INTERNATIONAL PACIFIC SALMON
FISHERIES COMMISSION

PROGRESS REPORT
No. 12

THE INFLUENCE OF PHYSICAL FACTORS ON THE DEVELOPMENT AND WEIGHT OF SOCKEYE SALMON EMBRYOS AND ALEVINS

BY

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the Fraser River System

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ABSTRACT

The effects of water velocity, daylight and dissolved oxygen on the development and weights of sockeye salmon embryos and alevins were investigated. Before hatching, embryos were unaffected by the range of velocities studied, but were affected by exposure to diffuse daylight and different levels of dissolved oxygen. After hatching, the weights of the alevins and their rates of weight gain were influenced by velocity and oxygen, and their mortality was influenced by high velocities, especially when exposed to diffuse daylight. The significance of the effects of the three factors on the ultimate survival of fry are discussed.

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INTRODUCTION

Historically, the sockeye salmon, Oncorhynchus nerka (Walbaum), have
enjoyed relatively virgin spawning streams and lake rearing areas in the Fraser
River system. In spite of this fact it has been determined from field
investigations that the rearing potential of some of the sockeye producing
lakes has never been utilized because the areas available for spawning have
physical limitations. Francois, Kamloops and Harrison Lakes are among the
notable examples of rearing areas not being fully utilized because of limited
fry populations.

Recently, certain spawning grounds for both sockeye and pink salmon have
become unstable because of sharp changes in the stream discharge caused by
extensive logging of the watershed. Extreme floods during the winter months,
causing the movement of a bed load and very low flows in the late summer and
early fall months, leaving spawning areas dry, have resulted in a significant
reduction in the measured egg-to-fry survival. These conditions require that
the International Pacific Salmon Fisheries Commission develop proven methods
for artificially increasing fry production if it is to fulfill its terms of
reference calling for the protection and extension of the sockeye and pink
salmon fisheries of the Fraser River.

Since the first hatchery was built on the Sacramento River in 1872,[1] it
has been well established that artificial propagation greatly increases
egg-to-fry survival. Therefore it is logical that the Commission should
consider artificial propagation and related hatchery operations as a possible
means of increasing fry production. However, the real value of hatcheries

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[1] See U.S. Comm. of Fish and Fisheries, 1878.

has become the subject of considerable controversy. Although hatcheries experience low mortalities during incubation, their success with sockeye and pink salmon for the most part, has been poor when measured in terms of adult returns.

From extensive studies on the relative efficiencies of natural and artificial propagation, Foerster (1938) concluded that artificial propagation provided no advantage over natural spawning as a means of maintaining a run. Because of these investigations all salmon hatcheries in British Columbia were closed in 1937. It is noted that in one particular stream, the Birkenhead River, an average of 24,500,000 sockeye eggs were spawned and incubated in a hatchery each year from 1905 to 1935.[1] While survival to the fry stage was increased significantly over that experienced in natural spawning and the subsequent fry, in large part, were planted back into the donor stream, the size of the Birkenhead sockeye run declined gradually. Thus the value of hatcheries for increasing fry production when measured in terms of adult returns is questionable.

It becomes necessary to examine hatchery operations to define and eliminate, if possible, any factors contributing to their poor success. Only by eliminating these adverse factors could the Commission consider salmon hatcheries as a method for increasing fry production for under-utilized natural rearing areas or as a substitute for unstable natural spawning grounds.

An examination of hatchery methods presently in use reveals several factors which differ from the natural environment. Hatchery environments do not have a gravel substrate for developing eggs and alevins, while in nature a gravel substrate is always present. Gravel cover in the natural redd eliminates high velocities and excludes light. In the hatchery environment velocities

[1]See Babcock 1902-1932, Canadian Dept. of Fish. Annual Reports and Canadian Dept. of Marine and Fish. Annual Reports.

are several times higher than in nature and the eggs are exposed to natural
or artificial light. The oxygen concentration of water in hatcheries is
usually near saturation while in nature the dissolved oxygen may never
approach saturation.

In this investigation the effect of three factors, velocity, light and
oxygen, on the development of eggs and growth of alevins was assessed. The
effect of substrate itself was not studied, but it is the presence and
character of substrate which is in large measure responsible for the variations
in the factors examined.

METHODS AND MATERIALS

The eggs used in the studies were taken from sockeye salmon spawning on
the spring-fed beach area in Cultus Lake, British Columbia. Twenty females
and ten males were used to obtain and artificially fertilize the eggs. After
thorough mixing, 18,000 eggs were measured out, water hardened and transferred
to the Sweltzer Creek Field Station located three miles from the spawning
beach.

Upon arrival at the station the eggs were placed in nine, seven foot
long troughs. Each trough was divided by baffle plates to accommodate two
wooden framed, plastic screened trays. The trays were subdivided into
20 compartments, each containing 50 eggs in an area of four square inches,
and positioned in the trough to assure only an upwelling flow. Screen covers
were placed over the trays to allow their submersion and the troughs were
covered to exclude light. After 24 hours the experimental environments were
introduced.

The range of velocities studied (75, 25, 15, 5, 1.5 and 0.5 mm/sec)
include those generally employed in hatchery operations. These values were

representative of the actual velocities between individual eggs in a single layer and were determined from the cross-sectional area of voids and the flow. Flow, and thus velocity, was controlled by adjusting the supply valve for each trough. Flows were checked daily by measuring discharge volumetrically. The velocity studies were under constant conditions of temperature (46.5°F), oxygen (11.9 mg/l) and darkness.

The effect of light was studied over the same range of velocities, but with the trough covers removed, exposing the eggs to diffuse natural daylight. The light intensity purposely did not exceed 2 foot candles and thus was not greater than the natural illumination experienced in most hatcheries.

The studies on the effect of oxygen were under constant conditions of temperature (46.5°F), velocity (5.0 mm/sec) and darkness. The oxygen concentrations studied (3.0, 6.0 and 11.9 mg/l) were restricted to the known non-lethal range for other salmonoids (Silver, et al., 1963). Two stripping towers, similar to those described by Fry (1951), were used to deoxygenate water to 3.0 and 6.0 mg/l. Water was passed downward through vertical ten foot long plastic pipes, six inches in diameter, against a counter flow of nitrogen gas which caused the removal of oxygen. A third tower was used to air equilibrate water by running it down through a column of air. The lower oxygen levels were obtained by adjusting the nitrogen flow through the stripping columns while the water flow remained constant at 1 gallon per minute. The flow of nitrogen was controlled by a two-stage pressure reducing valve and was measured by a ball displacement type flow meter. Dissolved oxygen determinations were measured twice a week by the unmodified Winkler titration method using .025N thiosulphate. The trough with the oxygen concentration at 11.9 mg/l (saturation) was the control trough and the alevins from it were considered the standard with which to compare the others.

