Factors that Influence Stranding of Juvenile Chinook Salmon and Steelhead Trout

by

Cindy Louise Monk

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Signature Cindy Louise Monk

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INTRODUCTION

Rivers regulated for hydroelectric power production are often characterized by daily flow level fluctuations due to constantly changing power demands with high outflow when energy demand is maximum and low outflow when energy demand declines. These fluctuations are more dramatic than normal flow changes in natural rivers influenced solely by tributary inflow and precipitation, and consequently, they may have adverse effects on anadromous fish adapted to natural flow regimes.

Anadromous fishes require species specific flow velocities and water depths to spawn and rear successfully (Reiser and Bjornn 1979). Hydropower induced flow fluctuations may adversely affect them in several ways. First, fluctuations can disrupt spawning activities and cause mortalities of eggs and alevins (Hamilton and Buell 1976; Graybill et al. 1979; Becker et al. 1981; Stober et al. 1982; Chapman et al. 1983; Fast and Stober 1984). Second, rapid and frequently changing flow levels can reduce production of important invertebrate food sources for rearing salmonids (Gislason 1980). Third, young salmonids that prefer shallow areas along the river margins, are vulnerable to entrapment in potholes and stranding on gravel bars exposed by lowered water levels due to flow fluctuations (Thompson 1970a, 1970b; Woodin et al. 1984; Woodin 1984;

Troutt et al. 1986; Jones and Stokes Associates, Inc. 1985; R. W. Beck and Associates 1987).

Gravel bar stranding is of concern to fisheries managers because of the cumulative mortality on the populations of both wild and hatchery produced juvenile salmonids within a river. Studies have shown that newly emerged steelhead trout (Oncorhynchus mykiss) and chinook salmon (O. tshawytscha) are the species most often found stranded on gravel bars by flow reductions, while chum (O. keta), pink (O. gorbuscha), and coho salmon (O. kisutch) also have been found stranded (Thompson 1970b; Phinney 1972, 1974a, 1974b; Hamilton and Buell 1976; Bauersfeld 1977, 1978; Graybill et al. 1979; Woodin 1984; Woodin et al. 1984). Stranding of juvenile salmon and steelhead trout longer than 100 mm has also been documented (Bauersfeld 1977; Graybill et al. 1979; Woodin et al. 1984; R. W. Beck and Associates 1987).

Factors that have been identified to contribute to the stranding susceptibility of fry belong to three general types: (a) biological factors, (b) physical environment factors, and (c) hydrological parameters due to natural as well as hydropower influence. Biological factors that influence the susceptibility of fry to stranding include species habitat preference, seasonal abundance, local distribution, fry size, and diurnal behavioral differences. Physical factors include the extent of gravel bars exposed due to flow fluctuation (due to channel shape), substrate size composition, gravel bar slope, and the presence of potholes on gravel bars subject to dewatering. Hydrological factors that affect stranding include rate of water depth reduction (dewatering rate), fluctuation amplitude (the difference between water levels before and after a flow reduction event), frequency of fluctuations, and the influence of tributary inflow. Past researchers have faced many difficulties in defining the relative importance of these factors in field studies due to uncontrolled environmental factors, high variation in the number of fry stranded on similar types of gravel bars, and the inaccurate counting of dead fry where they have burrowed into the substrate (Phinney 1974a; Bauersfeld 1977, 1978; Woodin 1984; Woodin et al. 1984).

An experiment was devised to study the phenomenon of fry stranding where flow levels, the dewatering rate, bar slope, and substrate composition were controlled. The primary objective of the experiment was to determine if fry stranding (surface and subsurface) varies with substrate size when fry are subjected to a controlled flow reduction while confined over a particular substrate. Secondary objectives were to evaluate the influence of varying factors such as dewatering rate, daylight, gravel bar slopes, and fry size on stranding. Another variable, section position with respect to the inflow manifold, was included in the analysis after obvious effects were noted while collecting data.

MATERIALS AND METHODS

Pond and Sections

The pond used for the setting of the stranding experiments was located in the Seward Park Fish Hatchery in Seattle, Washington. A 12.19 m diameter, concrete-lined pond was divided into 12 sections with Vexar plastic screens (opening diameter, 0.48 cm) mounted on wooden frames (Fig. 1). Nine sections of equal size and three smaller sections completely occupied the outer portion of the pond and extended inward toward the drain approximately 2.44 m. The sections were organized so that three large sections were grouped together in three locations in the pond. Three smaller sections into which inflowing water was piped separated the three groups of large sections. The inner 3.7 m diameter of the pond was left free of debris to serve as a drainage area. A gravity drain (diameter 22.07 cm) was located at the center of the pond, whose concrete pond bottom sloped toward it approximately 7 cm in a 6 m distance (1.2 percent gradient).

Plumbing

The plumbing in the pond was configured with polyethylene pipe and PVC (Fig. 1 and 2). A manifold was placed in each small section to deliver equal flows to each series of three large sections. Each manifold was capped on the end and perforated with fifteen 0.32 cm holes evenly spaced in

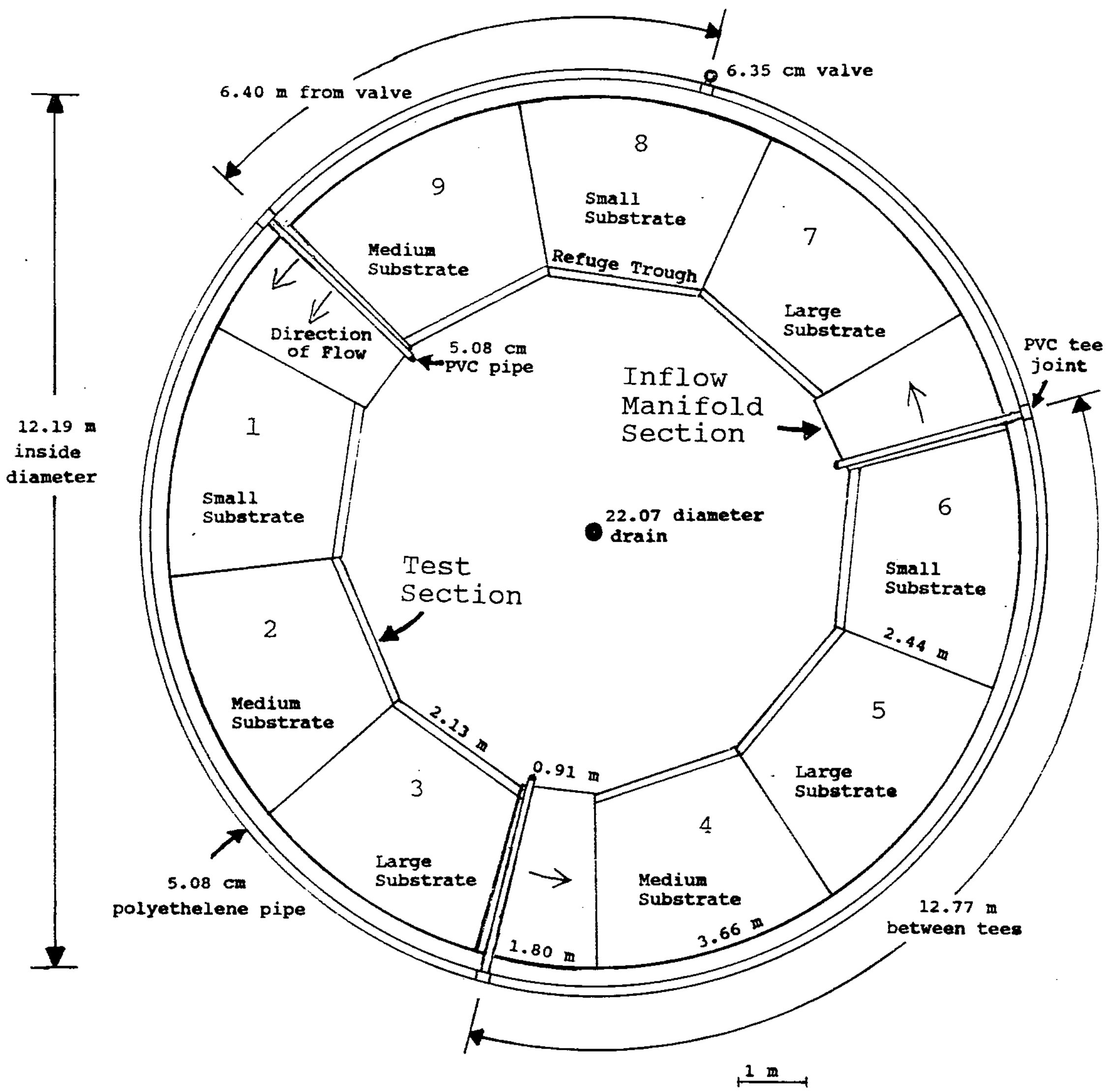

Figure 1. Experimental pond configuration for salmonid stranding experiments.

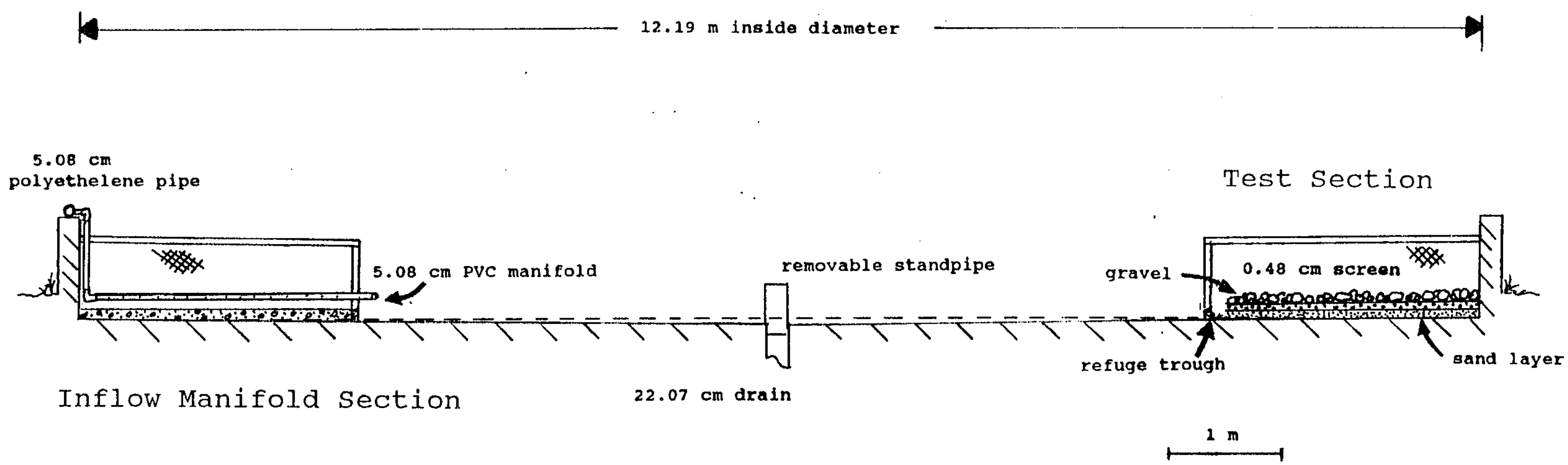

Figure 2. Cross section of experimental pond showing manifold in inflow section and one test section.

a longitudinal fashion such that flow could be delivered across the entire length of the pipe parallel to the pond perimeter.

The flow through the pond in the chinook fry experiment was approximately 170 l/min. The flow through the pond in the steelhead experiment was increased to approximately 390 l/min because the fry tended to wander around at the lower flow level rather than swimming upstream in the fashion most often observed in the field. Water depth in the pond was controlled with a standpipe in the central drain. Dewatering rates for the tests were controlled by substituting standpipes of varying sizes at equal time intervals. The heights of the ten standpipes used varied by 2.5 cm each from 15.5 to 38.0 cm.

Substrate

Sand and gravel were purchased in standard construction sizes that had been screened and sorted (with the exception of the cobbles) in the following forms:

(1) coarse sand, called builders' sand;

(2) a homogenous 0.5 cm size, called pea gravel;

(3) a homogenous 2.2 cm size, commonly called 7/8 inch;

(4) a homogenous 3.8 cm size, called 1-1/2 inch size; and

(5) a mixture of cobbles, called oversize, which ranged in size from 5 to 46 cm in diameter. The cobbles were hand sorted to remove stones less than 10 cm in diameter, which were subsequently included in the composition of medium size substrate. All of the gravel was rinsed thoroughly before initiating the tests.

With the framework in place, coarse sand was placed into the bottom of each screened section to a depth of approximately 9 cm to provide a compact base upon which to place additional substrate and impede undersurface flow. Each series of three sections contained one each of the three gravel composition types and the arrangement of these three different substrates was rotated in each series so that each type appeared in each of the positions with respect to an inflow manifold located upstream. The three series were randomly arranged one time for the entire experiment (Fig. 1).

The three gravel compositions tested were: (a) small, composed of 80 percent pea gravel and 20 percent 2.2 cm gravel; (b) medium, composed of 10 percent pea gravel, 60 percent 3.8 cm gravel, and 30 percent 5-10 cm gravel; and (c) large, composed of 10 percent pea gravel, and 90 percent 15 to 46 cm cobbles. These compositions were derived in the following manner. Pea gravel was layered into each section to a depth of about 7 cm on top of the compacted sand layer. Then, an additional 7 cm of pea gravel mixed with 2.2 cm gravel was spread onto the sections (numbered 1, 6, and 8) that were assigned the small gravel composition. A 5 cm layer of 2.2 cm gravel mixed with 3.8 cm gravel and 5 to 10 cm size gravel (small cobble) was placed in the sections (2, 4, and 9) which were assigned the medium gravel composition. Finally, cobbles ranging from 15 to 46 cm were placed in a single layer on top of the pea gravel layer in the sections (numbered 3, 5, and 7) which were assigned the largest substrate composition.

