

THE INFLUENCE OF WATER VELOCITY
AND DISSOLVED OXYGEN
ON THE DEVELOPMENT OF SALMONID EMBRYOS

by

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THE INFLUENCE OF WATER VELOCITY
AND DISSOLVED OXYGEN
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INTRODUCTION

A laboratory investigation was conducted to determine the influence of water velocity and dissolved oxygen on the development of embryos of chinook salmon, Oncorhynchus tshawytscha (Walbaum), and steelhead trout, Salmo gairdneri gairdneri Richardson. The experiments were performed during October, November, and December of 1958, and February, March, and April of 1959, at the Oak Creek Fisheries Laboratory of the Department of Fish and Game Management, Oregon State College. A wide range of water velocities was tested at different controlled oxygen levels, and the influence of these conditions on the growth, rate of development, and success in hatching of salmonid embryos was studied.

Ellis (4, p. 394) indicated that the deposition of silt on spawning grounds has a direct effect on fish populations. A great deal has been done to determine the effects of siltation on developing fish embryos since the publication of this work in 1937. Hobbs (7, p. 93), from his work in New Zealand, concluded that the extent of losses of fertilized ova in redds depended on the amount of very fine material in the redds prior to "eyeing" of the embryos. Shaw and Maga (11, p. 34-41) showed that

mining silt deposited on spawning beds during the time that salmon embryos were developing had a deleterious effect on the yield of fry. They concluded that deposition of silt at this time was a serious menace to natural propagation. Other workers have also indicated the adverse effects of siltation on developing salmonid embryos (10, p. 138) (12, p. 225-230) (14, p. 23).

According to Wickett (15, p. 933), high mortalities in nature of pre-eyed chum salmon, Oncorhynchus keta, eggs may be due to the embryos' receiving insufficient oxygen either because of very low apparent velocity¹ or very low dissolved oxygen content of the subgravel water. Cooper (3, p.52) concluded from his experiments on the Horsefly River in Canada that reduced survival rates of embryos and fry would be in proportion to the reduction of flow of water through the gravel, caused by deposition of sediment on gravel spawning beds. He further concluded that a certain apparent velocity is necessary to supply to all locations in a given type of gravel bed sufficient oxygen for maximum survival of salmonid embryos to be obtained.

1. Apparent velocity as defined by Pollard (9, p. 709) is the rate of seepage expressed as the volume of liquid flowing per unit time through a unit area (of solids plus voids) normal to the direction of flow.

The environmental factors affecting the production of pink salmon, Oncorhynchus gorbuscha, and chum salmon have been reviewed by Wickett (16, p. 1103-1126). He noted that different water levels during the early stages of embryonic development may result in variations in survival rate from year to year, and the numerical size of the offspring stock bears a close relation to these water levels. He attributed this to the change in flow of oxygen-bearing water past the eggs in the gravel. Wickett suggested also that survival increased with increase in the permeability of the gravel.

Investigations concerning oxygen consumption rate of salmonid embryos have been conducted by Lindroth (8, p. 583-594), Hayes, Wilmot and Livingstone (6, p. 377-395), and Alderdice, Wickett and Brett (1, p. 229-249). Hayes (5, p. 281-308) reviewed the growth, general chemistry, and temperature relations of developing salmonid embryos. Smith (13, p. 323-359) reviewed the general physiology of developing teleost embryos, including effects of environmental conditions on development.

Alderdice, Wickett and Brett (op. cit.) suggest that the availability of oxygen to salmon embryos may be dependent on the oxygen pressure in the microenvironment surrounding the egg. The potential utilization rate and physiological state of the embryo are influenced by

temperature, as is the oxygen pressure in the microenvironment. The oxygen content of the water which immediately surrounds the eggs may be affected by the rate of oxygen utilization if this water is not replaced at a sufficient rate.

This thesis presents the results of two experiments on the influence of water velocity and dissolved oxygen on the development of salmonid embryos. The experimental apparatus was designed in the hope that nearly laminar flows of water of known velocities would be developed. It is recognized that the measurement of true velocities² in gravel beds is regarded by Wickett (15, p. 936) as impossible. It is believed that the rates of flow developed during the two experiments discussed here can most nearly be expressed as true velocities.

2. True velocity, as defined by Pollard (op. cit.), is the actual velocity of flow through the interstitial spaces of the gravel. This differs from pore to pore.

EXPERIMENTAL APPARATUS, MATERIALS AND METHODS

Experimental Apparatus

The apparatus shown in Figures 1 and 2 was designed to provide developing salmonid embryos with a constant, nearly laminar flow³ of water of controlled velocity and dissolved oxygen concentration. The major components of the experimental equipment were three plastic aquaria, each of which was constructed to provide two independent, 75-liter experimental chambers. Thus, six different dissolved oxygen concentrations could be tested during a single experiment.

Each aquarium was fitted with plastic supports for holding the porous plates on which the developing embryos rested. The aquaria were constructed so that turbulent water from beneath the plates was in direct contact with only a very small air surface, and so that air bubbles could be removed from beneath the plates. Each aquarium was fitted with two inlet tubes beneath the plates and an overflow tube above the plates (Figure 3).

Four 9-inch-square filter plates rested on the supports provided in each independent experimental chamber.

3. Laminar flow, as defined by Pollard (9, p. 709), is flow in which the individual molecules of the liquid are considered never to cross each other's path.



Figure 1. Experimental apparatus used to study the influence of water velocity and dissolved oxygen on the development of salmonid embryos.

