

## RESPONSE OF MIGRATING CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) SMOLTS TO IN-STREAM STRUCTURE ASSOCIATED WITH CULVERTS

PAUL S. KEMP<sup>a,b\*</sup> and JOHN G. WILLIAMS<sup>a</sup>

<sup>a</sup> *Fish Ecology Division, Northwest Fisheries Science Center, NOAA Fisheries, 2725 Montlake Boulevard East, Seattle, WA 98112-2097, USA*

<sup>b</sup> *International Centre for Ecohydraulic Research, School of Civil Engineering and the Environment, University of Southampton, Highfield, Southampton SO17 1BJ, UK*

### ABSTRACT

Poorly designed culverts can impede upstream movements of fish under high flows when excessive water velocities create adverse conditions. Improvement in upstream fish passage efficiency may occur with placement of structures within culverts that increase hydraulic complexity and provide resting areas. The effects of structural modification on downstream migrants, however, are unknown. To address this gap in knowledge, the behaviour of Chinook salmon (*Oncorhynchus tshawytscha*) smolts was assessed in an experimental laboratory flume. Under light and dark conditions, fish were observed as they encountered either an unmodified aluminium channel (control) or one of two treatments: an 'intermediate' substrate (treatment channel lined with corrugated sheet) or a 'complex' substrate (addition of cobbles to the 'intermediate' treatment). More smolts passed the control channel than the treatment channels. Even with control of the variation in flow between channels, under light conditions more fish than expected passed the control channel when paired with the complex treatment. Smolts more frequently rejected both treatments than the control channel when light, and the complex treatment when dark, by swimming upstream against the flow after entry. The majority of fish moved through the flume facing downstream, although a greater proportion faced upstream when dark than when light, and entered the control channel. Velocity of downstream movement (ground velocity) was greater through the control channel than for the treatment routes, and slower than the mean water velocity, and under the dark condition. When mean water velocities were taken into account, the net velocity through the control channel was not significantly different to the intermediate, and lower than the complex channel. Juvenile Chinook salmon determined fine-scale variation in structural complexity and exhibited avoidance behaviour in the presence and absence of visual stimuli. Hydraulic stimuli influenced route selection exhibited by migratory juvenile salmonids. Copyright © 2008 John Wiley & Sons, Ltd.

KEY WORDS: fishways; culverts; turbulence; swimming-performance

Received 3 September 2007; Revised 30 May 2007; Accepted 19 June 2007

### INTRODUCTION

Culverts that commonly divert streams and rivers underneath roads, railways or other embankments, can impede the movements of migratory fish (Hendry *et al.*, 2003). Within the culvert barrel, water velocities that exceed the swimming capabilities of the target species, insufficient depth or excessive turbulence may prevent upstream migration (WDFW, 2003). The culvert may further impede migration if the inlet is blocked by the accumulation of sediment or debris, or if an excessive drop is eroded at the outflow. In recognition of the negative impacts culverts have had on populations of salmon (e.g. Ebbin, 2002), several state fish and wildlife agencies in California, Oregon and Washington, USA (e.g. CDFG, 2002; WDFW, 2003; ODFW, 2004) have published design criteria to minimize the occurrence of adverse conditions that block migratory fish. To alleviate problems of reduced efficiency during periods of high flow, weirs (e.g. Rajaratnam *et al.*, 1989) and baffles (e.g. Rajaratnam *et al.*, 1990) have been designed to enhance hydraulic heterogeneity within the culvert barrel to create areas of slack water in which fish may rest and where overall depth is increased. Similar results are also achieved through the placement or collection (e.g. Behlke *et al.*, 1991; Clay, 1995) of natural bedload substrate (e.g. cobbles and small boulders) and even riprap

\*Correspondence to: Paul S. Kemp, International Centre for Ecohydraulic Research, School of Civil Engineering and the Environment, University of Southampton, Highfield, Southampton SO17 1BJ, UK. E-mail: p.kemp@soton.ac.uk