Along the base of the screen nearest the drain in each test section, a depression (refuge trough) was left for a length of plastic pipe cut in half longitudinally to hold water as a refuge for fry trying to escape stranding. The plastic pipe was removed during the tests for steelhead since most of the fry appeared to hide underneath it rather than find refuge in it.

Mean particle diameter of the surface substrate of each section was measured for at least 40 stones along a transect in the center of each section from the concrete wall to the inner screen. This was done once for the entire experiment, since the substrate composition within each section remained unchanged between tests. Mean particle diameters in the combined sections for each of the three categories were 13.9 (sd = 4.75), 29.9 (sd = 11.39), and 70.6 (sd = 19.69) mm in the small, medium, and large substrate sections, respectively (Table 1). The oneway

Table 1. Diameter in millimeters of surface substrate particles by section and by substrate size category.

Section	Number Measured	Mean Diameter	sd	Maximum Diameter	Minimum Diameter
SMALL					
1	43	13.3	4.68	22.9	4.5
6	42	14.1	4.76	22.0	5.1
8	42	14.4	4.86	22.9	4.8
Combined	127	13.9	4.75	22.9	4.5
MEDIUM					
2	41	31.5	11.88	57.3	15.3
4	44	27.9	9.83	55.4	14.6
9	40	30.5	12.42	61.8	12.4
Combined	125	29.9	11.39	61.8	12.4
LARGE					
3	69	71.6	19.51	133.7	45.5
5	65	68.1	20.73	201.2	46.5
7	60	72.1	18.64	125.7	43.3
Combined	194	70.6	19.65	201.2	43.3

analysis of variance of substrate size by section was highly significant ($P < 0.0000$) indicating that the substrate compositions used were different.

Flow Velocity

Water velocities in the sections were measured 7 cm from the bottom at nine locations within each section during the series of tests with chinook in which the substrate surface was gently sloped (gentle series) and in the series of tests with steelhead in which the substrate surface was steeply sloped (steep series) and in the second series of tests in which the substrate was gently sloped (gentle series). Measurements were taken near the top, middle and toe of the slope in each of the upstream, midstream, and downstream parts of each section for a total of nine measurements. Velocities within sections varied widely resulting in high standard deviations for mean velocities (Table 2).

Mean velocities were slightly higher during the steelhead experiment in the sections of medium and large substrate, but velocity levels varied little between the sections of different substrate in the chinook experiment (Fig. 3). However, the mean velocity in sections immediately downstream of the inflow manifolds (sections 1, 4, and 7) was consistently higher than mean velocity in the sections following in the middle and last positions with

Table 2. Mean velocities in cm/sec in the chinook and steelhead tests grouped in series by slope. Chinook II represents tests numbered 7 through 18 of the chinook experiment. Steelhead II represents tests 7 through 19, and Steelhead III represents tests 20 through 25 of the steelhead experiment. Velocity was not measured in other tests.

Section	Chinook I	sd	Steelhead II	sd	Steelhead III	sd
1	4.2	1.58	7.9	2.02	8.4	2.66
2	1.6	1.51	4.0	3.21	6.3	2.30
3	2.0	2.00	5.2	2.43	6.1	2.51
4	2.6	1.96	8.6	1.99	9.7	2.06
5	0.6	0.51	4.4	0.78	5.3	2.12
6	1.6	1.61	4.4	2.86	4.7	2.23
7	4.0	1.64	10.6	3.35	9.7	2.62
8	0.7	0.49	3.3	1.60	5.0	1.80
9	1.7	1.64	4.9	1.76	5.3	2.29
Overall	2.1	1.95	5.9	3.44	6.7	2.98

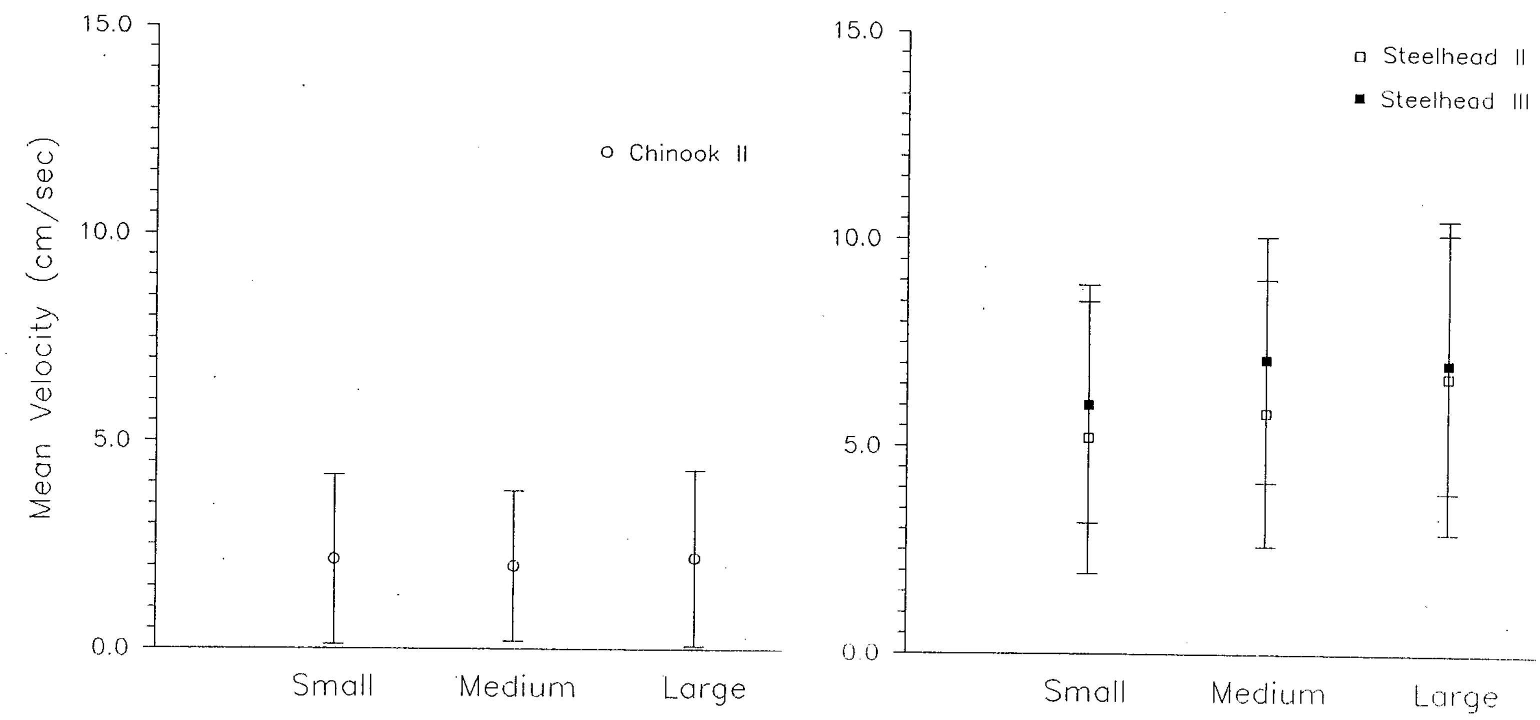

Figure 3. Mean velocity by substrate size category (three sections combined) for salmonid stranding experiments. Chinook II represents tests numbered 7 through 18 of the chinook experiment. Steelhead II represents tests numbered 7 through 19 and Steelhead III represents tests 20 through 25 of the steelhead experiment.

respect to the inflow manifold of each series of three sections (Fig. 4). The wide variation in velocity from section to section required that section position with respect to the inflow manifold be included as an additional variable in the analysis of stranded fry. The overall mean velocity in the gentle series for chinook was 2.1 (sd = 1.95) cm/sec, while the overall mean velocities in the steelhead tests were 5.9 (sd = 3.44) and 6.7 (sd = 2.98) cm/sec in the steep and second gentle series, respectively. A t-test showed that the mean velocities in the two steelhead series were not significantly different ($P = 0.1141$).

Water Depth

Depths of water flowing over the substrate surface in each section were measured at the same locations as velocity in the gentle series for chinook and in the steep and second gentle series for steelhead (Table 3). The mean depth of water flowing in the gentle series for chinook was 13.5 (sd = 2.33) cm in the gentle test series. The mean depths measured in the steep and second gentle series for steelhead were 14.1 (sd = 4.20) cm and 12.8 (sd = 2.33) cm, respectively. Analyses of variance of water depth within the gentle series for both chinook and steelhead showed that the mean depth differed significantly from section to section ($P < 0.0000$). However, analysis of variance of mean depth by section within the steep series with

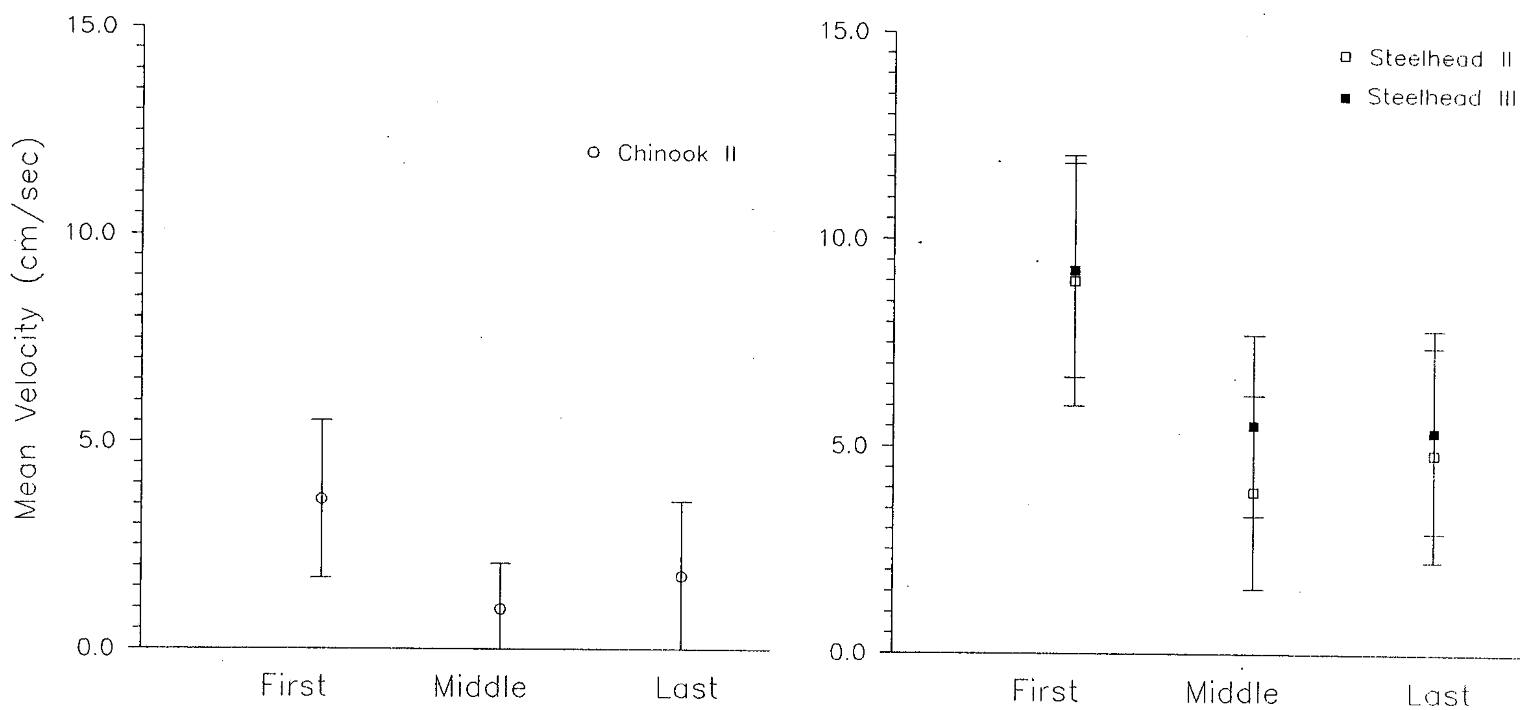

Figure 4. Mean velocity by section position with respect to the inflow manifolds (three sections combined) for salmonid stranding experiments. Chinook II represents tests numbered 7 through 18 of the chinook experiment. Steelhead II represents tests numbered 7 through 19 and Steelhead III represents tests 20 through 25 of the steelhead experiment.

Table 3. Mean depth in cm in the chinook and steelhead tests grouped in series by slope. Chinook II represents tests numbered 7 through 18 of the chinook experiment. Steelhead II represents tests numbered 7 through 19 and Steelhead III represents tests 20 through 25 of the steelhead experiment. Depth was not measured in other tests.

Section	Chinook II	sd	Steelhead II	sd	Steelhead III	sd
1	13.5	1.35	14.5	4.19	13.8	1.58
2	12.6	1.72	12.8	3.83	11.4	2.22
3	13.5	1.98	13.5	2.84	11.9	2.00
4	10.6	1.47	11.9	3.94	10.8	1.29
5	12.6	1.61	13.2	2.88	11.1	1.87
6	16.1	1.81	16.9	3.84	15.8	1.39
7	13.2	2.00	14.2	3.13	12.9	1.45
8	15.5	1.19	15.2	4.87	14.1	1.70
9	14.0	1.42	15.2	5.31	13.4	1.90
Overall	13.5	2.33	14.2	4.20	12.8	2.33

steelhead was not significant (P = 0.3368). The mean depth by section in the two steelhead series (second gentle and steep) were significantly different (P = 0.0129).

The mean depth by substrate size for each test series was slightly greater in the sections of small substrate than in sections of medium or large substrate (Fig. 5). The mean depth by section position with respect to the inflow manifold was slightly higher in the sections in the last position downstream of the inflow manifolds than in sections in the first and second positions (Fig. 6).

Experimental Design

For both fish species a randomized block design was selected to test the influence of the variables: substrate size, substrate slope, dewatering rate, and daylight on fry stranding. Each dewatering event in the pond represented a test which was characterized by substrate slope, dewatering rate, and day or night factors that were assigned according to the test desired. Tests were arranged so that each substrate size composition was utilized. Neither the positions of the substrates nor the positions of the inflow manifolds were changed during the entire test series. This lack of randomization for these factors limited the extent of valid inferential statistics that could be calculated.