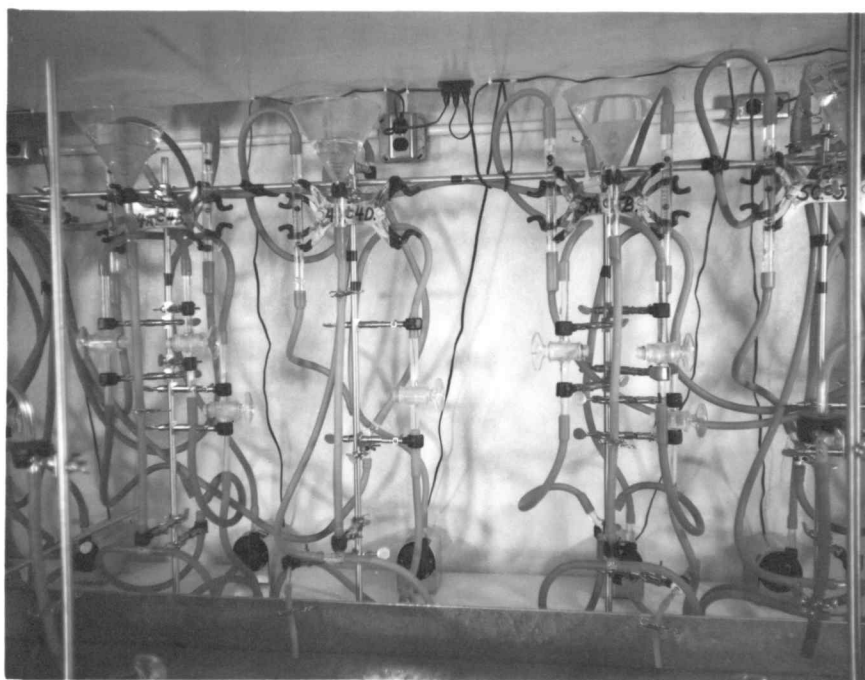
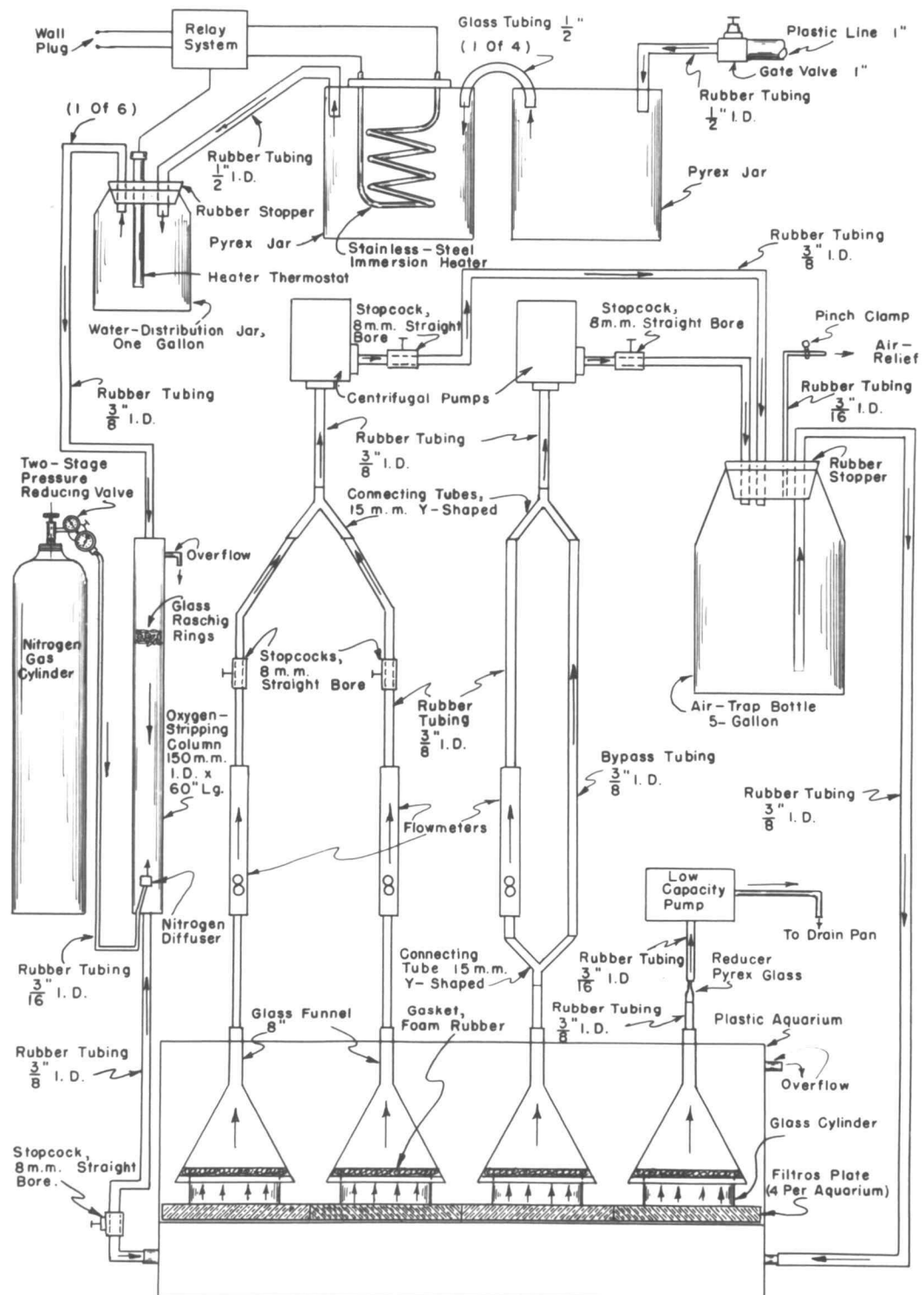


Figure 2. Components used for the control of water velocities.

These porous ceramic plates, composed essentially of silica, were manufactured by Filtros Incorporated, East Rochester, New York. They are one inch in thickness and permit a rather free passage of water. During the experiments, the plates acted as the resting place for the developing embryos and separated them from the turbulent inlet water which was introduced beneath the plates.

A pyrex-glass cylinder, 9 centimeters high and with an inside diameter of 13.8 centimeters, was sealed to each filter plate. The embryos rested on the plates, inside the cylinders. A polyethylene gasket held in place by a layer of sand was used as a seal in the chinook salmon experiment. A wax coating was used to seal the cylinders to the plates in the experiment with steelhead embryos. The purpose of these seals was to prevent any water not destined to pass among the embryos from flowing under the edges of the glass cylinders and disrupting the flow within the cylinders. A foam-rubber gasket was attached around the outside of each cylinder at its upper end to act as a seal between the cylinder and the eight-inch pyrex funnel inverted over it.

A discussion of the water-flow pattern through the entire system will serve to give an overall picture of the experimental apparatus (Figure 4). Water from a small, spring-fed stream was supplied through polyethylene pipe to



the constant-temperature experimental room. The water used for the chinook salmon experiment was not filtered, but the water for the steelhead experiment passed through a filtration system. Flow of water into a glass jar used to provide a constant head for the experiments was controlled with a one-inch gate valve. This jar was kept overflowing at all times. From here, the water was siphoned by means of U-shaped glass tubes to a second jar which held the thermostatically-controlled, stainless-steel immersion heater. The water then flowed to a one-gallon distribution jar which contained the heater thermostat and six outlet tubes. Water passed through these tubes to the tops of the six oxygen-stripping columns.

Dissolved oxygen was partially removed from the water passing down five of the columns by counterflows of nitrogen which were closely controlled by two-stage pressure-reducing valves. Air was passed through the water in the sixth column so as to provide a dissolved oxygen concentration at the air-saturation level. After leaving the columns, the water passed through eight-millimeter stopcocks for flow-rate control and then into the experimental chambers of the aquaria. Renewal water was supplied to each experimental chamber at a rate of approximately 600 milliliters per minute.

The embryos, resting on the filter plates inside the glass cylinders, received a flow of water when small centrifugal pumps with rubber housings and impellers were put into operation (Figure 2). Water from beneath the plates was drawn through the plates, past the eggs, through the funnels, through flowmeters, and then through rubber tubing to the pump intake connections. The flowmeters were of the ball-displacement type and measured the volumes of water passing the embryos. In order to achieve the highest velocities tested in the chinook salmon experiment, it was necessary to install bypass tubes in combination with some of the flowmeters (Figures 2 and 4). The flows thus obtained were more than double those obtainable with the flowmeters alone. Each bypass was calibrated with its respective flowmeter before the experiment began and after it was completed. The mean values of these calibrations were used in subsequent flow determinations. The readings obtained on the flowmeters were converted into milliliters per minute by means of a calibration chart provided by the manufacturer, the Manostat Corporation, New York, New York. The amount of water which flowed past the embryos was regulated by means of eight-millimeter stopcocks installed in the intake and output lines of the pumps.

