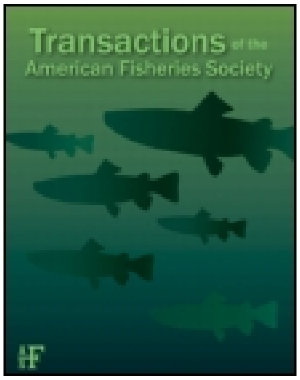

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Upstream Movement of Juvenile Coho Salmon in Relation to Environmental Conditions in a Culvert Test Bed

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ARTICLE

Upstream Movement of Juvenile Coho Salmon in Relation to Environmental Conditions in a Culvert Test Bed

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Abstract
We measured the upstream passage success of juvenile coho salmon *Oncorhynchus kisutch* in relation to select experimental factors in a culvert test bed at a salmon rearing facility on the Skookumchuk River in western Washington State. Passage success, the term used for the response variable, was defined as the number of fish in the headwater tank at the end of the test divided by the number of fish released in the tailwater pool at the beginning of the test (2- to 17-h test periods). Passage success was higher for large (139 mm fork length [FL]) than small (55 mm FL) fish, was higher at night than during the day, was not affected by shading, decreased as tailwater pool depth increased (22.9–53.3 cm), and did not differ significantly among the fish densities tested in the tailwater pool (35–141 fish/m^3). There was a clear, negative exponential trend in the response relationship between transformed (arcsine of the square root) passage success and culvert discharge (0.028–0.099 m^3/s; mean velocities, 0.59–0.98 m/s). The horizontal distribution of fish moving upstream that successfully exited the culvert into the headwater tank was skewed to the right side of the inlet where the reduced-velocity zone (RVZ) was located. This observation supported the RVZ hypothesis about upstream movement of juvenile salmon in a culvert—fish accomplish upstream movements in roughened culverts via pathways in the low-velocity, low-turbulence boundary layer. To facilitate salmonid passage at road crossings, the preferred resource management alternatives are bridges or stream simulation, but in situations where these approaches are constrained by cost or logistics, the hydraulic design of culverts may be appropriate. The findings from these experiments in the culvert test bed are applicable to hydraulic designs of culverts where upstream passage of juvenile salmon is a concern.

Culverts conveying stream discharge under roads and other obstacles can fragment habitats (Roni et al. 2002; Sheer and Steel 2006) and hinder or block upstream passage of juvenile salmon and other fishes (Warren and Pardew 1998; Gibson et al. 2005; Price et al. 2010). Until recently, most research and engineering focused on enhancement of the upstream passage of adult salmon through culverts (Copstead et al. 1998; Kahler and Quinn 1998; Moore et al. 1999). Optimal conditions for culvert passage by juvenile salmon, however, must be addressed because of the biological importance of this stage in the salmon life cycle (Behlke et al. 1991; Kahler and Quinn 1998). Although the primary movement usually attributed to juvenile salmon is downstream toward marine waters, research has indicated that upstream movement by juvenile salmon also occurs (Kahler and Quinn 1998; Kahler et al. 2001; Anderson et al. 2008). Relocation upstream in freshwater habitats presumably provides a survival advantage to these fish by reducing competition, improving feeding conditions, and decreasing predation (Murray

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and Rosenau 1989; Kahler et al. 2001; Roni et al. 2002). Any survival benefit of upstream dispersal, however, would be diminished or eliminated by culverts that inhibit habitat connectivity and upstream movement into otherwise productive freshwater habitats (Wofford et al. 2005; Sheer and Steel 2006).

Thousands of road culverts are barriers to fish movement, blocking thousands of kilometers of stream habitat nationwide. For example, Wilder and Barber (2008), in an ongoing inventory of fish passage barriers in Washington State, noted that 1,859 fish-bearing road crossings were blocking more than 5,000 linear kilometers of potential salmon habitat. Furthermore, where culverts are in critical habitats for salmon species listed under the Endangered Species Act, there is an undeniable legal impetus to improve upstream juvenile salmonid passage in culverts. Stream restoration work involving culverts to improve habitat connectivity is under way in earnest in many states and countries (Wall and Berry 2004; Cahoon et al. 2007; Peake 2008a; Price et al. 2010).

There are several standard approaches to improving passage conditions for juvenile salmon at road crossings. Bridges or stream simulation (creating natural conditions for water flow) over the extent of the floodplain is preferred by fisheries management agencies because natural streambed conditions may be recreated (Bates et al. 2003; Price et al. 2010; NMFS 2011). Large embedded pipe or bottomless arch culverts may be used where bridges or stream simulations are too costly or impractical. Another approach, the hydraulic design method (NMFS 2011), associates specific fish swimming capabilities with ambient hydraulic conditions; however, this approach is usually limited to low-gradient (0–1%) streams or culvert retrofits (replacing existing culverts with new culverts) because of constraints on the range of acceptable hydraulic conditions. Other approaches, such as the no-slope culvert, are also used. Many state and federal agencies have guidelines for culvert designs (NMFS 2001; Bates et al. 2003; MDT 2004; VFWD 2007; Love and Bates 2009; NMFS 2011).

Various factors can affect fish swimming abilities and motivation and thereby potentially affect successful upstream movement through a culvert (Lang et al. 2004; Hoffman and Dunham 2007; Peake 2008b). Such factors can include species, size, condition, nutrition, smoltification, competition, the presence of predators, and others. Environmental factors, such as season, time of day, light levels, water temperature, velocity, turbulence, and turbidity, can also influence upstream movements (Griffiths and Alderdice 1972; Powers et al. 1997; Kahler and Quinn 1998). In fact, juvenile salmon pass upstream in culverts with mean velocities higher than their swimming performance indicates is possible (Powers et al. 1997). There is a region of low velocity and low turbulence, called the reduced-velocity zone (RVZ), that forms in the lee of culvert corrugations or baffles (Barber and Downs 1996; Powers et al. 1997; Bates and Powers 1998; Richmond et al. 2007). The hypothesis, which may be called the "RVZ hypothesis," is that fish accomplish upstream movements in roughened culverts via pathways in the low-velocity, low-turbulence boundary layer (modified from Powers et al. 1997).