Three types of substrate were tested: small (13.9 mm mean diameter), medium (29.9 mm mean diameter), and large

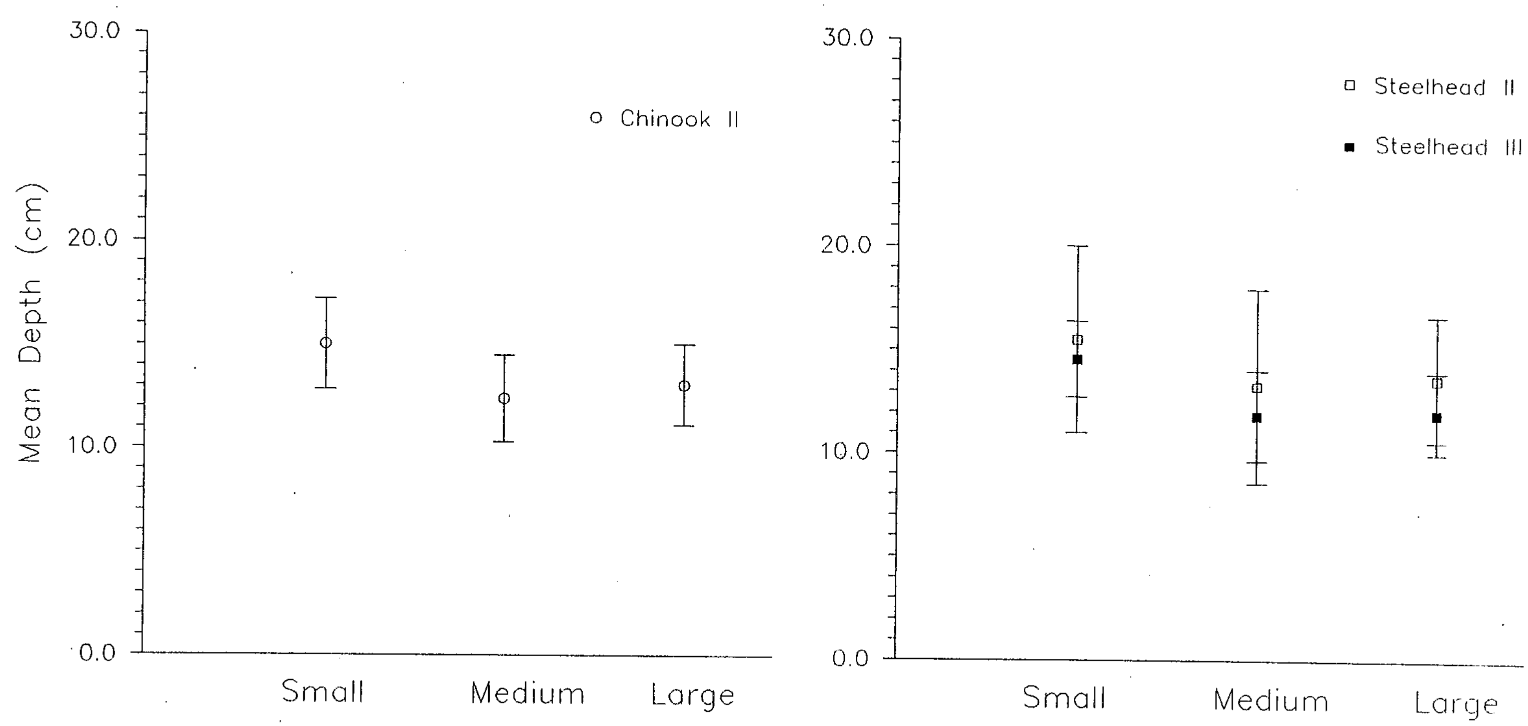

Figure 5. Mean depth by substrate size category (three sections combined) for salmonid stranding experiments. Chinook II represents tests numbered 7 through 18 of the chinook experiment. Steelhead II represents tests numbered 7 through 19 and Steelhead III represents tests 20 through 25 of the steelhead experiment.

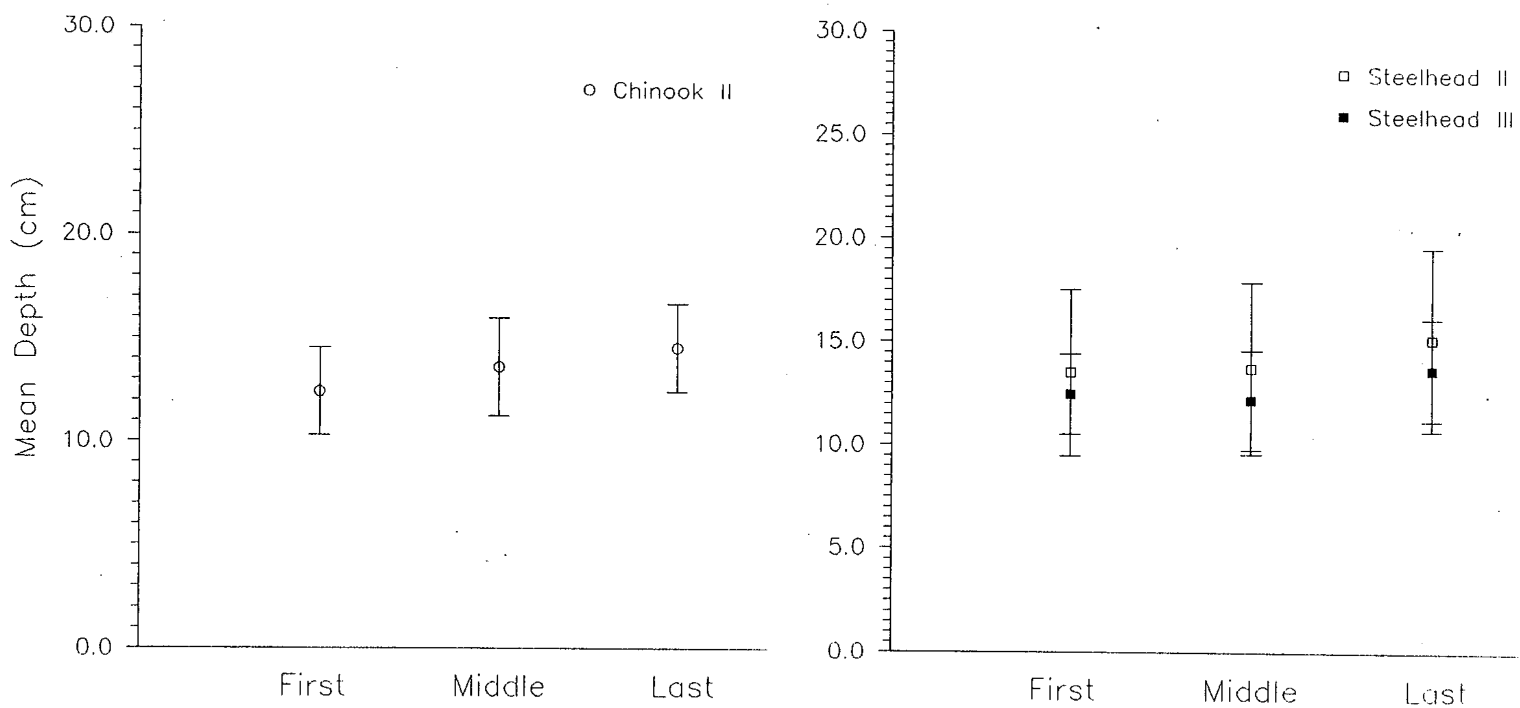

Figure 6. Mean depth by section position with respect to the inflow manifold (three sections combined) for salmonid stranding experiments. Chinook II represents tests numbered 7 through 18 of the chinook experiment. Steelhead II represents tests numbered 7 through 19 and Steelhead III represents tests 20 through 25 of the steelhead experiment.

(70.6 mm mean diameter). Two levels of each of the following factors were tested: substrate slope, dewatering rate, and daylight. The test results in numbers of stranded fry by test and by section was analyzed using analysis of variance for a randomized complete block design. A supporting analysis was performed using the nonparametric Friedman's test recommended by Zar (1974) for analyzing data from a randomized block experimental design which do not meet analysis of variance assumptions of normality and homoscedasticity. All statistical tests were calculated for the 0.05 significance level.

Species Tested

Two groups of approximately 3600 and 5500 fall chinook salmon fry were obtained from the Green River Hatchery near Auburn, Washington, and transported to Seward Park on February 28, 1986 and March 19, 1986, respectively. The fry numbered approximately 2150 fry/kg and 1980 fry/kg, respectively; these fry groups were mixed together prior to testing, placed into several 500 liter tanks, and were fed a maintenance ration of fish meal provided in small quantities several times per day. The water temperature at Seward Park was 7.2 degrees centigrade.

Ten thousand eyed stage eggs of winter run steelhead trout were obtained from the Cowlitz River Hatchery, near Toledo, Washington, and transported on June 4, 1986, to

Seward Park. They were placed into two stacked Heath incubation trays flushed continuously with water pumped from Lake Washington. Water temperatures during the subsequent incubation period ranged from 11.1 to 16.7 degrees centigrade. The steelhead eggs began hatching June 13 and were transferred to 500 liter tanks after yolk absorption. They began feeding by July 6 on a maintenance ration of fish meal administered in small quantities several times per day.

At least 24 hours before each experiment, fry were marked with powdered fluorescent dye applied onto their sides with compressed air (at 110 psi) as described by Pauley and Troutt (1988). Dye of four colors (pink, red orange, and yellow) applied in this manner was readily visible to the naked eye in the lateral line, and on the opercles and fins. Although the procedure left the fry stunned for several hours afterwards and killed 1 to 5 percent, the behavior of the fry appeared normal, including a resumption of feeding, within eight hours.

Substrate Slope

Substrate slope is the gradient of vertical change in the level of the substrate surface measured at a high elevation near the concrete wall and at a point near the lowest elevation at the edge of gravel nearest the central drain. The sand base in each section was used to form the test slope from the pond wall to the central drain. Then, the surface layer of substrate was raked to an even depth.

An automatic level and stadia rod were used to measure substrate surface slopes to achieve the desired gradient and to and to estimate the slope of the substrate surface in each section (Table 4). These estimations were based on measurements at nine locations within each section. Measurement points were located in each of the upstream, midstream, and downstream parts of each section in three places: (1) the highest part of the slope approximately 30 cm from the pond wall, (2) halfway down the slope, and (3) near the toe of the slope near the refuge channel.

The actual slopes tested for chinook were 5.1 (sd = 1.25) and 1.8 (sd = 1.48) percent gradients. These correspond to vertical changes of 10.3 and 3.6 cm over 203 cm of linear gravel surface for the tests of gently and steeply sloped substrate, respectively. For steelhead, the gentle slopes tested were 1.2 (sd = 0.63) and 0.9 (sd = 0.70) percent gradients which correspond to vertical drops of 1.8 and 2.4 cm over 203 cm of gravel surface. The steep slope tested was 3.6 (sd = 0.96) percent gradient which corresponds to a vertical drop of 7.3 cm over 203 cm of linear gravel surface.

Individual slope measurements varied widely within a section, but mean slopes by section were not significantly different from section to section within each series

Table 4. Mean substrate slope in percent vertical gradient in the chinook and steelhead tests grouped in series by slope. Chinook I represents tests numbered 1 through 6 and Chinook II represents tests 7 through 18 of the chinook experiment. Steelhead I represents tests 1 through 6, Steelhead II represents tests 7 through 19, and Steelhead III represents tests numbered 20 through 25 of the steelhead experiment.

Section	Chnk I	sd	Chnk II	sd	Sthd I	sd	Sthd II	sd	Sthd III	sd
1	4.2	1.12	1.7	1.72	1.0	1.01	3.8	0.84	1.0	0.59
2	5.3	1.14	1.7	1.61	2.0	0.77	3.6	1.58	1.0	0.44
3	5.9	1.23	2.7	1.79	0.8	0.27	3.1	0.67	0.5	1.07
4	5.4	0.77	1.7	1.19	1.3	0.59	3.0	0.61	1.1	0.59
5	4.9	1.76	1.4	0.65	1.2	0.58	3.4	0.85	0.6	0.43
6	5.1	0.97	1.8	1.25	1.1	1.03	3.8	0.49	1.1	0.91
7	4.6	1.11	1.6	0.79	1.0	0.71	3.8	1.12	0.8	0.60
8	5.3	0.83	2.6	1.14	1.0	0.69	3.7	0.59	1.0	0.67
9	4.7	1.24	0.7	1.66	1.1	0.49	4.0	0.86	0.9	0.36
Overall	5.1	1.25	1.8	1.48	1.2	0.63	3.6	0.96	0.9	0.70

(P = 0.5207; P = 0.4457; P = 0.3309; P = 0.6471; P = 0.8218). T-tests showed that the slope measurements in the steep and gentle series were significantly different in both the chinook (P < 0.0000) and steelhead (P < 0.0000) experiments. The mean slopes in the two gentle series (1.2 and 0.9 percent gradients) for steelhead were just significantly different at the 95 percent confidence level (P = 0.0489).

Tests Performed

Each test was repeated three times. In the case of chinook, the tests of the same factors were done on the same day or night, while for steelhead, each similar test was randomly assigned to a day and time during the entire experimental period to increase the validity of inferential statistics. However, the series of tests of gently sloped (gentle series) and steeply sloped (steep series) gradients were performed consecutively to minimize disturbing the gravel layers.

The dewatering rates tested in the chinook experiment were approximately 1.0 cm/min and 4.0 cm/min of vertical change in water depth in the slow and fast dewatering rate categories, respectively. In the steelhead experiment, dewatering rates tested were approximately 0.7 cm/min and 2.5 cm/min of vertical change in water depth in the slow and fast dewatering rate categories, respectively.