All studies were carried out using water pumped from Cultus Lake. The water temperature maintained in all troughs during the studies was 46.5°F, coinciding with the nearly constant temperature of the natural, spring-fed spawning area in Cultus Lake. This necessitated using a small amount of heated lake water during the winter months when the lake temperatures dropped below 46°F. Nitrogen supersaturation of the heated water was overcome by air equilibrating the water as it entered the troughs. The temperature of the supply was recorded on a Taylor thermograph with spot temperatures taken weekly on individual troughs.

The eggs were handled only when necessary. Dead eggs were not removed prior to blastopore closure. Thereafter dead eggs were removed and trays were cleaned weekly.

During the course of the study the alevins from each tray were sampled at 1,200, 1,600, 1,800, 1,900 and in some cases 2,000 temperature units, (Fahrenheit degree days after fertilization), excepting the control which was sampled every 100 temperature units after fertilization. All samples were preserved in 10% formalin and weight comparisons were based on averages of 20 individuals. Since the embryos and alevins in the control trough (11.9 mg/1 O_2) were sampled every 100 temperature units, their yolk weights were used to obtain a rate of yolk utilization with which to compare those exposed to the different velocities.

In the present paper embryo refers to the prehatching stage, alevin to post-hatching and fry indicates that period beyond complete yolk absorption. All embryos and alevins were carefully dissected from their yolk material, each part blotted on filter paper and weighed separately on an analytical balance. After the wet weights were measured the material was transferred to an oven, dried 24 hours at 98°C and reweighed.

The studies were terminated when the fry had experienced an obvious loss in weight following yolk absorption.

RESULTS

Velocity

The data obtained on the effect of six velocities on the weight of embryos and the subsequent alevins are summarized in TABLE 1. Under constant conditions of darkness and temperature, embryos from eggs exposed to the different velocities showed no significant wet weight differences at the time of hatching (1200 T.U.) when tested statistically by an analysis of variance (F = 2.33) or by Duncan's new multiple range test (see Steel and Torrie, 1960) of the differences among the means.

The exposure of alevins to the different velocities from hatching to yolk absorption (1200 to 1800 T.U.) resulted in large differences between certain groups. These data are presented in FIGURE 1 where the mean wet weight and the standard error of the mean are plotted. The data show that the weight of alevins was impaired by velocities greater than 15 mm/sec.

Observations during the study showed that in velocities greater than 15 mm/sec the alevins were forced to be more active to retain their position in the compartments than were alevins in the lower velocities. The relative severity of the exercise is not known. However, when the water flow was stopped momentarily during cleaning operations the alevins in the high velocity compartments would immediately drop to the bottom with marked hyperventilation. Therefore, it is believed that the lower weights of alevins in high velocities resulted from the forced activity and a consequent excessive expenditure of energy stores.

TABLE 1 — Mean wet and dry weights and standard errors of samples of sockeye embryos and alevins (N = 20) exposed to six water velocities during yolk utilization.

Temp. Units	Velocity mm/sec	Mean Wet Wt. mgs.	Standard Error	Mean Dry Wt. mgs.	Standard Error
1200*	75	42.43		8.93	
	25	43.92		8.92	
	15	45.10		9.37	
	5	43.42		9.09	
	1.5	44.71		9.90	
	0.5	44.34		8.20	
1600	75	98.05	$\pm$ 2.77	17.66	$\pm$ 0.47
	25	99.53	$\pm$ 1.79	17.50	$\pm$ 0.32
	15	107.78	$\pm$ 2.02	17.35	$\pm$ 0.35
	5	112.76	$\pm$ 2.16	18.62	$\pm$ 0.36
	1.5	112.53	$\pm$ 1.82	19.55	$\pm$ 0.32
	0.5	118.26	$\pm$ 1.83	19.01	$\pm$ 0.29
1800	75	121.82	$\pm$ 1.99	20.96	$\pm$ 0.44
	25	127.57	$\pm$ 2.83	21.95	$\pm$ 0.57
	15	140.09	$\pm$ 2.08	22.41	$\pm$ 0.46
	5	136.87	$\pm$ 1.46	23.56	$\pm$ 0.24
	1.5	134.39	$\pm$ 1.96	23.09	$\pm$ 0.38
	0.5	140.67	$\pm$ 2.59	21.30	$\pm$ 0.47
1900	75	111.06	$\pm$ 2.60	16.59	$\pm$ 0.48
	25	123.82	$\pm$ 2.17	19.05	$\pm$ 0.37
	15	128.87	$\pm$ 2.45	19.57	$\pm$ 0.44
	5	132.18	$\pm$ 1.54	19.30	$\pm$ 0.26
	1.5	130.04	$\pm$ 2.04	19.64	$\pm$ 0.37
	0.5	125.37	$\pm$ 1.82	18.64	$\pm$ 0.37