(e.g. McKinnon and Hnytko, 1985) within the culvert. Indeed, hydraulic complexity may benefit fish that minimize energetic expenditure by utilizing slow flowing areas in the lee of natural structures as foraging positions (Everest and Chapman, 1972; Morantz *et al.*, 1987), or extract energy from the associated vortices to enhance swimming performance (Hinch and Rand, 2000; Liao *et al.*, 2003). Indeed, Coutant (1998) suggested it would be surprising if anadromous fish that had evolved in turbulent rivers did not utilize the kinetic energy from turbulence to reduce the energetic costs of swimming. Therefore, it seems reasonable to assume that upstream migrating fish will perform better when passing through culverts containing natural substrate, over those that provide a smooth uniform bed.

Despite recognition of the impediments to upstream fish migration created by poorly designed culverts, and subsequent attempts to improve their effectiveness, low fish passage efficiency for many species may continue to result for three main reasons. First, the process of iterative design through the modification of existing inefficient structures does not always take into account an understanding of the ecology of the target species of fish. Second, most efforts to improve culverts have targeted upstream movements of commercially important adult salmonids. The requirements of other salmonid life stages and non-salmonid species are not well known. Third, because of a lack of understanding about the behaviour fish exhibit in response to conditions encountered at culverts, design efforts can generally only rely, at best, on information available about swimming capability.

Nearly all efforts to date designed to improve passage of fish at culverts have focused on adult upstream migrants. Little is known about passage of downstream migrants when they encounter culverts. However, recent research on seaward migrating juvenile salmonids, commonly referred to as smolts, suggests that they may not merely move through them with the flow. Kemp *et al.* (2005a) found in laboratory studies with smooth channels that most Chinook salmon (*Oncorhynchus tshawytscha*) smolts actively avoided overhead cover, a situation they would encounter at culverts. This suggested the need for additional research to determine if modified culverts that contained structural complexity designed to improve upstream passage would alter the behaviour of downstream Chinook salmon migrants. Here, the results of this research are presented.

## MATERIALS AND METHODS

### *Study area*

McNary Dam (467 river km upstream of the mouth) impounds the Columbia River (USA), where it forms the border between the states of Washington and Oregon (Figure 1). The dam creates a reservoir (Lake Wallula) that extends 103 km upstream. This concrete gravity-type run-of-river dam, operated by the US Army Corps of Engineers for hydropower production and navigation, has an earthen embankment at the southern abutment, is 2245 m long and rises 56 m above the streambed. The dam raises the normal water surface by approximately 26 m. The spillway (399 m long) consists of 22 vertical lift gates (each 15 m × 15 m) and is designed to accommodate a discharge of approximately 62 300 m<sup>3</sup> s<sup>-1</sup> during times of flood. Construction began in 1947 and was completed in 1954. All 14 Kaplan turbine units (capacity: 70 000 kW each) were in operation and producing power in February 1957.

For upstream migratory species, fish ladders situated on each shore of the dam use full overflow weirs along with submerged orifices to aid passage. Fish are monitored as they pass through counting stations and adult PIT-tag detection systems within the ladders. The juvenile bypass system, completed in 1981, is similar to those used at other collector dams on the Snake and Columbia Rivers (Matthews *et al.*, 1977; Gessel *et al.*, 1991). Extended-length submersible bar screens, installed in 1997, divert juvenile salmonids as they approach the turbines into vertical gatewells from which the fish can pass through orifices (0.3 m diameter) and enter the bypass channel (4 m wide and 3 m deep) that runs (internally) along the length of the powerhouse. Total flow through the bypass channel can approach 17–20 m<sup>3</sup> s<sup>-1</sup> when all turbine units are in operation.