In the chinook experiment, the steep series (5.1 percent surface slope gradient) was done at the beginning of the experimental period (tests numbered 1 through 6), and the gentle series (1.8 percent gradient) was subsequent in tests numbered 7 through 18. Tests were performed between April 20, 1986 and May 1, 1986, inclusive. With respect to slope and dewatering rate, for chinook salmon fewer tests were performed on the steep slope with a slow dewatering rate than on the gentle slope with a fast dewatering rate.

In the steelhead fry experiment, the 12 gentle tests were divided into two series of six tests each (1.2 and 0.9 percent surface slope gradients) which occurred at the beginning and end of the experiment (tests numbered 1 through 6 and 20 through 25). The 13 tests (tests numbered 7 through 19) of the steep series (3.6 percent gradient) were performed between the two gentle series. Tests were performed between July 9, 1986 and July 20, 1986, inclusive. For steelhead trout, each combination of factors was tested three times. Except that one test was repeated a fourth time (the test of steep slope, slow dewatering rate, and daytime). This additional test was included in the analysis.

Testing Procedures

The procedures for the test series for the two species were similar. The pond sections were carefully groomed to the appropriate slope with a rake prior to each test. Then the tallest (38 cm) standpipe was put into place and the water supply valve was opened to fill the pond. The chinook salmon experiments proceeded as follows:

1. When the water level was deep enough to entirely cover the gravel, 40 fish of a particular color mark were counted into each section beginning with Section 1 each time;

2. Fry were allowed to acclimate in the pond sections until the maximum depth was reached when the flow began draining over the top of the tallest central standpipe after about 30 minutes;

3. The flow at the water supply valve was reduced to a preselected mark on the valve stem and the fry were allowed to acclimate for one additional hour at the slower velocity. As time permitted, the behavior of the acclimating fry in one or more sections was observed. The movements and schooling behaviors were recorded. Behavioral observation of the fish was not attempted at night because of the difficulty in seeing the fry underwater. An ultraviolet light did not make the dye markings on the sides of the fish visible because of the dorsal orientation of the swimming fry;

4. The person changing the standpipes waded through one of the manifold sections, stood at the center near the drain for three minutes, then either removed the standpipe and stood at the center timing the dewatering rate until all the gravel surfaces were exposed, or removed the standpipe and immediately replaced it with one which was 2.5 cm shorter, waited for 60 seconds, then changed the standpipe for one 2.5 cm shorter every 60 seconds until the gravel in all sections was exposed. This procedure resulted in vertical changes in the level of water in the pond at rates of 4.0 cm/min and 1.0 cm/min;

5. At the end of each test, the water supply valve was closed and the pond was allowed to drain completely for at least one hour to ensure that any fry hiding under the gravel surfaces would be killed. The live fry in the refuge channel were immediately removed to a holding tank, and the fry stranded on the surface were collected. During night tests, a gas lantern provided illumination while removing the live fry from the refuge channel and while searching the substrate surface for stranded fry. Locations and total lengths of most stranded fry were recorded. Fry in the refuge channel of Sections 1, 2 and 3 were measured in at least one test replicate;

6. Steps 1 to 5 were repeated twice with fry marked with different colors;

7. At the conclusion of the third test, the gravel was searched just down to the compacted sand surface to locate fry stranded beneath the surface. Fry from different tests were distinguished by their dye marks.

The tests for steelhead were the same as for chinook except as follows:

1. The steelhead were not introduced to the pond until the water level was deep enough to begin draining over the tallest (38 cm) standpipe. Thirty-five fry (rather than 40) were counted into each section beginning with Section 1 each time;

2. Fry acclimated in the full pond sections for one hour and the pond inflow was not changed during this period;

3. During the dewatering period, the standpipes were either changed to one 2.5 cm shorter in intervals of 30 seconds or three minutes depending on the dewatering rate required. This procedure resulted in vertical changes in the water level in the pond of 0.7 cm/min and 2.5 cm/min. When possible, one or more observers recorded the behavior and movement of fry during the dewatering portion of the test;

4. Fry in the refuge channel of Sections 4, 5 and 6 were measured in the first and last tests of most test types;

5. Steps 1 to 5 were repeated three to four times with fry marked with different colors.

RESULTS

Fry Behavior

Chinook

During daytime acclimation, chinook were frequently observed schooling and swimming oriented upstream (Table 5). Other fry were scattered throughout a section, alternately swimming in place and wandering around, and occasionally nipping at floating particles. Many of the chinook schools were located in the deepest and fastest moving water of the section. Some fry exhibited a marked attraction to the manifold areas of high velocity and bubbly, turbulent flow and several fry were observed trying to swim through the screens between their section and the manifold area.

Two daytime observations of dewatering were made during the chinook tests. The schooling fry appeared to respond readily to flow level reductions, moving quickly downslope to the refuge channel area into the deepest water. Several fry were observed swimming back and forth along the barrier screens. A few fry swimming in place over cobble remained at their stations until the water was well below the tops of the cobble near them. As water levels receded, they were observed trying to wriggle into the substrate. Even though sufficient water remained for them to swim, the avenue of escape had been cut off and they were stranded subsequently.

Table 5. Behaviors of fry observed during acclimating and dewatering periods of tests. The symbol '-' indicates that a behavior was not observed, '+' indicates that a behavior was occasionally observed, and '++' indicates that a behavior occurred frequently.

Behavior Observed	Chinook		Steelhead	
	Acclimation	Dewatering	Acclimation	Dewatering
attraction to inflow areas	+	++	++	++
swimming in the shade	-	-	+	-
chasing other fry	-	-	++	+
nipping at particles	+	-	++	+
wandering	+	++	-	++
swimming in deepest water	+	++	+	++
rheotactic swimming	++	+	++	+
schooling	++	++	+	+
scattering	+	-	++	-
swimming in place	+	+	++	+
hiding in the substrate	-	+	+	++
swimming to the refuge	-	++	-	++
trapped in rocks in low water	-	++	-	++

Steelhead

During the daylight acclimation periods, steelhead were frequently observed scattered throughout the sections, swimming rheotactively, nipping at floating particles, and chasing other fry that passed near their swimming location (Table 5). The majority of fry were stationed near the screens in the areas of highest velocity and usually in the shade. Some steelhead seemed to try to swim through the screen barriers near the manifold section. A few fry wandered periodically around their sections during acclimation. Schooling of some steelhead was observed in the deeper corners of the sections where section velocities were greatest.

During daylight dewatering, steelhead tended to wander or swim towards the refuge channel near the end of dewatering, and showed an increased attraction to the areas of inflow. In sections with medium and large substrate, steelhead often were observed swimming in place until the water level in the section was below the tops of the largest stones. In contrast, fry in sections of small substrate generally began to leave their territories and move downstream and downslope when water levels were reduced to approximately 3 cm or less. They were often chased by other fry as they swam by stations where individual fry were swimming in place.

Some fry were observed moving in a random fashion, rather than down slope towards the refuge, as they picked their way through interstitial spaces in sections of large substrate. Frequently, fry congregated during dewatering in the locations of highest velocities in a section, such as immediately downstream of an inflow manifold section, which is where many were subsequently stranded. Fry forced out of territorial spaces tended to school together in the refuge channel and swim back and forth along the screen barrier.

Stranding by Test

Chinook

A total of 412 chinook were stranded in 18 tests, which was 6.4 percent of the total population tested (6480 fish). The number of chinook stranded ranged from 2 to 63 fry per test (Table 6). The most chinook stranded in the daytime test in which the substrate surface was gently sloped (1.8 percent gradient) and dewatering occurred at a rate of 4.0 cm/min (Table 7). The fewest fry were stranded in a daytime test of fast dewatering rate (4.0 cm/min) with substrate sloped at a 5.1 percent gradient. Analysis of variance of chinook stranding by test indicated that numbers of fry stranded differed significantly between tests ($P = 0.0163$). Friedman's test (Zar 1974) confirmed this significant difference ($P = 0.0043$).

Table 6. Total numbers of chinook salmon fry stranded in each test by pond section.

Section Number

	1	2	3	4	5	6	7	8	9	Total
Test										
1	0	1	0	0	0	0	0	1	0	2
2	0	0	0	0	0	9	0	0	2	11
3	0	0	1	0	1	0	0	1	5	8
4	0	0	1	0	1	6	1	1	0	10
5	0	1	0	0	2	0	1	0	0	4
6	0	0	0	0	1	0	3	1	1	6
7	0	0	3	0	28	4	3	0	2	40
8	2	1	7	3	3	2	14	0	1	33
9	2	2	7	1	9	1	4	0	1	27
10	0	2	1	1	0	0	1	1	3	9
11	0	3	3	1	23	2	2	1	0	35
12	0	0	13	2	3	0	6	0	3	27
13	0	2	7	6	18	1	4	0	3	41
14	1	1	5	2	11	0	3	0	0	23
15	0	0	2	1	9	0	0	1	0	13
16	0	3	25	1	14	0	17	0	3	63
17	0	0	13	1	6	2	13	1	4	40
18	0	0	6	6	1	0	5	0	2	20
Total	5	16	94	25	130	27	77	8	30	412

Table 7. Ranked numbers of stranded chinook fry by test showing categories of slope, dewatering rate, and day/night.

Test	Fry	Mean No. Stranded Section	sd	Slope	Dewater Rate	Day/Night Category
1	2	0.2	0.44	steep	fast	day
5	4	0.4	0.73	steep	fast	night
6	6	0.7	1.00	steep	fast	night
3	8	0.9	1.62	steep	fast	day
10	9	1.0	1.00	gentle	fast	night
4	10	1.1	1.90	steep	fast	night
2	11	1.2	2.99	steep	fast	day
15	13	1.4	2.92	gentle	slow	night
18	20	2.2	2.68	gentle	fast	day
14	23	2.6	3.57	gentle	slow	night
9	27	3.0	3.08	gentle	slow	day
12	27	3.0	4.27	gentle	fast	night
13	41	4.6	5.61	gentle	slow	night
8	33	3.7	4.36	gentle	slow	day
11	35	3.9	7.25	gentle	fast	night
7	40	4.4	8.97	gentle	slow	day
17	40	4.4	5.22	gentle	fast	day
16	63	7.0	9.27	gentle	fast	day

Steelhead

A total of 1806 steelhead were stranded in 25 tests, which was 22.9 percent of the total population tested (7875 fry). The numbers of steelhead stranded varied from 34 to 129 fry per test (Table 8). The most steelhead stranded in a night test with the fast dewatering rate (2.5 cm/min) and with the substrate sloped at a 1.2 percent gradient (Table 9). The fewest fry were stranded in a night test with the slow dewatering rate (0.7 cm/min) and with the substrate sloped at a 4.6 percent gradient. Analysis of variance indicated that steelhead stranding in the individual tests differed significantly (P = 0.0038) and Friedman's test confirmed this significant difference (P = 0.0032).

Stranding by Substrate Slope

Chinook

The majority (371) of stranded chinook were on the substrate sloped 1.8 percent, while 41 fry were stranded on the steeper substrate that was sloped 5.1 percent (Table 10; Fig. 7). The Mann-Whitney test (Zar 1974) of mean numbers of fry stranded in the steep (6.8 fry per test) and gentle series (30.9 fry per test) showed that significantly greater numbers of chinook were stranded in the gentle series tests (P = 0.0017).

Table 8. Total numbers of steelhead trout fry stranded in in each test by pond section.

	Section Number									
	1	2	3	4	5	6	7	8	9	Total
Test										
1	1	2	8	10	9	0	25	0	0	55
2	12	2	10	5	7	2	27	3	5	73
3	29	7	5	4	5	0	26	13	1	90
4	26	7	18	4	10	11	27	24	2	129
5	8	5	17	9	9	2	17	0	2	69
6	23	1	10	10	11	12	22	0	8	97
7	8	0	4	7	1	10	17	2	1	50
8	13	0	17	20	1	6	25	1	1	84
9	3	0	2	8	1	2	18	0	0	34
10	7	8	5	21	10	6	7	6	3	73
11	7	2	8	23	2	3	22	0	9	76
12	12	0	4	9	0	1	9	1	3	39
13	6	10	3	13	12	0	16	4	7	71
14	10	1	7	11	1	2	17	0	6	55
15	4	2	3	15	7	2	19	0	2	54
16	15	8	3	8	4	8	18	7	11	82
17	5	6	5	14	4	4	15	3	10	66
18	13	0	14	18	5	5	14	1	19	89
19	5	5	12	26	7	3	21	1	10	90
20	9	5	12	6	15	10	14	12	10	93
21	6	4	9	7	7	1	14	4	4	56
22	3	5	4	5	1	3	21	1	10	53
23	4	7	10	10	12	1	10	1	3	58
24	14	12	13	11	13	6	8	5	7	89
25	10	6	12	12	8	5	22	2	4	81
Total	253	105	215	286	162	105	451	91	138	1806

Table 9. Ranked numbers of stranded steelhead fry by test showing categories of slope, dewatering rate, and day/night.

Test	No. of Fry	Mean No. Stranded Per Sec.	sd	Slope	Dewater Rate	Day/Night Category
9	34	3.8	5.89	steep	slow	night
12	39	4.3	4.53	steep	slow	night
7	50	5.6	5.55	steep	fast	day
22	53	5.9	6.27	gentle	slow	day
15	54	6.0	6.60	steep	fast	day
1	55	6.1	8.21	gentle	fast	day
14	55	6.1	5.75	steep	slow	day
21	56	6.2	3.73	gentle	slow	night
23	58	6.4	4.28	gentle	fast	day
17	66	7.3	4.53	steep	slow	night
5	69	7.7	6.20	gentle	slow	day
13	71	7.9	5.23	steep	fast	night
2	73	8.1	7.88	gentle	fast	day
10	73	8.1	5.21	steep	fast	night
11	76	8.4	8.53	steep	slow	day
25	81	9.0	6.00	gentle	slow	night
16	82	9.1	4.86	steep	fast	night
8	84	9.3	9.60	steep	slow	day
18	89	9.9	7.22	steep	slow	day
24	89	9.9	3.41	gentle	fast	night
3	90	10.0	10.62	gentle	slow	night
19	90	10.0	8.44	steep	fast	day
20	93	10.3	3.35	gentle	fast	night
6	97	10.8	7.89	gentle	slow	day
4	129	14.3	9.66	gentle	fast	night

Table 10. Summary statistics for numbers of chinook fry stranded by section and by test for each factor level. Tests of equal means were made for each factor at a significance level of five percent (alpha = 0.05).