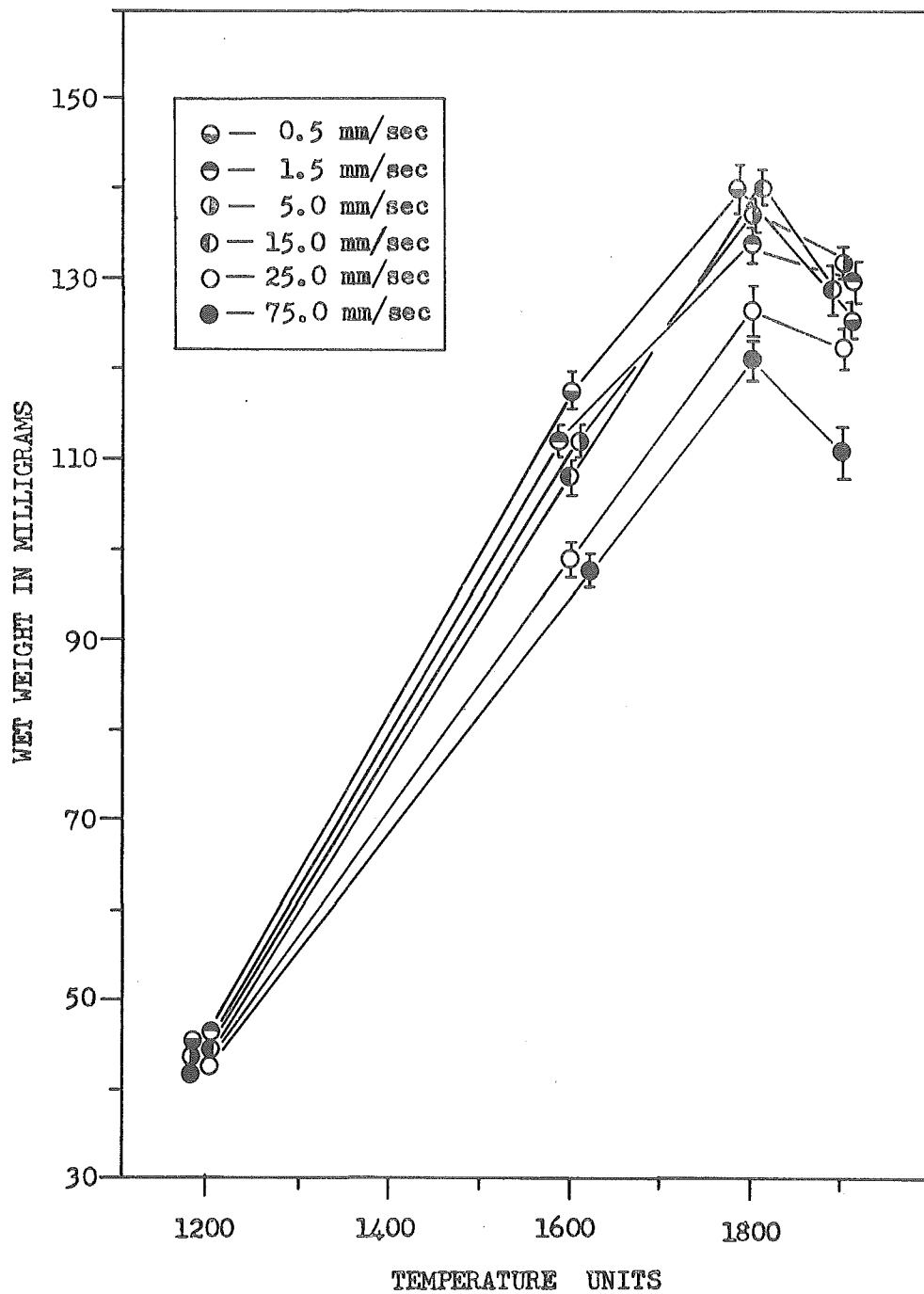*At 1200 temperature units N = 10.

FIGURE 1 – The mean wet weights and standard error of the mean of alevins held in six water velocities from hatching to complete yolk utilization.

Data on dry weight of embryos and alevins (TABLE 1) corroborate the conclusions reached on the basis of wet weights. Statistically no significant difference occurred until after hatching and then only in velocities greater than 15 mm/sec. At one particular stage (1800 T.U.) the sample taken from alevins in the velocity of 0.5 mm/sec showed a disproportionately low dry weight in comparison to its wet weight. These measurements, the wet and dry weights, would appear to be anomalous. However, it is believed that at this minimum velocity the water warmed slightly which would have hastened development (Hayes and Pelluet, 1945) and resulted in premature exhaustion of yolk material and starvation. Brett (1964) has shown that a decrease in lipid results in an increase in moisture among juvenile sockeye. Therefore, it is possible that starvation after yolk absorption could be evidenced as a loss in dry weight prior to a noticeable decrease in wet weight.

Measurements of the remaining yolk material on alevins in the different velocities were made at 1200 and 1600 temperature units. It was found that the yolk weights were very similar among the six lots. When the values were tested by an analysis of variance no statistically significant difference was found (F = 2.4) with the exception of the value for the alevins held in the lowest velocity. However, as explained previously the temperature in the low flow was slightly higher thus the temperature unit accumulation was actually greater than the 1600 units measured at the main water supply.