### *Experimental design*

The study used seaward migrating juvenile Chinook salmon diverted from the bypass system to an experimental through-flow flume (12 m long × 1.5 m wide × 0.75 m deep) at McNary Dam between 24 June and 9 July 2004. The

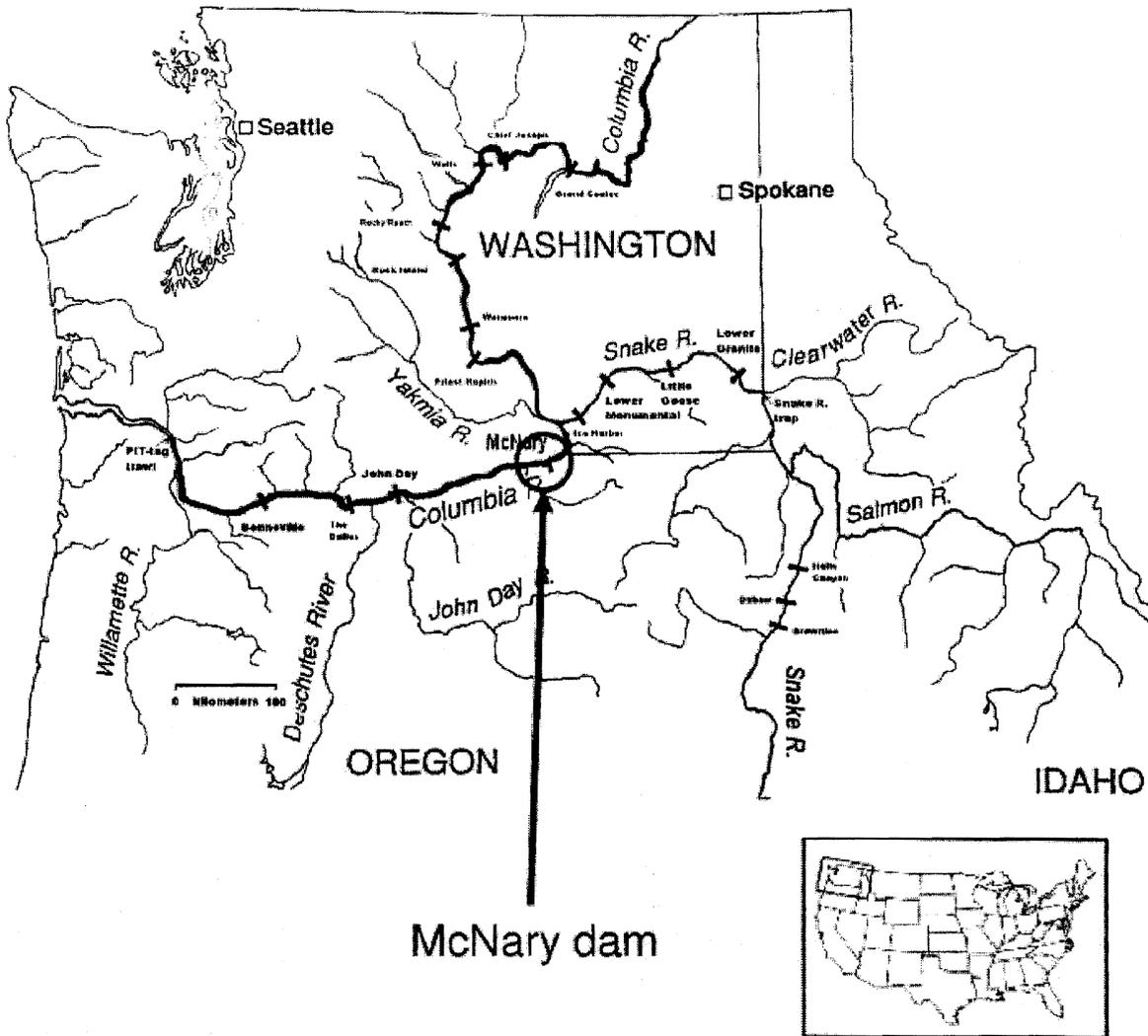


Figure 1. The study site was located at McNary Dam on the mid Columbia River, forming the Washington Oregon border, USA