	Total	Percent Stranded of Total Fry Tested	Mean No. of Fry Per test	sd	Mean No. Per Section	sd	Means Comparison P-values
SLOPE							
steep (5.1 %)	41	1.9	6.8	3.18	0.8	1.62	
gentle (1.8 %)	371	8.6	30.9	13.94	3.4	5.35	0.0017
DEWATERING RATE							
fast (4.0 cm/min)	235	5.4	19.6	17.66	2.2	4.40	
slow (1.0 cm/min)	177	8.2	29.5	9.79	3.3	5.02	0.1009
DAY/NIGHT							
night	168	5.2	18.7	12.61	2.1	3.85	
day	244	7.5	27.1	18.14	3.0	5.28	0.4524
SUBSTRATE							
small	40	1.9	2.2	2.44	0.7	1.58	
medium	71	3.3	3.9	2.82	1.3	1.54	
large	301	13.9	16.7	14.97	5.6	6.77	0.0000
POSITION							
first	107	5.0	5.9	6.00	2.0	3.53	
middle	154	7.1	8.6	8.69	2.9	5.74	
last	151	7.0	8.4	6.91	2.8	4.33	0.4643

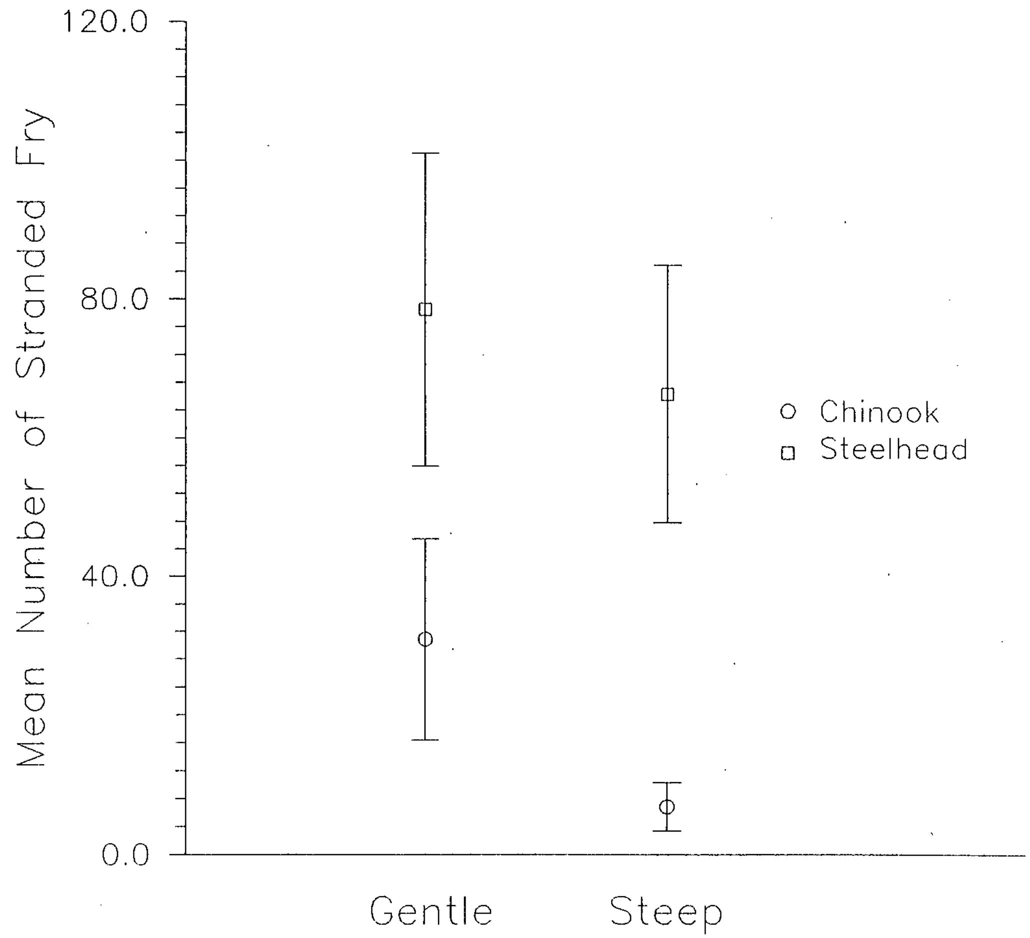

Figure 7. Mean number of stranded fry per test by substrate surface slope for salmonid stranding experiments.

Steelhead

Most (943) steelhead stranded on the substrate where slopes averaged 1.0 percent (the combined gentle series) (Table 11). The mean number of steelhead stranded in the gentle series were higher than in the steep series, but the large standard deviations of these means resulted in overlapping distributions (Fig. 7). The Mann-Whitney test of mean numbers of steelhead stranded in the two gentle slope series (85.5 and 71.7 fry per test) was not significant (P = 0.3785), which indicated no difference in stranding on 1.2 and 0.9 percent gradients. The Mann-Whitney test of mean numbers of steelhead stranded in the steep series (66.4 fry per test) and combined gentle slope series (78.6 fry per test) indicated no significant difference (P = 0.1823) in stranding on the two different of slopes tested.

Stranding by Rate of Dewatering

Chinook

The mean number of chinook stranded in tests with a slow dewatering rate (29.5 fry per test at 1.0 cm/min) was higher than in tests of the fast dewatering rate (19.6 fry per test at 4.0 cm/min), but the large standard deviations of these means resulted in overlapping distributions and no significant differences (P = 0.1009) (Table 10; Fig. 8).

Table 11. Summary statistics for numbers of steelhead fry stranded by section and by test for each factor level. Gentle1 represents steelhead tests numbered 1 through 6 and Gentle2 represents test 19 through 25. Tests of equal means were made for each factor at a significance level of five percent (alpha = 0.05).

	Total	Percent Stranded of Total Fry Tested	Mean No. Per Test	sd	Mean No. Per Section	sd	Means Comparison P-value
SLOPE							
steep (4.6 %)	863	21.1	66.4	17.83	7.4	6.44	
gentle (combined)	943	25.0	78.6	21.60	8.7	6.91	0.1823
gentle1 (1.2 %)	513	27.1	85.5	23.82	9.5	8.46	
gentle2 (0.9 %)	430	22.8	71.7	16.45	8.0	4.76	0.3785
DEWATERING RATE							
fast (2.5 cm/min)	917	24.26	76.4	21.34	8.5	6.46	
slow (0.7 cm/min)	889	21.71	68.4	19.20	7.6	6.89	0.5136
DAY/NIGHT							
night	903	23.9	75.3	24.47	8.4	6.28	
day	903	22.1	69.5	15.85	7.7	7.06	0.5136
SUBSTRATE							
small	449	17.1	18.0	13.21	6.0	6.22	
medium	529	20.2	21.2	9.01	7.1	5.66	
large	828	31.5	33.1	9.52	11.0	7.06	0.0000
POSITION							
first	990	37.7	39.6	10.37	13.2	7.13	
middle	358	13.6	14.3	10.47	4.8	4.61	
last	458	17.5	18.3	8.69	6.1	4.66	0.0000

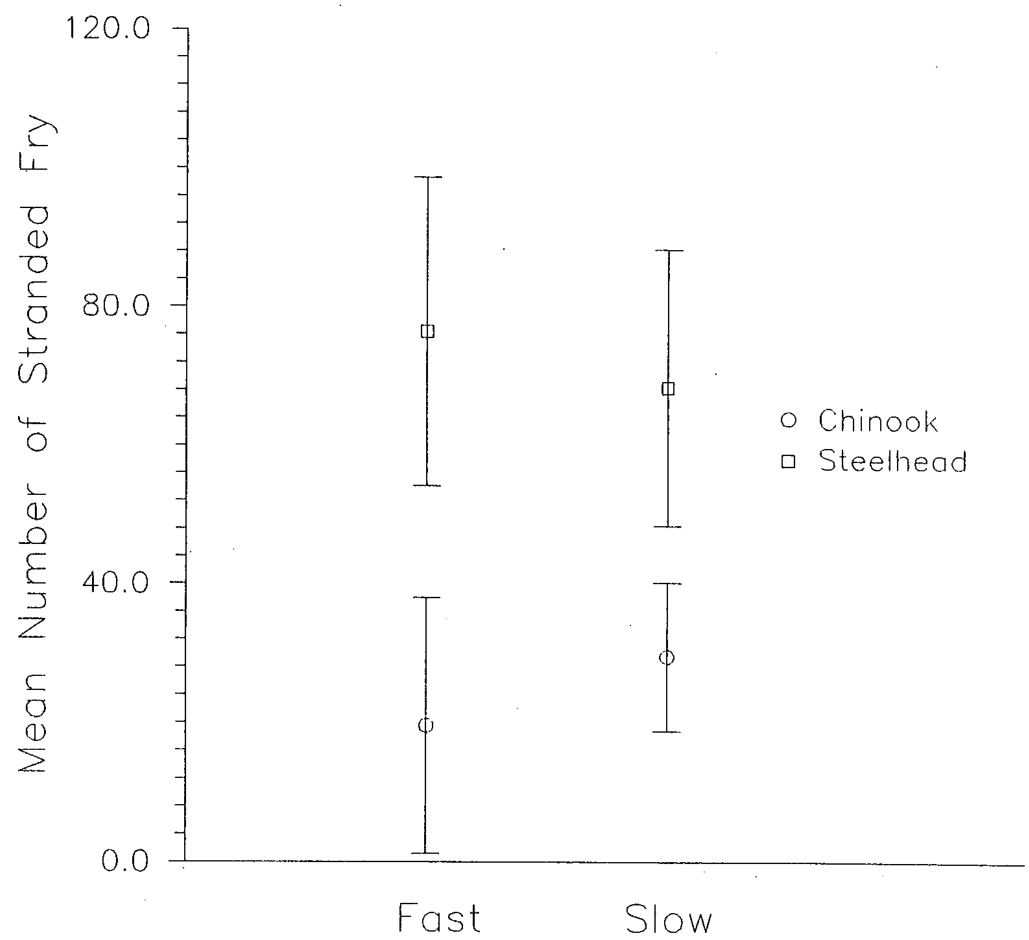

Figure 8. Mean number of stranded fry per test by rate of dewatering for salmonid stranding experiments.

Steelhead

The mean number of steelhead stranded in the tests with a fast dewatering rate (76.4 fry per test at 2.5 cm/min) was higher than in the tests with a slow dewatering rate (68.4 fry per test at 0.7 cm/min), but the large standard deviations of these means resulted in overlapping distributions and no significant differences (P = 0.5136) (Table 11; Fig. 8).

Stranding by Daylight

Chinook

The mean number of chinook stranded was higher in the day tests (27.1 fry per test) than in the night tests (18.7 fry per test), but the large standard deviations of these means resulted in overlapping distributions and no significant difference (P = 0.4524) (Table 10; Fig. 9).

Steelhead

Although equal total numbers of steelhead fry (903) were stranded in the 13 tests performed in the daytime and in the 12 tests performed at night (Table 11), the mean number of steelhead stranded was higher in the night tests (75.3 fry per test) than in the day tests (69.5 fry per test). The large standard deviations of these means resulted in overlapping distributions and no significant difference (Fig. 9).

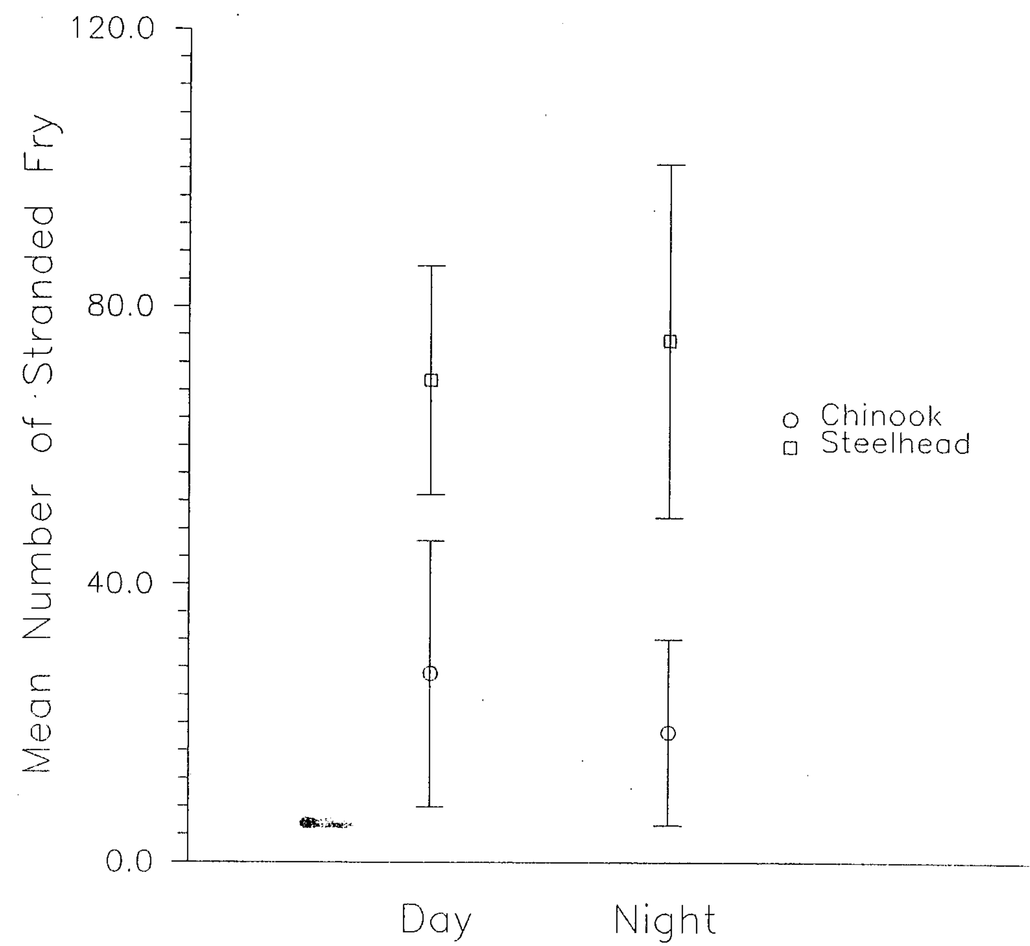

Figure 9. Mean number of stranded fry per test by night and day for salmonid stranding experiments.