The similarity of the rate of yolk utilization among the six groups is shown in FIGURE 2 where the dry yolk weights are plotted. The yolk weights of alevins from the six velocities (represented by circles) are plotted for 1200 and 1600 temperature units and the control (represented by squares) plotted for every 100 units. When a line is drawn through those values of the control (held in a constant velocity of 5.0 mm/sec) it is seen that the
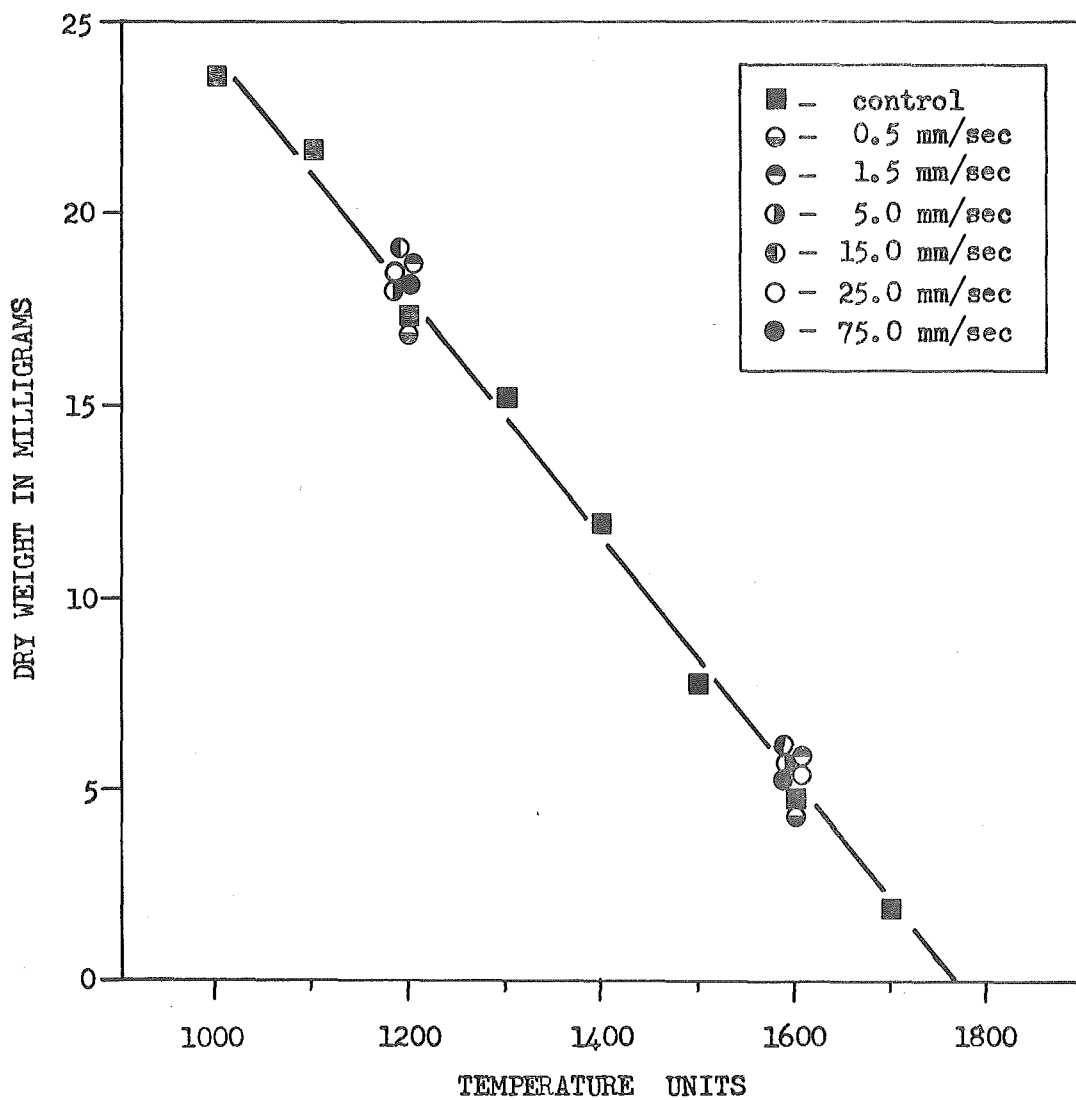
FIGURE 2 - The dry weight of the yolk material remaining in alevins from troughs with different water velocities during the period of yolk utilization.

absorption rate is nearly constant throughout the late embryonic and alevin stages. Moreover, the values for the six test lots do not deviate much from the control. These data indicate that rate of yolk utilization was the same among the different groups regardless of the velocity to which the alevins were subjected.

In general, mortalities among eggs and alevins in velocities of 0.5, 1.5, 5.0 and 15.0 mm/sec were low, not exceeding 5.0 per cent. However, in 25 and 75 mm/sec the mortalities were 24.5 per cent and 15.5 per cent, respectively. Over 65 per cent of the deaths in these higher velocities were experienced by the alevins shortly after emergence from their egg capsules. Most of the dying alevins had wisps of coagulated yolk near the surface of the yolk membrane and were blanched nearly colorless.

Light

Unlike velocity, light influenced the weight of embryos prior to hatching (1200 T.U. - TABLE 2). At hatching the mean weight of embryos held in diffuse light (7.82 mg) was significantly less (P $<$ 0.001) than those held in darkness (9.07 mg).

From hatching to yolk absorption, the mean weights of alevins held in light were significantly less (P $<$ 0.02) than those alevins held in darkness (FIGURE 3). However, rates of weight gain were similar for alevins held in either light or darkness. Thus, the initial difference in weight, induced by exposure to light during the embryonic stage, was maintained in subsequent stages to yolk absorption.

Similarly, the rate of yolk utilization among the light and dark exposed alevins was the same, but the embryos incubated in daylight averaged one milligram less dry yolk at hatching. This difference experienced as embryos

TABLE 2 — Mean dry weights and standard errors of samples of sockeye embryos and alevins (N = 20) exposed to daylight or darkness in six water velocities during yolk utilization.

| Temp. Units	Velocity mm/sec	DARKNESS		DAYLIGHT	
		Mean Dry Wt. mgs.	Standard Error	Mean Dry Wt. mgs.	Standard Error
1200*	75	8.93		8.22	
	25	8.92		7.82	
	15	9.37		8.25	
	5	9.09		8.08	
	1.5	9.90		7.10	
	0.5	8.20		7.43	
1600	75	17.66	$\pm$ 0.47	17.68	$\pm$ 0.47
	25	17.50	$\pm$ 0.32	15.91	$\pm$ 0.44
	15	17.35	$\pm$ 0.35	18.10	$\pm$ 0.33
	5	18.62	$\pm$ 0.36	18.36	$\pm$ 0.28
	1.5	19.55	$\pm$ 0.32	19.51	$\pm$ 0.32
	0.5	19.01	$\pm$ 0.29	18.10	$\pm$ 0.20
1800	75	20.96	$\pm$ 0.44	19.68	$\pm$ 0.54
	25	21.95	$\pm$ 0.57	21.03	$\pm$ 0.41
	15	22.41	$\pm$ 0.46	20.59	$\pm$ 0.47
	5	23.56	$\pm$ 0.24	21.36	$\pm$ 0.65
	1.5	23.09	$\pm$ 0.38	21.98	$\pm$ 0.60
	0.5	21.30	$\pm$ 0.47	19.86	$\pm$ 0.42
1900	75	16.59	$\pm$ 0.48	17.47	$\pm$ 0.51
	25	19.05	$\pm$ 0.37	15.62	$\pm$ 0.51
	15	19.57	$\pm$ 0.44	19.53	$\pm$ 0.39
	5	19.30	$\pm$ 0.26	17.49	$\pm$ 0.32
	1.5	19.64	$\pm$ 0.37	18.76	$\pm$ 0.39
	0.5	18.64	$\pm$ 0.37	17.46	$\pm$ 0.44