downstream end of the flume was separated into two channels of equal dimensions (2.45 m long  $\times$  0.75 m wide) by an aluminium partition. The control channel was left unmodified, while the walls and floor of the adjacent channel were lined with corrugated sheet (7.6 cm wavelength, 0.65 cm amplitude) to create a condition in which structural complexity was designated as 'intermediate'. Alternatively, eight cobbles/boulders (mean diameter = 19.6 cm, range = 13.3–22.9 cm) were randomly placed in the 'intermediate' channel to form a 'complex' treatment in which resulting flow patterns and turbulence were similar to those found in a moderate energy stream or river. Stone *et al.* (2003) observed that similar levels of turbulence were generated behind boulders with distinctly different geometries indicating the potential for a universal relationship. All flume surfaces were painted with a dull matt grey waterproof emulsion to minimize potential disturbance to the fish by an aluminium surface. The flume was enclosed within a darkened hide that blocked external light sources. Overhead fluorescent lighting provided illumination under the 'light' condition during which the mean visible illuminance was 1313.3 (SD  $\pm$  92.9) lux. Two infrared modules (power consumption 50 W each) emitted light between 840 and 1200 nm wavelength to allow recording of fish behaviour by an overhead low-light black and white CCD video-camera system during periods of darkness (illuminance was below that which would enable the observer to see unaided).

Table I. Summary of experimental trials conducted at McNary Dam to assess the route selection of downstream migrating juvenile fall Chinook salmon through a uniform aluminium channel, or one lined with either an intermediate or complex landscape, under light and dark conditions

Treatment landscape	Treatment illumination	Trials <i>n</i>	Total fish sample <i>n</i> (SD)	Mean fork length (mm) (SD)
Intermediate	Light	10	8786 (1140)	89.5 (9.2)
Intermediate	Dark	10	5769 (729)	89.0 (9.1)
Complex	Light	10	13 159 (1931)	89.0 (9.3)
Complex	Dark	10	4839 (405)	89.0 (9.6)

### Experimental protocol

A total of forty 10-min trials were conducted under light and dark conditions (Table I). The fish entered the flume via a 30 cm diameter orifice and were able to pass either the control or treatment route under one of four landscapes—illumination scenarios designated as (i) intermediate—light, (ii) intermediate—dark, (iii) complex—light or (iv) complex—dark. The position of the treatment channel relative to the control was alternated between trials to control for any lateral bias associated with fish behaviour or hydraulic conditions within the flume. Having passed through a channel, the fish were sampled from a separate and isolated collection tank (control or treatment), anaesthetized (MS-222) and measured (fork length) (Table I). Water temperatures ranged between 18.6 and 21.5°C (mean = 20.0°C) during the trials.

### Discharge, depth, velocity and turbulence

Mean flume discharge was  $78 \text{ l s}^{-1}$  (range =  $58\text{--}105 \text{ l s}^{-1}$ ). Under the 'intermediate' condition, the mean water depth was 10.9 cm (range = 9.4–13.0 cm) in the control channel and 9.8 cm (range = 8.7–11.5 cm) in the treatment channel. The control channel received a higher percentage of flow (mean = 58%, range = 52–65%) and water velocities (mean =  $53.9 \text{ cm s}^{-1}$ , range =  $48\text{--}64 \text{ cm s}^{-1}$ ) as greater channel roughness through the treatment section resulted in displacement of water and lower velocities (mean =  $43.3 \text{ cm s}^{-1}$ , range =  $34.8\text{--}52.2 \text{ cm s}^{-1}$ ).

Under the 'complex' condition, the mean water depth was 11.5 cm (range = 9.8–14.1 cm) in the control channel and 10.6 cm (range = 9.4–12.7 cm) in the treatment channel. On average, the control channel received 67% (range = 61–70%) of the total flume discharge with a mean water velocity of  $58.3 \text{ cm s}^{-1}$  ( $53.7\text{--}68.1 \text{ cm s}^{-1}$ ). The mean water velocity was  $34.3 \text{ cm s}^{-1}$  ( $29.4\text{--}41.1 \text{ cm s}^{-1}$ ) in the treatment channel.