Stranding by Substrate Size

Chinook

Of the total of 412 chinook stranded in the tests, the majority (301) were stranded in the sections of large substrate (Table 10), with medium and small substrate sizes stranding 71 and 40 chinook fry, respectively. Analysis of variance indicated that the effect of the three substrate size compositions on chinook stranding was highly significant ($P < 0.0000$). The large standard deviations of these means resulted in overlapping distributions (Fig. 10). The large substrate section in the middle position with respect to the inflow manifold stranded more chinook fry on average (7.2 fry per test) than any other section (Table 12), while the section of small substrate in the first position after an inflow manifold stranded the lowest average number of chinook (0.2 fry per test).

Steelhead

Of the total of 1806 steelhead stranded in the tests, 828 were stranded in the sections with large substrate, while the sections with small and medium substrate stranded 449 and 529 fry (Table 11). Analysis of variance indicated that substrate composition was highly significant for steelhead stranding ($P < 0.0000$). The large standard deviations of these means resulted in overlapping distributions (Fig. 10). The section of large substrate in the

Table 12. Ranked stranding of chinook fry by sections showing categories for position with respect to the inflow manifolds and substrate size.

Section	Mean No. of Fry Stranded	sd	Position Category	Substrate Category
1	0.3	0.67	First	Small
8	0.4	0.51	Middle	Small
2	0.9	1.08	Middle	Medium
4	1.4	1.88	First	Medium
6	1.5	2.50	Last	Small
9	1.7	1.57	Last	Medium
7	4.3	5.15	First	Large
3	5.2	6.44	Last	Large
5	7.2	8.54	Middle	Large

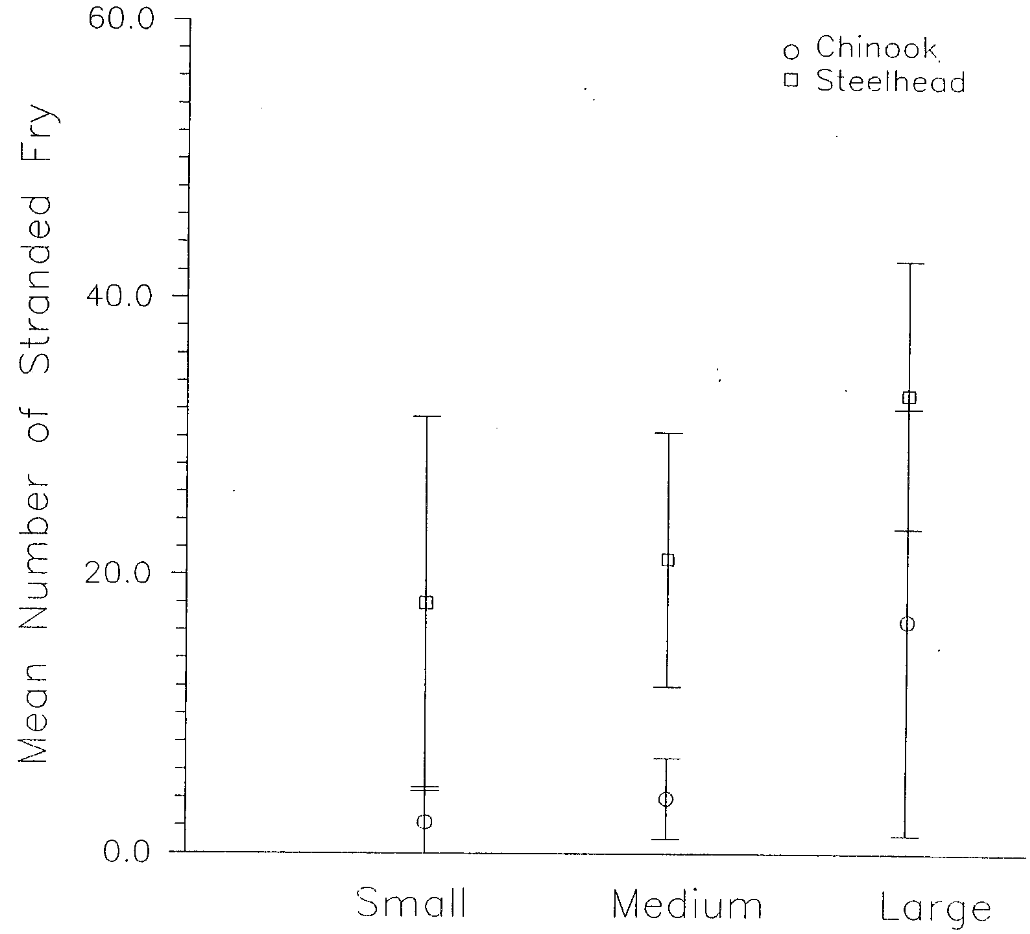

Figure 10. Mean number of stranded fry per test by substrate size category for salmonid stranding experiments.

first position after the inflow manifold stranded the greatest average number of steelhead (18.0 fry per test), while the section of small substrate in the middle position after the manifolds stranded the lowest mean number of fry (3.6 fry per test) (Table 13).

Stranding by Position with Respect to the Manifold

Chinook

Of the total of 412 chinook stranded in the tests, the total number (107) and mean number stranded in the sections immediately downstream of the three manifolds in the pond were less than were stranded in the sections in the middle (154) and last (151) positions away from the manifold, but the large standard deviations resulted in overlapping distributions (Table 10; Fig. 11). Analysis of variance indicated that chinook stranding was not significantly different in the sections in the three positions with respect to the inflow manifolds ($P = 0.4643$).

Steelhead

Of the total of 1806 steelhead stranded in the tests, the total number (990) and mean number stranded in the sections immediately downstream from the three manifolds in the pond were greater than were stranded in the sections in the middle (358) and last (458) positions from the manifold, with no overlap in standard deviation between the

Table 13. Ranked stranding of steelhead fry by sections showing categories for position with respect to the inflow manifolds and substrate size.

Section	Mean No. of Fry Stranded	sd	Position Category	Substrate Category
8	3.6	5.52	Middle	Small
2	4.2	3.44	Middle	Medium
6	4.2	3.61	Last	Small
9	5.5	4.56	Last	Medium
5	6.5	4.41	Middle	Large
3	8.6	4.84	Last	Large
1	10.1	7.11	First	Small
4	11.4	6.06	First	Medium
7	18.0	5.85	First	Large

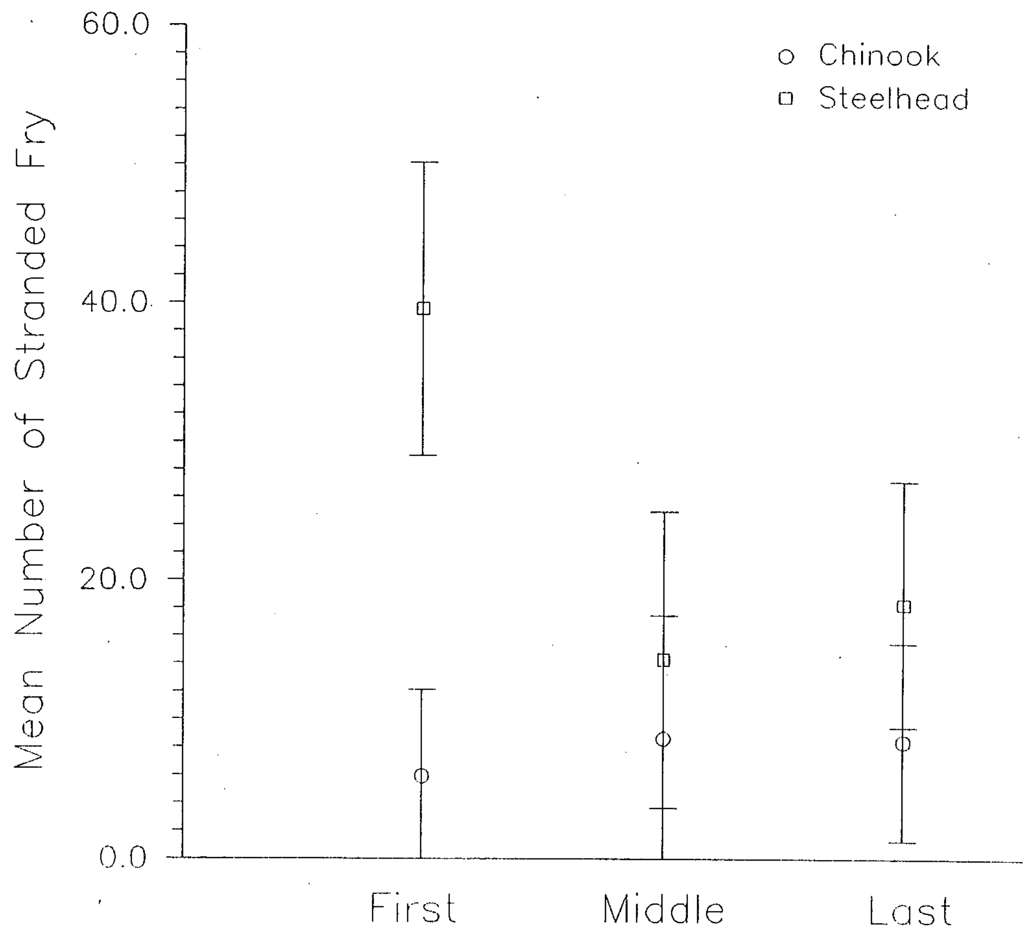

Figure 11. Mean number of stranded fry per test by section position with respect to the inflow manifold for salmonid stranding experiments.

first and the middle and last positions (Table 11; Fig. 11). Analysis of variance indicated that position of the section with respect to the manifold was highly significant for steelhead stranding ($P < 0.0000$).

Subsurface Stranding

Chinook

Overall, slightly more stranded chinook (213) were found on the surface of the substrate rather than beneath the surface (199 fry), but these numbers were not significantly different ($P = 0.5574$) (Table 14). A significantly ($P = 0.0027$) greater mean number of stranded chinook fry (2.0 fry per test) was found on the substrate surface in the sections of small substrate than beneath that substrate's surface (0.2 fry per test).

On the other hand, in the sections of medium and large substrate, more fry were stranded 1 to 12 cm beneath the substrate surface (2.4 and 8.4 fry per test) than on the surface of the substrate (1.6 and 8.3 fry per test), but the standard deviations were very large (Fig. 12). The differences between the surface and subsurface stranding were not significant in either the medium ($P = 0.2052$) or large substrate ($P = 0.8232$).

Table 14. Summary of stranded chinook fry by substrate size (three sections combined). Tests of equal means for surface and subsurface stranding were made at a significance level of five percent (alpha = 0.05).

SUBSTRATE CATEGORY	LOCATION	Total	Percent of Stranded Fry	Mean No. of Fry Test	sd	P-Values
small	surface	36	8.7	2.0	2.54	
	subsurface	4	1.0	0.2	0.43	0.0027
medium	surface	28	6.8	1.6	1.85	
	subsurface	43	10.4	2.4	2.11	0.2052
large	surface	149	36.2	8.3	9.23	
	subsurface	152	36.9	8.4	12.31	0.8232
Overall	surface	213	51.7	11.8	10.02	
	subsurface	199	48.3	11.1	12.80	0.5574

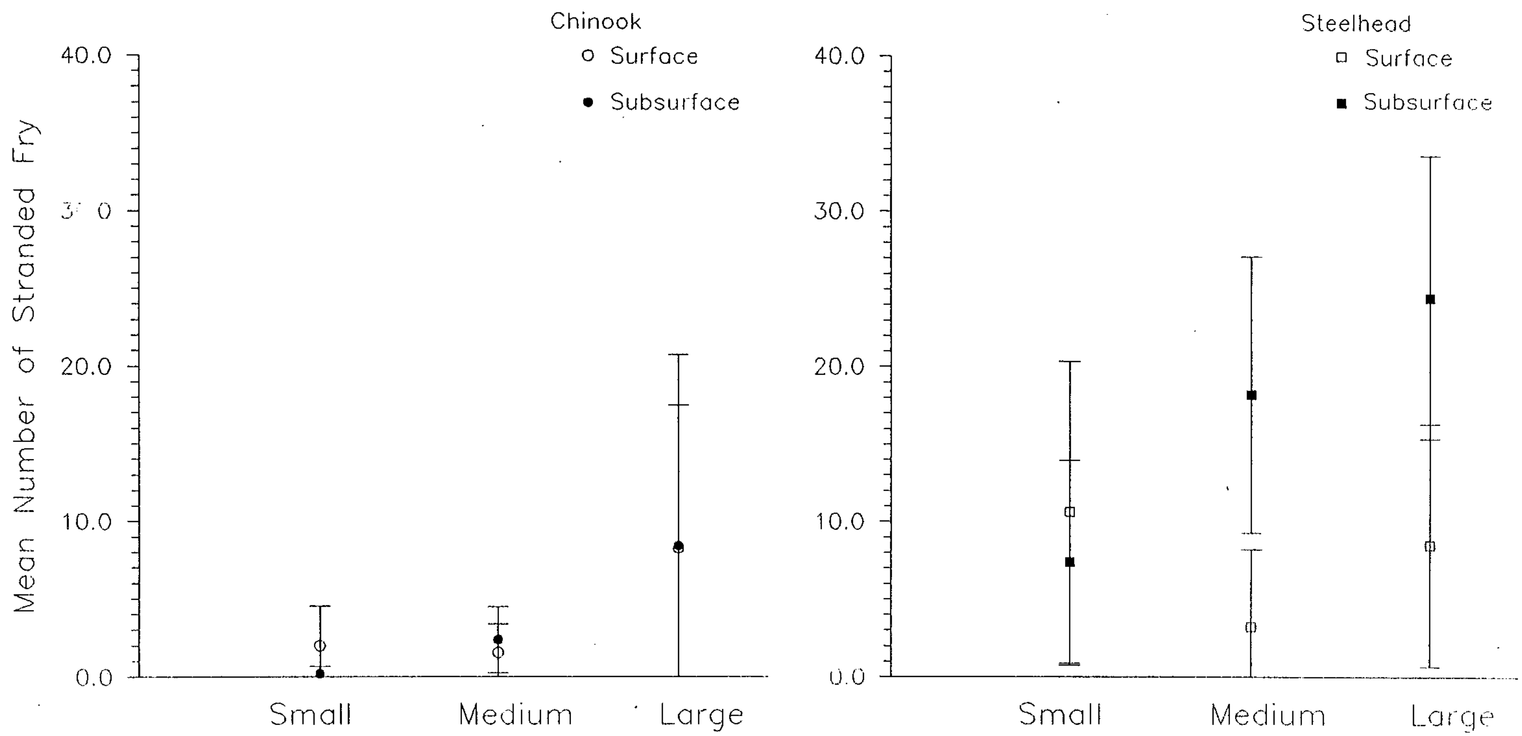

Figure 12. Mean number of surface and subsurface stranded fry per test by substrate size category for salmonid stranding experiments.