Water, after leaving the pump, entered a five-gallon bottle where some of the air which collected in the system

was trapped. This air was removed periodically by means of relief lines. From the air traps, the water was reintroduced into the experimental chambers, beneath the filter plates. Water which flowed past the embryos was in this way recirculated through the system except in the case of the low velocity in the steelhead experiment. The very low rates of flow necessary for this velocity were obtained by means of a low-capacity pump which delivered the water either to a graduated cylinder for flow measurement, or to a drain pan.

Two centrifugal pumps were used for each experimental chamber. One of these was used for maintaining the highest experimental velocity. The two intermediate velocities were maintained by the pumping capacity of the second centrifugal pump. The two delivery lines to this pump each contained a flowmeter for flow measurement, and a stopcock for flow-rate regulation.

Experimental Materials

The chinook salmon eggs were from fall-run fish obtained at the Oregon State Fish Commission's Oxbow Hatchery on the Columbia River. The steelhead trout eggs were from winter-run fish obtained at the Oregon State Game Commission's trout hatchery on the North Fork of the Alsea River.

The eggs used in each experiment were from a single female. The eggs were allowed to become water hardened before being transported to the Oak Creek laboratory. The temperature of the water in which the eggs were transported was changed over a period of about six hours to the temperature at which the experiment was to be performed.

Experimental Methods

Several days before the beginning of each experiment, renewal and recirculation flows of water were started. This allowed time for air to be cleared from the system. Temperature control of the renewal water and of the constant temperature room was also begun. The temperature of the room was maintained several degrees lower than the temperature of the renewal water. Oxygen concentrations were not brought to the desired levels until after the eggs were placed into the experimental chambers.

For the chinook salmon experiment, 140 eggs were placed inside each of the three cylinders in every experimental chamber. The eggs in each cylinder were divided into two groups, one containing 60 and the other 80 eggs. The group of 60 was used for hatching success determination, and the group of 80 was used for four periodic samples. For the steelhead experiment, a total of 60 eggs

was placed inside each glass cylinder. Each cylinder in this experiment contained an egg separator which was made of a stainless-steel band strung with nylon to form a grid. The nylon strands prevented the eggs from touching one another. Twenty eggs in each cylinder were designated for a sample to be taken prior to hatching for examination and measurement, and 40 were designated for determination of hatching success.

A constant effort was made to maintain the selected experimental conditions throughout each experiment. Records of experimental data were taken, and adjustments were made three times daily; once between the hours of 7:30 and 9:30 a.m., once between 1:00 and 4:00 p.m., and once between 9:00 and 12:00 p.m. At these times, flowmeter readings and water temperatures were recorded, as were the numbers of dead embryos and numbers of hatched fry. Water samples were siphoned from the experimental chambers for dissolved oxygen determinations. After all samples were taken and necessary data were recorded, adjustments of the apparatus were made.

Air which had accumulated in the system had to be removed before flow or oxygen concentration adjustment could be accomplished. Air which had accumulated at various points in the tubing was forced through the system and then removed from the air-trap bottles by means of the relief

lines provided. Air which collected beneath the plates was removed with an L-shaped squeegee which was inserted between the side baffles of the aquarium (Figure 3).

After the air was removed, the desired experimental velocities were obtained by manipulation of the stopcocks in the recirculation system (Figure 2). Oxygen concentrations were adjusted by either increasing or decreasing the flow of nitrogen gas to the oxygen-stripping columns after the rates of water renewal for the experimental chambers were adjusted.

Dissolved oxygen determinations were made using the Alsterberg (azide) modification of the Winkler method as described in Standard Methods for the Examination of Water, Sewage, and Industrial Wastes, tenth edition (2, p. 255-256). Dissolved oxygen concentrations were determined and recorded to the nearest tenth of a milligram. Some of the oxygen concentrations as reported here have been corrected to adjust for differences between the concentration at the sampling point and the concentrations in the water in the different cylinders. Correction factors were determined through a series of comparative tests. Water samples were at first taken from above the plates, and it was later found that the oxygen concentrations in the water beneath the plates were somewhat lower. The dissolved oxygen concentration at the lowest velocity in the steelhead

experiment was slightly lower than that at the other velocities. Apparently this condition was caused largely by an oxygen demand which developed in the filter plates. This oxygen demand did not cause a detectable decrease in the concentrations at the higher velocities.

The water used for the chinook salmon experiment was not filtered, and this made it periodically necessary to remove as much silt as possible from the plates and embryos. Silt deposited in the plates resulted in some flow reduction and disruption. A water filter was in operation during the steelhead experiment, and silt presented no problem.

Dead eggs or embryos were not removed until the developing embryos had reached the eyed stage. From this time on, dead embryos were removed as they occurred. Cumulative records of the numbers of dead embryos and numbers of hatched fry were kept.

Samples of embryos were taken during the course of each experiment for length measurements. Four samples of approximately 20 embryos each were taken during the chinook salmon experiment. The first sample was taken when all the embryos but those in the lowest dissolved oxygen concentration were eyed, and the last sample was taken when the first fry appeared in the experimental chamber with the highest dissolved oxygen concentration (control chamber).

Only one sample of approximately 20 embryos from each cylinder was taken during the steelhead experiment. This sample was taken four days prior to the hatching of the first embryo in the control chamber.

After the embryos were preserved in Bouin's solution, their chorions were removed, and the embryos were observed under a dissecting microscope. Lengths were measured in short increments to the nearest tenth of a millimeter with a pair of engineering dividers and a millimeter scale. The lengths were recorded, and the mean length and the range for each sample were determined.

Volumetric as well as length measurements were determined for the fry at the time of complete or nearly complete hatch. Complete hatch occurred at different times in the various experimental chambers, depending on the dissolved oxygen concentrations and the velocities. Samples of fry were taken so that measurements would correspond with these times. A second sample for length and volumetric measurements was taken from each cylinder in the steelhead experiment 17 days after complete hatch occurred. No measurements were made at a corresponding time for chinook salmon fry.

Length measurements of fry were determined to the nearest tenth of a millimeter with a pair of engineering dividers and a millimeter scale. Fry volume was determined

by the water displacement of the entire sample in either a 25 or 50-milliliter graduated cylinder after yolk sacs had been removed. Water was first removed from the fry by placing them on paper towels. All length and volume measurements of fry were determined with non-preserved specimens.

Mean water velocities, temperatures, and dissolved oxygen concentrations were calculated at the conclusion of each experiment. Correction factors for both water velocities and oxygen concentrations were necessary. Water velocities tended to decrease during any period. So that calculated means would not be biased downward by only the lowest velocity being determined for any period, an after-adjustment reading was included for each pre-adjustment reading. Mean oxygen concentrations reported here have been corrected for differences in oxygen concentration between sampling points and different cylinders.