Relatively few studies have related the upstream movements of juvenile salmon to the conditions in a field-scale culvert environment (Powers et al. 1997; Bates and Powers 1998; Bolton et al. 2002; Lang et al. 2004; Gregory et al. 2004). Culvert test flumes have been used to study the downstream movements of salmon smolts (Kemp and Williams 2008) and the upstream swimming responses of inanga *Galaxias maculatus* (Stevenson et al. 2008), various adult trout species, e.g., cutthroat trout *Oncorhynchus clarkii* and bull trout *Salvelinus confluentus* (Belford and Gould 1989; Burford et al. 2009), and warmwater prairie fishes, e.g., shiner *Notropis* spp., green sunfish *Lepomis cyanellus*, and dace *Phoxinus* spp. (Cahoon et al. 2007; Bouska and Paukert 2010), among others. Laboratory studies are common for the swimming performance of juvenile salmon (reviewed by Beamish 1978) and other fishes (Jones et al. 1974; Toepfer et al. 1999; Leavy and Bonner 2009). Several authors, though, urge caution in using laboratory swimming performance data as a basis for culvert design criteria because fish behavior and variable hydraulic conditions are not typically accounted for (Cahoon et al. 2007; Peake 2004). Basic research on the conditions related to the upstream passage of juvenile salmon in culverts and the RVZ hypothesis is needed to inform the design of culvert improvements where bridge or stream simulation solutions are not feasible.

This study assessed the upstream passage of hatchery-raised juvenile coho salmon *O. kisutch* in a culvert under various experimental conditions during tests in 2003 and 2004 using a specially constructed culvert test bed (Figure 1). The objectives were to determine general fish behaviors in the tailwater pool; the relationships between passage success and time of day/shading, tailwater pool depth, fish density in the tailwater pool, culvert discharge, and select hydraulic variables; and the horizontal distribution of fish passing upstream and exiting the culvert into the headwater pool. This research addresses the RVZ hypothesis and provides basic data on the upstream passage of hatchery-raised juvenile coho salmon in a culvert that fisheries managers can apply to stream restoration efforts.

STUDY SITE

The culvert test bed (CTB; Figure 1) is located at the Washington Department of Fish and Wildlife's (WDFW) coho salmon and steelhead *O. mykiss* (anadromous rainbow trout) rearing facility (hereafter "facility") on the Skookumchuck River near the town of Tenino in western Washington. The three main structures of the CTB are the tailwater (TW) pool, the culvert barrel, and the headwater (HW) pool. Mueller et al. (2008) provide side and plan view diagrams of the CTB. Its hydraulic capacity is 0.71 m^3/s. Slopes are adjustable up to 10% using an A-frame hoist assembly. Tailwater elevation is controllable using stop logs. The CTB is integrated into the facility's water supply system, which is gravity fed from the reservoir behind Skookumchuck Dam, located about 800 m upstream.

FIGURE 1. Photograph of the culvert test bed showing the culvert barrel and TW tank. The winch assembly is used to adjust the slope of the 1.83-m-diameter culvert barrel. The distance between posts in the railing is 3.05 m. [Figure available online in color.]

During the experiments reported herein, the CTB was configured as follows: 1.8 m round culvert, 12.2 m long, spiral corrugations (7.6 × 2.5 cm) with a right-hand pitch of 5°, unflattened ends, bare bed, and near-level slope (1.14%). These parameters are reasonably typical for culverts in the Pacific Northwest. We maintained at least 5% backwatering from the TW pool into the culvert barrel during the biological experiments to ensure that the culvert outlet was not a barrier to fish passage. Richmond et al. (2007), Mueller et al. (2008), and Morrison et al. (2009) used the CTB for hydraulic and biological research.

METHODS

Hydraulic Data

We studied the upstream passage of juvenile coho salmon in relation to hydraulic conditions in a culvert test bed. Hydraulic measurements included water surface level, culvert discharge, and water velocity (Richmond et al. 2007). Water surface levels were measured at 15 locations using manometer tubes tapped into the culvert barrel. Culvert discharge was measured with an Ultramag magnetic flowmeter located upstream of the HW tank. Water velocity measurements were made with a SonTek 16-mHz micro-acoustic Doppler velocimeter (ADV) for six culvert discharges and, except for tests at 0.085 m^3/s, corresponded to those studied during fish passage experiments, i.e., 0.029, 0.042, 0.057, 0.071, and 0.099 m^3/s. Hydraulic measurements were also collected at 11 cross sections approximately 2 m apart longitudinally and, for a given cross section, approximately every 2–5 cm vertically and every 20 cm laterally (Richmond et al. 2007). Average water velocity (V_{ave}) was calculated by dividing discharge (Q) as measured with the flowmeter by the wetted area (A) calculated from the depth ($V_{\text{ave}} = Q/A$). Maximum water velocity (V_{max}) was the highest value measured with the ADV. The turbulence intensity was defined as the root mean square (RMS) of the velocity at each measurement point calculated from a time series of N velocity measurements. As an example, the RMS calculation for the downstream velocity component for a given measurement location would be

$$\text{RMS}_u = \sqrt{\frac{1}{N}\sum_{x=1}^{N}(v_x - v_{avg})^2}.$$

where u is the downstream velocity component, x is the measurement point, and v_{avg} is the average of the velocity measurements.

The RVZ is the region on the right side of the culvert looking upstream, where velocity was about 36% of the velocity in the middle of the culvert. Secondary flow induced by the spiral corrugations in the culvert that are angled slightly downstream (5° right-handed pitch) causes asymmetries in the horizontal distribution of flow, thereby creating the RVZ.