Time-series water-velocity measurements through control and treatment channels were recorded using a SonTek acoustic Doppler velocimeter (ADV) at 10 MHz. This system used a probe with three receivers extending out at an angle from the transmitter to calculate the three-dimensional ( $u$  = downstream,  $v$  = across stream and  $w$  = vertical) water velocity. The probe was oriented into the current with the support assembly off to the side to minimize interference from the vertical pole on velocity readings in the sample volume. The probe was positioned so that all three receivers were within the water column. Velocities were recorded at each sampling point along the channel transects for no less than 20 s to collect a data point every 0.1 s and stored on a laptop computer. Relative turbulence intensity ( $K$ ) was calculated by dividing the standard deviation of the velocity by the mean. This dimensionless ratio is an expression of the relative intensity of turbulence, and represents one of the most ecologically relevant descriptors of turbulence (Robson *et al.*, 1999). A one-way ANOVA was used to assess whether  $K$  in each dimension differed between control and treatment channels under both landscape (intermediate and complex) conditions.

### Analysis of fish behaviour

Video records of each trial were reviewed to assess fish behaviour during passage through the flume.

*Channel passage.* The total number of fish that passed each channel was counted during each trial and relative proportions calculated. A residual proportion of passes through the control channel was calculated by subtracting

the observed value from that expected if passes were directly proportional to the volume of water that passed (control: intermediate = 0.58; control: complex = 0.67). Results close to 0 indicated little deviation from the expectation, whereas positive and negative values respectively indicated higher and lower proportions than expected. One-sample *t*-tests were used to investigate whether the proportion of fish that passed the control channel was equal (i.e. 0.5) when paired with the alternate treatments under the two illumination regimes. To control for the flow variation through the respective channels, and to assess the influence of illumination, one sample *t*-tests were used to test whether the mean residual value significantly deviated from a value of 0 for the trials conducted under each landscape—illumination condition.

*Channel rejection.* Channel rejection was defined as a smolt entering a channel then subsequently exiting it by swimming upstream against the flow. For each trial, the total number of rejections was divided by the total number of passes through each channel (rejection per pass). A three-way univariate analysis of variance was used to test whether rejection per pass (dependent variable) was influenced by three fixed factors: channel type (control vs. treatment); landscape pairing (control with intermediate or control with complex) and illumination (light vs. dark).

*Orientation.* The percentage of fish that entered the channels while oriented facing the flow was calculated for each trial. A two-way univariate ANOVA was used to assess the influence of light and treatment on the percentage of fish that entered the channels facing upstream. All proportions were arcsine square-root transformed prior to analysis.

*Travel velocity.* Ground velocity ( $\text{m s}^{-1}$ ) of downstream passage was calculated for ten randomly selected fish per channel per trial (total  $n = 10 \times 2 \times 40 = 800$ ) by counting the number of video frames (film speed = 30 frames per second) that elapsed as a fish travelled downstream between two points 1.5 m apart. As orientation influences rate of downstream movement in Pacific salmon smolts (Kemp *et al.*, 2005b), only those fish predominantly oriented downstream were considered. Paired *t*-tests were used to assess the influence of treatment and light on mean rate of passage by comparing within-trial means (treatment) and paired between-trial means (light). Net velocity (ground velocity minus mean mid-column water velocity) was used to control for variation in water velocities between channels. Positive and negative values represent net travel velocities that are respectively greater and lesser than the mean mid-column water velocity measured through the channel.

## RESULTS

### *Relative turbulence intensity*

Relative turbulence intensity in the downstream direction ( $u$ ) was significantly different between control and treatment channels under both the intermediate ( $F = 72.1$ ,  $p < 0.001$ ) and complex ( $F = 56.0$ ,  $p < 0.001$ ) pairings.  $K$  values recorded in the control and complex treatment were also significantly different ( $F = 4.7$ ,  $p < 0.05$ ) in the across stream dimension ( $w$ ).