EXPERIMENTAL RESULTS

Chinook Salmon

Hatching Success and Delay

While differences in water velocity had no apparent effect on hatching success of chinook salmon embryos, hatching was affected by the lowest dissolved oxygen concentration tested. Increased delay in hatching occurred with decreases in dissolved oxygen concentration. Differences in water velocity caused little or no delay in hatching.

Table 1 summarizes the results on hatching success and time of hatch. Time of hatch is expressed as age in days from fertilization for beginning, median, and complete hatch. It should be noted that the three experimental velocities tested were not equal for all experimental chambers, though it is believed that the velocity differences were not great enough for the results to have been influenced appreciably.

Total mortality of the embryos occurred at a dissolved oxygen concentration of 1.6 milligrams per liter at all velocities tested. The percentages of hatch were high at all concentrations between 2.5 and 11.7 mg./l., ranging from 92.3 to 100 percent. Hatching was successful

TABLE 1

Age in Days from Fertilization at Beginning,
Median, and Complete Hatch, and
Percent Hatch for Chinook Salmon Embryos

D.O. mg./l.	Velocity cm./hr.	Hatching			Percent Hatch
		Beginning	Median	Complete	
1.6	82	--	--	--	0
	568	--	--	--	0
	1313	--	--	--	0
2.5	88	48	51	54	95.1
	592	48	51	52	98.3
	1334	48	50	52	96.7
3.9	94	45	46	48	100
	576	44	46	48	100
	1238	45	46	48	100
5.6	97	45	46	47	96.7
	576	45	46	47	98.4
	1372	45	46	47	93.1
8.0	97	43	44	45	98.3
	576	44	44	45	98.3
	1362	42	44	45	95.0
11.7	94	42	43	45	100
	576	42	44	45	92.3
	1356	42	43	45	98.2

at all water velocities tested when the concentration of dissolved oxygen was 2.5 mg./l. or higher.

Embryos reared at dissolved oxygen concentrations lower than the control level, 11.7 mg./l., exhibited a delay in hatching time. The delay was greatest at the dissolved oxygen concentration of 2.5 milligrams per liter. The embryos reared at this oxygen level, as compared to those reared at the control level, were delayed six days for beginning hatch, seven to eight days for median hatch, and seven to nine days for complete hatch. Water temperatures in all experimental chambers were not equal (Table 2), and this could account for some of the differences in time of hatch. However, mean water temperatures at the dissolved oxygen concentrations of 3.9 and 8.0 mg./l. were equal, and a difference in hatching time of zero to three days for beginning hatch, two days for median hatch, and three days for complete hatch was evident at these concentrations. The largest differences in hatching time between embryos reared at the various water velocities occurred at a dissolved oxygen concentration of 2.5 mg./l., but these differences were not great, and may not have been significant.

Embryo and Fry Growth

Differences in growth, indicated by linear measurements of embryos and linear and volumetric measurements of

TABLE 2

Means and Ranges of Water Temperature, Velocity, and Oxygen Concentration
for the Experiment with Chinook Salmon Embryos

Experimental Chamber Number	Temperature °C.		Dissolved Oxygen mg./l.		Cylinder	Velocity ¹ cm./hr.	
	Mean	Range	Mean	Range		Mean	Range
1	11.3	9.3-13.0	8.0	6.8-9.6	A	97	82-128
					B	576	556-654
					C	1362	1132-1457
2	11.2	9.2-13.0	1.6	0.6-5.1	A	82	20-350
					B	568	332-798
					C	1313	916-1604
3	11.1	9.5-13.1	5.6	3.4-6.5	A	97	54-112
					B	576	536-608
					C	1372	1004-1444
4	11.0	9.3-13.5	2.5	.9-4.3	A	88	20-357
					B	592	262-781
					C	1334	1042-1500
5	11.3	9.9-13.7	3.9	2.4-5.9	A	94	42-350
					B	576	350-684
					C	1238	850-1496
6	11.4	10.0-13.8	11.7	10.0-13.2	A	94	30-112
					B	576	442-764
					C	1356	1032-1510

1. Power failure eight days after experiment began reduced all velocities to zero for two hours.

newly-hatched fry, were apparent between embryos reared at the different levels of dissolved oxygen tested. Differences in growth between embryos reared at the different water velocities tested at each dissolved oxygen concentration were also apparent. With decreasing levels of dissolved oxygen or water velocity, there was a decrease in the mean size of the embryos and fry. Growth subsequent to hatching was not determined for chinook salmon fry.

Table 3 presents the size data for the four samples taken during the experiment. Means and ranges of dissolved oxygen concentrations and water velocities for the different cylinders are given in Table 2. The embryos reared at higher levels of dissolved oxygen concentration were consistently larger than those reared at the lower levels. Some of the embryos sampled 14 days after fertilization already indicated increases in length at the higher concentrations over those reared at the lower oxygen concentrations. These differences in length between embryos reared at the different oxygen concentrations became greater, percentagewise, as the embryos became older, as indicated by samples taken 24, 35, and 41 days after fertilization. Differences in the mean lengths of embryos reared at the different velocities, while possibly present in the younger embryos, were not very apparent until the embryos became older.

TABLE 3

Mean Lengths and Ranges in Millimeters of Chinook Salmon Embryos
at Various Times During Development

Velocity in cm./hr. ¹	Days After Fertili- zation	Dissolved Oxygen Concentration in Mg./l.					
		1.6	2.5	3.9	5.6	8.0	11.7
92	14	2.5 (1.5-3.2)	5.3 (4.6-5.7)	6.0 (5.5-6.5)	5.6 (5.0-6.0)	6.0 (5.5-6.7)	6.3 (6.0-6.7)
	24	3.2 (2.0-4.0)	10.0 (9.3-11.0)	11.7 (11.0-12.2)	12.0 (11.0-13.0)	12.3 (11.2-13.0)	14.3 (13.8-15.0)
	35	3.7 (3.0-4.5)	13.4 (12.0-14.0)	15.5 (15.0-16.0)	16.0 (15.0-17.0)	17.2 (16.2-18.0)	19.6 (19.0-21.0)
	41	4.1 (2.5-5.0)	14.3 (13.7-15.8)	16.7 (15.5-18.0)	18.2 (14.0-19.0)	19.9 (19.0-20.3)	21.3 (20.0-22.0)
577	14	3.0 (2.4-3.4)	5.3 (5.0-5.7)	6.1 (5.6-6.5)	5.9 (5.3-6.1)	6.2 (5.7-6.7)	6.3 (5.9-6.8)
	24	3.9 (2.9-5.0)	8.9 (8.3-10.0)	12.0 (11.5-13.0)	11.9 (11.0-13.0)	12.0 (11.5-12.7)	14.4 (13.5-15.0)
	35	4.2 (3.0-5.5)	13.6 (13.0-14.1)	15.6 (15.0-17.0)	15.8 (15.0-16.5)	17.8 (17.0-19.0)	20.0 (19.0-21.0)
	41	4.7 (3.5-7.0)	14.9 (13.5-16.0)	17.5 (16.3-18.3)	18.8 (18.0-19.8)	20.3 (19.5-21.3)	21.6 (20.0-22.5)