Biological Data Collection

Test fish were hatchery-raised juvenile coho salmon obtained from rearing ponds at the Skookumchuck facility. Water velocities in the ponds were relatively low even as water was continually flowing through the ponds. The acclimation water velocities for the fish in the ponds were much lower than most velocities under test conditions in the CTB. Furthermore, test fish were presumably not exhausted, a precondition that could have biased results. Test fish were subjected to minimal stress resulting from transportation because the close proximity of the facility to the CTB allowed us to hand-carry the fish in 19-L buckets from the pond to the CTB.

We tested three size-classes of juvenile coho salmon in April and May 2003 and November 2004. The first group was composed of relatively large juveniles (104–177 mm fork length [FL]; mean, 139 mm). A smaller size-class of juvenile coho salmon (40–61 mm FL; mean, 55 mm) composed the second group of fish. The smaller fish were used in all remaining 2003 experiments. During the November 2004 experiments, the final group of juvenile coho salmon tested ranged from 61 to 126 mm FL and averaged 93 mm FL. Test periods lasted 2−17 h.

For a given trial, test fish were subjected to a consistent sequence of events that started when the fish were captured using a dip net in a rearing pond and that ended when the fish were deposited in a holding raceway or a second rearing pond after the test was completed. Fish were not fed between the time of capture and testing. Immediately before testing, the allotment of test fish was counted and transported in buckets of water from the rearing pond to the test bed TW pool. With the culvert test bed operating at the prescribed flow and experimental conditions, the fish were released by emptying pails into the TW pool (Figure 2) to start the test. Test fish commenced swimming immediately upon being introduced into the TW pool.

To terminate a trial, the flow was turned off and at the same time the screens at the ends of the culvert barrel were lowered to isolate the fish in one of three areas: the TW pool, culvert barrel, or HW pool. Fish were retrieved from each area and separately counted and measured. In the TW pool, a net-pen (Figure 2) was used to confine and aid in the recapture of test fish. The net was constructed from 0.48-cm nylon mesh netting with 2.5-cm-diameter polyvinyl chloride frame. The net was raised and lowered along with the false floor to adjust the TW pool depth. Gaps around the sides were sealed with foam and neoprene material. Fish remaining in the net-pen were removed with dip nets as the flow subsided at the end of each trial. To retrieve fish that remained in the culvert, a researcher walked the length of the culvert and used small dip nets to recover them. In the HW pool, a drain valve was opened to allow personnel to enter the tank and dip-net the fish into a bucket. After retrieval, test fish were anesthetized, measured (nearest FL), examined for general condition, and returned to a net-pen located in the holding raceway or to a second rearing pond separate from the main hatchery population so that the fish were not used again in experiments.

FIGURE 2. Photograph of the culvert emptying into the TW tank and associated net-pen. The net-pen is 1.83 m wide. [Figure available online in color.]

We used a combination of high-resolution, low-light-capable underwater and above-water cameras to observe fish movement and behavior during the experiments. All cameras were monochrome charge-coupled devices with 1.27- and 0.85-cm image sensors capable of low-light operation and high resolution. A camera at the outlet in the TW pool was positioned to view fish moving upstream into the culvert from both sides. A camera in the HW pool was located just beyond the culvert barrel. To enable viewing during the night periods, above-water and underwater infrared illuminators (880 nm) were used in conjunction with each camera. This wavelength is beyond the spectral visual range of juvenile salmonids (Bowmaker and Kunz 1987; Lythgoe 1988). The videotape was played back through the multiplexer during postprocessing activities, allowing individual or multiple camera scenes to be viewed on the same monitor. In 2004, we used a digital video recording system that stored footage on digital video disks for review later.

For each trial, we logged measurements of water temperature and turbidity using an instrument with a probe in the HW pool. We recorded the water surface elevations in the HW and TW tanks at the beginning of each trial, in addition to measuring culvert discharge with a flowmeter and culvert water surface levels with a manometer, as mentioned earlier.

TABLE 1. Experimental conditions by experiment related to the upstream movement of juvenile coho salmon; nd = no data.

Number of trials	Period	Mean fork length (mm)	Number of test fish	Duration (h)	Flow (m^3/s)	Shade	Temperature (°C)	TW pool depth (cm)	TW pool volume (m^3)	TW fish density (number/m^3)
Time of day (test 1; Apr 8–15, 2003)										
2	Day	139	20	4–6	0.057	No	nd	42.5	3.17	6
1	Dusk	139	20	4	0.057	No	7	42.5	3.17	6
4	Night	139	20	7.5–17	0.057	No	6.5	42.5	3.17	6
Time of day (test 2) and shade (Apr 22–May 8, 2003)										
3	Day	55	20	3	0.057	No	7–8	42.5	3.17	6
3	Dusk	55	20	3	0.057	No	7–8	42.5	3.17	6
3	Night	55	20	8.5–10	0.057	No	7–8	42.5	3.17	6
3	Day	55	20	3	0.057	Yes	7–8	42.5	3.17	6
3	Dusk	55	20	3	0.057	Yes	7–8	42.5	3.17	6
3	Night	55	20	8–10	0.057	Yes	7–8	42.5	3.17	6
Tailwater pool depth (Nov 8–13, 2004)										
4	Night	93	120	3	0.043	No	6–8	22.9	1.70	71
4	Night	93	200	3	0.043	No	7	38.1	2.83	71
4	Night	93	280	3	0.043	No	6.5–7	53.3	3.96	71
Fish density in tailwater pool (Nov 15–20, 2004)										
4	Night	93	60	3	0.043	No	8	22.9	1.70	35
4	Night	93	120	3	0.043	No	8	22.9	1.70	71
4	Night	93	240	3	0.043	No	8	22.9	1.70	141
Culvert discharge (May 19–30, 2003)										
1	Night	55	200	3	0.028	No	8	34.8	2.58	71
1	Night	55	200	3	0.043	No	8.5	35.6	2.66	71
1	Night	55	200	3	0.057	No	8	36.8	97	71
1	Night	55	200	3	0.071	No	8	38.1	100	71
1	Night	55	201	3	0.085	No	8	39.1	103	71
1	Night	55	200	3	0.099	No	8.5	39.9	105	71

Experimental Conditions

Time of day and shading.—Between April 8 and April 15, 2003, seven preliminary trials were conducted with the available fish (mean FL, 139 mm): four overnight, one at dusk, and two during daylight (Table 1). For these trials, the duration was not standardized and the data were not normalized for duration. The duration of the overnight trials ranged from 7.5 to 17 h; the longer night periods included some day and dusk conditions. The day trials were 4 and 6 h long and the dusk test was 4 h long. Trials were conducted with 20 fish per test.