*Channel passage.* A significantly greater proportion of smolts passed the control channel when paired with the intermediate treatment when light (one sample *t*-test:  $t = 2.4$ ,  $df = 9$ ,  $p < 0.05$ ) and dark ( $t = 12.0$ ,  $df = 9$ ,  $p < 0.001$ ), and with the complex channel when light ( $t = 2.5$ ,  $df = 9$ ,  $p < 0.05$ ) and dark ( $t = 6.1$ ,  $df = 9$ ,  $p < 0.001$ ) (Figure 2). When light, the proportion of smolts that passed the control channel was significantly greater than expected based on flow when paired with the complex treatment ( $t = 3.9$ ,  $df = 9$ ,  $p < 0.05$ ). There was no significant difference for the three alternate treatments (intermediate—light, intermediate—dark and complex—dark).

*Channel rejection.* Rejections per pass were higher for the treatment channels ( $F = 39.8$ ,  $p < 0.001$ ) and under the dark condition ( $F = 5.7$ ,  $p < 0.05$ ) (Figure 3). There was no significant influence of landscape pairing on rejection. However, a significant ( $F = 5.0$ ,  $p < 0.05$ ) interaction between landscape pairing and channel type indicated that the difference was greater when complex (mean = 0.34 rejection per pass) was paired with control (mean = 0.13) than when intermediate (mean = 0.24) was paired with the control channel (mean = 0.14). Further, a significant ( $F = 6.2$ ,  $p = 0.02$ ) interaction between landscape pairing and light showed that a significantly ( $F = 6.7$ ,  $p = 0.01$ ) higher rate of rejection occurred when dark (mean = 0.30) than when light (mean = 0.18) when the control channel was paired with the complex treatment. When intermediate was paired with the control channel the mean rates of rejection was 0.19 when both dark and light.

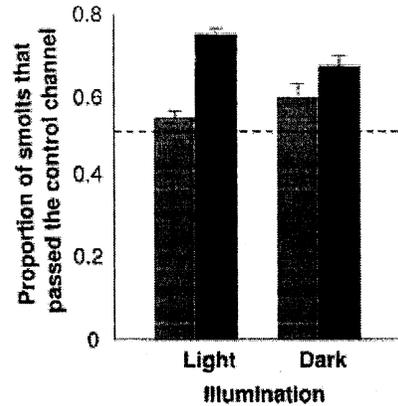


Figure 2. The proportion (with standard error) of smolts that passed a uniform aluminium control channel when paired with an adjacent treatment channel lined with either an intermediate (grey bars) or complex (solid bars) landscape in an experimental flume when light and dark. The dashed line represents that proportion expected if passage through the two channels were equal

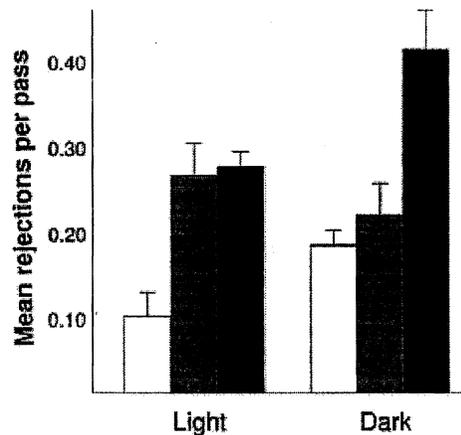


Figure 3. Mean (with standard error) rejection of uniform control (clear bars), intermediate (grey bars) and complex (solid bars) landscaped channels under light and dark conditions by actively migrating smolts

**Orientation.** The majority of smolts travelled through the flume facing downstream. However, a significantly greater percentage ( $F=153.3$ ,  $p < 0.001$ ) entered the channels facing upstream when dark (mean 12.3%,  $SE = 1.4\%$ ) than when light (mean 0.6%,  $SE = 0.3\%$ ). Treatment did not influence orientation, and there was no significant interaction between light and treatment.