TABLE 3 (cont'd)

Velocity in cm./hr. ¹	Days After Fertili- zation	Dissolved Oxygen Concentration in Mg./l.					
		1.6	2.5	3.9	5.6	8.0	11.7
1347 ²	14	3.0 (1.9-3.2)	5.5 (4.5-6.0)	6.1 (5.6-6.6)	5.5 (5.1-6.0)	6.2 (6.0-7.0)	6.3 (5.5-6.7)
	24	4.1 (3.0-5.0)	10.4 (10.0-11.0)	12.3 (11.5-13.0)	12.0 (11.0-13.0)	12.2 (11.0-13.0)	14.5 (13.0-15.0)
	35	4.7 (4.0-5.7)	14.0 (13.2-15.0)	15.9 (15.1-17.0)	16.3 (15.5-17.0)	14.8 (17.0-18.6)	19.9 (19.0-21.0)
	41	5.2 (4.0-6.0)	14.9 (14.0-16.0)	17.5 (16.3-19.0)	18.8 (18.0-20.0)	20.2 (19.0-21.0)	22.2 (21.5-23.0)

1. Indicated as means calculated from the mean velocities of all experimental chambers.
2. 1238 cm./hr. at dissolved oxygen concentration of 3.9 mg./l. not included in calculation of mean.

The differences in growth at different oxygen concentrations shown by embryo measurements were also shown in measurements of fry (Table 4). Fry reared at the higher dissolved oxygen levels were consistently larger, both in length and in volume, than those reared at lower concentrations. While, as would be expected, the greatest size difference occurred between fry reared at 2.5 mg./l. and those reared at 11.7 mg./l. of dissolved oxygen, differences existed between fry reared at 8.0 and 11.7 milligrams per liter. Mean size differences between embryos reared at 2.5 and 11.7 mg./l. ranged from 4.5 to 5.1 millimeters in length and from .040 to .066 milliliters in volume. Percentagewise, differences in volume were much greater than were differences in length.

At all dissolved oxygen concentrations studied, the fry reared at the lowest and intermediate velocities, approximately 92 and 577 centimeters per hour respectively, were shorter than those reared at the highest velocity, approximately 1347 centimeters per hour. The greatest difference occurred at the dissolved oxygen concentration of 3.9 mg./l., where the fry reared at the highest velocity averaged 1.2 millimeters larger than those reared at the lowest velocity. At 2.5 mg./l. the mean volume of the fry reared at the highest velocity was nearly twice that of the fry reared at the lowest velocity. Increases in volume of

TABLE 4

Mean Lengths and Ranges and Mean Volumes of Chinook Salmon Fry at Hatch

Velocity ¹ in cm./hr.	<u>Dissolved Oxygen Concentration in mg./l.</u>					
	1.6	2.5	3.9	5.6	8.0	11.7
<u>Length in Millimeters</u>						
92	--	18.7	20.0	21.6	22.5	23.6
		(17.8-19.8)	(19.5-20.6)	(21.0-22.0)	(22.0-23.0)	(23.0-24.5)
577	--	19.4	21.0	22.4	22.9	23.9
		(18.5-21.0)	(20.2-21.5)	(21.5-22.8)	(22.5-23.0)	(23.5-24.5)
1347 ²	--	19.7	21.2	22.5	23.2	24.8
		(19.4-20.0)	(20.5-21.9)	(22.1-23.0)	(22.5-24.0)	(24.0-25.0)
<u>Volume in Milliliters³</u>						
92	--	.017	.033	.042	.053	.083
577	--	.020	.037	.050	.066	.066
1347	--	.033	.043	.050	.066	.073

1. Indicated as means calculated from the mean velocities of all experimental chambers.
2. 1238 cm./hr. at dissolved oxygen concentration of 3.9 mg./l. not included in calculation of mean.
3. Volumes of fry without yolk sacs.

fry with increasing velocity were apparent at all concentrations of dissolved oxygen tested up to and including 8.0 milligrams per liter.

Abnormalities and Fry Survival

External examination of chinook salmon embryos indicated that abnormal development occurred only at the lowest dissolved oxygen concentration tested. Embryos reared at 1.6 mg./l. of dissolved oxygen exhibited grossly abnormal development at the three levels of water velocity tested. No differences in the incidence of abnormal growth between the levels of water velocity could be detected.

Post-hatching survival was affected by the lowest dissolved oxygen concentration in which hatching occurred. The percent mortalities within seven days after hatching for fry reared at a dissolved oxygen concentration of 2.5 mg./l. and at 88, 592, and 1334 cm./hr. were 29.3, 23.7, and 8.5 percent respectively. Velocity, too, would seem to have influenced survival at this concentration. The percentages of mortality at other levels of dissolved oxygen ranged from 6.9 to 0 percent.

Steelhead Trout

Hatching Success and Delay

In the experiment with steelhead embryos, hatching success was reduced at the lowest dissolved oxygen concentration tested, but apparently it was not influenced by the water velocities tested. Time of hatch was delayed by reduced levels of dissolved oxygen and water velocity.

Time of hatch, expressed as beginning, median, and complete hatch, and percentages of hatch are given in Table 5. Dissolved oxygen concentrations are expressed as mean values for each experimental chamber. Mean values for each cylinder are given in Table 6. Water velocities are expressed as means for the different cylinders. Table 6, in addition to presenting means and ranges for oxygen and velocity, also gives temperature means and ranges.

Hatching success at 2.6 mg./l. of dissolved oxygen and above ranged from 72.5 to 87.5 percent. Total mortality occurred at the dissolved oxygen concentration of 1.6 milligrams per liter. Two embryos hatched at this level, but they were greatly deformed and did not survive. Where hatching did occur, no apparent relationship existed between hatching success, dissolved oxygen concentration, and water velocity.

Fry reared at a concentration of 2.6 mg./l. of dissolved oxygen as compared to those reared at 11.2 mg./l.

TABLE 5

Age in Days from Fertilization at Beginning,
Median, and Complete Hatch, and
Percent Hatch for Steelhead Trout Embryos

D.O. ¹ mg./l.	Velocity cm./hr.	Hatching			Percent Hatch
		Beginning	Median	Complete	
1.6	6.3	--	--	--	0
	33.7	--	--	--	0
	148.0	--	--	--	0
	749.6	--	--	--	0
2.6	5.6	42	44	46	79.5
	33.7	41	43	44	85.0
	152.6	41	42	43	78.0
	747.6	40	41	43	79.5
4.2	6.1	37	38	40	80.0
	36.2	37	38	39	82.5
	143.6	36	37	39	80.0
	735.6	36	37	39	82.5
5.7	6.0	37	39	39	87.5
	32.7	36	37	40	84.2
	154.0	36	37	38	82.5
	650.2	36	37	38	85.0
7.9	6.4	35	36	37	72.5
	35.7	35	36	36	87.2
	152.6	35	36	37	85.4
	742.4	35	35	36	66.7
11.2	6.2	35	36	37	77.5
	32.2	35	36	36	85.0
	149.5	34	36	36	80.1
	720.8	35	36	36	72.5