Steelhead

The majority (1051) of stranded steelhead were recovered from subgravel locations, while significantly fewer (469) fry were found on the surface ($P < 0.0000$; Table 15). Sections with small substrate were the only sections in which a greater number of fry (223) were found on the surface of the substrate rather than beneath the surface (155 fry), but the Mann-Whitney test indicated that these numbers were not significantly different ($P = 0.4420$).

On the other hand, subsurface stranding in the medium and large substrate sections was significantly greater than surface stranding ($P < 0.0000$). The large standard deviations resulted in overlapping distributions for the small and large substrates (Fig. 12).

Fry Lengths

Chinook

Mean lengths of chinook used in the test varied from 43.8 (sd = 3.3) mm to 49.3 (sd = 3.4) mm (Table 16). Analysis of variance indicated that fry used in some tests were significantly larger ($P < 0.0000$) in total length than the mean length of fry in other tests.

The t-test comparing mean lengths of fry that escaped and stranded in individual tests was significant ($P = 0.0026$) in one case (Test 10), but an overall t-test for combined tests failed to show any difference ($P = 0.4873$)

Table 15. Summary of stranded steelhead by substrate size (three sections combined). Tests numbered 6, 14, 22, and 25 were not evaluated. Tests of equal means were made for each pair of means at a significance level of five percent (alpha = 0.05).

SUBSTRATE CATEGORY	LOCATION	Total	Percent of Stranded Fry	Mean No. of Fry Per Test	sd	P-Value
small	surface	223	14.7	10.6	9.73	
	subsurface	155	10.2	7.4	6.61	0.4420
medium	surface	68	4.5	3.2	4.95	
	subsurface	382	25.1	18.2	8.91	0.0000
large	surface	178	11.7	8.5	7.81	
	subsurface	514	33.8	24.5	9.12	0.0000
Overall	surface	469	30.9	22.3	12.91	
	subsurface	1051	69.1	50.1	13.52	0.0000

Table 16. Mean lengths, standard deviations, and comparative statistics of total lengths of chinook fry by test. Tests of equal mean lengths escaped and stranded chinook were made with a signficance level of five percent (alpha = 0.05).

	Combined Fry			Escaped fry			Stranded fry			
Test	No.	Mean	sd	No.	Mean	sd	No.	Mean	sd	P-Values
1	115	44.1	3.3	114	44.1	3.3	1	45.0	0.0	
2	10	46.6	3.0	-	-	-	10	46.6	3.0	
3	1	47.0	0.0	-	-	-	1	47.0	0.0	
4	3	44.7	3.1	-	-	-	3	44.7	3.1	
5	119	46.9	3.3	115	47.0	3.2	4	45.0	4.3	0.2262
6	5	43.8	2.4	-	-	-	5	43.8	2.4	
7	152	46.0	3.6	112	46.0	3.6	40	46.0	3.7	0.9598
8	31	45.1	3.0	-	-	-	31	45.1	3.0	
9	26	44.2	5.1	-	-	-	26	44.2	5.1	
10	126	47.3	3.1	117	47.5	3.0	9	44.3	2.6	0.0026
11	35	45.9	4.4	-	-	-	35	45.8	4.4	
12	27	45.5	4.1	-	-	-	27	45.5	4.1	
13	145	46.6	3.7	104	46.8	3.6	41	46.0	3.8	0.2419
14	22	45.5	4.6	-	-	-	22	45.5	4.6	
15	13	46.6	3.1	-	-	-	13	46.6	3.1	
16	149	48.4	3.6	86	48.3	3.9	63	48.6	3.3	0.7040
17	40	47.3	3.8	-	-	-	40	47.3	3.8	
18	20	49.3	3.4	-	-	-	20	49.3	3.4	
Overall	1039	46.5	3.8	648	46.6	3.7	391	46.4	4.0	0.4873

in mean lengths of fry that were stranded (46.4 mm) or escaped (46.5 mm) (Table 16). A t-test indicated that there was no significant difference (P = 0.9292) in total lengths of fry that were stranded on the surface (46.4 mm; sd = 4.08) or subsurface (46.4 mm; sd = 3.92) of the substrate.

Steelhead

Mean lengths of steelhead used in the tests varied from 32.1 (sd = 1.7) mm to 34.2 (sd = 1.8) mm (Table 17). Analysis of variance of mean fry length by test indicated that fry in some tests were significantly larger (P < 0.0000) than fry in other tests.

T-tests comparing lengths of escaped and stranded fry in individual tests were significant in three cases (P = 0.0303; P = 0.0039; P = 0.0017), and the overall t-test for combined tests indicated that the mean length of fry that escaped (33.0 mm) was significantly larger than that of fry that stranded (32.9 mm) (P = 0.0282). A t-test indicated that there was no significant difference (P = 0.9889) in mean length between fry stranded on the surface (32.9 mm; sd = 1.65) or beneath the substrate (32.9 mm; sd = 1.52).

Table 17. Mean lengths, standard deviations, and comparative statistics of total lengths of steelhead fry by test. Tests of equal mean lengths escaped and stranded chinook were made with a signficance level of five percent (alpha = 0.05).

	Combined Fry			Escaped fry			Stranded fry			
Test	No.	Mean	sd	No.	Mean	sd	No.	Mean	sd	P-Values
1	123	32.7	1.5	69	33.0	1.3	54	32.4	1.6	0.0303
2	71	32.3	1.4	-	-	-	71	32.3	1.4	
3	128	32.1	1.7	65	31.6	1.8	63	32.5	1.6	0.0039
4	110	32.5	1.4	26	32.8	1.4	84	32.4	1.4	0.2290
6	90	32.2	1.5	65	32.1	1.6	25	32.4	1.4	0.3848
7	136	34.0	1.5	90	34.1	1.6	46	33.7	1.2	0.1619
8	150	33.3	1.6	77	33.7	1.6	73	32.9	1.5	0.0017
9	121	33.4	1.8	89	33.5	1.7	32	32.9	1.9	0.0815
10	89	33.3	1.6	48	33.3	1.6	41	33.3	1.6	0.9569
11	26	34.2	1.8	-	-	-	26	34.2	1.8	
12	10	33.7	1.8	-	-	-	10	33.7	1.8	
13	25	33.4	1.5	-	-	-	25	33.4	1.5	
14	96	32.7	1.5	82	32.9	1.4	14	32.1	1.9	0.0676
15	86	32.5	1.2	73	32.5	1.2	13	32.6	1.1	0.6776
16	66	34.0	1.7	59	34.0	1.7	7	33.6	1.5	0.5269
18	86	32.8	1.4	86	32.8	1.4	-	-	-	
19	69	32.3	1.5	69	32.3	1.5	-	-	-	
20	26	32.9	1.7	-	-	-	26	32.8	1.7	
21	12	33.6	1.7	-	-	-	12	33.6	1.7	
22	90	33.4	2.1	85	33.4	2.1	5	33.8	1.9	0.6657
23	75	32.6	1.7	70	32.5	1.7	5	32.8	0.8	0.7282
24	45	33.8	1.9	40	33.9	1.9	5	33.2	1.3	0.4520
25	3	34.0	1.0	-	-	-	3	34.0	1.0	
Overall	1733	33.0	1.7	1093	33.0	1.7	640	32.8	1.6	0.0282

DISCUSSION

Stranding Behavior

Behavior of fry that results in stranding on gravel bars is not well understood. Fry that inhabit the shallow areas of a river often do not respond to flow reductions in ways that will allow them to avoid stranding on gravel bars. Both natural and artificially induced fluctuations of flow levels result in exposed areas of gravel bar with which fry are associated.

Stranding of salmonid fry occurs because the appropriate response that allows fry to avoid stranding is inhibited by biological and environmental factors. A major biological factor that influences the vulnerability of salmonid fry to stranding is habitat preference which is a function of species and age. When fry are by biological necessity (due to their requirements for space, food, and limited swimming stamina) located in areas of gravel bar subject to dewatering, then other environmental factors come into play: substrate size composition, slope of the substrate surface, rate of dewatering, time of day of dewatering, and perhaps other characteristics of the channel morphology and river flow which were not studied here. The vulnerability of salmonid fry to strand seems to be influenced by characteristics of the habitat that is exposed by a flow reduction. In the present study when substrate was large and the slope was nearly flat, fry frequently were unable to make an appropriate choice to move down slope with the receding water level to avoid stranding. Also, water drainage from the gravel bar or beneath the surface gravel seemed to attract fry to locations that would be dewatered. Evidently, characteristics of the habitat or familiarity with a certain territory induces fry to remain in a location in spite of decreasing velocity and depth, and the rates tested made no difference in this stranding effect.

It has been documented that fry prefer habitat with species specific water velocities and depths (Everest and Chapman 1972; Reiser and Bjornn 1979). Thus, in a natural river where flow levels do not change quickly or with much frequency, fry become accustomed to inhabiting certain areas of gravel bar. River flow level reductions due to hydropower operations are much faster and more frequent than natural flow reductions, hence, fry are subjected to a regime of changes with which they cannot cope. Evidently there is nothing in their adaptive history that urges them to leave their accustomed gravel bar habitat during a rapid flow reduction to avoid mortality.

Published observations of behavior of fry during flow reductions in field studies are nonexistent. Observations in the present study suggest that at least several factors can influence stranding: velocity, substrate size, substrate slope, and dewatering rate. Also, time of day of the flow reduction may have some effect, although it was not significant in a Mann-Whitney test.

Care was taken to design the gravel surfaces and flow conditions to mimic riparian gravel bars to avoid creating an unrealistic model of the real world that would result in abnormal behavior of fry. Measured velocities, depths, and substrate size compositions were within the ranges reported for chinook and steelhead fry habitat in streams (Everest and Chapman 1972; Thompson 1972; Reiser and Bjornn 1979; Stober et al. 1982). The surface gravel sizes selected for testing were similar to that which is found on natural river bars, although the composition was probably more homogenous with less interstitial fine sediment particles than occurs on river bars. The lack of interstitial fines is particularly important, since stranding of fry under the substrate surface occurred more often in the present experiment than previously recorded in field studies. The incidence of higher stranding in these laboratory tests than in field studies may have been made possible by readily available interstitial hiding places.

Fry were observed swimming rheotactively over particular stations, nipping at drifting particles and otherwise exhibiting behavior much as described by for fry within natural stream environments (Chapman 1962; Edmundson 1968; Lister and Genoe 1970; Brix 1974). Both species of fry in the present study, but steelhead in particular, exhibited a strong tendency to remain at a station over a certain group of stones during the acclimation period and for a large part of the dewatering period. Steelhead are territorial during their freshwater residence (Everest and Chapman 1972), which may explain their reluctance to abandon certain swimming stations during flow reductions. Hamilton and Buell (1976) described similar behavior for chinook fry in the Campbell River, British Columbia. Such "territorial tenacity" results in delayed movement of fry toward habitat that would be safe from dewatering. This territorial tendency was most evident over the sections of large substrate, less so over the medium substrate and rare over the fine substrate.

Chinook were much more successful than steelhead at avoiding stranding which was apparently due to their tendency to swim in groups, which spent most of the acclimation period in the deepest water over the refuge channel. However, some chinook occasionally stranded as a group when they lingered too long on the upper part of the slope. These occasions resulted in the largest numbers of chinook stranded per test during the experiment. Such group strandings occurred in sections of large substrate that were gently sloped (1.8 percent gradient). This suggested that some characteristic of the gently sloped surface covered by cobble provided the fry a false sense of security and inhibited an appropriate response to avoid stranding.

Section Position

Position of the sections with respect to the inflow manifold was necessarily included in the analysis due to its strong effect on steelhead fry stranding. The steelhead showed a significantly greater tendency to strand in sections in the first position with respect to the inflow manifolds which had higher mean velocities than in sections in the middle and last positions.

Steelhead exhibited a strong attraction to the source of inflowing water coming under the screen which separated their graveled section from the inflow section and frequently were found stranded beneath the gravel or cobble along the screen. A strong attraction to areas of high water velocity was also observed where steelhead fry swam up the slope of a Skagit River gravel bar from which water was draining following a flow reduction. This behavioral tendency may represent an attempt by fry to swim into tributary waters or sloughs to avoid the strong currents in the mainstem river as preferred shallow habitat of a gravel bar becomes exposed in a flow reduction. Obviously, such behavior is counterproductive when fry delay swimming towards deeper water habitat where they would be safe from stranding. Chinook did not exhibit this behavior to the same degree as steelhead since schools quickly formed and remained primarily in the deep upstream portion of the refuge channel during dewatering.