From April 22 to May 9, 2003, we conducted experiments to determine the effects of two experimental factors, time of day (dusk, night, or day) and shade (shade or no shade). Six trials each were conducted during day, dusk, and night using small juvenile fish (mean FL, 55 mm; Table 1). During three of the six trials for each time of day, canvas was placed over the HW and TW pools and the culvert to provide shade. Thus, each time of day–shade treatment was tested three times. Shade conditions were randomized among the trials. The day and dusk trials were 3 h in duration. The overnight trials ranged from 8 to 10.5 h in duration. All trials in this experiment were conducted with 20 fish per test, 0.057 m^3/s discharge, 5% backwater, a 3.5-cm TW pool depth, and 71 fish/m^3.

Tailwater pool depth.—During November 2004, using the available fish (mean FL, 93 mm), we conducted an experiment using three TW pool depths: 22.9, 38.1, and 53.3 cm (Table 1). Pool depth is the distance from the net-pen floor in the TW pool to the water surface at the culvert outlet. We randomized the order of the pool depths over two 3-d blocks. For logistical reasons, a given pool depth was tested twice per night. Thus, each pool depth was tested four times. The factors held constant included the night time of day, 3-h duration, 0.043-m^3/s discharge, 5% backwater, and fish density (71 fish/m^3). To maintain consistent fish density, we adjusted the number of test fish for each pool depth: 120 fish for 22.9 cm, 200 fish for 38.1 cm, and 280 fish for 53.3 cm.

Fish density in the tailwater pool.—We performed a fish density experiment in November 2004. Three fish densities in the TW pool were tested: 35, 71, and 141 fish/m^3 (Table 1). Trials were conducted at the pool depth that had the best passage success, namely, the shallow pool depth (22.9 cm). Two trials per night were performed over six consecutive nights. Thus, the three fish densities were each tested four times. The order of the fish density treatments was randomized for a given set of three successive trials. The factors held constant included the time of day (night), 3-h duration, 0.043-m^3/s discharge, 5% backwater, and 22.9-cm pool depth. We adjusted the number of test fish to establish the fish density treatments under a constant pool volume (1.7 m^3): 60 fish for 35 fish/m^3, 120 fish for 71 fish/m^3, and 240 fish for 141 fish/m^3.

Culvert discharge.—For small fish, we measured the relationship between fish passage success and culvert discharge (Table 1). Two trials were performed each night for three successive nights using available fish (mean FL, 55 mm). Six culvert discharges were tested in random order: 0.029, 0.043, 0.057, 0.071, 0.085, and 0.099 m^3/s. Thus, each culvert discharge was tested once during this experiment. Two hundred fish were used for each trial. Therefore, fish density in the TW pool was approximately 71 fish/m^3 for each trial because TW pool volume only varied from 2.6 to 3.0 m^3 as discharge increased (Table 1). The factors held constant included the time of day (night) and 3-h duration. Backwatering was about 5% and varied little among the culvert discharges tested. The distance from the bottom of the culvert barrel to the floor of the net-pen in the TW pool was set at 2.1 cm, providing TW pool depths ranging from 2.9 to 3.3 cm for the culvert discharges and the TW stop log condition in the culvert discharge experiment.

Horizontal distribution.—To address whether the fish used the low-velocity pathway within the culvert, we quantified the horizontal locations of fish successfully passing through the culvert and into the HW pool using taped video observations from the underwater camera in the HW pool. We divided the culvert flow inlet into five areas: right, right-center, middle, left-center, and left. We analyzed video from the culvert discharge trials (Table 1) with high passage success values—discharges 0.028 and 0.042 m^3/s—to maximize the number of observations of fish moving into the HW pool.

Statistical Methods

For a given trial, the primary response variable, called passage success (PS), was defined as the number of fish in the HW pool at the end of the test divided by the number of fish released in the TW pool at the beginning of the test, expressed as a percentage. Fish recovered outside the TW net-pen or missing after the test were not included in the denominator. Because the night trials were about three times as long as the day and dusk trials (Table 1), passage success was normalized by dividing it by test duration, producing passage success (PS) per hour.

The Kruskal–Wallis test, a nonparametric test employed in analysis of variance (ANOVA; Sokal and Rohlf 1981) was applied separately to the three experimental factors—time of day and shading, TW pool depth, and fish density in the TW pool. Passage success per se and PS/h were the dependent variables in such comparisons. The significance level was 0.05.

Nonlinear regression methods (Sokal and Rohlf 1981) were used to assess the relationship between passage success and culvert discharge. Correlation methods (Sokal and Rohlf 1981) were applied to assess the association between passage success, water velocity, and turbulence intensity. Passage success was transformed using the arcsine of the square root and correlated with four hydraulic variables: average water velocity in the culvert (V_{ave}), average velocity in the RVZ (V_{rvz}), maximum water velocity in the culvert (V_{max}), and the RMS of the velocity in the RVZ (RMS_{rvz}) (Table 2).

RESULTS

Hydraulic Conditions

A range of hydraulic conditions was studied (Table 2). Average water depth in the culvert varied from 9.1 to 16.8 cm. The lowest average water velocity was 0.59 m/s (for a discharge of 0.029 m^3/s), and the highest was 0.98 m/s (for a discharge of 0.113 m^3/s). Water surface profiles revealed an inlet drop at the HW tank and backwater conditions for all flows measured (Richmond et al. 2007). Backwatering was about 0.6 m up the culvert at culvert discharges 0.042–0.113 m^3/s. At all discharges

TABLE 2. Summary of hydraulic measurements and calculations from velocimeter data collected in the culvert. Abbreviations are as follows: V = velocity, RMS = root mean square of velocity, ave = average, max = maximum, and rvz = reduced-velocity zone.

