.1)	8.24 (7.5-9.0)	3.03 (2.8-3.4)	3.89 (3.5-4.4)	3.0 (3.0-3.1)
59	99	38.1 (36.0-42.0)	69.5 (57.03-99.43)	6.7 (1.61-20.71)	8.51 (8.0-9.0)	3.04 (2.7-3.6)	4.32 (4.0-4.6)	3.1 (3.0-3.2)

Table 4. Morphological development of steelhead trout alevins from hatching to yolk absorption. Values are means and ranges for groups of 10 fish.

Days after hatching	Percent yolk absorbed	Total length (mm)	Dry body weight (mg)	Dry yolk weight (mg)	Caudal fin height (mm)	Dorsal fin height (mm)	Pectoral fin height (mm)	Eye diameter (mm)
1	0	19.0 (18.0-20.0)	6.5 (4.4-9.6)	44.6 (38.1-49.2)	2.10 (1.7-2.4)	0.73 (0.6-0.9)	0.95 (0.7-1.2)	1.8 (1.7-2.0)
4	17	20.0 (19.0-21.0)	8.0 (6.32-9.36)	36.8 (29.8-44.3)	2.40 (2.1-2.8)	0.90 (0.7-1.1)	1.2 (0.9-1.4)	1.84 (1.7-2.0)
9	31	22.3 (21.0-23.0)	11.93 (9.08-13.72)	30.89 (23.85-36.58)	3.60 (3.1-4.0)	1.16 (1.0-1.3)	1.66 (1.5-2.0)	1.96 (1.8-2.0)
11	38	22.5 (21.5-23.5)	15.0 (11.78-17.86)	27.59 (22.6-34.12)	3.88 (3.2-4.2)	1.28 (1.0-1.5)	1.84 (1.2-2.0)	1.96 (1.8-2.0)
18	64	25.2 (23.5-26.5)	22.0 (17.4-25.0)	15.9 (10.2-21.5)	4.54 (4.1-5.1)	1.89 (1.5-2.2)	2.43 (1.8-2.7)	2.04 (1.9-2.3)
25	91	27.8 (26.5-28.5)	28.69 (23.87-31.6)	4.2 (0 - 8.1)	5.94 (5.5-6.0)	2.66 (2.3-2.9)	3.05 (2.9-3.3)	2.31 (2.2-2.4)
30	96	28.3 (27.0-30.0)	27.68 (20.34-35.66)	1.96 (0 - 4.71)	6.31 (5.8-7.0)	2.60 (2.1-3.0)	3.1 (3.0-3.8)	2.27 (2.1-2.5)

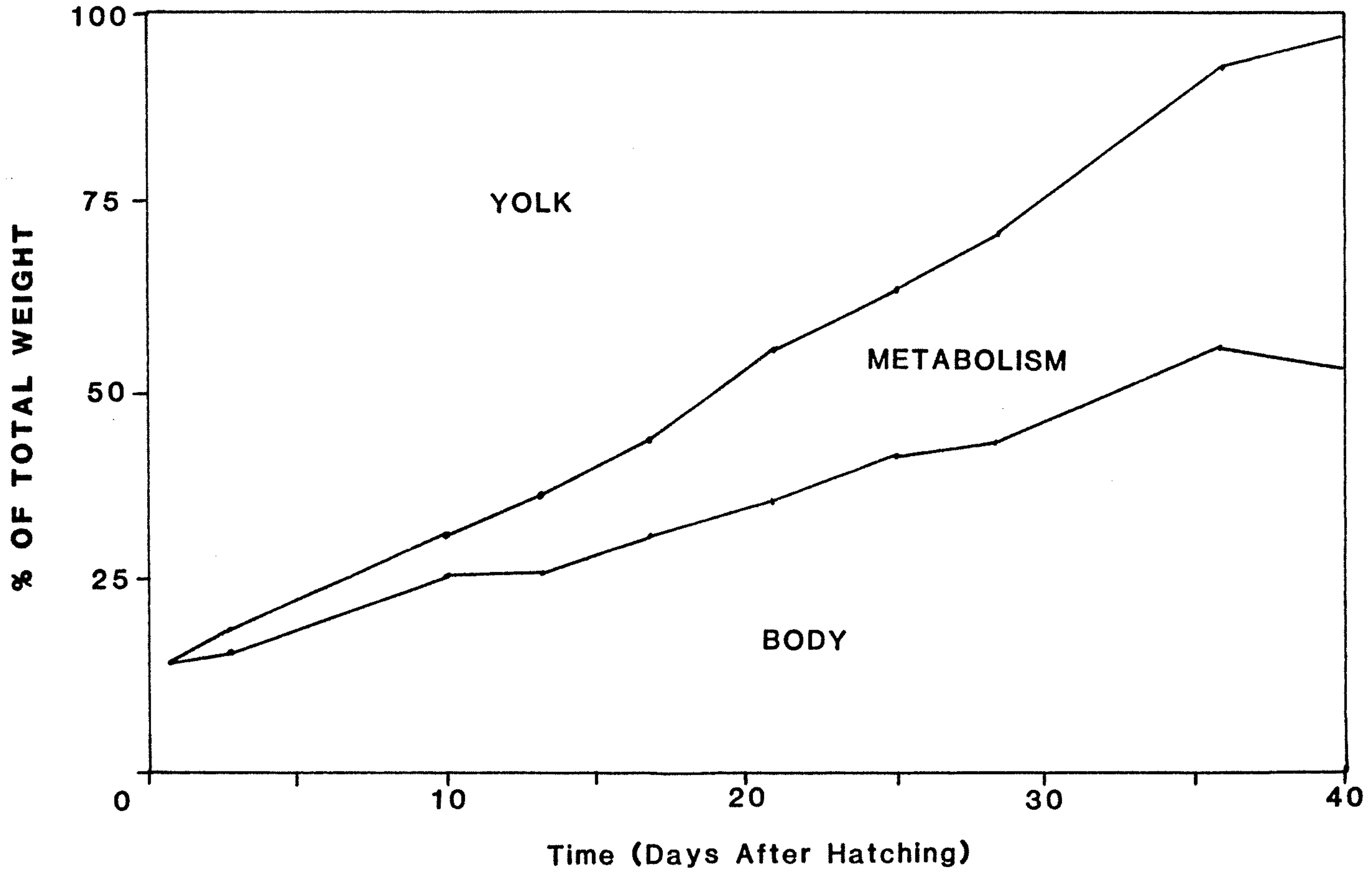


Fig. 8. The energy budget of chum salmon alevins from hatching to yolk absorption. The total energy available to an alevin at hatching (day 0) consists of yolk and body tissue. Utilization of the yolk material for body growth and metabolism is plotted against time after hatching.

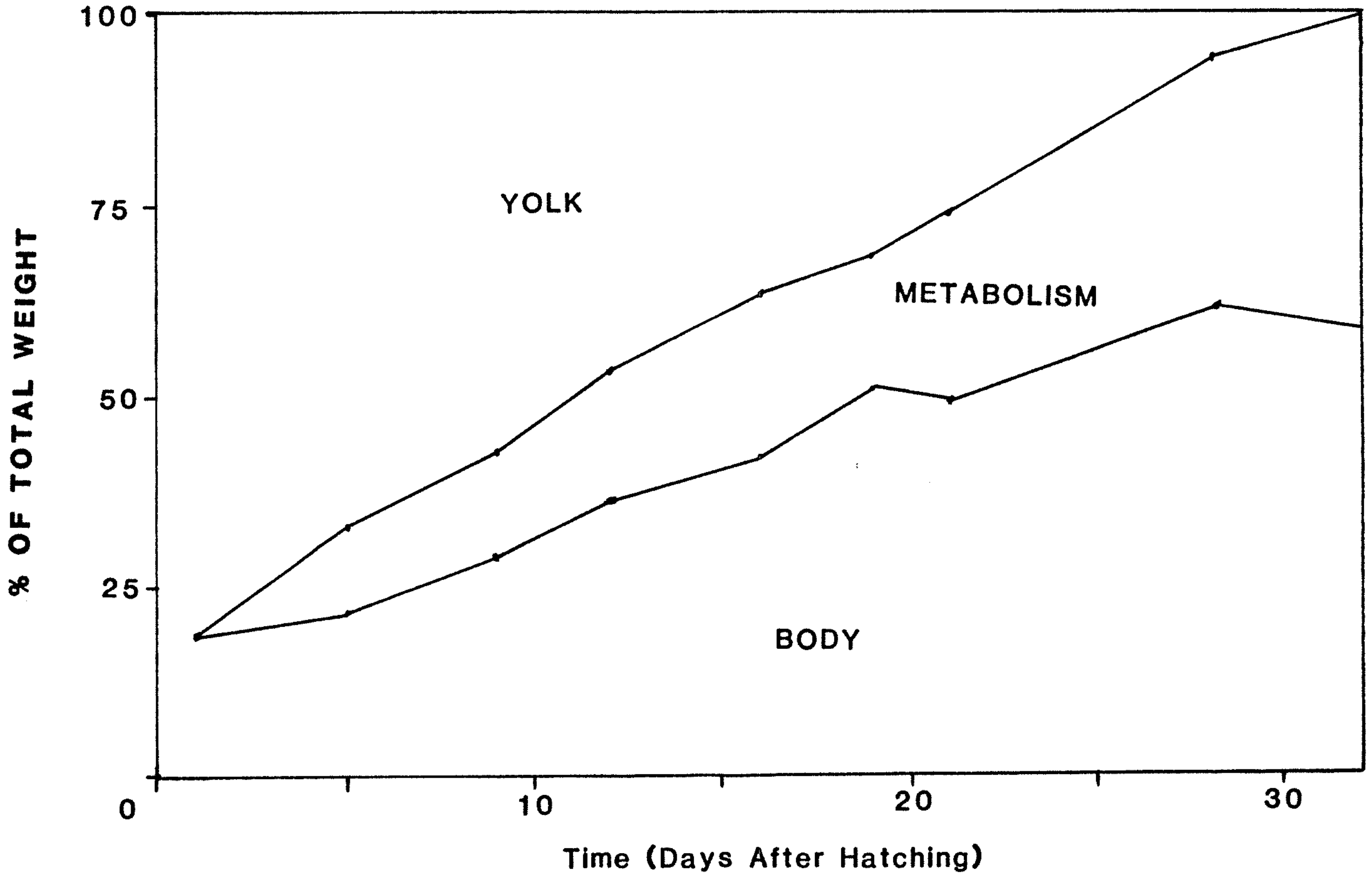


Fig. 9. The energy budget of coho salmon alevins from hatching to yolk absorption. The total energy available to an alevin at hatching (day 0) consists of yolk and body tissue. Utilization of the yolk material for body growth and metabolism is plotted against time after hatching.

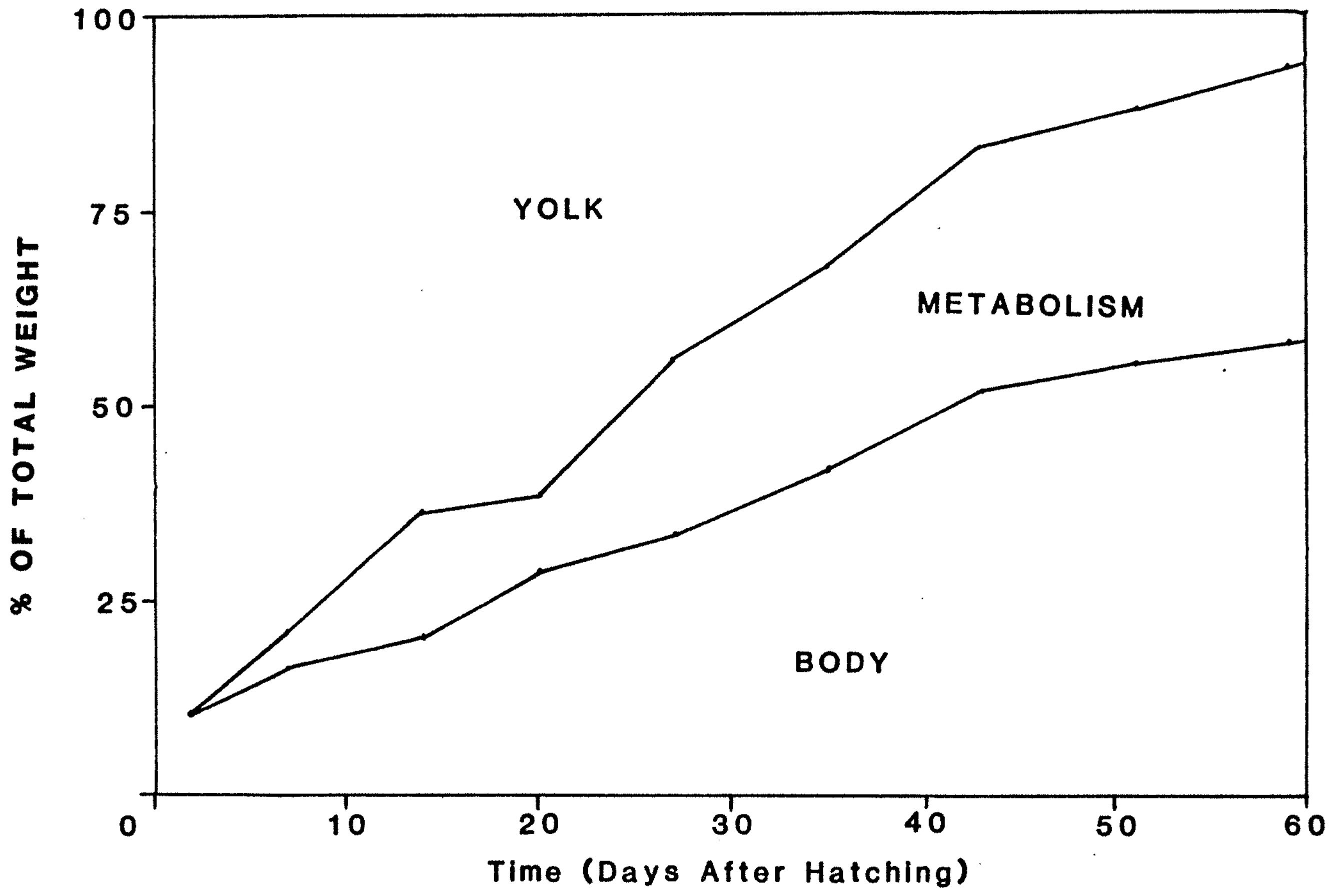


Fig. 10. The energy budget of chinook salmon alevins from hatching to yolk absorption. The total energy available to an alevin at hatching (day 0) consists of yolk and body tissue. Utilization of the yolk material for body growth and metabolism is plotted against time after hatching.

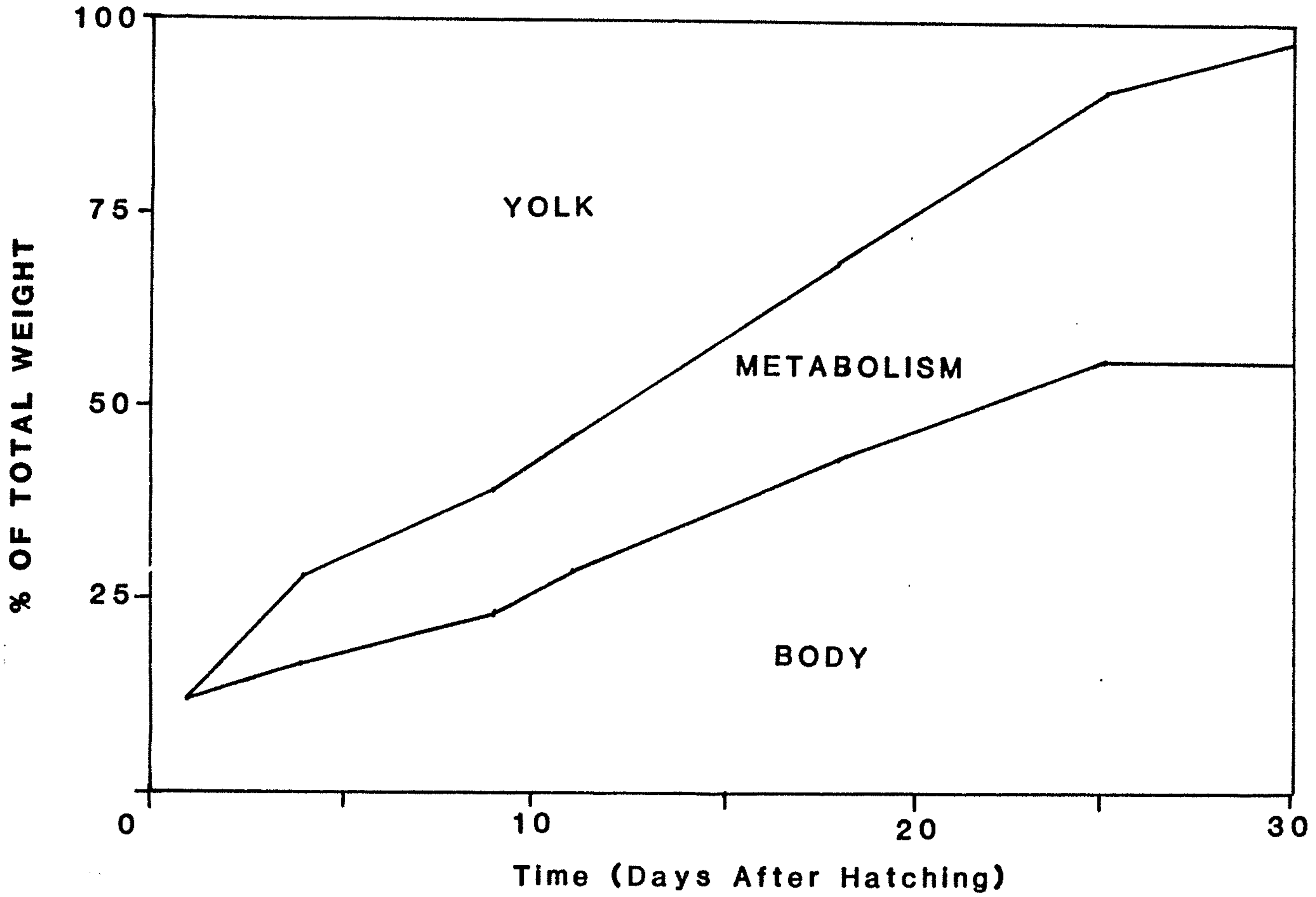


Fig. 11. The energy budget of steelhead trout alevins from hatching to yolk absorption. The total energy available to an alevin at hatching (day 0) consists of yolk and body tissue. Utilization of the yolk material for body growth and metabolism is plotted against time after hatching.

chinook had a much higher efficiency (57.1%) than chum (46.5%), coho (49.2%) or steelhead (49.7%). The smaller weight at hatching and higher yolk efficiency of the chinook suggest that it may have hatched at an earlier stage of development than the other species.