*At 1200 temperature units N = 10.
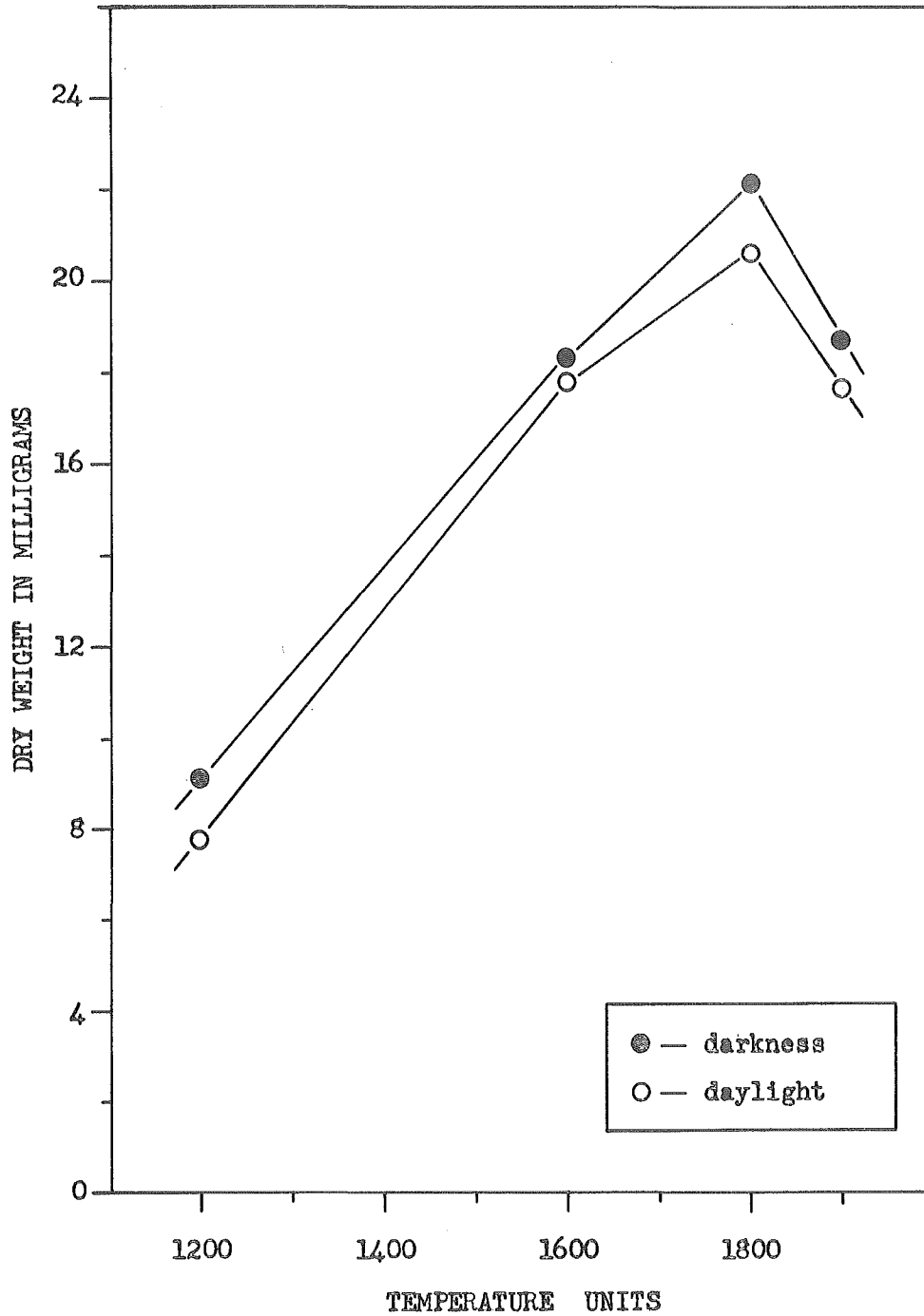
FIGURE 3 — The mean dry weights of alevins held in darkness and of alevins held in daylight during the period of yolk utilization.

persisted through the alevin stage and hence the light exposed alevins reached yolk absorption three days sooner than those in darkness.

Observations of the alevins exposed to light showed that they possessed a strong photonegative response during the whole of the yolk sac period. Although the light intensity did not exceed two foot candles, the newly hatched alevins preferred the dark corners of the compartment. This photoresponse persisted while the alevins remained at the bottom of the tray. Once the alevins left the bottom and entered the "swim-up" period they did not avoid the light as strongly. After "swim-up" and into the fry stage they continued to avoid the light, but would leave their protective shadows to nip at particles of food. Alevins exposed to light left the bottom of their compartments two weeks before those in the darkened compartments.

The cumulative mortality both in the alevins exposed to light and in those held in darkness was less than 5 per cent when in the velocities below 25 mm/sec but, the alevins exposed to light and water velocities of 25 mm/sec or greater experienced over 70 per cent mortality as compared to less than 25 per cent among those held in darkness in the same velocities. Most of the mortality occurred just after hatching and again the deaths were characterized by small wisps of coagulated yolk appearing at the surface of the yolk membrane. Most of the dying alevins appeared to be blanched as though circulation was inadequate.

Oxygen

Low oxygen concentrations have been shown to affect the rate of development of the embryos of chum salmon (Alderdice, et al., 1959), embryos and alevins of lake trout (Garside, 1959), steelhead, and chinook salmon (Silver, et al., 1963). In each case rate of development decreased with progressively lower oxygen concentrations. Similarly, in this study the development of sockeye embryos

or alevins was retarded when exposed to low oxygen concentrations. Newly hatched alevins (1200 T.U.) incubated at low oxygen concentrations showed less yolk utilization, retarded development of fins and pigmentation, and were smaller than alevins incubated at high oxygen concentrations (TABLE 3).

TABLE 3 - The comparative advancement of alevins at hatching from three oxygen concentrations.

Description	O_2 Concentration in mg/l		
	3.0	6.0	11.9
T.U. to 50% hatching	1200	1200	1200
Length in mm	16.3	18.6	19.7
Yolk sac shape	spherical	longitudinal	longitudinal
Pigmentation	lightly on head	on head and starting on back	on head and back
Visibility of the dorsal and anal fin rays	Not visible	Distinguishable	Readily visible
Caudal fin development	Forming	Forming	Well advanced

Retardation of development and growth at low oxygen concentrations was even more apparent after hatching. To reach the fry stage (identified by the complete absorption of the yolk material), alevins incubated in 3.0 mg/l required two weeks longer than those held at 6.0 mg/l and three weeks longer than those held at 11.9 mg/l.