Culvert discharge (m^3/s)	Water depth (cm)	V_{ave} (m/s)	V_{max} (m/s)	V_{rvz} (m/s)	RMS_{ave} (m/s)	RMS_{max} (m/s)	RMS_{rvz} (m/s)
0.029	9.1	0.59	0.90	0.25	0.13	0.20	0.12
0.043	12.2	0.67	0.94	0.24	0.14	0.21	0.13
0.057	13.4	0.70	1.00	0.24	0.14	0.22	0.13
0.071	14.6	0.89	1.18	0.28	0.15	0.23	0.13
0.099	16.8	0.95	1.25	0.33	0.17	0.25	0.14
0.113	16.6	0.98	1.39	0.34	0.18	0.29	0.13

measured, the streamwise velocity and turbulence intensity distributions were skewed toward the left side of the culvert (looking upstream). In addition to spatial variability, Richmond et al. (2007) noted pronounced temporal variability in the hydraulic conditions, as evidenced by a 10-s time series of streamwise velocities that ranged from 0 to 0.75 m/s.

Biological Findings

General behavior.—Milling and feeding on insects and plankton were the most common behaviors observed in the TW pool. Territorial/aggressive behavior was also noted, more so during the day than at night and especially near the culvert entrance. Fish were occasionally seen schooling during the dusk and night periods. Most fish entered the culvert briefly (1–2 s) before being washed back into the TW pool during many trials. Some fish entering the culvert, however, remained inside for 10–30 s before falling back into the TW pool.

A few fish were observed in real-time video successively moving from the TW into the culvert and then into the HW pool. Swimming location in the culvert barrel, however, could not be observed consistently because there was only one video camera in the culvert barrel. As an example, one fish swam the length of the culvert in 2.5 min and another in 4 min. Video observations revealed that a few fish fell back into the culvert after they had entered the HW pool, but the video data were not systematically processed to estimate the proportion of fish falling back after entering the HW pool.

Time of day and shading.—The movements upstream in the culvert test bed by large juvenile coho salmon (Table 3) were not statistically different between day and night (Kruskal–Wallis test; $P = 0.105$). The large juvenile coho salmon that moved up the culvert had no difficulties entering or swimming upstream or exiting during the trial at 0.057 m^3/s discharge.

More small juvenile coho salmon (mean FL, 55 mm) moved upstream into the HW pool at night (mean, 23%) than during the dusk or day periods (means, 9% and 3%, respectively) (Table 3). Statistical analysis using PS/h to account for the differing durations among the day, dusk, and night periods showed no significant differences (Kruskal–Wallis test; $P = 0.195$). Because passage success was generally highest at night, subsequent tests were conducted after dark.

Shading of the TW and HW pools produced no difference in passage success for small fish (Kruskal–Wallis test; $P = 0.963$); therefore, the tanks were not shaded in subsequent trials.

TABLE 3. Fish passage results for experiments at the culvert test bed. Duration is the total duration of the set of tests for a given factor level; PS is passage success for all tests combined for a given factor level; SD of PS is the standard deviation of passage success values for the individual tests for a given factor level; na = not available.

Factor	Factor level	Number of tests	Duration (h)	Number of fish, TW pool	Number of Fish, culvert	Number of fish, HW pool	PS (%)	PS per hour (%)	SD of PS (%)
Time of day (test 1)	Day	2	10	33	0	7	17.5	1.8	10.6
	Dusk	1	4	17	0	3	15.0	3.8	na
	Night	4	50.5	12	0	47	79.7	1.6	14.3
Time of day (test 2)/shade	Day/no	3	9	58	0	2	3.3	0.4	2.9
	Day/yes	3	9	59	0	1	1.7	0.4	2.9
	Dusk/no	3	9	51	2	6	10.2	1.1	14.0
	Dusk/yes	3	9	56	0	4	6.7	0.7	7.6
	Night/no	3	21	40	6	13	22.0	1.1	30.5
	Night/yes	3	36.5	44	2	14	23.3	0.6	2.9
Pool depth	Shallow	4	12	284	7	188	39.2	3.3	11.4
	Middle	4	12	599	11	190	23.8	2.0	11.2
	Deep	4	12	1,083	2	26	3.1	0.3	2.4
Fish density	Low	4	12	152	1	86	35.8	3.0	28.1
	Middle	4	12	316	7	156	32.5	2.7	20.5
	High	4	12	800	39	121	12.6	1.1	14.0
Discharge	0.029	1	3	167	1	32	16.0	5.3	na
	0.085	1	3	198	0	3	1.5	0.5	na
	0.057	1	3	197	1	2	1.0	0.3	na
	0.071	1	3	196	0	3	1.5	0.5	na
	0.043	1	3	194	0	6	3.0	1.0	na
	0.099	1	3	199	0	1	0.5	0.2	na

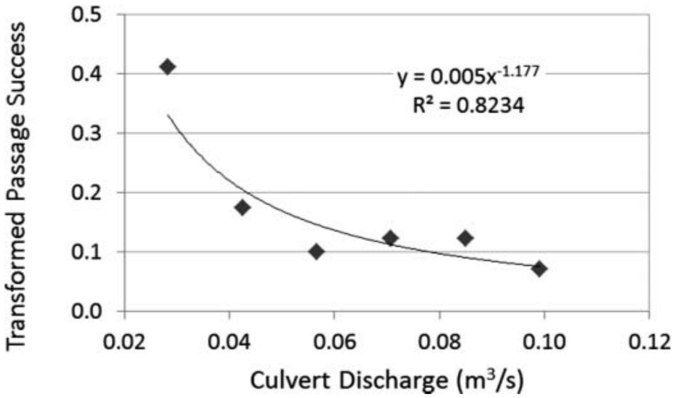

FIGURE 3. Power function relationship between culvert discharge and transformed passage success (arcsine of the square root of the passage success proportion). Mean size for juvenile coho salmon was 55 mm FL. All tests were conducted at night. Hydraulic conditions are summarized in Table 2.