Other aspects of development are plotted from hatching to yolk absorption in Figures 12, 13, 14 and 15. The morphological index (percent of final length) for total length at hatching is 65% in chum, 66% in coho, 67% in steelhead and only 57% in chinook. Thus the chinook was the least well developed by both weight (11%) and length (57%) at hatching.

One also notices the low state of fin development for each of the species at hatching (Figures 12, 13, 14 and 15). There is a pattern of development with the caudal fin more advanced than the pectoral fins and the dorsal fin least developed in all four species. The caudal fin in the coho salmon is the only one that at hatching was more than 50% of its height at emergence. Since the caudal fin is responsible for forward propulsion in the swimming fish one would predict that the ability to swim in these newly hatched alevins was not well developed. Likewise, the dorsal fin (used in stabilization and maintenance of an upright position) was only 22, 26, 16 and 28% of its height at emergence in chum, coho, chinook and steelhead. The chinook also had the least well developed dorsal fin. This poor fin development coupled with small body size and large yolk sac limit the mobility of the newly hatched alevin.

Observations made on swimming ability of alevins in several other test apparatus confirm the fact that at hatching the alevin is unable to swim. Figure 16 summarizes the development of a chum salmon from hatching to yolk absorption with observations on mobility at various stages. At 50% yolk absorption the alevin is capable of swimming quite well. From data in Table 1, at 48% yolk absorption the chum alevin is 33% longer than at hatching and

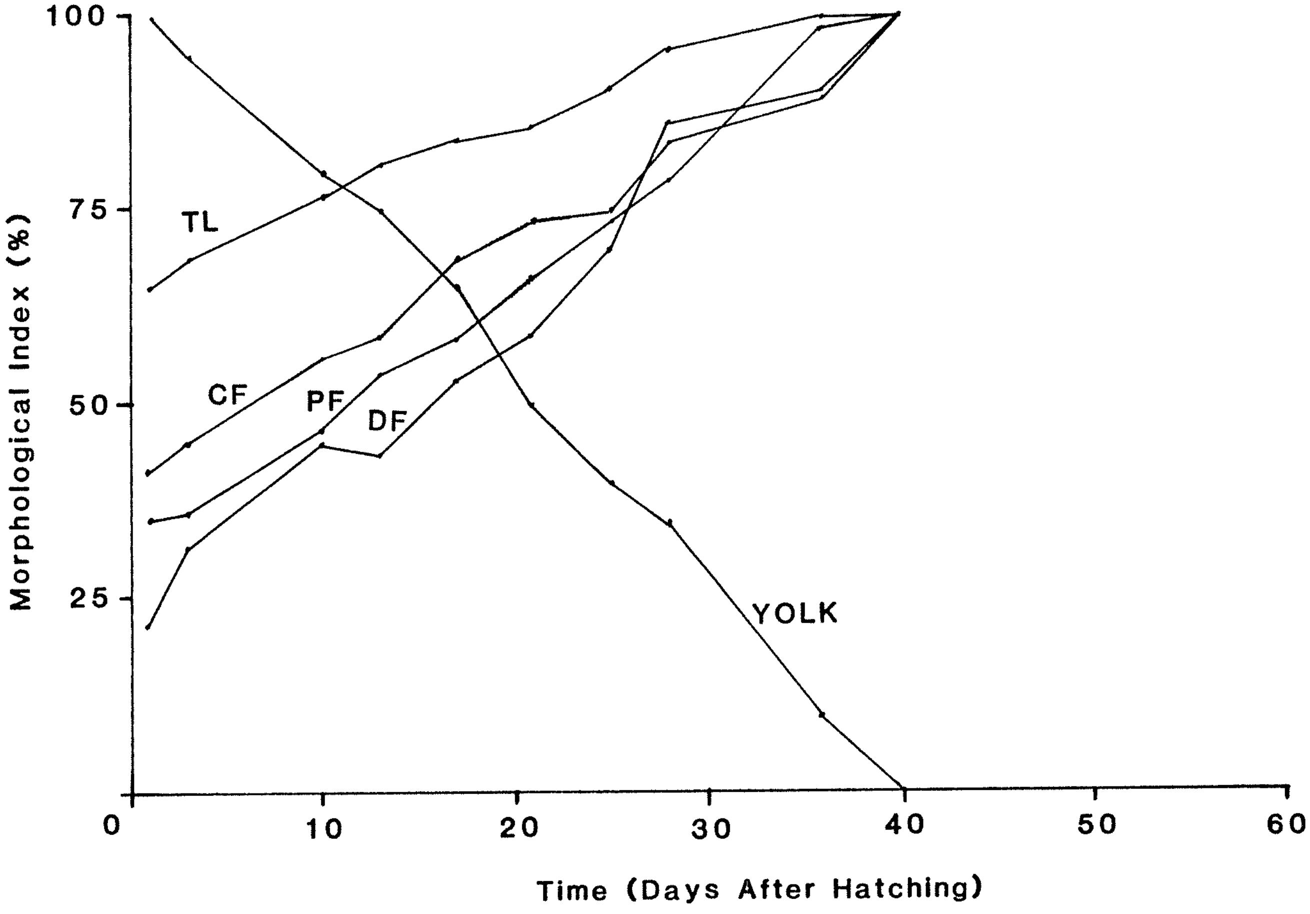


Fig. 12. Morphological development (total length; caudal, pectoral, and dorsal fin heights; and percent yolk remaining) of chum salmon plotted against time. Each data point is the mean from 30 fish.

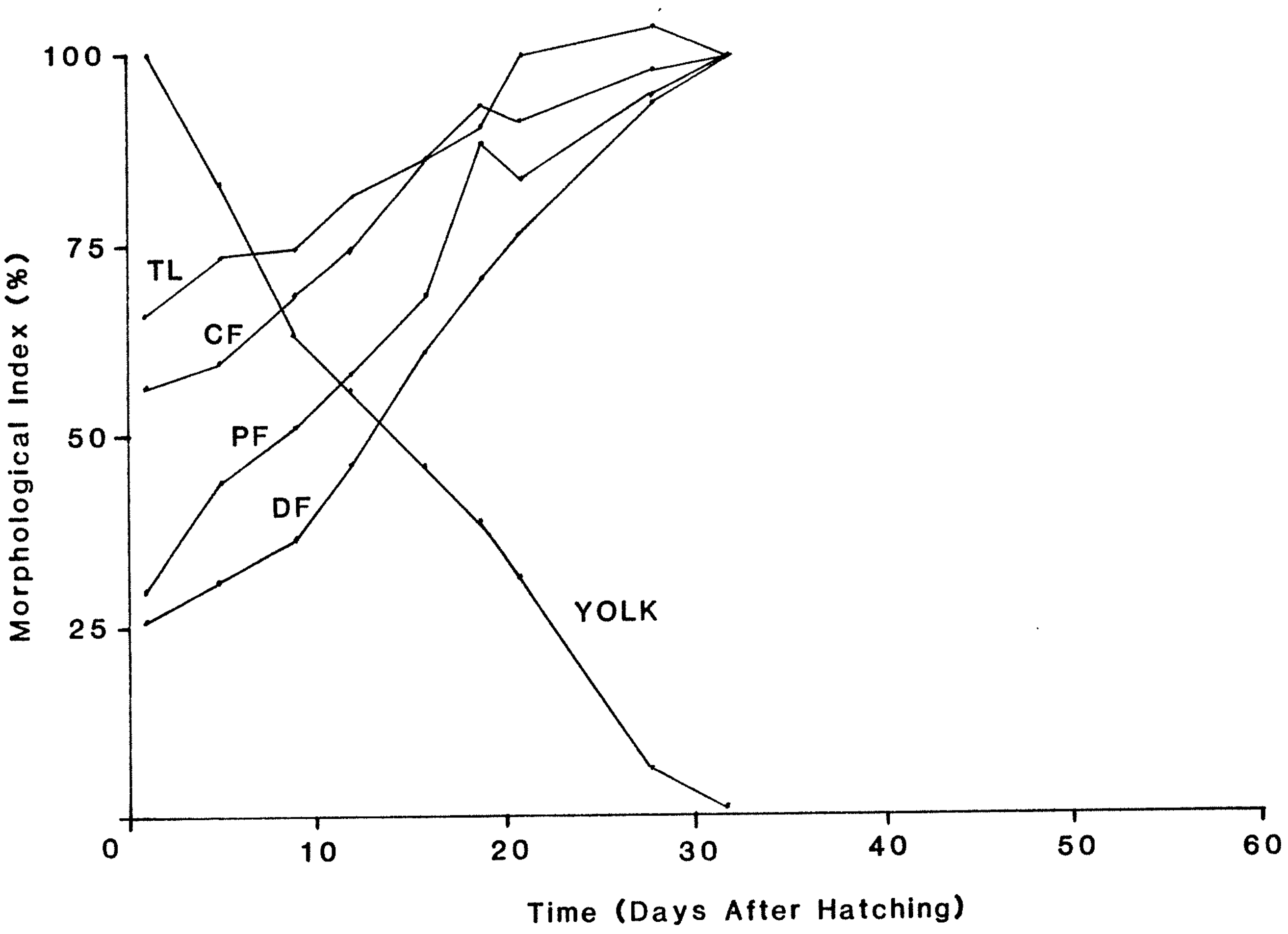


Fig. 13. Morphological development (total length; caudal, pectoral, and dorsal fin heights; and percent yolk remaining) of coho salmon plotted against time. Each data point is the mean from 30 fish.

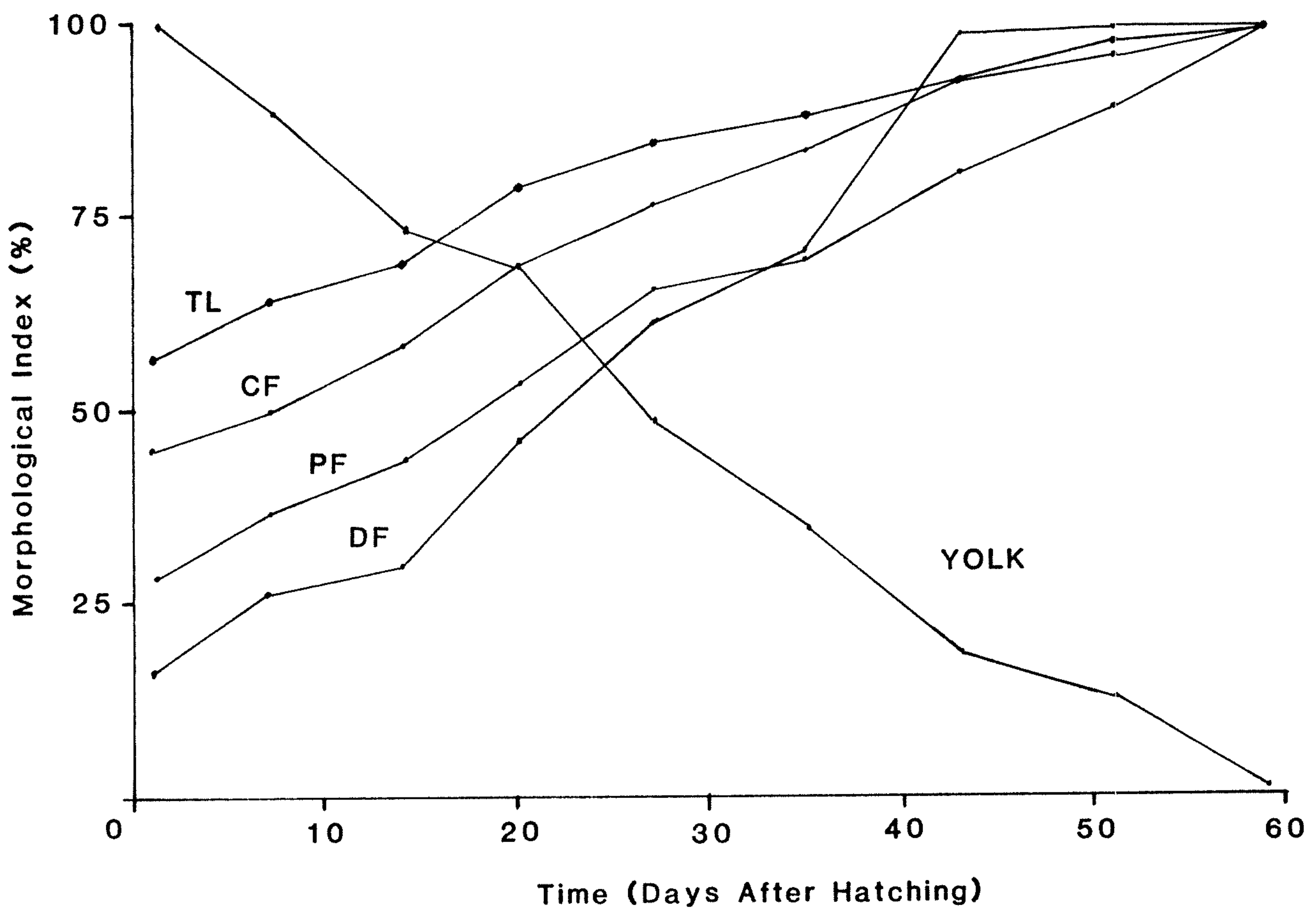


Fig. 14. Morphological development (total length; caudal, pectoral, and dorsal fin heights; and percent yolk remaining) of chinook salmon plotted against time. Each data point is the mean from 10 fish.