Perhaps a more dramatic example of the effect of a hypoxial environment on alevins can be shown by differences in their growth after hatching (FIGURE 4). Alevins incubated at low oxygen concentrations were not only smaller at hatching but their subsequent rate of growth was less than that of alevins incubated at higher oxygen concentrations. Thus, at 1200 temperature units, the group held at 3.0 mg/l weighed 21.2 mg less than the group held at 11.9 mg/l, but this difference had increased to 44.8 mg at 1800 temperature units.
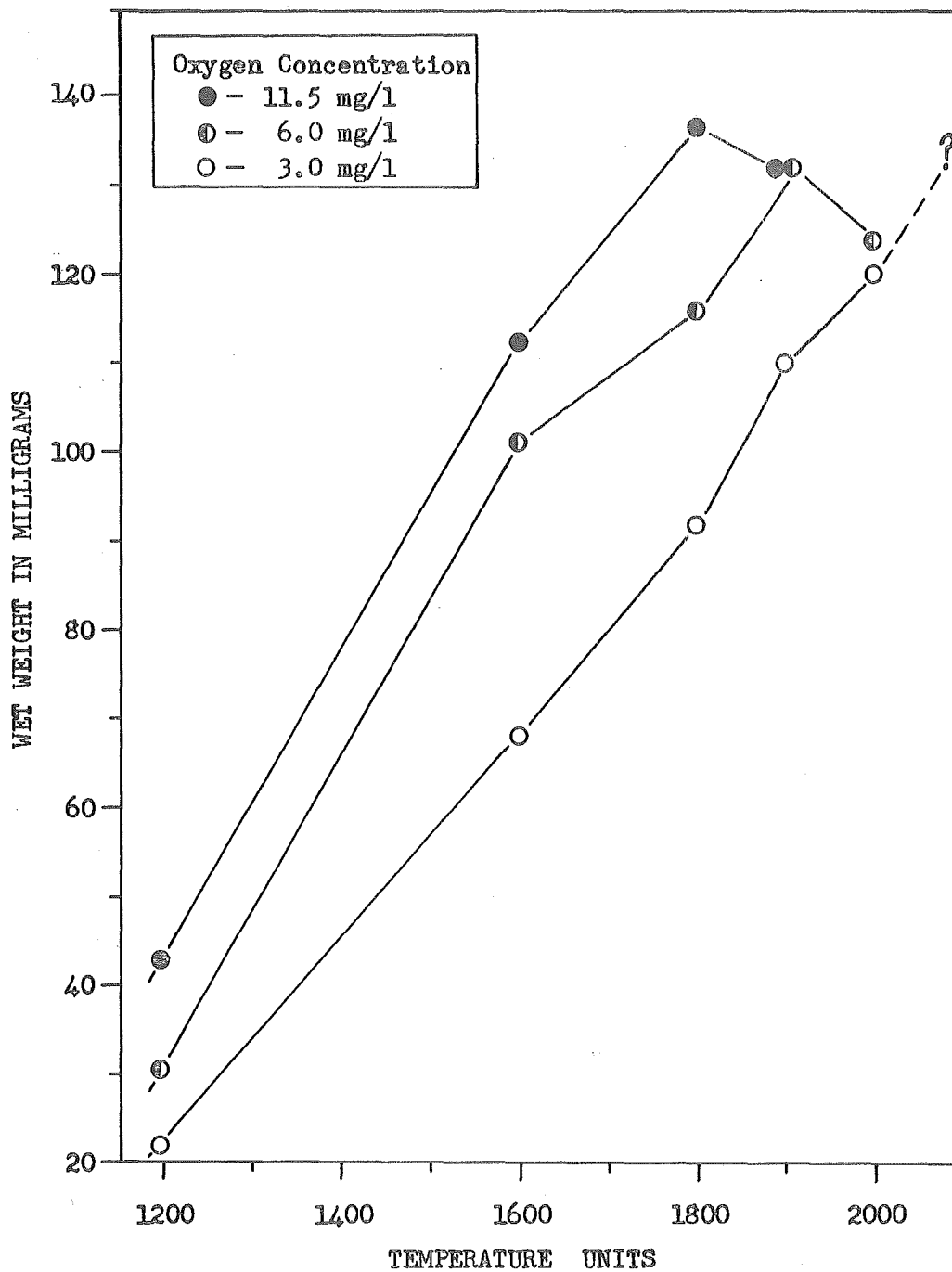
FIGURE 4 - The mean weights of sockeye salmon alevins held in one of three oxygen concentrations during the period of yolk utilization.

The exact date of yolk absorption and hence the greatest weight attained prior to starvation is not known for those alevins incubated at 3.0 mg/1 oxygen concentration. The study was terminated at 2000 temperature units while they still possessed 2.25 mg of dry yolk. However, based on rate of yolk absorption (FIGURE 2) and on body weight gained for yolk weight lost, 2.25 mg of dry yolk would have been consumed in one week and produced a gain of approximately 9 mg in body wet weight, thus placing them near the weight of alevins incubated in 11.9 mg/1 dissolved oxygen.

It is of interest that other investigators (Silver, et al., 1963 and Shumway, et al., 1964) have reported a delay both in development and hatching time among salmon eggs incubated under hypoxial conditions. In the present study, although development was retarded, hatching time was not influenced by oxygen concentration.

There were no deformities among the alevins in the study and the mortality during incubation was less than 6.0 per cent in any one concentration. Most of the deaths occurred at hatching.

DISCUSSION

Velocity

It is believed that prior to hatching the only effect of water velocity on developing embryos is through its role in transferring sufficient dissolved oxygen to the surface of the egg membrane and in removing waste products. Certain investigations have demonstrated the effect of low velocity, and hence its ability to provide sufficient oxygen, on the size of steelhead and chinook salmon embryos (Silver, et al., 1963) and silver salmon embryos (Shumway, et al., 1964). These investigators have shown that size is influenced by water velocity, and in the case of chinook salmon, velocities even up to 1350 cm/hr would result in larger fry.

In the present study at oxygen saturation even the lowest velocity of 0.5 mm/sec (180 cm/hr) was adequate to provide sufficient oxygen to the surface of the egg membrane and hence velocity did not affect the size of the embryos. Daykin (1965), using data on steelhead embryos (from Silver, et al., 1963), calculated that 11.2 mg/l dissolved oxygen would provide full oxygen uptake down to the velocity of 175 cm/hr. Since the egg sizes of steelhead and Cultus sockeye are comparable, these data confirm the present results.