Tailwater pool depth.—Passage success decreased significantly as TW pool depth increased (Kruskal–Wallis test; $P = 0.012$). Mean passage success was 39, 24, and 3% for the shallow, middle, and deep pools, respectively (Table 3). Therefore, the shallow pool depth (22.9 cm) was used to conduct the experiment on the relationship between passage success and fish density in the TW pool.

Tailwater fish density in the tailwater pool.—Mean passage success was 36, 33, and 13% for the low, middle, and high densities, respectively (Table 3). Statistical analyses showed that passage success did not differ significantly among the fish densities tested (Kruskal–Wallis test; $P = 0.174$) because the variability in passage success was high.

Culvert discharge.—Passage success decreased from 16% at 0.029 m^3/s to 1% at 0.057 m^3/s (Table 3). At 0.099 m^3/s, passage success decreased to 0.5% (Table 3). There was a clear trend in the response relationship between transformed passage success and discharge (power function fit $R^2 = 0.82$; Figure 3).

Water velocity and turbulence intensity.—We used culvert discharge data to study the relationship between passage success and four water velocity and turbulence intensity variables: average velocity over an entire cross section; average velocity in the RVZ; maximum velocity over an entire cross section; and RMS velocity (i.e., turbulence intensity) in the RVZ. Using the arcsine-square-root transformation of passage success, the Pearson correlations between passage success and the four hydraulic variables were negative and ranged from –0.61 for average velocity in the RVZ to –0.93 for turbulence intensity in the RVZ. The relationships between transformed passage success and the hydraulic variables (Figure 4) were significant ($P \leq 0.05$) for V_{ave} and RMS_{rvz} but not for V_{rvz} ($P = 0.20$) and V_{max} ($P = 0.06$).

Horizontal distribution of fish exiting the culvert into the headwater tank.—The horizontal distribution of fish exiting the culvert after passing upstream was skewed to the right (looking upstream; Richmond et al. 2007). We observed 3.5 times as many fish moving into the HW pool on the far right side of the culvert inlet than on the far left. In the culvert tested, the RVZ is on the right side (Richmond et al. 2007).

DISCUSSION

This study used a sequential, adaptive approach to investigate factors related to upstream passage of juvenile hatchery coho salmon in a culvert test bed. The investigations included characterizing hydraulic conditions; performing repeatable, quantitative trials of juvenile fish passage success under various test conditions; and revisiting the hydraulic characterizations as necessary (Pearson et al. 2005). The biological experiments reported in this article were intended to determine the conditions that induce juvenile salmon to swim upstream (Pearson et al. 2005); it should be noted, however, that the study design did not allow differentiation between motivation and swimming capability. For fish motivated to move upstream, their capabilities and adaptive behaviors interacted with the culvert's physical structure and hydraulic conditions to determine passage success. Indeed, the variability in passage success among individuals may have been related to variability in motivation to swim upstream against the current (McDonald et al. 2007).

Nonhydraulic Factors Influencing Passage Success

The time-of-day and shading experiments revealed the importance of fish size as an experimental factor. Based on daytime observations in a smaller culvert system of different configuration, Powers et al. (1997) concluded that under some circumstances smaller juvenile coho salmon would exhibit greater upstream movement than larger coho salmon. The reason for this difference was thought to be that small fish would better use the corrugations as resting areas. We observed, however, that at the same discharge (0.057 m^3/s) the larger fish moved upstream in greater percentages and in apparently shorter times than small fish. For example, we observed some large fish successfully traversing the culvert in about 20 s, compared with 2–4 min for small fish under similar conditions. Our findings are consistent with the positive relationships between fish size and upstream passage reported by Adams et al. (2000) for brook trout *S. fontinalis* (65−210 mm total length), Burford et al. (2009) for various trout species (45−127 mm mean FL by site), and Lang et al. (2004) for various juvenile salmonids (coho salmon, Chinook salmon *O. tshawytscha*, and steelhead; 76−381 mm FL).

Our trials showed that movement upstream was stronger at night than during the day, although the trials with the larger juveniles were limited in the number of replicates because of the seasonal availability of the larger fish from the hatchery. Increased replication with larger juveniles would have offered us greater power to detect differences. Trials with and without