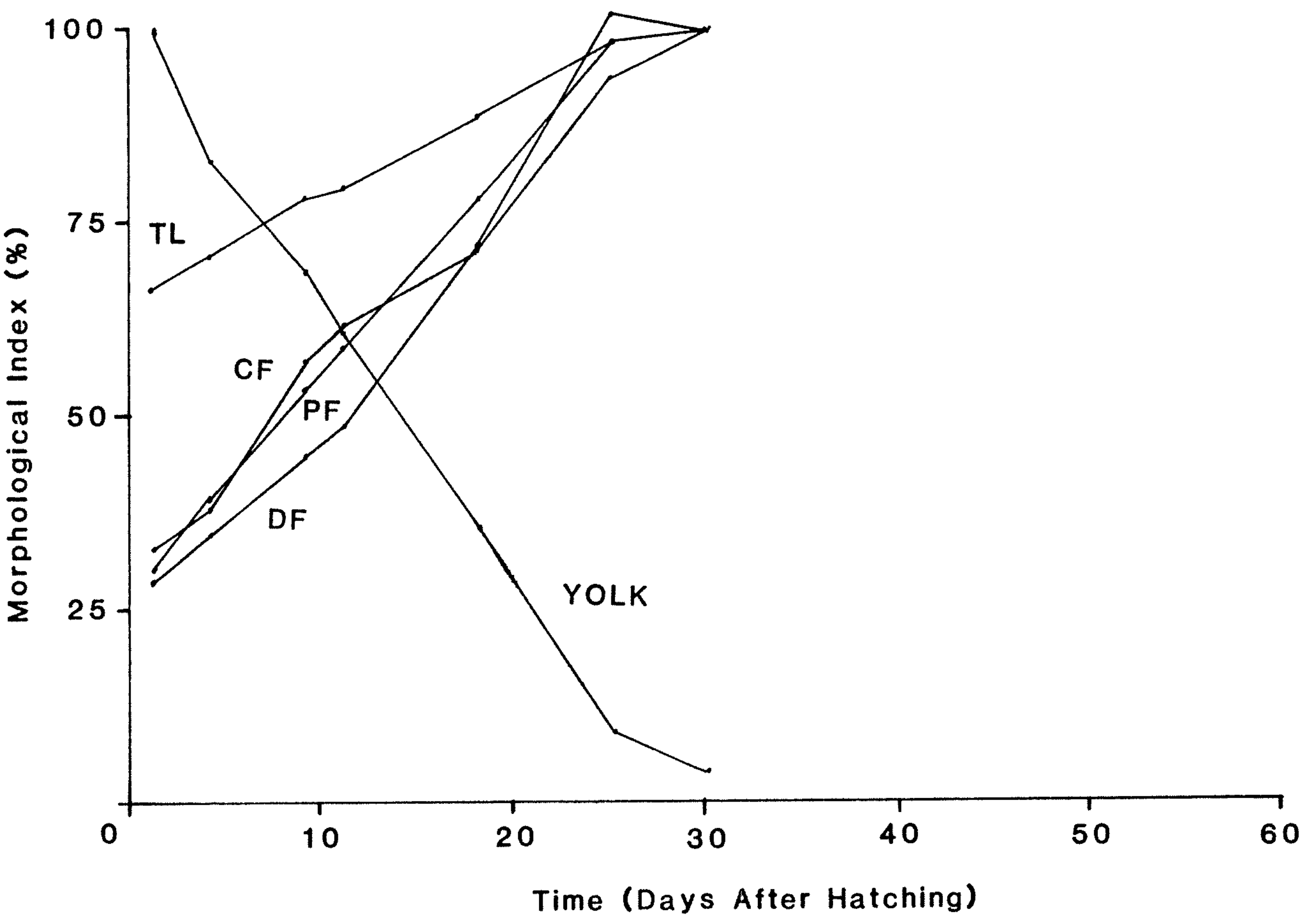


Fig. 15. Morphological development (total length; caudal, pectoral, and dorsal fin heights; and percent yolk remaining) of steelhead trout plotted against time. Each data point is the mean from 10 fish.

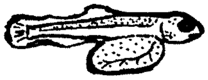
	Days after Hatching	Percent Yolk Remaining	Movement
	0	100	--
	1	99	Alevin on side on bottom; no direction to movement; short bursts (3-6 sec) of spinning around yolk sac.
	11	75	Alevin able to maintain upright position and swim for short distances on bottom; return to side position when not swimming or supported by walls.
	22	50	Alevin capable of swimming on bottom for long periods and maintaining upright position while resting; swim up off bottom for short periods.
	29	25	Alevin swimming in water column or resting on bottom when not swimming.
	41	0	Alevin swimming continuously in water column.

Fig. 16. Morphological development of chum salmon from egg to yolk absorption with observations on mobility at various stages.

its caudal, dorsal and pectoral fins are 77%, 65% and 89% longer than they were at hatching. By day 29 (75% yolk absorption) the alevin is capable of swimming for long periods of time in the water column. These alevins still rest on the bottom between swimming episodes.

3.2 Metabolic Rate Studies

The rate of oxygen consumption from hatching to yolk absorption at 4, 8 and 12°C is shown in Figures 17, 18, and 19 for chum, coho and steelhead trout, respectively. Insufficient data on chinook alevins preclude their representation here.

The chum salmon alevins had a lower rate of oxygen consumption on day five (190 $ulO_2/g/hr$) at 8°C than either the coho (290 $ulO_2/g/hr$) or steelhead (263 $ulO_2/g/hr$). However, near the end of yolk absorption the steelhead trout had the highest rate at 8°C (1050 $ulO_2/g/hr$) with the chum intermediate (868 $ulO_2/g/hr$) and the coho alevins the lowest (719 $ulO_2/g/hr$). Oxygen consumption per gram of alevin body weight increased throughout development from hatching to yolk absorption. Also, on each test date the alevins had higher rates of oxygen consumption at higher test temperatures.

3.3 Dewatering Studies

The results of experiments on the survival of alevins in single, long-term dewatering studies are presented in Table 5 for chum, coho, and chinook salmon and steelhead trout. Survival time decreased significantly as development proceeded in all four species.

The percent survival is plotted against dewatering time on "Log-probability" paper for each of the tests conducted from hatching to yolk absorption in Figures 20, 21, 22, and 23. The LT_{50}'s determined from these

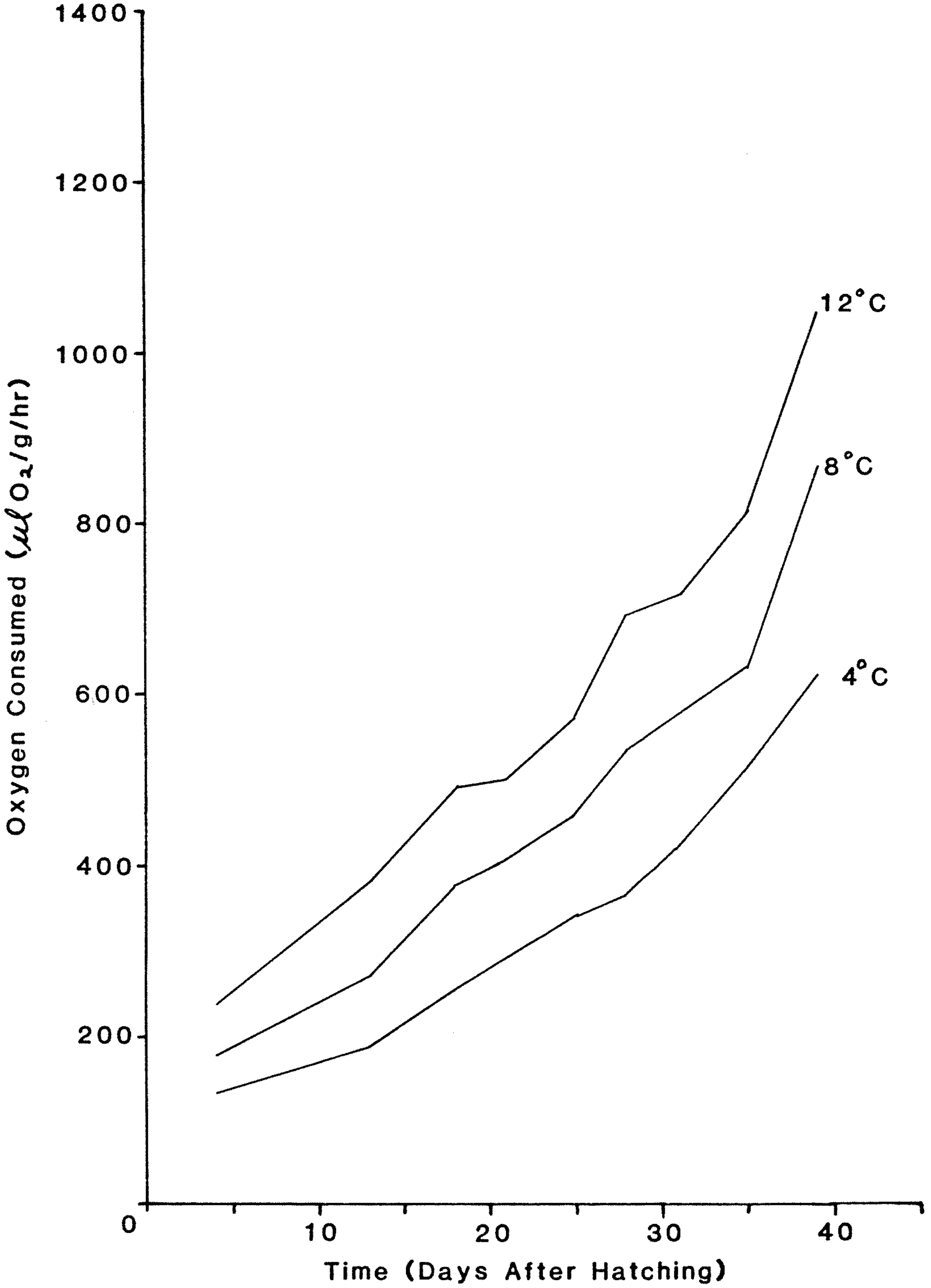


Fig. 17. Rate of oxygen consumption from hatching to yolk absorption for chum salmon alevins at 4, 8, and 12°C.

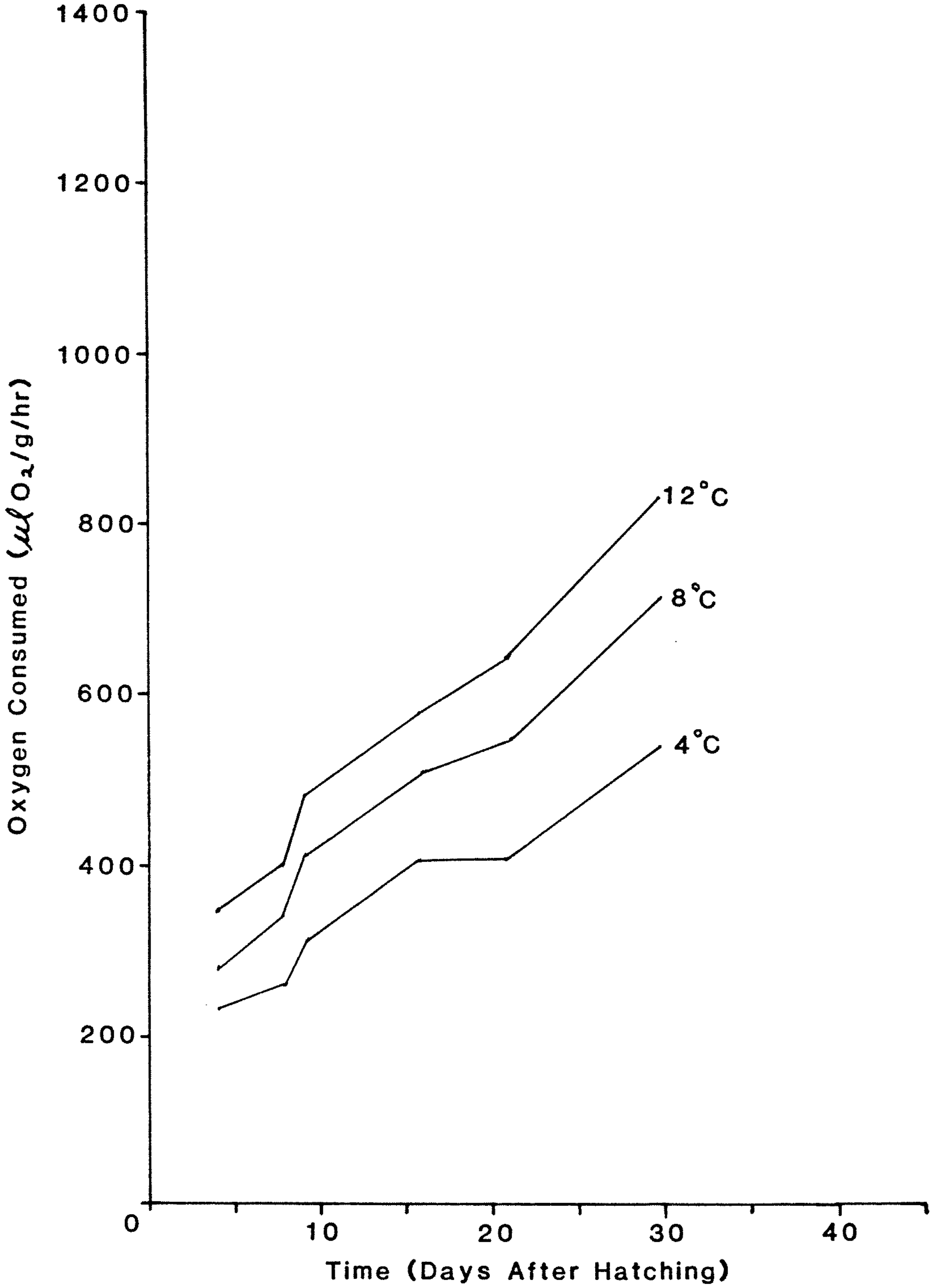


Fig. 18. Rate of oxygen consumption from hatching to yolk absorption for coho salmon alevins at 4, 8, and 12°C.

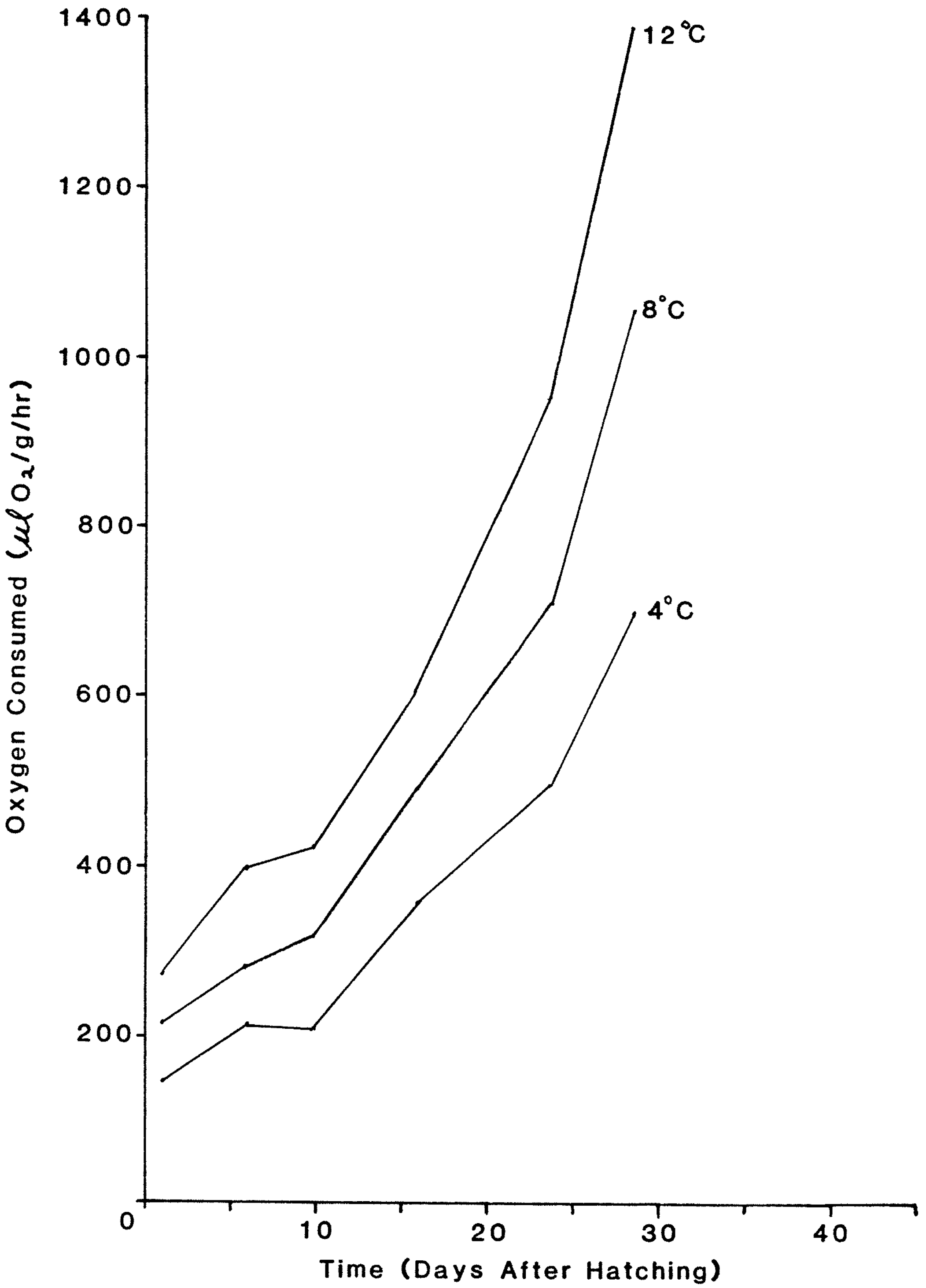


Fig. 19. Rate of oxygen consumption from hatching to yolk absorption for steelhead trout alevins at 4, 8, and 12°C.

Table 5. Percent survival during single dewaterings of chum, coho, and chinook salmon and steelhead trout alevins from hatching to yolk absorption.