The influence of velocity is altered once the embryo leaves the protection of the egg membrane. Surface area suddenly increases and the alevin is susceptible to conditions previously not experienced as a spherical form. In an environment where substrate restricts water velocity the alevin can proceed in development with little requirement of energy for activity. But, in the absence of a substrate, typical of the artificial environment, the alevin is at the mercy of the velocity. If high enough the immediate result from velocity can be the death of many of the alevins. The principal cause of death from high velocity is not known, although hyperactivity as a lethal factor (Black, 1958) has been shown to occur in some instances among various fishes.

The more prolonged sublethal effect of high velocity is the requirement imposed on the energy stores of the alevin at the inevitable sacrifice of growth. Size is believed to be a factor influencing the ability of fry to survive. In studies by the Commission, size affected the vulnerability of sockeye fry to predation. While fry averaging over 300 mg and 32 mm in weight and length experienced less than 48 per cent mortality when placed in a tank with rainbow trout, fry of the same age but averaging less than 300 mg and 32 mm in weight and length suffered a greater than 57 per cent loss.

It is of interest that the rate of yolk utilization was nearly constant among the alevins in the six velocities studied. These data would indicate that from hatching the yolk absorption rate is constant for a given temperature and oxygen concentration and is not influenced by a greater requirement of energy for exercise. Moreover this suggests that rate of yolk absorption is at a maximum, since greater demands were not met by an increase in yolk utilization. Therefore, since conversion of yolk provides an energy pool for activity, maintenance and growth, an increased energy demand by one of these processes must decrease the energy available for the others. Hence, growth is sacrificed among alevins subjected to high velocities to satisfy the energy demand of increased activity, but the rate of yolk utilization remains unchanged.

Light

The effect of light on the development of salmon embryos, alevins and fry has long been a debatable issue. Perhaps the argument was precipitated from the fact that salmon eggs and the subsequent alevins are never exposed to daylight in their natural environment. As early as 1916, E. V. Smith (1916) reported differences between light and dark exposed chinook salmon embryos and alevins. He concluded that those exposed to daylight were smaller, hatched sooner, absorbed the yolk faster and experienced a higher mortality than alevins raised in darkness. Similarly, experiments conducted by the Commission (Internat. Pacific Salmon Fish. Comm., 1957) on sockeye salmon have shown that light exposed eggs hatch earlier, and that alevins exposed to light were more active, experienced higher mortality and showed a poorer performance in swimming tests than alevins raised in darkness.

Several investigators (Bell & Hoar, 1950; Eisler, 1957; and Perlmutter & White, 1962), have studied the effect of various types of artificial light

and have found that generally light will retard development, cause higher
mortalities and slow yolk utilization. Regardless of this seemingly good
evidence most hatcherymen still fail to cover eggs from natural or artificial
light.

In the present paper, data on the effect of even very diffuse daylight gave
detectable differences comparable to results found by previous investigators.
The weight differences between light and dark exposed embryos were significant.
Moreover, at hatching the alevins exposed to daylight averaged less yolk which
indicates poorer efficiency in yolk conversion and therefore accentuates the
overall effect from light exposure during development. But after hatching
the alevin weights were not affected by exposure to light, although the
initial difference persisted through the alevin stage.

It appears that in the higher velocities ($\bar{>}$ 25 mm/sec), where the alevins
were required to maintain position by actively swimming, exposure to daylight
substantially increased their mortality over that experienced by alevins in
darkness. However in the lower velocities ($<$ 25 mm/sec) where vigorous
exercise was not required, the mortality was low in all groups.

Perhaps the influence of light on the ultimate survival of the fry is not
obvious while it is protected in the laboratory or hatchery trough. Certainly
the size of the fry when released may influence their ability to survive as
discussed previously. However, it is probable that diurnal exposure to
light also alters some of the normal behavioral responses of fry and renders
them more susceptible to predation when released into the rigors of natural
selection. Although light exposed alevins upon reaching the fry stage retain
a photonegative response and avoid bright light, they appear to be less
startled from overhead movement than fry having been raised in darkness. This

same behavior is more obvious in wild smolts held in confinement. The wild fish are very cautious and seek protection whereas the pond raised smolts are almost indifferent to outside movement. Admittedly this is generalizing the influence of many factors involved in producing such a different response in pond raised and wild fish, however it is believed that such an analogy is justified.

Oxygen

The effect of continuous exposure to low oxygen concentrations during incubation on the ultimate survival of sockeye alevins is debatable. Rate of development and growth are dependent on oxygen concentration as well as temperature. Therefore it is necessary that one appreciate the magnitude of delay resulting from the hypoxial environment when comparing embryos or alevins raised in different oxygen concentrations. Some investigators have used hatching time as a standard for comparison, but unless specifically chosen the results from such a criterion can be deceiving. In the present study hatching occurred at 1200 temperature units among eggs regardless of the three different oxygen concentrations under which they were incubated. When measurements of the newly hatched alevins were compared large differences existed between the test groups. Upon examination of the alevins using criteria based on developmental stages (Pelluet, 1944; Garside, 1959) the test groups were found to be separated in their advancement by as much as 200 temperature units. This suggests that when delay occurs in the hatching time from hypoxial conditions it is not proportional to the delay in development. Hatching is a physiological event and unless demonstrated that it coincides with the same anatomical stage of development it has limited value as a standard for comparison.

Silver, et al. (1963) using data collected up to and shortly after hatching, state that very small sac fry (alevins) having been reared at very low oxygen concentrations cannot be expected to survive. Natural spawning redds, however, can be exposed to very low oxygen concentrations during much of the incubation period. In this situation, although newly hatched alevins might be relatively small and weak, their condition would not necessarily reflect their ability to survive. Their small size may be due to emergence from the egg capsule at a relatively early stage of development. This situation occurs on the natural spawning beach in Cultus Lake. The sockeye spawners use the whole of an upwelling spring-fed area to build their redds. In 1963 those redds on the periphery of the spring area experienced very poor percolation and consequently measurements of the dissolved oxygen were as low as 3.0 mg/l. The analyses of dissolved oxygen on water samples taken from the redds with a large syringe was based on the technique of Scholander, Van Dam, Claff and Kanwisher (1955) and on the unmodified Winkler titration methods. Excavation of redds during hatching exposed whole nests of very small alevins showing the same characteristics that appeared among those incubated at 3.0 mg/l in the laboratory. Regular samples from the nests revealed that the alevins did survive and emerge.