1. Mean dissolved oxygen concentrations for each cylinder are given in Table 6.

TABLE 6

Means and Ranges of Water Temperature, Velocity, and Oxygen Concentration
for the Experiment with Steelhead Trout Embryos

Experimental Chamber Number	Temperature °C.		Cylinder	Dissolved Oxygen mg./l.		Velocity ¹ cm./hr.	
	Mean	Range		Mean	Range	Mean	Range
1	9.5	7.5-10.0	A	7.9	7.4-9.0	35.7	23.2-80.4
			B	7.9	7.4-9.0	152.6	102.4-322.0
			C	7.9	7.4-9.0	742.4	695.6-749.6
			D	7.7	7.2-7.8	6.4	6.0-6.8
2	9.5	8.0-10.0	A	2.6	2.1-3.2	33.7	29.2-50.8
			B	2.6	2.1-3.2	152.6	116.4-177.2
			C	2.6	2.1-3.2	747.6	702.8-756.8
			D	2.5	2.0-3.1	5.8	5.6-6.0
3	9.3	7.8-10.1	A	5.7	5.0-6.9	32.7	29.2-39.2
			B	5.7	5.0-6.9	154.0	130.0-188.8
			C	5.7	5.0-6.9	650.2	498.0-749.6
			D	5.5	4.8-6.7	6.0	5.6-6.4
4	9.3	7.9-10.0	A	1.6	1.0-3.6	33.7	30.8-80.4
			B	1.6	1.0-3.6	148.0	93.6-158.4
			C	1.6	1.0-3.6	749.6	720.8-777.6
			D	1.4	.8-3.4	6.3	.4-7.6
5	9.7	8.2-10.4	A	4.2	3.6-10.4	36.2	31.2-63.8
			B	4.2	3.6-10.4	143.6	88.4-158.4
			C	4.2	3.6-10.4	735.2	669.2-807.0
			D	4.0	3.4-10.2	6.1	5.2-6.6
6	9.5	7.6-10.1	A	11.2	10.5-12.0	32.2	26.2-48.2
			B	11.2	10.5-12.0	149.5	121.6-164.4
			C	11.2	10.5-12.0	720.8	576.0-756.8
			D	11.0	10.3-11.8	6.2	5.9-6.5

1. Power failure seven days after experiment began reduced all velocities to zero for 12 hours.

were delayed five to seven days for beginning hatch, five to eight days for median hatch, and seven to nine days for complete hatch. A smaller delay was apparent at concentrations of 4.2 and 5.7 mg./l., but none was apparent at 7.9 milligrams per liter. At 4.2 and 5.7 mg./l., a one to two-day delay occurred for beginning hatch, a one to three-day delay occurred for median hatch, and a two to four-day delay occurred for complete hatch.

Fry reared at the lowest velocity at 2.5 mg./l. of dissolved oxygen reached the time of beginning hatch two days later and median and complete hatch three days later than the fry reared at the highest velocity at the same concentration. Comparable results can be found at the intermediate velocities and at dissolved oxygen concentrations up to and including 5.7 milligrams per liter.

Embryo and Fry Growth

Linear measurements of embryos and linear and volumetric measurements of newly hatched fry indicated that growth was adversely affected by reductions of dissolved oxygen concentration and water velocity. Differences in size of fry at the various dissolved oxygen concentrations were apparent 17 days following complete hatch.

A sample of embryos from each cylinder was taken four to five days before hatching began at the dissolved oxygen

concentration of 11.2 mg./l., and the mean lengths and ranges for these samples are given in Table 7. The smallest embryos, at every dissolved oxygen concentration except 11.2 mg./l., occurred at the lowest velocity. The largest embryos were those reared at 11.2 mg./l. of dissolved oxygen. The mean lengths of these embryos ranged from 5.1 to 6.3 millimeters longer than those of the embryos reared at a dissolved oxygen level of 2.6 milligrams per liter. Embryos reared at 1.6 mg./l. of dissolved oxygen were deformed, making meaningful measurements difficult, if not impossible, to obtain.

The linear and volumetric measurements of steelhead fry at time of hatch and 17 days following the complete hatch for each cylinder are given in Tables 8 and 9. Measurements of newly hatched fry were made shortly after complete hatch occurred in an individual cylinder. Thus, the measurements were taken at different times but at the same relative stage of development for each group of fry. Likewise, measurements made 17 days after hatch was complete in the different cylinders were made at different times but at the same relative stage of development.

The largest fry at hatching were those reared at the control level, 11.2 mg./l. of dissolved oxygen, and the smallest fry were those reared at 2.6 milligrams per liter. The largest fry reared at any one dissolved oxygen

TABLE 7

Mean Lengths and Ranges in Millimeters of Steelhead Trout Embryos
30 Days Following Fertilization

Velocity in cm./hr. ¹	Dissolved Oxygen Concentration in Mg./l. ³					
	1.6	2.6	4.2	5.7	7.9	11.2
6.1	4.2 (3.5-5.0)	9.6 (8.0-10.6)	12.2 (11.7-12.5)	13.2 (12.6-13.8)	14.4 (14.0-15.0)	15.9 (15.0-16.4)
34.0	5.1 (4.4-5.7)	10.3 (8.2-11.0)	13.3 (12.8-13.7)	14.0 (13.2-15.5)	15.1 (14.2-15.8)	15.5 (14.1-16.2)
150.1	5.6 (4.7-6.5)	10.7 (9.2-11.6)	13.5 (11.7-14.1)	14.2 (13.1-15.7)	15.3 (14.3-16.0)	15.9 (15.2-16.9)
739.1 ²	5.6 (5.0-6.0)	10.7 (9.0-12.0)	13.8 (13.0-14.5)	14.4 (13.1-15.5)	15.5 (14.7-16.0)	15.8 (14.9-17.1)

1. Indicated as means calculated from the mean velocities of all experimental chambers.
2. 650.2 cm./hr. at dissolved oxygen concentration of 5.7 mg./l. not included in calculation of mean.
3. Mean dissolved oxygen concentrations for each cylinder are given in Table 6.