Species	Days after hatching	Dewatering time (hr)								
		0.5	1	2	4	8	12	24	36	48
Chum	1			94	89	83	72	66	53	36
	13		92	90	62	57	38	7		
	15		84	64	52	34	21	1		
	18		58	53	32	33	16			
	31		31	18	6	19				
	37	48	16	13						
Coho	1			99	86	77	52	34	13	2
	5			77	90	74	49	26	3	
	9			92	70	63	21	9		
	11		90	76	62	30	9			
	12			69	51	52	14			
	21		66	48	36	17	4			
	27		51	33	14	1				
	34	2	3							
Chinook	1			100	100	100	81	67	22	2
	8				97	94	72	62	18	2
	16			81	54	41	14	3		
	19			74	56	32	17	2		
	24		94	84	42	14	9			
	29		92	93	41	14				
	34	71	29	0	3					
	42	87	1							
Steelhead	2				84	77	36	13	4	
	8			81	70	48	31	13		
	14			69	38	30	11	2		
	23		58	42	13	10	2			
	29	18	16	2						

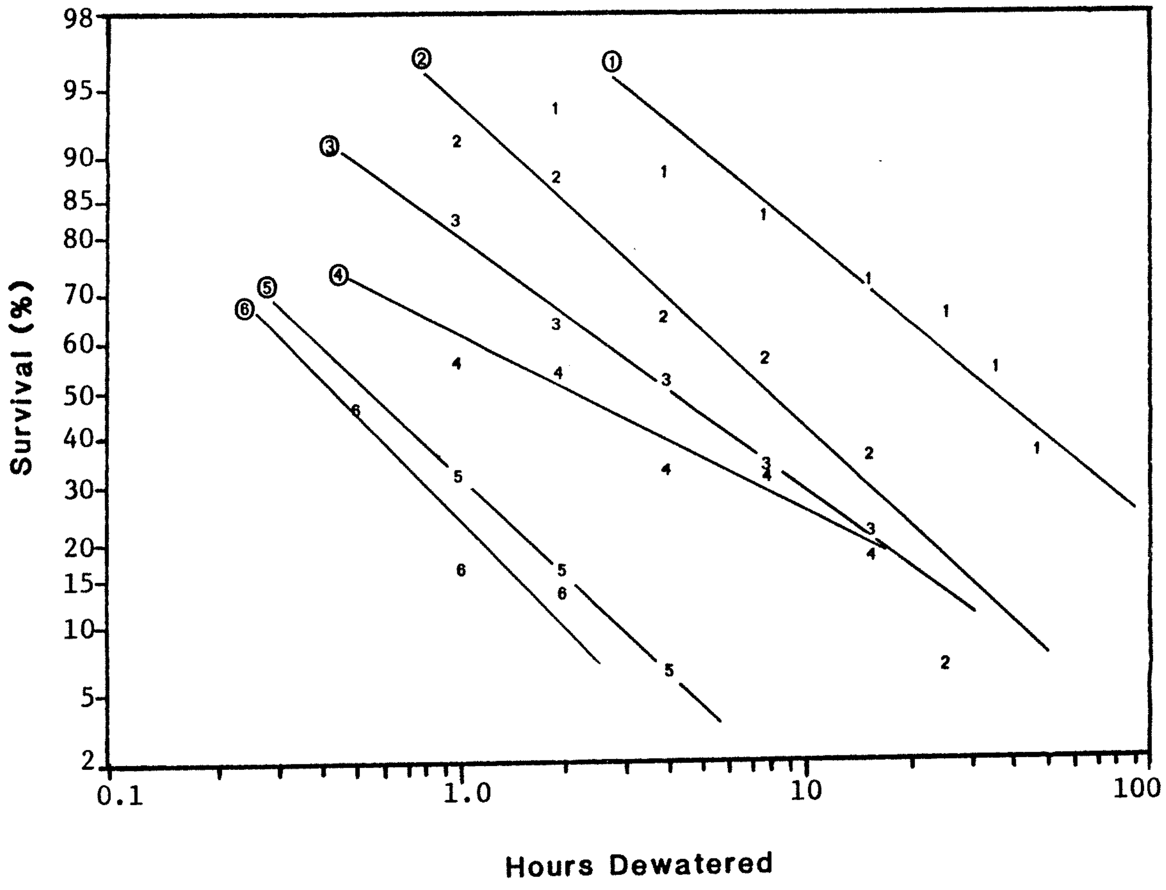


Fig. 20. The percent survival of chum salmon alevins dewatered at various stages of development. Line 1 = day 1 after hatching; 2 = day 13; 3 = day 15; 4 = day 17; 5 = day 18; and 6 = day 27.

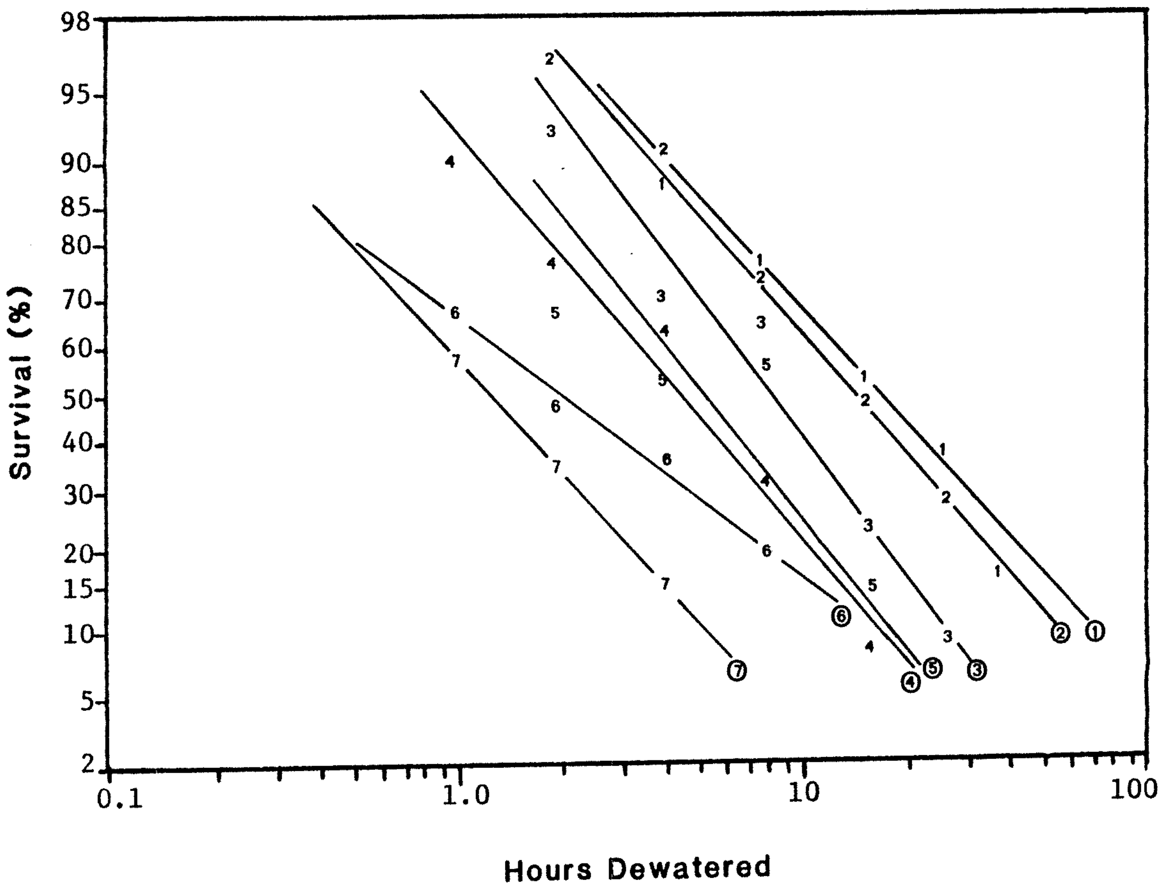


Fig. 21. The percent survival of coho salmon alevins dewatered at various stages of development. Line 1 = day 1 after hatching; 2 = day 5; 3 = day 9; 4 = day 11; 5 = day 12; 6 = day 21; and 7 = day 27.

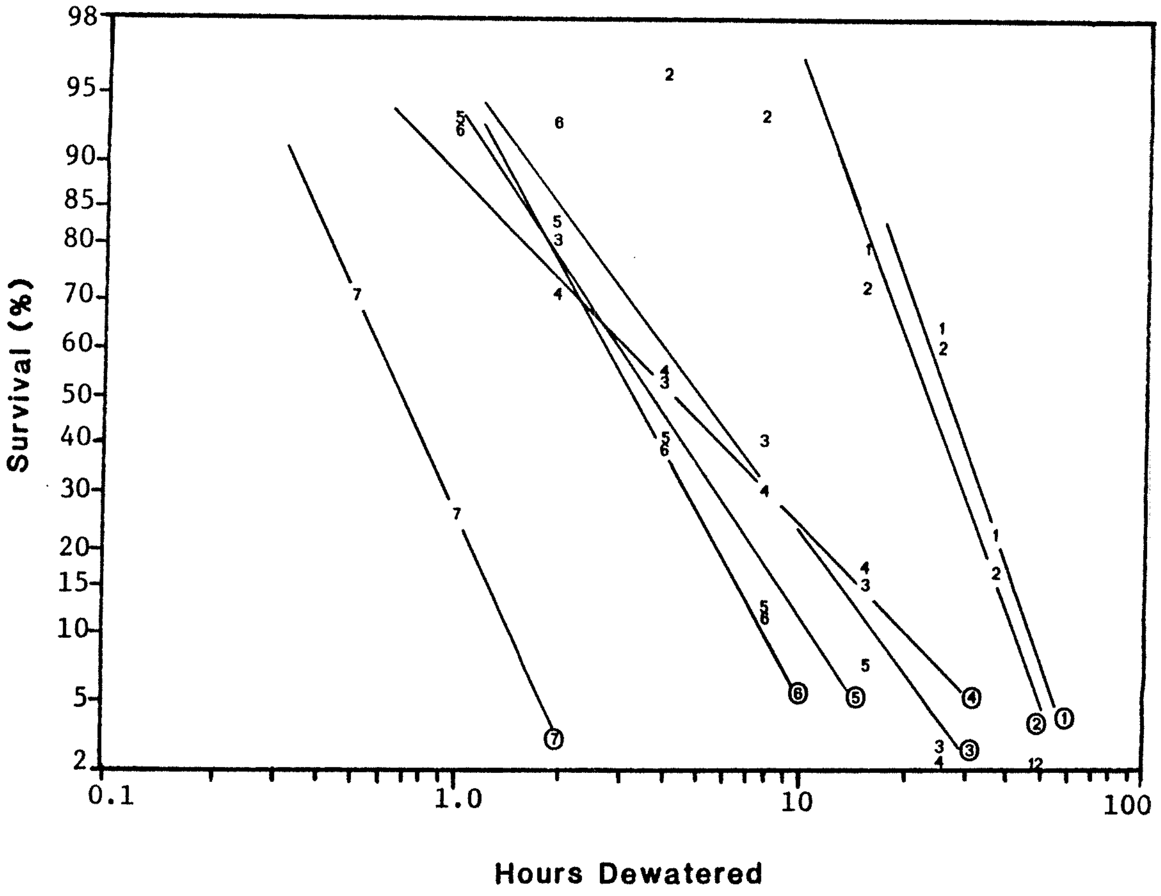


Fig. 22. The percent survival of chinook salmon alevins dewatered at various stages of development. Line 1 = day 1 after hatching; 2 = day 8; 3 = day 16; 4 = day 19; 5 = day 24; 6 = day 29; and 7 = day 34.

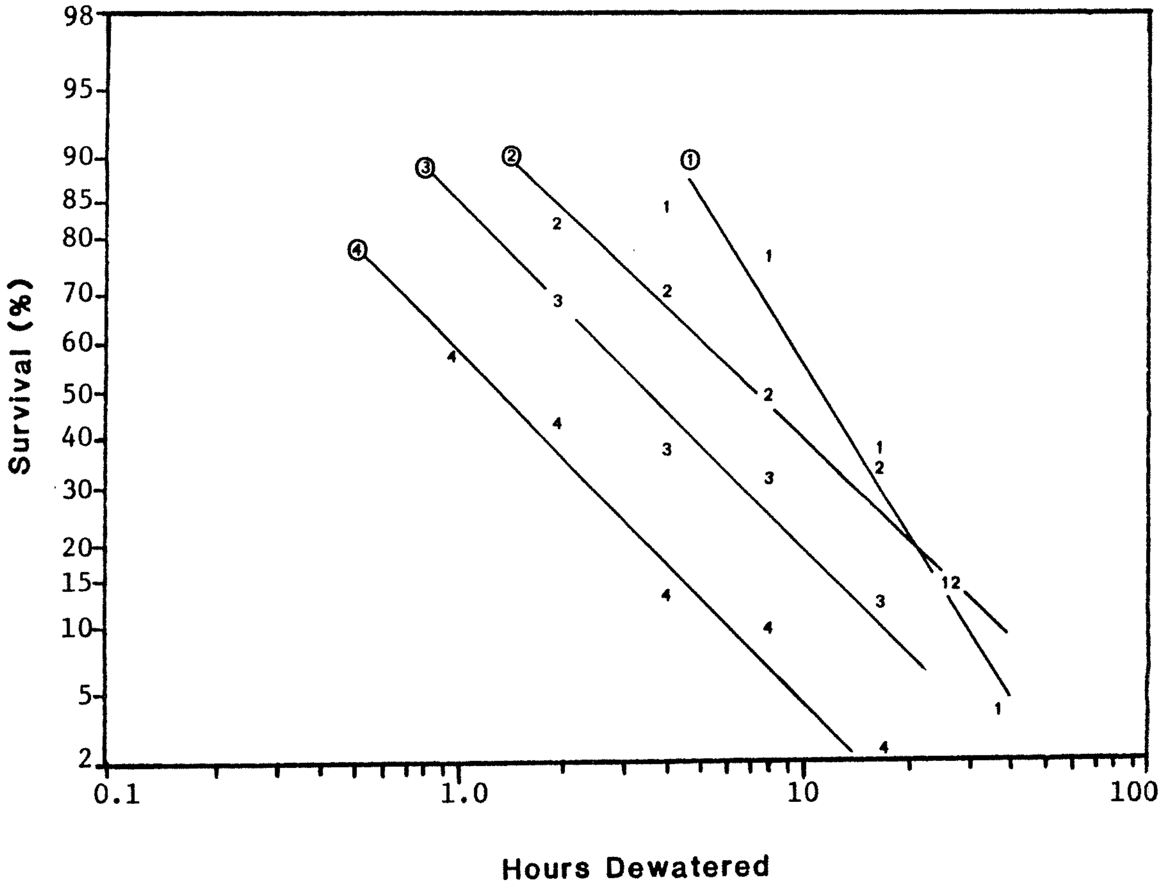


Fig. 23. The percent survival of steelhead trout alevins dewatered at various stages of development. Line 1 = day 2 after hatching; 2 = day 8; 3 = day 14; and 4 = day 23.

graphs are plotted against days after hatching to yield a 50% survival curve for each species (Figure 24). The LT_{50} on day one was 34 hours for chinook, 29 hours for chum, 17 hours for coho, and 13 hours for steelhead. Thus the survival time for chinook was almost three times as long as that for steelhead at hatching. Newly hatched chum alevins also had a longer survival time than either coho or steelhead.

The regression lines converged as days after hatching increased so that by day 20 the LT_{50}'s were 4.6 hours for chinook, 2.6 for chum, 2.3 for coho, and 1.8 for steelhead. The regression lines were not plotted below 0.4 hours because the LT_{50}'s approached but never reached the X-axis (50% mortality never occurred at 0 hours dewatered).

3.4 Alevin Behavior Experiments

3.4.1 Movement under favorable conditions

The results of experiments on the intragravel movement of alevins under conditions of adequate velocity, dissolved oxygen, and darkness are presented in Table 6 for chum, coho, and chinook salmon and steelhead trout. Alevins of all four species made downward migrations after hatching. Chum salmon had the greatest number of alevins (36%) making successful migrations through the 20 cm of gravel. Other alevins had moved to locations away from the egg burial site but were not counted unless they were in the compartments. Chinook salmon alevins made the fewest successful downward migrations (17%).