**Travel velocity.** Downstream-oriented fish travelled through the control channel more rapidly than through the treatment channel when paired with both intermediate ( $t=5.1$ ,  $df = 18$ ,  $p < 0.001$ ) and complex ( $t=9.1$ ,  $df = 19$ ,  $p < 0.001$ ) landscapes (Figure 4). Overall, the fish tended to travel downstream slower than the mean current velocity. After taking the mean mid-column water velocity through each channel into account, there was no significant difference in mean net travel velocity between the control (mean =  $-0.31$ ,  $SE = 0.12 \text{ m s}^{-1}$ ) and intermediate (mean =  $-0.22$ ,  $SE = 0.09 \text{ m s}^{-1}$ ) landscape. The net travel velocity through the control (mean =  $-0.53$ ,  $SE = 0.11 \text{ m s}^{-1}$ ) channel was significantly lower, albeit barely ( $t = -2.1$ ,  $df = 15$ ,  $p = 0.049$ ), than through the complex (mean =  $-0.36$ ,  $SE = 0.06 \text{ m s}^{-1}$ ) treatment. Travel through the three channel types was significantly more rapid when light (control:  $t = 16.3$ ,  $df = 18$ ,  $p < 0.001$ ; intermediate:  $t = 7.2$ ,  $df = 8$ ,  $p < 0.001$ ; complex:  $t = 9.4$ ,  $df = 9$ ,  $p < 0.001$ ) than when dark.

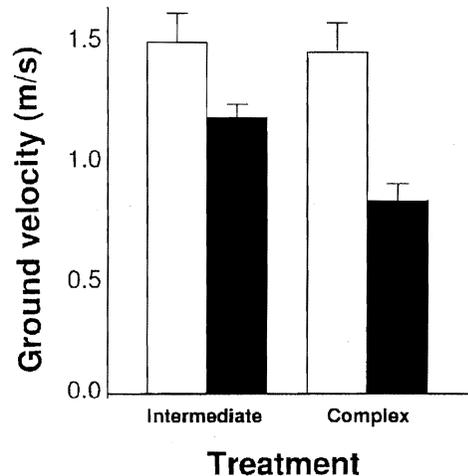


Figure 4. Downstream ground velocity ( $\text{m s}^{-1}$ ) of passage (with standard error) by smolts that selected either the uniform control (clear bars) or treatment (solid bars) channels

## DISCUSSION

Poorly designed and maintained culverts can severely restrict the upstream migration of anadromous fish (Hendry *et al.*, 2003). Yet, efforts to improve conditions (Rajaratnam *et al.*, 1989, 1990; Behlke *et al.*, 1991; Clay, 1995) generally do not consider potential effects on downstream migrating fish. This appears short sighted. Indeed, Bates (1992) observed that the practice of retrofitting culverts with structures that might improve fish passage had become fashionable in the absence of considering the needs of juvenile salmonids and speculated that the turbulence created might in some instances block downstream migration.

The results of research presented indicate that when given a choice, actively migrating juvenile Chinook salmon selected a passage route that had the least substrate roughness and associated turbulence. Seaward migrating smolts, apparently responding to visual stimuli, tended to elicit pre-emptive avoidance of a complex landscape when light, and selected a uniform landscape in which hydraulic diversity was low. When dark, fish relied heavily on alternative non-visual senses and were more likely to avoid the complex landscape having encountered it, by swimming in the upstream direction. It is unclear whether the behaviour exhibited was in response to a sudden environmental change, or avoidance of specific hydraulic conditions. However, this finding contradicts the assumption that smolts should always utilize the kinetic energy created under turbulent conditions to reduce the energetic costs of swimming (Coutant, 1998), and so are expected to select routes where bed features more closely mimic natural substrate in preference to a smooth uniform channel.

Avoidance by juveniles of in-stream structures may prove disadvantageous if they impede downstream movement, create an excessive energetic cost needed to avoid hydraulic conditions, or provide refuge for predators. Interestingly, in a conceptual model, Goodwin *et al.* (2006) speculated that migrating juvenile salmon may swim towards higher velocities in order to minimize turbulence or change in velocities associated with cobbles or boulders projecting into the flow field. In this study, downstream-oriented fish travelled more slowly through the flume when they passed through a hydraulically complex landscape. It remains unclear whether fish perceived in-stream structures as physical obstructions to passage, *per se*, or if the observed avoidance reflected altered behaviour in response to the hydraulic conditions experienced.