TABLE 8

Mean Lengths and Ranges in Millimeters of Steelhead Trout Fry
at Hatch and 17 Days After Hatch

Velocity in cm./hr. ¹	Dissolved Oxygen Concentration in Mg./l. ⁴					
	1.6	2.6 ³	4.2	5.7	7.9	11.2
<u>At Hatch</u>						
6.1	--	15.2	16.8	17.5	18.5	19.4
	--	(14.6-15.9)	(15.5-17.7)	(16.6-18.2)	(18.0-19.2)	(18.8-20.0)
34.0	--	15.3	17.4	18.1	19.1	19.9
	--	(14.1-16.3)	(16.8-18.0)	(16.4-19.1)	(18.2-19.9)	(19.4-20.5)
150.1	--	16.0	17.9	18.9	19.3	19.7
	--	(14.0-17.7)	(17.2-18.7)	(18.0-20.0)	(18.4-20.0)	(19.1-20.4)
739.1 ²	--	16.5	18.6	19.2	19.6	20.0
	--	(15.3-17.7)	(17.7-19.1)	(18.7-20.0)	(18.7-20.4)	(19.5-20.8)
<u>17 Days After Hatch</u>						
6.1	--	--	22.7	25.2	--	--
	--	--	(20.7-23.7)	(23.8-26.0)	--	--
34.0	--	20.7	24.5	25.4	27.0	26.5
	--	(18.5-22.1)	(23.0-25.5)	(23.5-27.1)	(25.9-27.8)	(25.5-28.1)
150.1	--	22.4	25.8	25.7	27.9	26.9
	--	(21.4-24.0)	(23.6-26.9)	(23.6-27.0)	(26.9-28.7)	(23.8-28.8)
739.1	--	22.1	25.9	26.3	--	27.7
	--	(20.3-24.9)	(23.4-27.0)	(23.2-27.9)	--	(26.1-29.0)

1. Indicated as means calculated from the mean velocities of all experimental chambers.
2. 650.2 cm./hr. at dissolved oxygen concentration of 5.7 mg./l. not included in calculation of mean.
3. Abnormal fry not included.
4. Mean dissolved oxygen concentrations for each cylinder are given in Table 6.

TABLE 9

Mean Volumes in Milliliters of Steelhead Trout Fry
at Hatch and 17 Days After Hatch¹

Velocity in cm./hr. ²	Dissolved Oxygen Concentration in Mg./l. ³					
	1.6	2.6	4.2	5.7	7.9	11.2
<u>At Hatch</u>						
6.1	--	.010	.015	.021	.024	.029
34.0	--	.015	.020	.023	.025	.030
150.1	--	.015	.021	.030	.020	.030
739.1 ⁴	--	.015	.028	.028	.030	.030
<u>17 Days After Hatch</u>						
6.1	--	--	.070	.087	--	--
34.0	--	.046	.082	.100	.110	.118
150.1	--	.055	.100	.120	.129	.122
739.1	--	.066	.110	.108	--	.133

1. Volumes of fry without yolk sacs.
2. Indicated as means calculated from the mean velocities of all experimental chambers.
3. Mean dissolved oxygen concentrations for each cylinder are given in Table 6.
4. 650.2 cm./hr. at dissolved oxygen concentration of 5.7 mg./l. not included in calculation of mean.

concentration generally occurred in the cylinder with the highest velocity, and the smallest fry in that with the lowest velocity. These size differences were shown by both linear and volumetric measurements (Tables 8 and 9).

At the dissolved oxygen concentration of 4.2 mg./l., the fry reared at the lowest velocity (6.1 cm./hr.) averaged 1.8 millimeters shorter than those reared at the highest velocity (approximately 739.1 cm./hr.). Volumetric measurement of these same fry showed that those at the highest velocity had nearly twice the volume of those at the lowest velocity. Fry reared at the lowest velocity at 11.2 mg./l. of dissolved oxygen also had nearly twice the volume of those reared at the lowest velocity at 4.2 milligrams per liter.

Fry at the lowest velocity at 5.7 mg./l. of dissolved oxygen averaged 1.7 millimeters shorter than those at the highest velocity in the same concentration. The fry reared at the lowest velocity at 5.7 mg./l. of dissolved oxygen averaged 1.9 millimeters shorter than those reared at the lowest velocity at 11.2 milligrams per liter. Volumetric measurement of these same fry showed that nearly the same differences in size were caused by an increase in water velocity from 6.1 cm./hr. to 650.2 cm./hr. at 5.7 mg./l. of dissolved oxygen as were caused by an increase in dissolved

oxygen concentration from 5.7 to 11.2 mg./l. at the low velocity.

Fry reared at the highest velocity at a particular dissolved oxygen level usually averaged larger than those reared at the lowest velocity of the next higher oxygen concentration tested. At the oxygen concentration of 4.2 mg./l., the mean fry length at the highest velocity was 18.6 millimeters. The mean fry length at the lowest velocity in 5.7 mg./l. of dissolved oxygen was 17.5 millimeters. Comparable results can be found at dissolved oxygen concentrations of 5.7 and 7.9 milligrams per liter. These differences are also apparent when mean fry volumes rather than mean fry lengths are considered.

Table 6 shows that the mean dissolved oxygen concentrations at the low velocities tested were 0.1 to 0.2 milligrams per liter lower than at other velocities. A small part of the reduction in fry size with reduction in velocity may be due to this. How small this oxygen effect would be can be judged by noting in Tables 8 and 9 the magnitude of the size differences of the fry reared at adjacent test concentrations at the same velocities.

Fry reared at the test concentration of 5.7 mg./l. of dissolved oxygen averaged smaller at 34 cm./hr. than at the highest velocity at 4.2 mg./l. of dissolved oxygen. Comparable results can be found at dissolved oxygen

concentrations of 5.7 and 7.9 milligrams per liter. Means and ranges for water temperatures, oxygen concentrations, and velocities in each cylinder are given in Table 6.

Abnormalities and Fry Survival

Abnormal development of steelhead embryos occurred only at the two lowest levels of dissolved oxygen tested. At 1.6 mg./l., all embryos exhibited abnormal development, and none survived through the hatching stage. At 2.6 mg./l., the following percentages of abnormalities occurred at the velocities indicated: 5.8 cm./hr., 9.4 percent; 33.7 cm./hr., 24.4 percent; 152.6 cm./hr., 19.1 percent; 747.6 cm./hr., 14.9 percent. Abnormal development was apparent in these cases as twisted or deformed tails or backs and abnormal structure of the nervous system, especially the brain. Most deformed embryos reared at 2.6 mg./l. of dissolved oxygen survived through the hatching stage.

Uncontrollable factors occurred during the experiment which prevented the determination of fry survival.

DISCUSSION

These laboratory experiments were conducted in order to gain more information concerning the influence of water velocity and dissolved oxygen on developing salmonid embryos. Conditions in nature cannot usually be controlled, and it is difficult to relate the success of embryonic development to specific environmental circumstances. Laboratory studies reported here have made it possible to relate certain developmental phenomena to known environmental conditions.

It is not entirely clear, however, to what extent the conditions studied in these experiments can be related to natural conditions. This applies particularly to the water velocities and flow patterns studied. Exact measurement of velocities under natural conditions is hardly possible, and flow patterns in natural gravel beds are much more complex than those developed in the experimental apparatus. Water flow through a granular material, such as spawning gravel, has been studied by Pollard (9, p. 709), and he gives the following definitions:

- | | |
|----------------|---|
| Laminar flow | - Flow in which the individual water molecules never cross each other's path. |
| Turbulent flow | - Flow in which volumes of water cross and recross each other's path though the flow within each volume may be laminar. |

Apparent velocity - The rate of seepage expressed as the volume of liquid flowing per unit time through a unit area (solids plus voids) normal to the direction of flow.

True velocity - The actual velocity of flow through the interstitial spaces. This differs from pore to pore.