The majority of alevins in each of the four species tested demonstrated a positive rheotactic response by migrating through the gravel into the current and "falling" into the upstream compartments (1 and 2). The pooled results were tested for randomness using Chi-square and the null hypothesis (50:50 distribution) was rejected for each species ($P < .001$ for chum and steelhead;

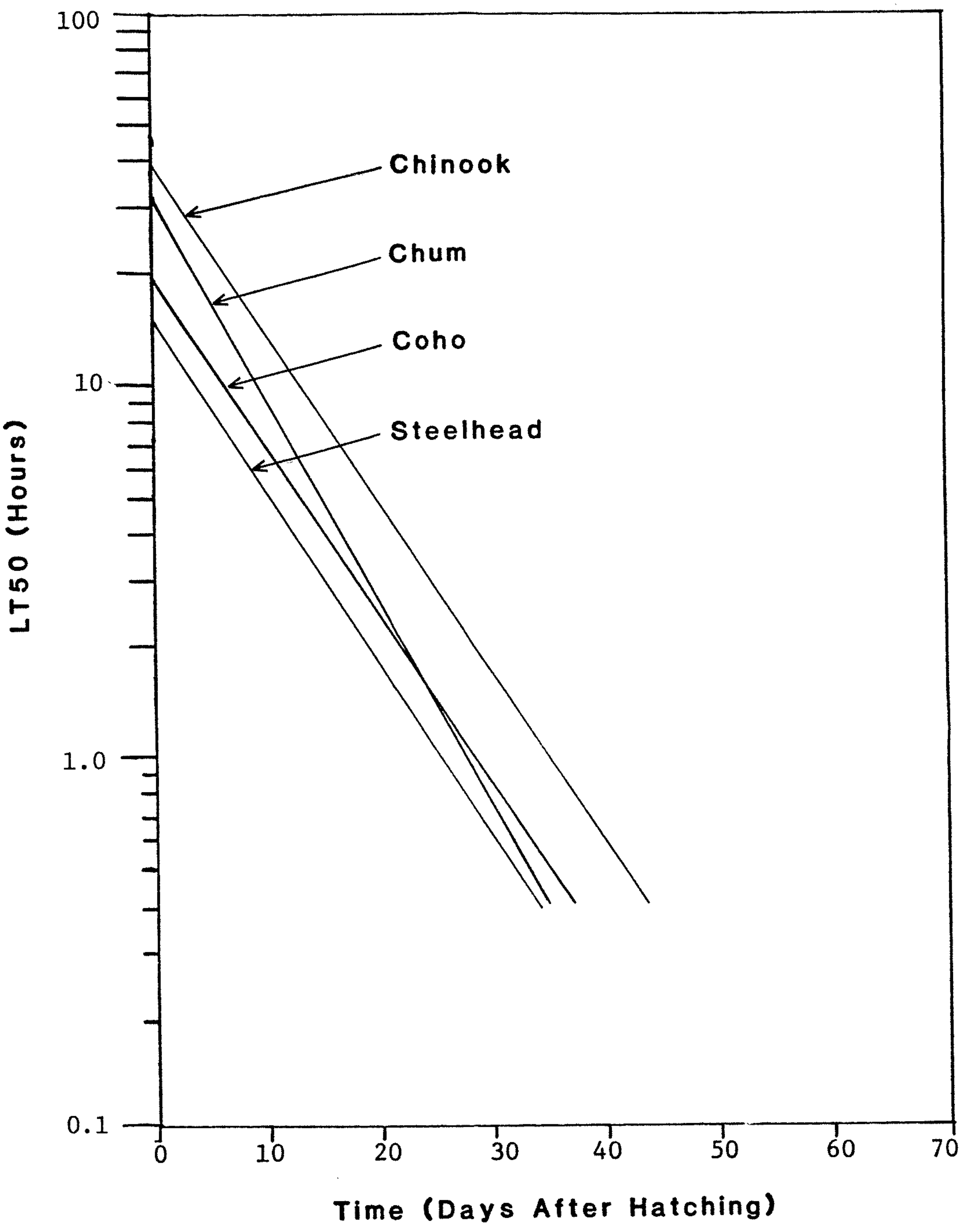


Fig. 24. The 50% survival curves for chinook, chum, and coho salmon and steelhead trout alevins in successive dewatering experiments from hatching to yolk absorption. The curves were determined by regression of LT_{50}'s (time to 50% mortality) against time in days after hatching.

Table 6. The number of chum, coho, and chinook salmon and steelhead trout alevins observed in compartments after migrating down through 20 cm of gravel. Numbers indicate compartment nearest inlet (1) or outlet (4) for determination of rheotactic behavior. Three groups of 100 alevins were tested for each species except steelhead.

		Compartment				
Species	Test	1	2	3	4	Total
Chum	1	13	16	9	4	42
	2	8	14	8	1	31
	3	14	12	6	3	35
	Mean	11.7	14	7.7	2.7	36
Coho	1	7	12	10	2	31
	2	10	9	11	5	35
	3	9	11	5	0	25
	Mean	8.7	10.7	8.7	2.3	30.3
Chinook	1	0	9	6	0	15
	2	2	8	3	0	13
	3	4	10	7	2	23
	Mean	2	9	5.3	0.7	17
Steelhead	1	14	11	4	0	29
	2	10	17	9	1	37
	Mean	12	14	6.5	0.5	33

0.01 $< P <$ .005 for coho; and .05 $< P <$ .025 for steelhead.)

3.4.2 Downward intragravel movement.

Tables 7, 8, and 9 report the percentage of chum and coho salmon and steelhead trout that were unable to move downward through screens of designated mesh sizes at different stages of development. This experiment was designed after the chinook incubation period so chinook alevins were not tested. The mean total weight, head depth and width, and greatest body depth are also reported for comparison in determining what limited downward movement. The chum and coho alevins were approximately the same weight (71.5 mg vs 69.3 mg) on the first day after hatching. However, the majority of the chum alevins (67%) passed through the number 7 seive (2.80 mm mesh size) while no coho were successful. In fact, only 11% of the coho migrated through the number 6 seive (3.33 mm) while 55% were stopped by it, and 26% were unable to pass through the number 5 seive (3.96 mm). Steelhead trout, which were only 71% as large as the chum, had alevins migrating through both the number 7 and the number 8 seive (2.36 mm) meshes, but in fewer numbers than chum.

Greatest body depth (6.73 mm) of chum alevins apparently was not the factor limiting downward migration as 100% successfully passed through the number 5 (3.96 mm) mesh sieve. The head depth and width averaged about 2.78 mm and 67% of the alevins passed through the number 7 (2.80 mm) mesh. The range, however, for head depth was from 2.56 to 3.0 mm and 23% of the alevins tested migrated through the number 8 (2.36 mm) mesh.

The coho alevins on day one had a mean head width of 3.35 mm and the number 6 mesh (3.33 mm) stopped 55% of them. Also, all but 2% of the steelhead alevins, whose mean head width was 2.36 mm on day one, were stopped by the number 8 (2.36 mm) screen. However, 45% were stopped by the 2.80 mm screen and 15% by the 3.33 mm screen, so other factors (i.e., firmness of yolk

Table 7. Morphometric measurements of chum salmon alevins from hatching to yolk absorption. The percentage of alevins unable to move downward through screens of designated mesh sizes (mm) is shown for each developmental size.

Days after hatching	% Yolk absorbed	Total weight (mg)	Head depth (mm)	Head width (mm)	Greatest body depth (mm)	Sieve size (mm)					
						4 (4.76)	5 (3.96)	6 (3.33)	7 (2.80)	8 (2.36)	10 (2.00)
1	0	71.5	2.77	2.79	6.73			12	21	44	23
3	4	70.1	2.9	2.82	6.6			19	47	30	4
10	18	68.5	3.28	3.23	6.53			10	48	42	
13	25	64.3	3.28	3.05	6.58			9	55	36	
21	48	57.1	3.73	3.84	7.21			41	47	12	
25	58	55.5	3.83	3.6	6.83		6	55	38	1	
28	65	52.6	4.22	3.66	6.88		24	54	22		
36	92	44.9	4.85	4.32	6.22	1	43	54	2		

Table 8. Morphometric measurements of coho salmon alevins from hatching to yolk absorption. The percentage of alevins unable to move downward through screens of designated mesh sizes (mm) is shown for each developmental size.

Days after hatching	% Yolk absorbed	Total weight (mg)	Head depth (mm)	Head width (mm)	Greatest body depth (mm)	Sieve size (mm)				
						4 (4.76)	5 (3.96)	6 (3.33)	7 (2.80)	8 (2.36)
1	0	69.3	3.0	3.35	6.63	8	26	55	11	
5	17	61.9	3.25	3.35	6.83		5	66	29	
9	36	59.5	3.50	3.76	6.68		5	59	30	6
12	43	57.1	3.78	4.01	6.38		6	57	34	3
19	61	56.9	4.09	3.94	6.17	1	9	74	16	
21	68	51.8	4.22	4.45	6.17		15	73	12	
28	94	46.7	4.47	4.42	5.36		28	69	3	
32	99	40.9	4.42	4.60	5.16	2	52	46		

Table 9. Morphometric measurements of steelhead trout alevins from hatching to yolk absorption. The percentage of alevins unable to move downward through screens of designated mesh sizes (mm) is shown for each developmental size.

Days after hatching	% Yolk absorbed	Total weight (mg)	Head depth (mm)	Head width (mm)	Greatest body depth (mm)	Sieve size (mm)					
						4 (4.76)	5 (3.96)	6 (3.33)	7 (2.80)	8 (2.36)	10 (2.00)
1	0	50.6	2.08	2.36	6.33		4	15	45	34	2
9	31	42.79	2.72	2.87	5.82	1	6	31	38	23	1
18	64	37.9	3.38	3.63	5.03	1	3	30	46	20	
30	96	29.6	3.71	4.09	4.24	1	4	69	24	2	

sac) appear to influence movement.

As development of alevins proceeded there was a corresponding increase in the number of alevins that were stopped by each screen. On day 36 the chum alevins mean head depth was 4.85 mm (range 3.86 to 5.31) and yet 99% moved through the number 4 mesh (4.76 mm). One possible explanation is that the meshes were measured from one corner to an adjacent corner. Thus the number 4 mesh (4.76 mm) would actually be 6.73 mm from one corner to the opposite corner. Since the head is an oval the alevin may be able to twist in such a manner as to maneuver through the opening.

3.4.3 Movement and velocity

Results of experiments on the behavior of chum, coho, and chinook salmon and steelhead trout alevins in relation to velocities of 0 (zero), 40 (low), and 120 (high) cm/min are reported in Tables 10, 11, 12, and 13. The 3x3 factorials show the percentage of alevins migrating into the current (positive rheotaxis) and the percentage demonstrating negative rheotaxis for each category of velocity and developmental stage. Similar patterns emerged in each of the four species studied. For alevins tested within several days after hatching the high flow had few positively rheotactic alevins but from 17 to 30% were negative. In the low flow what little movement occurred appeared to be random. Slightly more movement occurred in the 0 flow, but again appeared to be random.

At the approximate midpoint between hatching and complete yolk absorption, the high flow studies found a tendency for more alevins to migrate upstream in all species except chum. The low flow had more positive than negative movement. The tests with no flowing water had random movement in all species but coho where 53% went "upstream" and 27% went down.

Tests during the late developmental stage resulted in alevins in the high

	DEVELOPMENTAL STAGE		
VELOCITY	Early	Middle	Late
High	3/27	13/17	30/13
Low	7/10	13/7	23/13
No Flow	10/13	20/33	37/43

Table 10. Experimental block design for chum salmon alevin rheotactic response to no flow (0.0 cm/min), low velocity (40 cm/min), and high velocity (120 cm/min), at early (just hatched), middle (≈ 50% yolk absorption), and late (near emergence) developmental stages. The upper number in each block represents the percentage of alevins moving into the current and the lower number is the percentage going downstream.

		DEVELOPMENTAL STAGE		
		Early	**Middle**	**Late**
VELOCITY	**High**	0 / 17	30 / 17	23 / 10
	Low	10 / 3	40 / 13	43 / 17
	No Flow	17 / 20	53 / 27	40 / 57

Table 11. Experimental block design for coho salmon alevin rheotactic response to no flow (0.0 cm/min), low velocity (40 cm/min), and high velocity (120 cm/min), at early (just hatched), middle (≈ 50% yolk absorption), and late (near emergence) developmental stages. The upper number in each block represents the percentage of alevins moving into the current and the lower number is the percentage going downstream.

VELOCITY	DEVELOPMENTAL STAGE		
	Early	Middle	Late
High	3/30	27/20	46/17
Low	16/7	37/13	30/3
No Flow	6/17	27/20	33/46

Table 12. Experimental block design for chinook salmon alevin rheotactic response to no flow (0.0 cm/min), low velocity (40 cm/min) and high velocity (120 cm/min), at early (just hatched), middle (≈50% yolk absorption), and late (near emergence) developmental stages. The upper number in each block represents the percentages of alevins moving into the current and the lower number is the percentage going downstream

		DEVELOPMENTAL STAGE		
		Early	Middle	Late
VELOCITY	High	0 / 23	16 / 7	30 / 7
	Low	3 / 7	7 / 0	23 / 7
	No Flow	10 / 17	33 / 23	30 / 40

Table 13. Experimental block design for steelhead trout alevin rheotactic response to no flow (0.0 cm/min), low velocity (40 cm/min), and high velocity (120 cm/min), at early (just hatched), middle (≈ 50% yolk absorption), and late (near emergence) developmental stages. The upper number in each block represents the percentage of alevins moving into the current and the lower number is the percentage going downstream.

flows demonstrating strong positive rheotaxis for all four species. The low flow studies also found positive movement. The no velocity tests had random movement for all species.

3.4.4 Movement and Dissolved Oxygen

The results of experiments on the movement of chum, coho, and chinook salmon and steelhead trout alevins in response to dissolved oxygen levels are reported in Tables 14, 15, 16, and 17. The number of alevins that moved during the early developmental stage (less than 20% of the yolk absorbed) was insufficient for analysis.

Alevins tested at the middle developmental stage (40-60% yolk absorbed) avoided the 2 mg/L concentration. A range of 95.3 to 98.8% of those alevins responding were observed to have moved into the 6 mg/L arm of the tank in the 6 vs. 2 mg/L tests. In the second test series (8 vs 4 mg/L) the alevins also avoided the lower oxygen level with from 71.6 to 78.5% moving into the high O_2 arm. In the third test series (10 vs 6 mg/L) the range of alevins preferring the higher O_2 level was from 59.6 to 70.8%. The chum and coho did not show a significant difference from random distribution at the 0.05 level of significance in the 10 vs. 6 mg/L tests. The chinook and steelhead showed significant difference from random distribution in this test. The alevins in the control tests were randomly distributed.

Tests performed during the late developmental stage generally had more alevins moving and also had a greater percentage preferring the higher oxygen levels than in the middle stage. In the first series of tests over 98% of the chum, coho and steelhead that moved preferred the 6 mg/L concentration over 2 mg/L. From 75.7 to 84% selected the higher level in the 8 vs 4 mg/L tests, and 64.9 to 75% chose the higher level in the 10 vs 6 mg/L tests. The controls for all species had random distribution of alevins.

Table 14. The responses of chum salmon alevins to different dissolved oxygen levels in a two-choice test apparatus. The alevins were tested at middle (40-60% yolk absorption) and late (>80% yolk absorption) developmental stages.

Oxygen levels		Preference				
High	Low	High	Low	No response	% High	χ^2
Middle Developmental Stage						
6	2	81	4	165	95.3	69.75***
8	4	68	23	159	74.7	22.25***
10	6	56	38	156	59.6	3.45
10 (Control)	10 (Control)	25	29	96	46.3	0.30
Late Developmental Stage						
6	2	111	2	137	98.2	105.14***
8	4	82	16	152	83.7	44.45***
10	6	72	38	139	64.9	10.41**
10 (Control)	10 (Control)	26	37	97	41.3	1.92

**P < 0.01. ***P < 0.001.

Table 15. The responses of coho salmon alevins to different dissolved oxygen levels in a two-choice test apparatus. The alevins were tested at middle (40-60% yolk absorption) and late (more than 80% yolk absorption) developmental stages.

Oxygen levels		Preference				
High	Low	High	Low	No response	% High	χ^2
Middle Developmental Stage						
6	2	81	2	167	97.6	75.19***
8	4	53	21	176	71.6	13.84***
10	6	43	27	180	61.4	3.66
10 (Control)	10 (Control)	24	14	112	63.2	2.63
Late Developmental Stage						
6	2	83	1	166	98.8	80.05***
8	4	87	28	135	75.7	30.27***
10	6	54	25	171	68.4	10.65**
10 (Control)	10 (Control)	26	24	100	52.0	0.08

**$P < 0.01$. ***$P < 0.001$.

Table 16. The responses of chinook salmon alevins to different dissolved oxygen levels in a two-choice test apparatus. The alevins were tested at middle (40-60% yolk absorption) and late (>80% yolk absorption) developmental stages.

Oxygen levels		Preference				
High	Low	High	Low	No response	% High	χ^2
Middle Developmental Stage						
6	2	57	2	191	96.6	51.27***
8	4	51	14	185	78.5	21.06***
10	6	46	19	185	70.8	11.21***
10 (Control)	10 (Control)	21	16	113	56.8	0.93
Late Developmental Stage						
6	2	77	6	167	92.7	60.73***
8	4	50	15	185	76.9	18.85***
10	6	63	21	166	75.0	21.00***
10 (Control)	10 (Control)	14	26	110	35.0	3.60

***P < 0.001.

Table 17. The responses of steelhead trout alevins to different oxygen levels in a two-choice test apparatus. The alevins were tested at middle (40-60% yolk absorption) and late (>80% yolk absorption) developmental stages.