As shown previously the most obvious effect from continuous exposure of sockeye eggs and alevins to low oxygen is the delay imposed on development and growth. Those raised at low oxygen concentrations eventually arrived at the fry stage at nearly the same weight as the controls raised at saturation. The significance of the delay upon the subsequent fry survival has not been determined. However, if emergence must be precisely correlated with the environmental cycle of the lake, and if natural incubation normally occurs in an environment with the dissolved oxygen below saturation, then it may be

necessary for the fry to experience that environment in order to emerge at the time most advantageous to them.

It often has been reported that hatchery incubation causes the alevins to reach yolk absorption sooner than natural incubation even when the incubation temperatures are the same. Investigations by Pyper and Vernon (Internat. Pacific Salmon Fish. Comm., MS.) showed oxygen concentrations often moderately low in six streams surveyed. This condition no doubt is typical of salmon spawning areas in general and would even be accentuated with regard to the micro-environment of eggs in a redd when exposed to low gravel velocities. When considering the delay in the alevins' development from exposure to low oxygen concentrations and the high oxygen concentrations enjoyed by the hatchery environment, it seems reasonable to suggest that the factor most responsible for the accelerated development among hatchery alevins is the difference between the oxygen concentrations of the two environments.

SUMMARY

The exposure of sockeye salmon embryos and alevins to conditions of water velocity, daylight and dissolved oxygen common to the standard hatchery environment, but seldom experienced in nature, have been shown to cause effects believed to be adverse and responsible, in part, for the poor survival of hatchery fry when released into the rigors of the natural environment. The investigation on the effects of the three environmental factors have shown:

1. Embryos from eggs exposed to velocities between 0.5 mm/sec and 75 mm/sec showed no statistically significant weight difference at hatching. After hatching velocities greater than 15 mm/sec required nearly continuous exercise of the alevins which resulted in significantly smaller fry upon yolk absorption. The rate of yolk absorption seemingly was unaffected by exercise but mortality was greater among those in the high velocities.

2. When eggs were exposed to diffuse natural daylight the subsequent alevins at hatching were smaller and possessed slightly less yolk than alevins from eggs incubated in darkness. The growth rate after hatching appeared to be the same under darkness or daylight. Alevins exposed to daylight reached "swim-up" time sooner and, as fry, were not as frightened of daylight or overhead movement. Mortality was very high among light exposed alevins held in high velocities. The cause of death is not known.

3. The most obvious effect of exposure of sockeye eggs and alevins to low concentrations of oxygen was the delay in development. Regardless of oxygen concentration during incubation, the weights of the fry upon yolk absorption were nearly the same.

LITERATURE CITED

Alderdice, D.F., W.P. Wickett and J.R. Brett. 1958. Some effects of temporary exposure to low dissolved oxygen levels on Pacific salmon eggs. J. Fish. Res. Bd. Can., 15:229-250.

Babcock, J.P. 1902-1932. Spawning-beds of the Fraser River. British Columbia Fisheries Dept. Report, 1901-09, 1911-31. Victoria, B.C.

Bell, G.M. and W.S. Hoar. 1950. Some effects of ultra violet radiation on sockeye salmon eggs and alevins. Can. J. Res., D, 28:35-43.

Black, E.C. 1958. Hyperactivity as a lethal factor in fish. J. Fish. Res. Bd. Can., 15:573-586.

Brett, J.R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. J. Fish. Res. Bd. Can., 21:1183-1226.

Canada Department of Fisheries. 1931-1935. Annual Report, V.1-6, 1930/31-1935/36. Ottawa.

Canada Department of Marine and Fisheries, Fisheries Branch. 1905-1930. Annual Report, V.38-63, 1904/05-1929/30. Ottawa.

Daykin, P.N. 1965. Application of mass transfer theory to the problem of respiration of fresh eggs. J. Fish. Res. Bd. Can., 22:159-171.

Eisler, R. 1957. Some effects of artificial light on salmon eggs and larvae. Trans. Am. Fish. Soc., 87:151-162.

Foerster, R.E. 1938. An investigation of the relative efficiencies of natural and artificial propagation of sockeye salmon (Oncorhynchus nerka) at Cultus Lake, British Columbia. J. Fish. Res. Bd. Can., 4:151-161.

Fry, F.E.J. 1951. A fractionating column to provide water of various dissolved oxygen content. Can. J. Tech., 29:144-146.

Garside, E.T. 1959. Some effects of oxygen in relation to temperature on the development of lake trout embryos. Can. J. Zool., 37:689-698.

Hayes, F.R. and D. Pelluet. 1945. The effect of temperature on the growth and efficiency of yolk conversion in the salmon embryo. Can. J. Res., D, 23:7-15.

International Pacific Salmon Fisheries Commission. 1957. Annual Report for 1956, 32 pp.

Pelluet, D. 1944. Criteria for the recognition of developmental stages in the salmon (Salma salar). J. Morph., 74: 395-407.

Perlmutter, A. and E. White. 1962. Lethal effect of fluorescent light on the eggs of brook trout. Prog. Fish Cult., 24:26-30.

Pyper, J. and E.H. Vernon. MS. Physical and biological features of natural and artificial spawning grounds of Fraser River sockeye. Internat. Pacific Salmon Fish. Comm., 98 pp.

Scholander, P.F., L. Van Dam, C.L. Claff and J.W. Kanwisher. 1955. Micro gasometric determination of dissolved oxygen and nitrogen. Biol. Bull., 109:328-334.

Shumway, D.L., C.E. Warren and P. Doudoroff. 1964. Influence of oxygen concentration and water movement on the growth of steelhead trout and coho salmon embryos. Trans. Am. Fish. Soc., 93:342-356.

Silver, S.J., C.E. Warren and P. Doudoroff. 1963. Dissolved oxygen requirements of developing steelhead trout and chinook salmon embryos at different water velocities. Trans. Am. Fish. Soc., 92:327-343.

Smith, E.V. 1916. Effects of light on young salmon. Puget Sound Marine Sta. Pub., 1:89-107.

Steel, R.G.D. and J.H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co. Inc., New York, 107-109.

United States Commission of Fish and Fisheries. 1878. Commissioner's Report, 1875-76, 23 pp.