The apparatus used for these experiments was designed to develop, as nearly as possible, laminar flows and to make accurate velocity measurements possible. Silt deposition in the filter plates and improper sealing of the cylinders to the plates disrupted the flows in the chinook salmon experiment. These difficulties were corrected for the steelhead experiment, and it is believed that nearly laminar flows and accurate velocity measurements were obtained.

Investigations by Alderdice, Wickett, and Brett (2, p. 229-249) have shown that temporary exposure of chum salmon embryos at various developmental stages to conditions of low dissolved oxygen results in abnormal development, delay in hatching, and increased mortality. These investigators subjected embryos at different developmental stages to depressed levels of dissolved oxygen for a period of seven days, and then allowed the embryos to complete their development at the air-saturation level. "Critical dissolved oxygen levels" were defined by these workers as being the levels above which respiratory rate is unmodified

by the amount of oxygen available. From studies of the respiration rates of embryos at different stages, these workers determined that critical levels ranged from one mg./l. in early stages of development to seven mg./l. just before hatching occurred. At concentrations below these levels, differences in growth, rate of development, and hatching success might be expected. Unpublished data from experiments at Oregon State College in which embryos were held under constant dissolved oxygen levels throughout their development have shown that differences in growth and rate of development can occur at dissolved oxygen concentrations as high as seven or eight milligrams per liter.

In the laboratory experiments presented here, chinook salmon and steelhead trout embryos reared throughout their incubation period at dissolved oxygen concentrations not far below the air-saturation level exhibited differences in growth and rate of development, and those raised at very low levels failed to hatch. Total mortality occurred at the dissolved oxygen concentration of 1.6 milligrams per liter.

It is conjectural as to how important might be small differences in the size of embryos or of fry at time of hatch. A considerable reduction in size, such as occurred in steelhead fry reared at all water velocities in 2.6 mg./l. of dissolved oxygen and at the low velocity

(6.1 cm./hr.) in 4.2 mg./l. of dissolved oxygen, would undoubtedly be of some importance. Subsequent survival of these fry in nature would probably be affected by their weak condition.

Alderdice, Wickett and Brett (op. cit.) concluded that for early developmental stages of salmon embryos, temporary exposure to oxygen levels of from 0.25 to 0.92 mg./l. though not lethal, may result in the production of deformities. When embryos at a later stage of development were exposed to a dissolved oxygen concentration of 0.32 mg./l., total mortality occurred. In the present study, when chinook salmon and steelhead embryos were subjected to oxygen levels of 1.6 mg./l. for their entire incubation period, total mortality occurred. Abnormal development of steelhead embryos was evident at a concentration of 2.6 mg./l. of dissolved oxygen.

In the experiment with chinook salmon embryos, the water velocities studied were not low enough to produce very large differences in size shown at time of hatch except at the oxygen concentration of 2.5 milligrams per liter. A velocity of six cm./hr. at concentrations of 4.2 and 5.7 mg./l. of dissolved oxygen caused a considerable reduction in the size of steelhead embryos, and a velocity of 34 cm./hr. also caused some reduction. In view of these data, a water velocity of six cm./hr. could

produce serious growth reduction at dissolved oxygen concentrations of 5.7 mg./l. or less at a temperature near 9.5° centigrade. If the water velocities developed in the steelhead experiments approached the true velocity values as is believed, and if anything comparable to true velocities may be considered to exist in spawning gravel, the velocity of six cm./hr. can probably be considered detrimental to developing salmonid embryos. If rates of linear flow must be measured and expressed in terms of apparent velocity in spawning gravels, then much higher numerical values for velocity must probably be considered as being detrimental to the development of salmonid embryos.

SUMMARY

1. The influence of water velocity and dissolved oxygen on the growth, rate of development, and success in hatching of chinook salmon, Oncorhynchus tshawytscha (Walbaum), and steelhead trout, Salmo gairdneri gairdneri Richardson, embryos was studied at the Oak Creek Fisheries Laboratory of the Department of Fish and Game Management, Oregon State College. The experimental apparatus used in this laboratory investigation was designed to deliver to developing salmonid embryos constant, nearly laminar flows of water of known velocity and dissolved oxygen content.

2. During the course of each of two experiments, cumulative records of the numbers of dead embryos and numbers of hatched fry were kept. Also, samples were taken to determine the size and condition of the developing embryos prior to hatching. Length and volumetric measurements of fry were made at the time of hatch, and the same measurements were made 17 days following the time of hatch in the experiment with steelhead trout.

3. Rate of embryonic development was delayed at reduced levels of dissolved oxygen and water velocity. Salmonid embryos reared at dissolved oxygen concentrations of 2.5 and 2.6 mg./l. were delayed in reaching the time of hatch by as much as nine days, as compared to embryos

reared at dissolved oxygen levels of 11.7 and 11.2 milligrams per liter. Smaller delays were apparent at concentrations up to and including 5.6 and 5.7 mg./l. of dissolved oxygen. Steelhead embryos reared at the lowest velocity (approximately 6.1 cm./hr.) at 2.6 mg./l. of dissolved oxygen were delayed in reaching beginning, median, and complete hatch by as much as three days, as compared to those reared at the highest velocity at the same concentration. Similar but smaller delays occurred at 4.2 and 5.7 mg./l. of dissolved oxygen.

4. Linear measurements of embryos and linear and volumetric measurements of fry indicated that differences in growth occurred at the different levels of dissolved oxygen and water velocity tested. With decreasing levels of dissolved oxygen or water velocity, there were decreases in mean sizes of embryos and fry. Mean size differences were apparent between embryos reared at air-saturation levels and embryos reared at all tested levels of dissolved oxygen below that of saturation; the greatest differences being between those reared at saturation and those reared at the lowest concentration in which hatching occurred. Volumetric measurements of steelhead and salmon fry made at the time of hatch showed that the fry reared at the highest velocities (approximately 739 and 1347 cm./hr.) were nearly twice the volume as those reared at the lowest

velocities (approximately 6.1 and 92 cm./hr.) at dissolved oxygen concentrations of 2.5 and 4.2 milligrams per liter. Smaller, but comparable, differences were apparent between fry reared at different velocities at oxygen concentrations up to and including 7.9 and 8.0 milligrams per liter. In the steelhead experiment, size differences resulting from an increase in velocity from 6.1 to 739.1 cm./hr. at 4.2 mg./l. of dissolved oxygen were nearly as great as the differences resulting from an increase in dissolved oxygen concentration from 4.2 to 11.2 milligrams per liter.

5. External examination of chinook salmon and steelhead trout embryos indicated that abnormal development occurred at 1.6 mg./l. of dissolved oxygen. Total mortality occurred at this level. Some steelhead embryos exhibited abnormal development at a dissolved oxygen concentration of 2.6 milligrams per liter. These embryos survived through the hatching stage.

6. It is suggested that water velocities of about 6 cm./hr. at dissolved oxygen concentrations of 5.7 mg./l. or less could produce serious growth reduction of salmonid embryos at water temperatures near 9.5° C. If the water velocities developed under experimental conditions are comparable to those in spawning gravel, then the growth reduction resulting from a water velocity of 6 cm./hr. at

dissolved oxygen concentrations of 5.7 mg./l. or less could influence fry survival in nature.

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