Oxygen levels		Preference				
High	Low	High	Low	No response	% High	χ^2
Middle Developmental Stage						
6	2	83	1	166	98.8	80.05***
8	4	57	20	173	74.0	17.78***
10	6	56	26	168	68.3	10.98***
10 (Control)	10 (Control)	29	16	105	64.4	3.76
Late Developmental Stage						
6	2	87	0	183	100	87.0***
8	4	79	15	156	84.0	43.57***
10	6	65	34	151	65.7	14.79***
10 (Control)	10 (Control)	25	31	94	44.64	0.64

***$\underline{P} < 0.001$.

3.4.5 Movement and Photobehavior

Tables 18, 19, 20, and 21 report the results of studies on the photobehavior of chum, coho, and chinook salmon and steelhead trout alevins. The chum and chinook salmon, with 43.3 and 54.2% of the alevins in the light compartment, were not significantly different from random (50:50) on the first day after hatching. The coho (33.3% in the light) and steelhead (40.8%) were photonegative on day one.

In all four species there was an increase in photonegative behavior during the first 10 to 15 days after hatching. In the chum salmon this photonegative response was fairly constant from day 6 to day 22 with 3.3 to 9.2% of the alevins in the light compartment. The other three species had similar but shorter periods of photonegative behavior.

Alevins of all four species demonstrated a decrease in photonegative behavior when 50 to 60% of the yolk had been absorbed. The chinook had the earliest photoreversal and was neutral to light by the time 53% of the yolk was absorbed. The chum and coho were randomly distributed by 65 and 71% yolk absorption, respectively. The steelhead alevins were not neutral to light until 91% of their yolk had been absorbed.

The phototactic response (percentage of alevins in the light) for each species is plotted against time (in days after hatching) in Figures 25, 26, 27, and 28. The overall patterns of photobehavior are similar for all four species.

Table 18. The results of chi-square analysis of the photobehavior of chum salmon alevins from hatching to yolk absorption.

Days after hatching	% Yolk absorbed	Preference		% Light	χ^2
		Light	Dark		
1	--	52	68	43.3	2.13
2	2	42	78	35.0	10.80**
3	4	40	80	33.3	13.33***
4	6	34	86	28.3	22.53***
5	9	31	89	25.8	28.03***
6	10	5	115	4.2	100.83***
11	20	4	116	3.3	104.53***
14	28	7	113	5.8	93.63***
18	40	11	109	9.2	80.03***
19	42	4	116	3.3	104.53***
22	48	7	113	5.8	93.63***
25	58	14	120	11.7	70.53***
28	65	53	67	44.2	1.63
32	79	72	48	60.0	4.80*
37	92	74	46	61.7	6.53*
40	97	92	28	76.7	34.13***

*$P < 0.05$. **$P < 0.01$. ***$P < 0.001$.

Table 19. The results of chi-square analysis of the photobehavior of coho salmon alevins from hatching to yolk absorption.

Days after hatching	% Yolk absorbed	Preference		% Light	χ^2
		Light	Dark		
1	--	40	80	33.3	13.33***
5	17	23	97	19.2	45.63***
9	36	13	107	10.8	73.63***
12	43	4	116	3.3	104.53***
16	54	10	110	8.3	83.33***
19	61	34	86	28.3	22.53***
22	71	70	50	58.3	3.33
28	94	72	48	60.0	4.80*
32	99	85	35	70.8	20.83***

*$P < 0.05$. ***$P < 0.001$.

Table 20. The results of chi-square analysis of the photobehavior of chinook salmon alevins from hatching to yolk absorption.

Days after hatching	% Yolk absorbed	Preference		% Light	χ^2
		Light	Dark		
1	--	65	55	54.2	0.83
4	7	31	89	25.8	28.03***
8	15	35	85	29.2	20.83***
10	18	29	91	24.2	32.03***
15	27	16	104	13.3	64.53***
18	30	10	110	8.3	83.33***
21	34	4	116	3.3	104.53***
25	46	10	110	8.3	83.33***
28	53	60	60	50.0	0.00
36	67	64	56	53.3	0.53
43	81	74	46	61.7	6.53*
51	87	79	41	65.8	12.03***
59	99	91	29	75.8	32.03***

$^{*}P < 0.05$. $^{***}P < 0.001$.

Table 21. The results of chi-square analysis of the photobehavior of steelhead trout alevins from hatching to yolk absorption.

Days after hatching	% Yolk absorbed	Preference		% Light	χ^2
		Light	Dark		
1	--	49	71	40.8	4.03*
4	17	18	102	15.0	58.80***
8	28	11	109	9.2	80.03***
11	38	10	110	8.3	83.33***
15	53	13	107	10.8	73.63***
20	72	41	79	34.2	12.03***
25	91	60	60	50.0	0.00
30	96	76	44	63.3	8.53**

$*P < 0.05$. $**P < 0.01$. $***P < 0.001$.

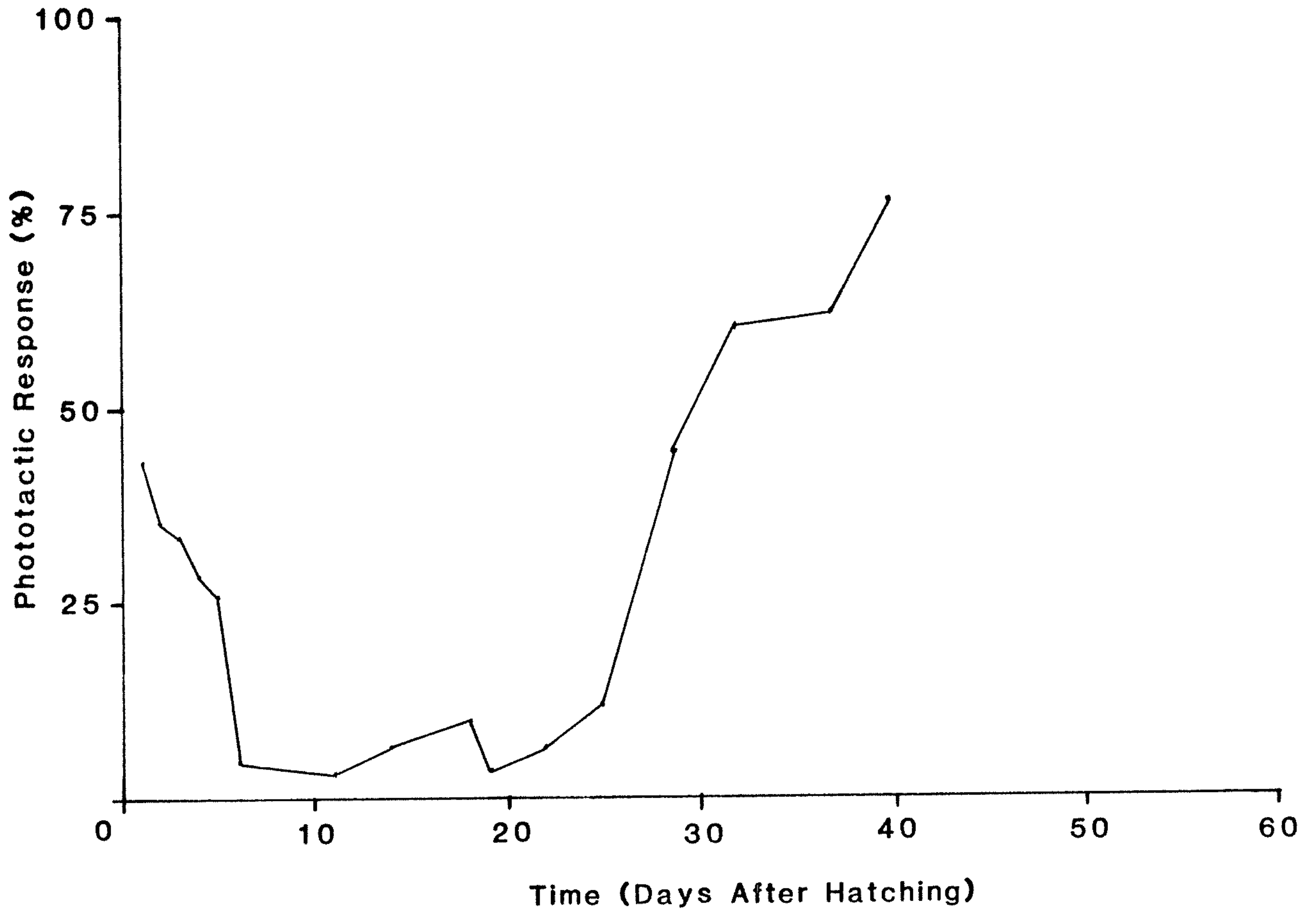


Fig. 25. Photobehavior of chum salmon alevins from hatching to yolk absorption. Each data point represents the mean percentage of 30 alevins in the light compartment of four separate light-dark choice tests.

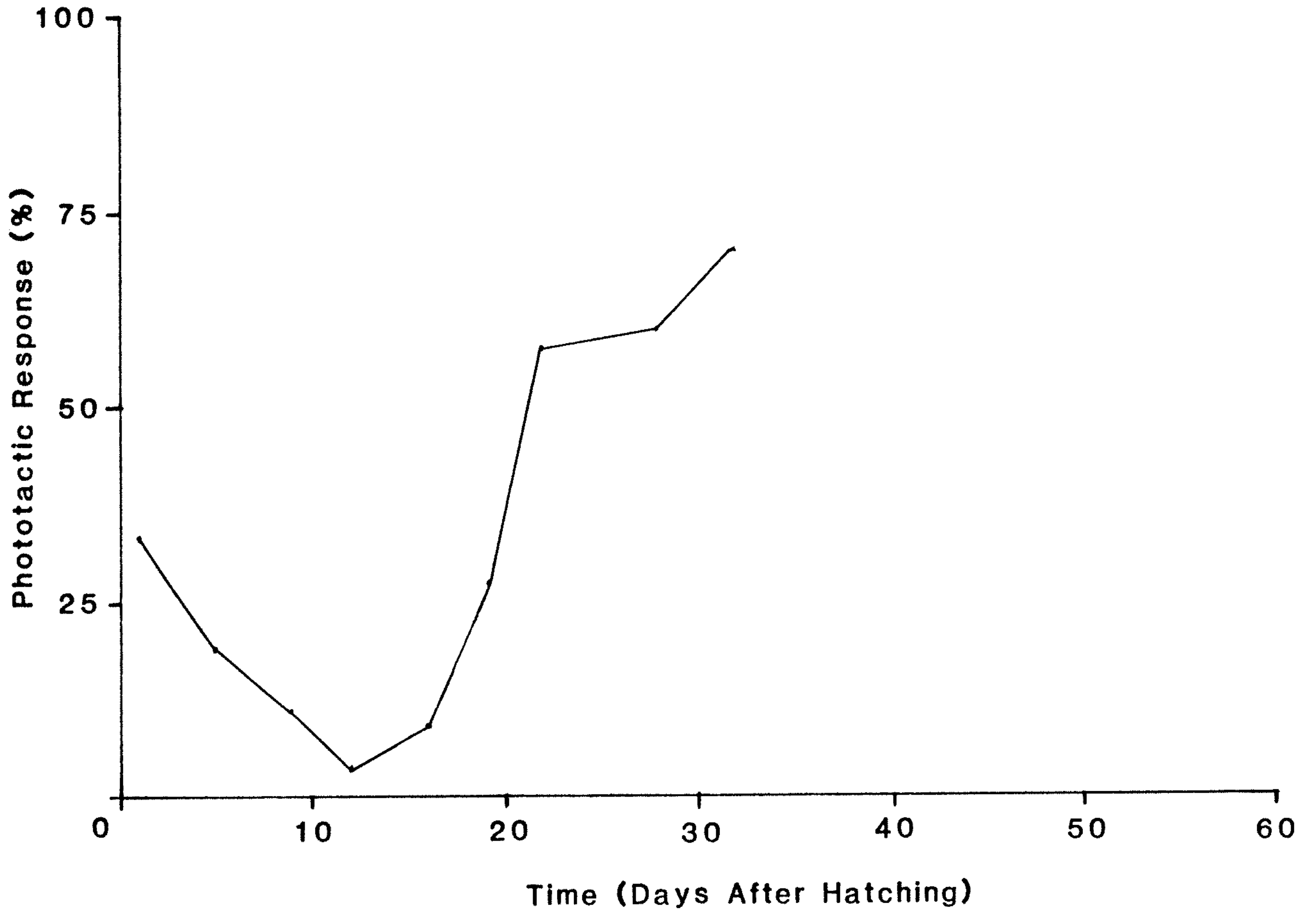


Fig. 26. Photobehavior of coho salmon alevins from hatching to yolk absorption. Each data point represents the mean percentage of 30 alevins in the light compartment of four separate light-dark choice tests.

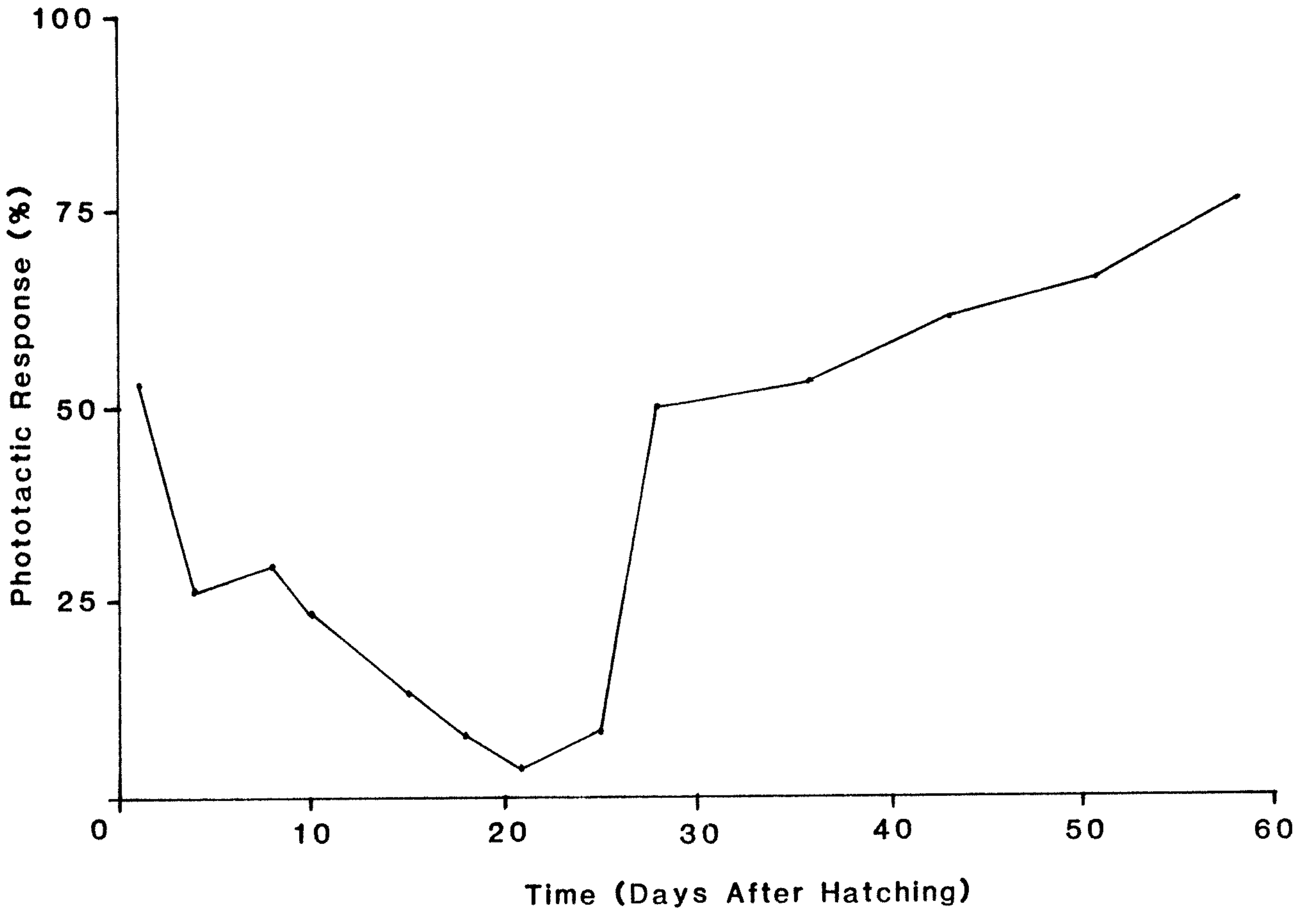


Fig. 27. Photobehavior of chinook salmon alevins from hatching to yolk absorption. Each data point represents the mean percentage of 30 alevins in the light compartment of four separate light-dark choice tests.