No other researchers have examined the effect of water flow velocity on the susceptibility of fry to stranding. Since fry habitat is typically defined by water depth and velocity (Reiser and Bjornn (1979)), it seems that velocity may be an extremely important factor that affects stranding that should be addressed in any future studies.

Substrate Size

There was a clear relationship between increased numbers of both stranded species with increasing size of the substrate. These results corroborate what previous field observers hypothesized regarding the effect of increased substrate size on fry stranding (Hamilton and Buell 1976; Bauersfeld 1978; Woodin et al. 1984). Hamilton and Buell (1976) hypothesized that the length of time required for fry to orient to deeper water during a dewatering event is protracted over areas of rough substrate on gravel bars because the water tends to percolate down through the coarse gravel and boulders of the bars and traps fry "as in a sieve". Phinney (1974a) also observed that salmon fry tended to seek safety by entering "pockets of water" in the streambed, and that larger streambed material provided them with deeper "refuge pockets". The present study confirmed these observations most dramatically in the sections of large substrate in which fry were often seen swimming within water pockets between the cobbles as water levels receded.

Even when the water level was reduced to the degree that water pockets were isolated between exposed cobble tops, the fry remained in the "refuge pockets" where the water level was still deep enough to swim, providing apparent safety. As the water levels continued to fall, the pockets eventually dewatered as well, leaving the fry stranded on the sand and pea gravel layer under the larger stones after escape routes were eliminated. In contrast, fry in sections of small substrate tended to respond readily to flow reductions and typically moved down the slope to the refuge channel as the section dewatered.

Observations by R. W. Beck and Associates (1987) on the Skagit River indicated that gravel bars composed of small substrate (less than 7.6 cm) stranded more steelhead and chinook fry than bars composed of large substrate (greater than 7.6 cm). The difference in observed effects between the present study and R. W. Beck and Associates' (1987) conclusion that more fry stranded on smaller substrate may be due to the differences in substrates examined. The proportion of fine particles in the surface substrate of sections of medium and large substrate in the present experiment was far less than that typically observed on river bars and the R. W. Beck and Associates'

(1987) study did not examine subsurface stranding. A higher percentage of fines would be expected to result in a greater component of subsurface stranding on the medium and large substrates than typically observed on natural river bars.

Subsurface Stranding

Many of the fry stranded in the present experiment were stranded in subsurface locations. Several other researchers have reported finding significant numbers of fry stranded on river bars by removing surface rocks (Phinney 1974a; Bauersfeld 1978; Woodin et al. 1984). Use of substrate as a refuge by juvenile salmonids has been recognized by many researchers (Thompson 1970b; Phinney 1974b; Bauersfeld 1977; Stober et al. 1982; Woodin 1984). Fast and Stober's (1984) study of intragravel incubation documented the migration of alevins through substrate to avoid undesirable conditions such as low oxygen, low water velocity, low water levels, and light. Mason (1976) showed that coho fry had a tendency to use substrate as a refuge after emergence. The author observed startled fry diving into substrate interstitial spaces during field studies on the Skagit River as well as in the present experiment.

In the present study, fry appeared to slip down into interstitial spaces during struggles on the dewatered surface. No resurfacing was observed after the gravel was dewatered. The struggles of the fry seemed random and some ended up under the edge of rocks or among small stones that rendered them invisible to the initial surface inspection. Such fry were not found until the surface layer of 1 to 12 cm of substrate was overturned or removed.

Surface gravel used in the present experiment was probably more permeable than gravel observed in various field studies, because the medium and large substrate sections lacked the component of fine particles that one would normally find on river gravel bars. The mean sizes of fry stranded above and beneath the substrate surface were not significantly different for either species which suggests that fine particles in the substrate posed no obstacle to burrowing fry in the size ranges tested. Surface substrate permeability may explain why all stranding, but in particular, subsurface stranding, was more extensive than observed in field studies. Nevertheless, in the sections of small substrate, which most closely resemble gravel bar substrate in composition, stranding density was sometimes much greater than reported in previous field studies.

Extent of Stranding

The numbers of chinook and steelhead killed by stranding in these experiments were 6.4 and 22.9 percent of the total populations used. These proportions seem significant when projected to a population of millions of fry in a major river where stranding could be on the order of thousands of fry killed during each flow reduction. Biologists have asserted that mortalities of salmonid fry due to stranding within rivers regulated for hydroelectric power production are significant (Phinney 1974a; Bauersfeld 1978; Graybill et al. 1979; Stober et al. 1982; Woodin et al. 1984).

Densities of stranded fry observed in field studies have varied widely, apparently subject to seasonal fry abundance, local environmental conditions, and adult spawning distributions (Stober et al. 1982; R. W. Beck and Associates 1987). Densities of chinook stranded on gravel bars in the Skagit River have been reported from 0.3 fry per sq meter (Graybill et al. 1979) to 2.9 fry per sq m (Phinney 1974a). Bauersfeld (1977) observed stranding on Columbia River gravel bars in much lower densities that varied from 0 to 0.004 fry/sq m.

Densities of stranding observed in the present experiment under all conditions were much greater (up to 4 fry per sq m for both species) than those reported in field observations. These differences in the extent of fry stranding could be due to several reasons: (1) differences in the densities of numbers of fry subjected to dewatering, (2) differences in behavior of confined and wild fry,

(3) differences in the severity of the factors tested, or (4) differences in the stranding vulnerability of fry tested.

Field researchers found that the density of fry is highly variable from one gravel bar to another and from one day to another due to spawning ground distribution of the adults and the dispersion characteristics of fry (Stober et al. 1982; Woodin 1984; R. W. Beck and Associates 1987). This unpredictable variability in fry abundance makes the results of field experiments difficult to interpret. The present experiment attempted to avoid variability in fry densities and low numbers, such as 0.015 fry per sq m observed by Graybill et al. 1979, both of which complicated analysis of previous field studies. This was done by using fry in each section at densities of approximately 5.7 chinook per sq m and 5.0 steelhead per sq m.

Fry in the present study generally behaved much as other researchers have documented from field observations. Therefore, any differences in behavior of confined and wild fry is not believed to account for differences in stranding between the field studies and the present experiment. Vulnerability of fry to stranding is dependent on where and when flow reductions occur. Many researchers believe that stranding vulnerability may be related to fry size, because fry move to different parts of the river as they grow (Graybill et al. 1979; Stober et al. 1982). Of course, in the present experiment the fry could not leave their test sections to search for a habitat where no dewatering occurred. Thus, fry may have been subjected to dewatering that they would not normally have been subjected to in a river environment.

The sizes of steelhead used in the present experiment were comparable to the size ranges of stranded steelhead fry reported by by other researchers (Graybill et al. 1979 (34 to 55 mm); Stober et al. 1982 (mean sizes 31.3 to 50 mm); Woodin et al. 1984 (mean sizes 40.9 to 55.3 mm); R. W. Beck and Associates 1987 (30 to 45 mm)). Escaped steelhead in the present study were slightly larger than stranded fry, which suggests that size may have had an influence on stranding.

On the other hand, there was no difference in the size of chinook that escaped or stranded in the present study. The chinook tested were somewhat larger than the observed mean size of chinook fry stranded in field studies by Graybill et al. (1979) (41.6 mm) and Woodin (1984) (41.5 mm), although well within the size ranges of stranded chinook reported by others between 30 and 58 mm (Phinney 1974a; Bauersfeld 1977, 1978; R. W. Beck and Associates 1987). One would expect larger chinook to be less susceptible to stranding, yet densities of chinook stranded in the present experiment occasionally far exceeded densities reported by other researchers.

The substrate slope and daytime factors studied in the present experiment are comparable to factors studied in field research. Only the dewatering rates tested were faster than has been observed in rivers regulated for hydroelectric power production (Graybill et al. 1979; Bauersfeld 1977; Stober et al. 1982; R. W. Beck and Associates 1987). This factor may be one cause for the large number of stranded fry observed in the present experiment relative to riverine studies.

Substrate Slope

The present experiment indicated that greater numbers of fry were stranded in tests of gentle slope than in tests of the steep slope, although the means comparison was not significant for steelhead. The finding of greater stranding at lesser gradients is similar to that observed by field researchers where slopes less than five percent stranded the majority of fry (Phinney 1974b; Bauersfeld 1978; R. W. Beck and Associates 1987).

R. W. Beck and Associates (1987) hypothesized that the effect of gravel bar slope on stranding is due to accentuated hydrological effects. For example, for a given flow reduction, dewatering of gravel bar habitat occurs much more rapidly on bars with gradual slopes than on bars with steep slopes since the water's edge must travel farther on a gradual slope than on a steep slope to reach the same low point. Thus, fry must react more quickly to avoid stranding. Simultaneously, a nearly level substrate surface may obscure the cues required to orient tiny fry to the location of the moving river's edge since decreased water depths would be associated with decreased velocities or water flow originating from the gravel bar (i.e., draining out of the gravel bar which is perpendicular to the river's edge) which could attract fry away from the safety of the waters edge.

Daylight

The observations of the effect of day and night were consistent with the Skagit River observations of Woodin et al. (1984) who showed that greater numbers of chinook stranded during daylight dewatering, while greater numbers of steelhead stranded at night. Earlier researchers have recorded conflicting results regarding day versus night stranding for salmon fry. Thompson (1970a, 1970b) concluded from field observations made in the Skagit River in 1969 to 1970 that more chinook were stranded by dewatering at night than in daytime. Likewise, Bauersfeld (1977) observed that stranding of chinook fry due to ship wash (wakes) in the Columbia River was most likely at night. He concluded that juvenile chinook did not inhabit the nearshore waters during daylight hours. Hamilton and Buell (1976) also postulated, based on their observations in the

Campbell River, that more stranding of chinook and coho fry occurred during night time flow reductions because of disorientation of fry due to loss of visual stimuli.

Stober et al. (1982) found a similar relationship for steelhead, but R. W. Beck showed insignificant differences in stranding of steelhead between daylight and darkness although the mean number of fry stranded per test in darkness was higher than in daylight. The results of the present experiment suggest conclusions similar to Stober et al. (1982). They concluded that the difference in stranding of chinook salmon and steelhead during daylight was due to behavioral differences. Steelhead in nearshore areas appeared to be more easily frightened and used visual cues in daylight to avoid stranding, while salmon fry did not. Stober et al. (1982) hypothesized that steelhead may be "genetically keyed" to protect themselves from dropping water levels since they normally emerge from the gravel at times when natural river flows are likely to be dropping.

Moreover, salmon fry appear to have a reduced orientation to the substrate during hours of darkness resulting in a greater tendency for the fry to remain in the water column during a dewatering event and thereby move down slope as flow level declines (Woodin et al. 1984). In daylight, salmon fry appear to be "either actively seeking refuge in the substrate at dawn or reacting to the combined stimulus of light and reduced flow by seeking refuge in the substrate" where they subsequently stranded (Woodin et al. 1984).

Rate of Dewatering

There was no statistical difference in stranding between the two rates of dewatering for either species. Field studies have shown mixed results due to dewatering rate. Phinney (1974b) reported one occasion in the Lewis River where stranding mortality was less at a faster dewatering rate (approximately 1 cm/min) performed two days before a test of slower dewatering (approximately 0.5 cm/min). Others have also observed that stranding of salmon fry increased with increased dewatering rate (Bauersfeld 1977, 1978; Graybill et al. 1979).

Woodin et al. (1984) found that the relationship of greater stranding at faster dewatering rates held only for dewatering during daylight. They were studying vertical reductions in water depth at rates of 0.02 to 0.06 cm/min which were measured near Rockport on the Skagit River. Bauersfeld (1977) studied dewatering rates of 0.05 to 0.36 cm/min measured at gauges below The Dalles and Bonneville Dams on the Columbia River when he observed stranding of chinook fry in densities varying from 0 to 0.004 fry per sq m. Thompson (1970b) recorded a vertical change of water depth of 0.26 cm/min which produced stranding densities of up to 0.4 fry per sq m.

R. W. Beck and Associates (1987) reported consistently higher mean numbers of both chinook and steelhead stranding at faster dewatering rates studied in the Skagit River. However, analysis of variance tests showed significant effects only for stranding of chinook, but they found that rate of dewatering had no effect on stranding susceptibility of steelhead fry.

Summary

Fry stranding in the present study was clearly influenced by substrate size composition and a large proportion of fry were stranded beneath the substrate surface in sections of medium and large substrate. This result implied that past studies may have overlooked subsurface stranding of fry to some degree, and hence, underestimated the impact of flow fluctuations on stranding of juvenile salmonids. The results clearly show that fry will seek refuge from stranding beneath the substrate surface when conditions permit such behavior. However, the lack of fine substrate particles among surface stones in the present study may have provided an avenue to attempt to escape that fry in a river environment would not have available.

Stranding of steelhead was influenced by the section position from the manifold, apparently due to the higher mean velocities in the sections that immediately followed the inflow manifolds. The influence of dewatering rate and daylight on stranding were not significant in the present study and slope was significant only for chinook.

The severity of stranding observed in the present study which was greater than in previous field studies can be attributed to the controlled interaction of biological and environmental factors present in the tests. In these experiments, fry of a size vulnerable to stranding were confined in relatively high density to an evenly sloped "habitat" of permeable substrate that would dewater completely (except for a refuge channel). These fry were then subjected to a more rapid rate of dewatering than they would experience in natural rivers and in most hydropower regulated rivers.

In contrast, fry in a river would likely be found in lower densities and would be segregated to different habitats by species and size. Also, fine particles in substrate compositions would inhibit burrowing in substrate and force fry to seek other means of escape. Each of these factors would mitigate the vulnerability of fry to stranding in a river environment.

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