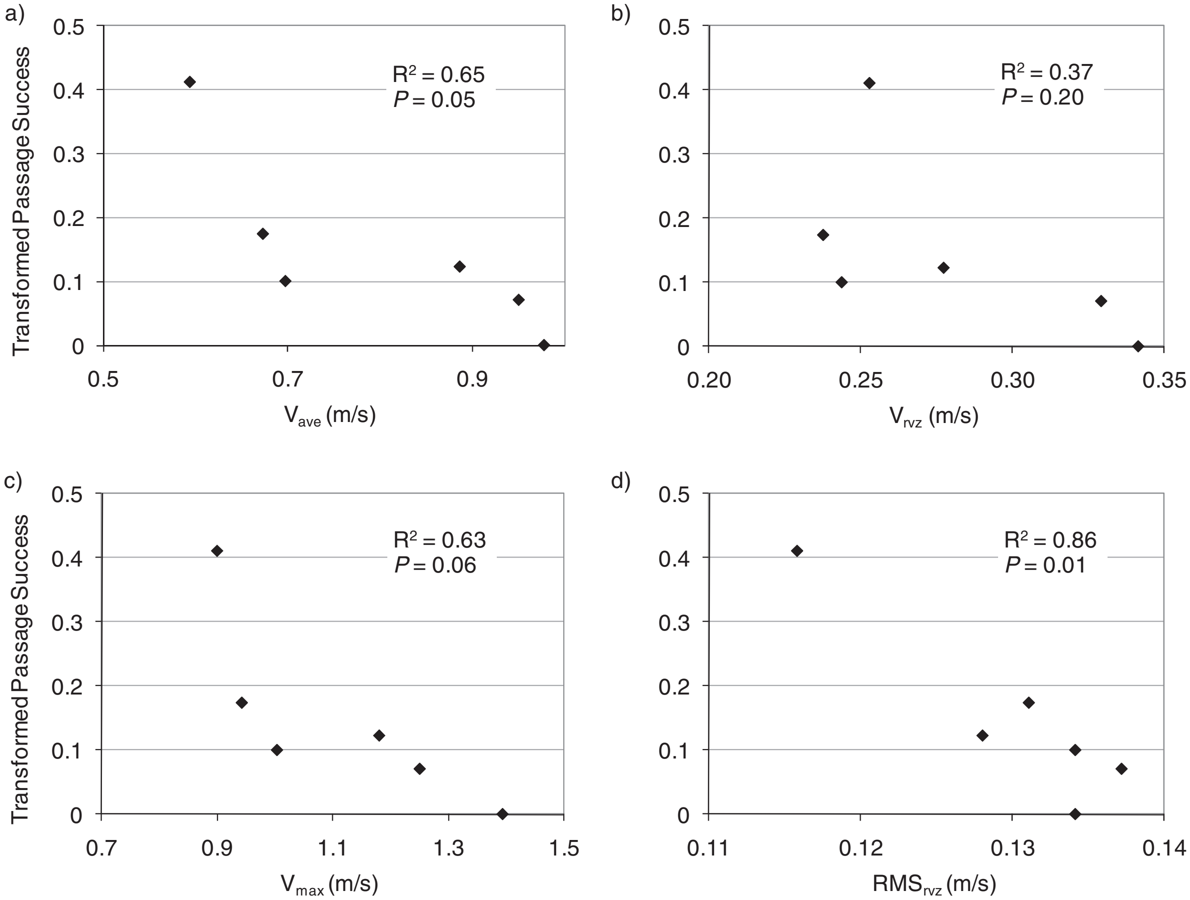

FIGURE 4. Transformed passage success (arcsine of the square root of passage success proportion) versus (**a**) mean velocity in the culvert, (**b**) mean velocity in the reduced-velocity zone, (**c**) maximum velocity in the culvert, and (**d**) root-mean-square velocity in the reduced-velocity zone. The mean size of the juvenile coho salmon was 55 mm FL. All tests were conducted at night. Hydraulic conditions are summarized in Table 2.

shade over the tanks during the daytime indicated that diel behavior was related to time of day rather than to ambient light conditions. Field observations at culverts by U.S. Forest Service researchers indicated that juvenile coho salmon moved primarily at night (M. Furniss, U.S. Forest Service, Corvallis, Oregon, personal communication). Therefore, future culvert passage experiments with juvenile coho salmon should be conducted at night without additional lighting or shading of the HW or TW pools. We are not aware of other studies documenting day–night patterns of upstream movement of juvenile salmon.

Some perspective on our results comes from field research indicating that in general upstream movement is common in juvenile coho salmon (Kahler and Quinn 1998; Kahler et al. 2001). The mean percentage of tagged and recovered juveniles (mean FL, 59–70 mm) moving in four western Washington streams varied between 28% and 60% (Kahler et al. 2001). Contrary to expectation, upstream rather than downstream movement was predominant (Kahler et al. 2001). The average passage success values that we observed in the culvert test bed during the TW pool depth (39%) and fish density (36%) experiments are at the low end of the range of the upstream movements (defined as the percentage of movers) in natural streams (28–62%) reported by Kahler et al. (2001).

Juvenile movement increased significantly as the depth of the downstream pool decreased both in the field observations of Kahler et al. (2001) and in the pool depth experiment here. Also, Kahler et al. (2001) found that fish moved from habitats with lower fish densities. In our study, density differences in passage success were not statistically significant. Because the habitat units from which coho salmon juveniles moved had low densities, Kahler et al. (2001) suggested that the mechanism behind movement was not displacement by competition for space but rather poor habitat quality. Furthermore, the fish that moved were not smaller and showed higher growth rates than those that did not move, further suggesting that the moving fish were not being displaced by competitive exclusion.

The data suggest that conditions related to season and temperature other than the factors specifically tested in our study also influence passage success. The influence of fish size is usually taken to relate to swimming performance, which increases with fish size. However, fish size is confounded by seasonal changes in the ambient test conditions (e.g., water temperature) and perhaps also by seasonal differences in the external cues (e.g., light, stream discharge) and internal drivers (e.g., feeding, refuge) governing upstream movement. Swimming performance for a given fish size is known to vary with water temperature. Griffiths and Alderdice (1972) concluded from their investigation of the influence of temperature on critical swimming speed that juvenile coho salmon are well adapted to maintain a high level of swimming performance over a broad range of temperatures, especially cooler temperatures. They found that the swimming speed of juvenile coho salmon at 2°C was only half that at 20°C but that swimming speed decreased abruptly above 20–22°C (Griffiths and Alderdice 1972). Although passage success did not appear to be related to temperature variation (6–8°C) in our TW pool depth experiment, a winter cold snap did appear to influence fish behavior during later experiments on leaping ability (Pearson et al. 2005). The results from the TW pool depth trials indicate that passage success rates for the same conditions are close on a given day but vary more substantially among days. The reason for this variability among days is unknown.

Besides seasonal changes in swimming performance related to size and water temperature, the external cues and internal drivers for upstream movement may differ by season. The motivation to move upstream—either as spontaneous, voluntary activity or as rheotaxis-induced activity (McDonald et al. 2007)—could be affected by seasonal differences in environmental conditions. Kahler et al. (2001) observed that not only did juvenile coho salmon move upstream more than expected in the summer but that a portion of the juvenile fish showed “exploratory” behavior, moving upstream and downstream and then returning to their points of origin. Kahler et al. (2001) suggest that habitat quality is the ultimate driver of summer movement and that both upstream and exploratory movement may confer an adaptive advantage when dewatering or other adverse conditions occur during the summer. Fall upstream movement may be related to finding overwintering habitat.