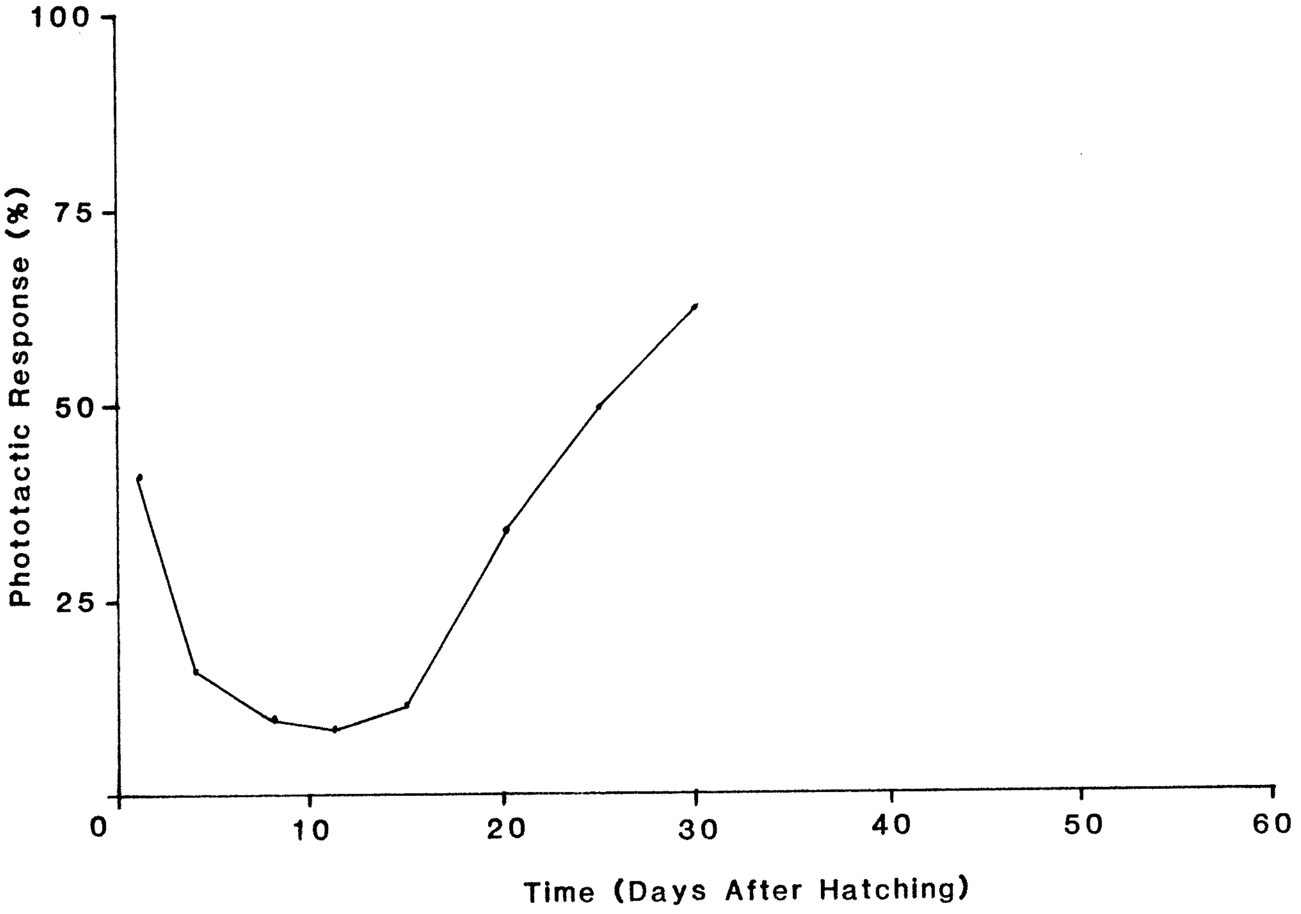


Fig. 28. Photobehavior of steelhead trout alevins from hatching to yolk absorption. Each data point represents the mean percentage of 30 alevins in the light compartment of four separate light-dark choice tests.

4.0 DISCUSSION

4.1 Morphological Development

The size of a salmonid alevin at yolk absorption is the result of numerous interrelated factors. Egg size is one of the most important biological factors affecting alevin size. The initial size of the egg varies both between and within species of salmonids (Rounsefell 1957; Bagenal 1966; Bakkala 1970; Koski 1975; Kazakov 1981). Egg size is influenced by the age, size and physiological condition of the female, time of spawning, and arrangement of ova in the ovaries (Koski 1975; Kazakov 1981). Egg size can also vary within a single female salmonid. The egg weights within an Atlantic salmon female ranged from 30 to 90 mg (Privolnev et al. 1964, in Kazakov 1981). A correlation exists between the size of the eggs and the resulting embryos and alevins (Gray 1928; Bagenal 1969; Fowler 1972; Koski 1975; Kazakov 1981). Studies have shown that larger fry are less susceptible to capture by predators (Parker 1971; Beall 1972; Walker 1974) and capable of out-competing their smaller conspecifics for feeding territories (Mason 1976). The smaller fry were driven out of experimental stream channels in Mason's study. When placed in replicate channels without competition these smaller fry grew to be as large as the fish in the original channels. This population regulatory mechanism assures that the largest fry will survive and also provides for dispersal of the species to previously un-utilized areas of the stream whenever available. Thus large size at emergence is advantageous in avoiding predation and in competition for better feeding territories.

A balancing mechanism in nature that limits the size of emerging fry is gravel size. Numerous studies have shown that smaller alevins have a higher survival to emergence rate than larger alevins (Bjornn 1969; Koski 1975;

Phillips et al. 1975). Koski (1975) believed that larger alevins were unable to migrate through the interstitial spaces in smaller gravel. Bams (1969) noted that emergence movements were slow, and that alevins alternated long periods of rest with periods of activity. Average speed of travel was determined by size of the interstices within the gravel (Bams 1969). Alevins that could not migrate through the gravel used up their available yolk supplies and died of starvation before emerging.

The yolk supply available to an alevin is a fixed quantity dependent upon the initial egg size. The yolk is utilized for body building and metabolism. Metabolism can be divided into maintenence and activity. Maintenance requirements are generally considered to be stable (Bams 1969). As an alevin increases its activity it increases the total amount of yolk (energy) that is used in metabolism and decreases the amount available for body growth. This results in a smaller sized fry at emergence (Bams 1969). Similarly, removal of a portion of the yolk of a developing alevin results in a smaller fry at yolk absorption (Gray 1928).

In a theoretical model, Bams (1969) assumed that about 30% of the yolk was required for metabolism from fertilization to emergence. Alevins that were more active (i.e., in a hatchery environment) would have a higher percentage of yolk used for activity and a resultant smaller body size at emergence.

The four species in the present study were reared under hatchery conditions. The yolk conversion efficiency, from hatching to yolk absorption, ranged from 46% in chum to 57% in chinook. Efficiencies calculated using similar dry weight methods for other species of salmonids ranged from 42 to 70% (Gray 1926; Gray 1928; Hayes and Pelluet 1945; Marr 1966; Blaxter 1969). Thus the species studied here had yolk conversion efficiencies well within the range reported in other salmonid studies. Marr (1966) found that yolk efficiency could be increased by rearing alevins on grooved substrate (for support), in darkened chambers, and with a high water turnover. Alevins decrease their activity in the dark, and high flow rate increased the oxygen level available for respiration.

The morphological development of the alevins increased from hatching to yolk absorption. The level of fin development for each of the species is of great importance in the mobility of the alevins. Bams (1969) observed that the caudal fin was used for propulsion in locomotion of alevins in wide crevices in the gravel. The caudal fin on day one was less than 50% of its final size at complete yolk absorption in three of the four species studied here. And in all four species the caudal fin was in a more advanced stage of development than the pectoral and dorsal fins. This may be due to the fact that in nature the alevin is supported by gravel at this stage of development and doesn't need stabilization from the dorsal and pectoral fins. The caudal fin would be expected to be more developed because it is the primary source of locomotion. Thus the poor fin and body musculature development and the large yolk sac limit the open water swimming ability of the newly hatched alevin. Thomas et al. (1969) attributed the increased swimming ability of older chinook alevins to the decrease in yolk sac volume. While the yolk sac is important, the development of the fins, both for propulsion and for stabilization in the water column are equally important.

Other experiments in this study indicated that newly hatched alevins were capable of downward intragravel movement. This movement resulted from undulating, snake-like motions in which the alevins wiggled between the pieces of gravel. Thus the alevins were capable of movement in the environment in which they would occur in nature. As morphological development proceeds the alevins body size and fin development increase and yolk size decreased such that they were prepared to swim in the open water when emergence occurred.

4.2 Metabolic Rate Studies

Studies on the metabolic rate of chum and coho salmon and steelhead trout demonstrated that there was an increase in oxygen consumption from hatching to yolk absorption. Previous studies have shown that the rate of oxygen consumption increased from fertilization to hatching in other salmonids. Hayes et al. (1951) found that oxygen uptake rose from about 0.2 ul/egg/hr at fertilization to 3.4 ul/egg/hr at hatching in Atlantic salmon. The salmonid egg is not always able to increase its oxygen uptake from the surrounding water as its metabolic rate increases. Daykin (1965) suggested that eggs deposited in the substrate act as oxygen "sinks" with the oxygen level at the egg surface always less than the surrounding water, even at high velocities. Previous studies of the effect of low dissolved oxygen levels on various salmonids have shown that survival occurs at levels of 2.5 mg/L or less but that development was retarded and alevins were smaller at hatching (Hayes et al. 1951; Alderdice et al. 1958; Garside 1959, 1966; Silver et al. 1963; Shumway et al. 1964). Reductions in velocity had a similar effect. Hayes et al. (1951) found that hatched alevins could obtain twice as much oxygen as unhatched embryos in the same water. This caused premature hatching of salmonid eggs in low oxygen water to occur as an adaptation of the embryo to increase its oxygen uptake (Alderdice et al. 1958).

Several studies have shown that the oxygen demand of larval fish also increased with age (Sharmardina 1954; Semko 1954). Tamarin and Komarova (1972) however, reported that maximum respiration in chum salmon occurred when about half of the yolk sac had been absorbed. This peak occurred at the time of complete transition to gill respiration, after which oxygen consumption decreased. No explanation or reason for the decrease was given.

The oxygen consumption rate of the chum and coho salmon and steelhead trout increased with increasing ambient water temperature. Alevin development is strongly affected by water temperature. At higher temperatures less time is required for development. This increase in developmental rate increased the metabolic rate and hence the oxygen consumption rate also rose. Lindroth (1942) reported the same effect of temperature on oxygen consumption rates.

4.3 Dewatering Studies

Experiments where alevins at successive stages of development were subjected to one-time, long-term dewatering indicated that survival was inversely related to time in days after hatching. Thus the greater degree of development in the alevin, the shorter the survival time when dewatered. The initial survival time (LT_{50}) ranged from 13 hours for steelhead to 34 hours for chinook. This original disparity decreased as alevin development increased.

Two possible reasons exist for the decrease in survival time of developing alevins. First, the metabolic rate as measured by oxygen consumption increases rapidly as development occurs. On day five, the oxygen consumption rate was lower in chum salmon than in either the coho salmon or steelhead trout. This difference, although slight, may account for the difference in early survival time. Information on chinook respiration rates might help to resolve this problem. The second possible explanation for the decrease in survival time was that the alevins developed a strong vascular net on the surface of the yolk sac which aids in respiration (Disler 1953; Smirnov 1953; Soin 1966). As the alevins develope, the size of the yolk decreases and its ability to supply oxygen decreases proportionately. Smirnov (1953) reported that in the developing embryo the gills do not begin to develop until the vascular system of the skin is fully developed. As the gills developed and began to function the capillaries in the skin degenerated because they were no longer necessary for respiration. Kryzhanovsky (In Smirnov 1953) suggested that the well developed vascular system in the yolk sac of the salmonids was analogous to that of the viviparous Cyprinidontiformes that suffered low dissolved oxygen levels by reason of being within the maternal body cavity. The chinook alevins had the lowest body weight as a percentage of total weight (body plus yolk) at hatching which may account for their longer survival time when dewatered. This theory assumes that respiration through the vascular system of the yolk sac assists or replaces respiration across the gills. Generally the gills, with a surface area between 10 and 60 times that of the rest of the fish's body, are the more important site of respiration (Parry 1966). However, the gills form a sieve-like structure that requires respiratory water flow along the secondary lamellae to maximize gill surface area for gas exchange (Hughes 1966). Saxena (In D. J. Randall Gas Exchange in Fish 1970) found that the secondary lamellae collapse and stick together when fish are in air. Thus the surface area of the gills available for respiration is greatly reduced when water is not being pumped through them. This would increase the importance of any accessory/secondary respiratory systems such as the vascular system of the yolk sac. Thus the survival time of the dewatered alevin would be expected to decrease as its respiration rate goes up, and its secondary respiratory surface (yolk sac) decreases.

4.4 Alevin Behavior Experiments

4.4.1 Movement Under Favorable Conditions

Alevins of chum, coho, and chinook salmon, and steelhead trout made downward intragravel migrations within 48 hours after hatching in conditions that were considered favorable for incubation. Chum salmon had the highest percentage of alevins migrating (36%) and chinook salmon had the lowest number (17%). This difference in numbers of fish moving was attributed to fewer chinook being able to move through the substrate interstices because of their larger size. Other studies have reported that larger numbers of smaller fish were successful in migrating through selected gravel substrates (Bjornn 1969; Koski 1975; Phillips et al. 1975).

Bams (1969), in laboratory observations of sockeye salmon, reported that pre-emergent alevins did not normally move through the gravel. They could be experimentally induced to move by reducing the water flow. Alevins in early developmental stages burrowed randomly through the gravel. Bams (1969) suggested that this random dispersal had adaptive value in spreading the alevins throughout a larger volume of water. Upon increasing the water flow the alevins ceased moving (Bams 1969).

Other studies have reported alevin movement did occur under favorable conditions. Dill and Northcote (1970) reported that coho alevins moved downward within a day after hatching. Further observations found alevins moving both laterally and vertically within the gravel prior to emergence. Dill (1967) found similar results in field studies of chum salmon. Studies by Roth and Geiger (1963) on brown trout, Carey and Noakes (1981) on rainbow trout, and Carey (in press) on brook and lake charr found that alevins moved downward after hatching. Differences in these results may be due to the different species tested and the different substrates used. Dill and Northcote (1969) had greater numbers of alevins moving downward in large gravel (3.2-6.3 cm) than in small gravel (1.9-3.2 cm).

It has been suggested that downward movement was the result of negative phototaxis (Roth and Geiger 1963; Dill and Northcote 1970; Carey and Noakes

1981; Carey in press). In the present study movement occurred even when extreme care was taken to exclude light from the experimental tanks. In Carey and Noakes (1981) study there was no difference in the magnitude of alevin movement over a range of light energies tested. Also, Roth and Geiger (1963) and Heard (1964) found that light penetrated only a few centimeters into the gravel and thus was probably not responsible for movement.

One possible reason for the movement observed in many of these studies is the dispersal theory suggested by Bams (1969). At hatching the alevin is closely associated with numerous other newly-hatched alevins and/or eggs which may be dead and decaying. Random dispersal of the alevins would increase the distance between alevins and move them away from their dead siblings.

Alevins of all four species demonstrated a positve rheotactic response by migrating into the current. Positive rheotaxis would have adaptive value in giving direction to the random dispersal in Bams (1969) theory. This upstream movement would assist the alevins in reaching higher quality water above their dead siblings.

4.4.2 Downward Intragravel Movement

Chum salmon alevins were able to migrate downward through smaller "interstitial" openings than similar sized coho salmon alevins and in greater numbers than the smaller steelhead trout. The factor that apparently limits the size of "interstitial" opening that an alevin can migrate through is greatest head diameter. Chum alevins had smaller head diameters than coho of the same approximate size but somewhat larger than steelhead alevins. The size of "interstitial" opening that alevins of all three species could migrate through decreased as alevin development progressed.

Several theories may be fowarded as to why chum salmon have an adaptive advantage in intragravel movement. Chum salmon often spawn in side channels or sloughs that may be more susceptible to water level fluctuations than coho or steelhead spawning areas. Chum salmon also spawn in areas that are influenced by tidal fluctuations. These water level fluctuations on chum spawning grounds may have resulted in the evolution of increased intragravel movement to avoid mortality from dewatering.

The experiments performed in this study tested the downward movement of alevins. This downward movement became more restricted by interstitial space size as alevin body size increased. This brings about the possibility of alevins migrating downward through interstitial gravel spaces that would later block their emergence migrations by stopping the upward passage of the larger, more developed alevins. Upward migration may be controlled by factors other than head diameter. With increased body strength the emerging alevins may wedge into crevices and enlarge the opening by prying its body upward. Gravity may also aid the upwardly mobile alevin. Bams (1969) reported that sockeye alevins, when confronted with a sand barrier during emergence migrations, would exhibit butting behavior. By thrusting its head into the sand the alevin loosened the grains of sand which fell downward past the fish and opened a tunnel for passage.

Koski (1975) however, found that survival to emergence decreased 1.26% for each 1.0% increase in sand in the gravel. Other studies have also found lowered survival in gravel with higher sand concentrations (Bjornn 1969; Phillips et al. 1975). These studies also demonstrated that smaller fry were more successful at emerging from higher sand concentrations than larger fry. Koski stated that the amount of sand in the spawning gravel was an index of the "living space" available for the developing alevins. He felt that a more meaningful measurement would be the percentage of voids within the gravel. Existing methods for gravel analysis are based on particle size from which the porosity of the streambed is inferred. Direct measurement of interstitial spaces using the McNeil Sampler or Freeze cores is impossible because of disruption of the gravel. Walkotten and Bryant (1976) proposed injecting epoxy resin into the substrate to bond gravel samples for direct measurement of interstitial spaces in salmonid redds. This method would increase information on alevin movement in the intragravel environment.

4.4.3 Movement and Velocity

Studies of the effects of velocity on alevin movement and rheotaxis have shown that movement shortly after hatching was random in the 0 and 40 cm/min velocities and apparently negatively rheotactic at 120 cm/min. Tests at the middle developmental stage had alevins demonstrating positive rheotaxis in the high and low flows and random in three of four species at zero velocity. At the late developmental stage the alevins were positively rheotactic in the high and low flows and random in the no velocity tests.

The random movement of all four species and at all life stages (except the middle stage in coho) in zero velocity indicates that when alevins had no current to orient to they dispersed randomly. These results are similar to the observations of Bams (1969) on sockeye salmon alevins. When water flow was experimentally stopped the alevins dispersed randomly. Bams (1969) suggested that this random dispersal was normal behavior when alevins were stressed. However, when alevins are stressed in the presence of current they generally orient into the current.

The negative rheotaxis of the newly hatched alevins in high velocity may be the result of the current carrying the alevins downstream through the large substrate. Dill and Northcote (1970) reported a negative rheotactic behavior in the downward movement of coho alevins in large gravel. This movement in Dill's experiment may also be the result of higher velocity carrying alevins downstream rather than active negative rheotaxis on the fishes part. High water velocities have been responsible for downstream displacement of embryos and alevins in other studies (Crisp 1981; Ottaway and Clarke 1981).

The alevins of all species demonstrated a positive rheotactic response in both low and high velocities during the middle and late developmental stages. This positive rheotaxis may have adaptive value in locating areas that have not had dissolved oxygen levels decreased from water reuse by sibling alevins or increased biological oxygen demand of decaying embryos. Pre-emergent chum alevins showed a decrease in length and weight when reared downstream from conspecifics in Japanese-style incubation channels (Bams and Lam 1983). The researchers concluded that deteriorating water quality (mainly dissolved oxygen) measurably reduced alevin development rate, growth rate, and yolk conversion efficiency. The minimum dissolved oxygen level in the channels was 6.21 mg/L. In natural redds the oxygen level may be considerably lower.

Emerging alevins generally demonstrate a positive rheotactic behavior. Chapman (1962) found that the coho moved downstream in small numbers shortly after emerging from the gravel. He did not determine if this downstream movement was an inate migratory urge or just displacement by current. Other studies by Mason and Chapman (1965) indicated that the earliest emerging coho fry occupied the most upstream areas of the study stream. Later studies by Mason (1976) indicated that coho fry showed a positive current response with 68-82% moving upstream following emergence. Neave (1955) and Hoar (1956) showed that pink, chum, and sockeye salmon fry usually migrated as individuals and were negatively rheotactic. Observations of newly emerged chum salmon in the present study indicated that these fry were positively rheotactic for several days after emerging. For several more days the chum fry alternated between swimming into the current or swimming with it. Thus results of these studies on pre-emergent alevins are in agreement with results of other studies on early emergent fry of the same species.

4.4.4 Movement and Dissolved Oxygen

The results of studies on the movement of chum, coho and chinook salmon and steelhead trout alevins in response to two sources of water that differed only in their dissolved oxygen content indicated that the alevins moved away from the lower oxygen source and toward the source with higher oxygen levels. This response was observed in each series of tests with different oxygen levels. This ability to detect and migrate to the source with a higher oxygen level may be important to the survival and growth of the alevins. The strong avoidance of the 2 mg/L water was expected as survival declines at or below this level (Shepard 1955; Herrmann et al. 1962; Davis 1975; Koski 1975; Brett and Blackburn 1981). The avoidance of the 4 mg/L water was not as strong as in the first series but was still significant (72 to 84%). An avoidance of the 6 mg/L water occurred in six of the eight tests. Thus the alevins avoided water with dissolved oxygen levels in the incipient sublethal threshold zone of 4.5 to 7.0 mg/L (Hayes et al. 1951; Wickett 1954; Alderdice et al. 1958; Whitmore et al. 1960; Herrmann et al. 1962; Davis et al. 1963; Randall and Smith 1967; Randall et al. 1967; Holeton 1971; Davis 1975; Brett and Blackburn 1981; Coble 1982; Bams and Lam 1983). This sublethal threshold zone is the level that will just support the maximum rate of growth.

Previous research has indicated that avoidance of hypoxic water occurred because fish generally became more active and randomly dispersed until areas of higher dissolved oxygen were encountered (Bams 1969; Randall 1970). Shepard (1955) reported that brook trout demonstrated a violent increase in activity when subjected to oxygen deficient water.

Whitmore et al. (1960) found that chinook fry avoided oxygen concentrations of 1.5, 3.0, and 4.5 mg/L at high temperatures. A decrease in avoidance, attributed to lower temperatures, occurred in the fall. Chinook did not avoid oxygen levels of 6 mg/L at any time. Coho salmon fry avoided all oxygen levels, including 6 mg/L, but not as strongly as chinook salmon at levels below 4.5 mg/L.

Salmonids must possess some physiological receptor for detecting low oxygen levels in water. Powers and Clarke (1942), in studies of brook and rainbow trout, concluded that there was respiratory control involving oxygen receptors in the gill arches. Randall and Smith (1967) found that rainbow trout increased their breathing rate and amplitude in response to hypoxia. Research has been conducted in an attempt to determine the location of the oxygen receptors in fish (Holeton 1977). Two locations are currently favored. The first set of receptors are believed to be located in the efferent arterial bloodstream. The second set of receptors are believed to be in contact with the inspired water. The probable location in rainbow trout is the anterodorsal surface of the anterior pair of gill arches (Randall and Smith 1967; Holeton 1977). Thus there is current evidence that fish are capable of determining the oxygen content of water and responding with physiological adaptations such as increased ventilation and decreased heart rate. The data in the present study indicated that salmonid alevins may also respond with a directed movement from low to high oxygen levels in water.

4.4.5 Movement and Photobehavior

Experiments on the photobehavior of developing alevins indicated that there was no initial response to light in the chum and chinook salmon. The steelhead trout were slightly photonegative and the coho alevins were the most strongly photonegative of the four species on the first day after hatching. As alevin development progressed photonegative behavior increased until less than 10% of the alevins remained in the light compartment. These results are very similar to those reported by Stuart (1953) for brown trout and Atlantic salmon.

Observations made during the present study indicated that newly hatched alevins were unable to make sustained swimming motion with any directional control. Alevin movement during the first several days after hatching consisted of laying on their sides and "spinning" around their yolk sacs. The initial neutral photobehavior may be due to the alevins inability to move into the darker compartment. The increasing photonegative behavior may actually be the result of greater alevin mobility as fin development and yolk absorption proceeded. Dill (1977, 1982) also observed this "spinning" behavior during the first days of development of the pink salmon, Atlantic salmon, and rainbow trout. Dill (1982) called this period the "righting phase" in which the alevins attempted to achieve and maintain an upright position. Alevins observed in substrate did not demonstrate this behavior as their bodies were supported by gravel.

Several other studies (Carey and Noakes 1981; and Carey in press) reported an initial strong photonegative behavior in rainbow trout and brook charr (*Salvelinus fontinalis*) alevins. This initial photonegative behavior gradually decreased as the alevins developed. Ostrander (personal communication) in recent studies of rainbow trout alevins found results similar to those reported in the present study.

The magnitude of the negative photoresponse was similar for all four species during the middle developmental stages. The initiation of the transition to photopositive response began when 53 to 61% of the yolk had been absorbed. This photoreversal occurred most rapidly in the chinook salmon, with an equal distribution of alevins between the light and dark compartments when only 53% of the yolk had been absorbed. The chum and coho became photoneutral at 72 and 68% yolk absorption, respectively. Steelhead trout did not reach this photoresponse transition until 91% of their yolk was absorbed.

One possible explanation for this difference in timing of photoreversal is the range in sizes of the species studied. Bams (1969) suggested that photonegative behavior was an adaptation to keep the alevins in the safety of the gravel. Other studies have shown that smaller fry have a higher survival to emergence rate than larger fry (Bjornn 1969; Koski 1975). Therefore, it would be adaptive for transition to photopositive behavior to occur earlier in the development of larger alevins. This would allow them to initiate emergence migrations with sufficient yolk supplies to ensure successful emergence from the gravel.

Mason (1976), in studies on coho fry, found that the pronounced photonegative behavior was progressively reduced as emergence proceeded but remained photonegative throughout his study. In a concurrent study of fry actually emerging from a redd, however, he found no difference between the numbers emerging during the day or night. Mason refers to this retention of photonegative response as hiding behavior in which the fry use the gravel as a refuge.

Studies of sockeye salmon report that emergence occurs mainly at night (Heard 1964; Bams 1969). Bams (1969) found that sockeye were negatively phototactic throughout their entire intragravel development and that any light inhibited emergence. It has been suggested that this tendency of certain species to emerge only at night may be an adaptation to avoid predators (Bams 1969; Godin 1980). No explanation as to why it does not occur in all species has been proposed as yet.

Temperature may also influence the diel emergence timing within certain species. Godin (1980) found that pink salmon emerge mainly at night at temperatures below 13°C, but randomly with respect to light at 15°C. Dill (1970) had more rainbow trout emerging during the day at 10°C and more at night at 15°C. Thus different species, or even stocks of fish, may demonstrate different photobehavioral responses during their development.

Some evidence that photobehavior may be genetic has been reported by Carey (in press). He found different magnitudes of photoresponse in brook charr (strong response) and lake charr (weak response). Hybrid progeny demonstrated an intermediate photobehavioral response.

The negative photobehavior of alevins prior to emergence is probably an adaptation to keep them in the gravel during incubation when they would be most susceptible to predation. The reversal of this behavior (at least in most species) at emergence allows the alevins to enter the water column above the substrate and begin the next stage of their life histories as free swimming fry.

4.5 Management Implications

The intragravel survival of embryos and alevins is an important fisheries concern of interest to water managers of hydroelectric, irrigation and other projects that cause water level fluctuations in rivers. A primary purpose of this research was to determine the survival time of alevins in dewatered environments and behavioral adaptations which may lead to the avoidance of the effects of dewatering (i.e., intragravel movement).

The survival time of dewatered alevins decreased as development from hatching to yolk absorption progressed. This decrease in survival time was believed to be the result of the increased respiration rate of the alevins and also the decreased surface area of the vascularized yolk sac which may act as a secondary respiratory organ. The LT_{50} was used as an index to compare the lengths of survival time between various stages of development and also between species. This data could be used as a guide to determine the maximum length of short-term dewatering which alevins at various stages of development could survive. The sublethal effects of dewatering were not studied in this research. Previous studies by Reiser and White (1981) found that long-term dewatering of embryos did not affect their final length or weight when compared to control fish that had not been dewatered. More research on the sublethal effects of dewatering should be conducted.

The survival time of alevins dewatered in a natural redd may differ substantially from those of alevins dewatered under laboratory conditions. In the natural situation the air temperature around the dewatered alevins may vary due to freezing or insolation from the sun. These and other factors may lower the survival rate of dewatered alevins in redds. Thus caution should be exercised in applying these results to actual field situations.

Management decisions are complicated when dewatering from even a single incident occurs in a river system where embryos and alevins from several salmonid species are incubating at different stages of development. Unfortunately, as alevin development increases and dewatering survival time decreases the susceptibility of alevins to dewatering is increased due to upward emergence migrations through the gravel. Thus smaller water level fluctuations will expose emerging alevins to dewatering conditions when their survival expectations are lowest.

These studies indicate that under controlled laboratory test conditions downward movement of alevins did occur after hatching. The alevins demonstrated the ability to actively move through gravel similar to that found in natural redds. Such movement in the natural redds may, however, be limited by intrusion of sediments into the gravel and/or the confines of the redd as constructed by the adult salmon. Movement under laboratory conditions may not parallel that in natural redds. One factor that may limit movement in redds is the intrusion of sediment into the gravel interstices during the several months of incubation between egg deposition and hatching. The gravel substrate used in the laboratory experiments approximated that collected from actual redds in the Skagit River. The samples were taken from the Skagit River redds within several weeks after spawning which may have limited the amount of sediment intrusion to a level lower than would be present after several months.

Another factor which may limit downward alevin movement in nature is the redd design. The female salmon constructs a redd to a limited depth by removing the sediment and smaller gravel. She then deposits the eggs in the interstitial spaces between the remaining larger gravel and covers the nest. Thus the eggs are already near the bottom of the redd at deposition and downward movement may be limited by bedrock or sediment layers in the gravel substrate beneath the redd. Thus movement of alevins to avoid dewatering in the natural situation may be restricted by several factors. Caution must be used in applying these laboratory criteria to management until appropriate field studies are conducted which define the natural limitations for each species and substrate type in the affected stream or river.

5.0 Summary

1. The chinook salmon alevins were the largest in total weight (body and yolk) at hatching. The chum and coho were about the same size while the steelhead were the smallest of the four species studied. Alevins of all four species had poorly developed fins at hatching and were unable to swim. Swimming movement was also restricted by large yolk sacs which represented 81 to 89% of the total dry weight of the alevin at hatching. Swimming ability increased as body and fin development proceeded and yolk sac decreased. The conversion efficiency of yolk to body weight ranged from 46% in chum to 57% in chinook salmon alevins.
2. The chum salmon alevins had the lowest metabolic rate, as measured by oxygen consumption, at hatching. The metabolic rate of chinook alevins was not studied. All three species increased the amount of oxygen consumed per gram of total weight from hatching to total yolk absorption. Oxygen consumption rate was measured at 4, 8, and 12°C and was found to be greater at higher temperatures for each species. The steelhead trout alevins had the highest oxygen consumption rate at total yolk absorption of the three species.
3. Experiments where alevins at successive stages of development were subjected to one-time, long-term dewatering indicated that survival was inversely related to time in days after hatching. The initial time to 50% survival (LT_{50}) ranged from 13 hours in steelhead to 34 hours in chinook alevins. Thirty days after hatching the LT_{50}'s ranged from .6 hours in steelhead to 1.6 hours in chinook. The decrease in survival time was attributed to the increase in metabolic rate and decrease in yolk sac size. The highly

vascularized yolk sac surface acts as a secondary respiratory organ.

4. The results of experiments on the intragravel movement of alevins under conditions of adequate velocity, dissolved oxygen, and darkness indicated that all four species made downward migrations within 48 hours after hatching. Chum salmon had the greatest number of alevins moving downward through 20 cm of gravel. The larger chinook alevins made the fewest successful downward migrations. The difference in number of alevins moving was attributed to size, however, chinook salmon usually spawn in larger substrate than other species of salmon. Alevins of all four species demonstrated a positive rheotaxis by migrating into the current.

5. Chum salmon alevins were able to migrate downward through smaller sieve mesh sizes than similar sized coho salmon alevins and in greater numbers than the smaller steelhead trout. The factor that apparently limited the size of opening an alevin could migrate through was greatest head diameter. Chum salmon had smaller head diameters than coho alevins of the same approximate size but were somewhat larger than steelhead alevins. The size of opening that alevins of all three species could move through decreased as alevin development progressed.

6. Studies of the effects of velocity on alevin movement and rheotaxis indicated that movement after hatching was random at zero and low velocities and negatively rheotactic at high velocities. The negative rheotaxis at high velocities may be the result of strong flow carrying the alevins downstream through the large substrate. Tests at middle and late alevin developmental stages indicated that alevin movement was positively rheotactic in the high and low flows

and random in the no velocity tests.

7. Studies on the movement of alevins in response to dissolved oxygen concentrations indicated that the alevins of all four species moved away from the lower oxygen concentration and toward the water source with higher oxygen levels. The percentage of alevins moving toward the higher oxygen was greatest in the 6 vs. 2 mg/L tests, intermediate in the 8 vs. 4 mg/L and lowest at 10 vs. 6 mg/L. The number of alevins responding was greater at the later stages of development.

8. Studies of photobehavior indicated that alevins became increasingly photonegative as development increased. This increase in photonegative behavior was attributed to an increase in the ability of alevins to respond to the light stimulus and move into the dark compartment as fin development and yolk absorption progressed.

   The magnitude of negative photoresponse was similar for all four species during the middle developmental stages. The initiation of the transition to photopositive behavior began when 53 to 61% of the yolk had been absorbed. The transition was completed before emergence began in each species. Photoreversal was most rapid in chinook and slowest in steelhead trout alevins. The earlier transition to photopositive behavior may allow the larger chinook alevins to initiate upward migrations with sufficient remaining yolk supplies to ensure successful emergence from the gravel.

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