Another nonhydraulic factor affecting passage success is the level of exhaustion of the test fish. Lee-Jenkins et al. (2007) found that there was a delay in return to normal swimming activity when rainbow trout were exhausted. Although the test fish were presumably not exhausted at the beginning of the trials, any fish that made repeated attempts or a sustained attempt to transit upstream in the culvert surely expended energy reserves. Whether this activity reached the point of exhaustion is unknown, as are the effects of exhaustion on the results.

Hydraulic Factors Influencing Passage Success

The relationships we determined between passage success for hatchery-raised juvenile coho salmon and various hydraulic factors (including culvert discharge, water velocity [average, maximum, and RVZ], and RMS velocity) correspond to the findings from previous studies. Gregory et al. (2004) examined the performance of juvenile cutthroat trout and steelhead passing upstream in various culverts in western Oregon. For the best analog to our work, the Big Noise Creek culvert (a concrete box culvert 30 m long with a slope of 1.5% and no baffles), passage success was 0% at 0.396 m^3/s. Using a test culvert (a spiral corrugated culvert 12.2 m long with no baffles), Powers et al. (1997) and Bates and Powers (1998) reported 20% passage success for upstream-moving juvenile hatchery coho salmon (55−65 mm FL) for a flow regime with 0.64 m/s V_{ave} and 0.79 m/s $V_{\max}$. This compares well with the 16% passage success we observed at a discharge of 0.029 m^3/s, 0.59 m/s V_{ave}, and 0.90 m/s $V_{\max}$.

The hydraulic characteristics within the culvert that are relevant to fish passage are different in the inlet, barrel, and outlet zones. The culvert inlet (upstream, HW end) is characterized by lower average cross-sectional velocities and more uniform cross-sectional velocity distributions than in the culvert barrel and the absence of an RVZ (described further below). The lack of an RVZ in this region means that there is a short, critical section at the inlet where juvenile salmon would be required to burst through high-velocity, moderate-turbulence water to pass upstream into the HW pool. The barrel region composes the majority of the culvert length where the flow is primarily governed by bed resistance and TW elevation. Based on ADV data, the barrel is composed of high-velocity and high-turbulence water in the center core of flow, moderate-velocity and high-turbulence water on the left side of the culvert, and low-velocity and low-turbulence water in the upper right corner of the flow (the RVZ). Water velocity in the RVZ continues to be below 0.6 m/s even at the higher discharges, indicating that if fish can find this area and maintain their position in it, then the likelihood of passage through the barrel region is increased. Because the asymmetry in hydraulic conditions across the culvert is caused by the 5° pitch in the spiraled corrugations, it would be useful for the designers of culvert retrofits to investigate which commonly manufactured combinations of spiral angle, amplitude, and length maximize the RVZ’s cross-sectional area.

The outlet zone at the downstream TW end of the culvert is the first section that fish must pass before entering the barrel section. If backwatered, depth of flow is increased and velocity is reduced; however, at larger discharges (>0.057 m^3/s) the mean velocity can still be higher than the 0.3-m/s prolonged swimming abilities of these fish. Therefore, once a juvenile coho salmon enters the culvert there is a critical time period for it to find the RVZ on the right side. Juveniles moving upstream are more likely to find the RVZ of the culvert if they start on the right side, especially at higher flows. Mueller et al. (2008) reported that most juvenile coho salmon (mean FL, 103 mm) entered the culvert barrel from the TW pool in the middle and at the surface of the outflow. Collectively, these observations indicate that where a juvenile salmon enters the culvert at the outlet could influence its passage success.

Mean velocity values and deviations about the average RMS may not tell the whole story, however; extreme turbulent events may need to be considered as well. In our case, the time series of hydraulic data revealed important characteristics other than the mean and RMS parameters (Richmond et al. 2007). For example, there were numerous moments when the instantaneous velocity was either above or below the RMS range. Bursts of extreme velocity could significantly affect fish, especially relatively small juveniles that can easily be flushed out of the RVZ into the faster core current. Such extreme bursts result from coherent structures of either high-velocity fluid from the flow core or low-velocity fluid from the bed and can be characterized by their size, rotation, and frequency by looking at the turbulent length scales, vorticity, and spectral distribution of the flow, respectively. Further investigation of these parameters in future studies may help to describe the degree and frequency of flow intermittency in the RVZ. The time series also illustrates that the nature of the hydraulic environment actually experienced by a fish is both complex and dynamic (Richmond et al. 2007). The determinants of fish passage success may derive from the way in which the velocity and turbulence interact or the amount of time that the combination of velocity and turbulence are below a certain (but as yet unknown) value.

In conclusion, our results demonstrate the usefulness of coupling the measurements of hydraulic conditions and fish behavior in a rigorous experimental framework. We suggest, however, several improvements to future studies of this type. First, approaches to statistical design and analysis need to be interwoven with the hydraulic considerations and are best established at the outset of the project. For example, we now know that turbulence and not just velocity plays a role and needs to be taken into account in the design, measurement, and analysis. Second, individual-based data from marked fish, such as those with passive integrated transponder (PIT) tags and receiving antennas appropriately shielded from the steel structures of the test bed, would permit more thorough examination of the complexities of the fish behaviors than using posttrial counts (Lang et al. 2004; Bouska and Paukert 2010). For example, the use of PIT-tagged fish would yield data on fish transit times up and down the culvert barrel, descriptive statistics on the number of attempts to move upstream per individual, and associations between biological responses and abiotic and biotic covariates. Lastly, future studies might address the biological responses of wild juvenile coho salmon and other salmonid species as well as examining other variables that may affect passage success, such as culvert diameter, slope, and shape.

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