Downstream-oriented smolts tended to move through the flume slower than the mean water velocity. This observation reflects active exploration of the channel by the fish in the form of subtle changes in direction as they utilized currents to aid downstream transport. The smolts were not obliged to pursue linear trajectories downstream as are water particles. Instead, the fish continuously moved from one wall to the other as they moved through the flume, and on occasions switched orientation and temporarily faced the flow. It appears, therefore, that even at the fine-scale, mean water velocity is a poor proxy for the velocity of downstream movements of fish.

Smolts moved slightly more rapidly through the complex than the uniform landscape when variation in mean mid-column water velocity through the opposing channels was controlled for. This finding appears to support the suggestion that turbulent conditions, such as those created by in-stream structures, will enhance velocities of downstream migration as fish select those regions where velocities are greater than that of the bulk flow (Coutant and Whitney, 2000). However, calculations of mean water velocity through the complex channel were based on measures taken along transects and that included the low velocity areas downstream of the cobbles that actively moving fish rarely utilized in addition to rapid flowing currents between the structures. Hence it would be expected that where hydraulic patterns are complex, the net travel velocities of fish that take swift flowing paths by slaloming between boulders will be greater than those based on the more homogenous velocities measured in the control channel, even though actual velocity of downstream movement may be lower. To understand how in-stream structures influence actual swimming performance, net velocity should be based on fine-resolution measurements attained for both the fish and water particles along the nonlinear paths travelled.

The majority of smolts passed through the flume oriented downstream when both light and dark. However, orientation towards the flow was more common in the absence of visual cues than in the light. For those fish that did face the flow, they had more time to process mechanosensory information during their slower progression downstream (Kemp *et al.*, 2005b). This allowed them to more effectively avoid entrance into areas they did not apparently find suitable as they used a sudden burst of swimming upstream when they encountered them. Further, smolts that travelled predominantly headfirst downstream did so at a slower rate when dark than when light.

Overall, passage through the flume was not excessively delayed as a result of behavioural avoidance exhibited by the smolts because they were able to select an alternative route. This, however, will rarely occur when encountering culverts in the field. Delayed migration may result in elevated energetic costs as fish either hold station or actively swim upstream away from the structure. A culvert may act as a 'prey-trap' if migrants concentrate in the immediate upstream vicinity of a culvert and suitable habitat exists for piscivorous predators. Ultimately, if overall fitness corresponds to arrival at the estuary during optimum conditions, a delayed migration may have important implications for survival. Such costs will accumulate on those systems where migrants encounter a series of culverts on route to the sea.

The findings presented have important implications for the management of migratory fish. Under the experimental conditions described, downstream migrating smolts more likely avoided a channel similar in landscape to that associated with a modified culvert, than one with a uniform, simple substrate. When considered in conjunction with the findings of Kemp *et al.* (2005a) in which smolts avoided areas of continuous overhead cover, it is suggestive that modified culverts may delay the seaward migration of juvenile salmonids, despite facilitating the upstream movement of adult fish. However, further experimental research is needed to ascertain whether the primary factor influencing the decision-making process was encountering an environmental change, or a predetermined preference/avoidance for specific hydraulic features. Field studies are now needed to investigate whether culverts do indeed impede downstream migration of juvenile salmonids by initiating avoidance reactions. The implication of delayed migration for individual fitness also needs assessment.

#### ACKNOWLEDGEMENTS

We acknowledge the practical support provided by Michael Gessel (NOAA National Marine Fisheries Service) and Brad Eby (United States Army Corp of Engineers); and comments provided by an anonymous reviewer. This work was performed while the author held a National Research Council Research Associateship Award.

#### REFERENCES

- Bates K. 1992. Fishway design guidelines for Pacific salmon. *Working paper 1.6*. Washington Department of Fish and Wildlife. Olympia, WA, 98501-1091.
- Behlke CE, Kane DL, McLean RF, Travis MD. 1991. Fundamentals of culvert design for passage of weak-swimming fish. *Final report*. Alaska DOT&PF and USDT, Federal Highway Administration, FHWA-AK-RD-90-10. 177 p.
- CDFG. 2002. *Culvert criteria for fish passage*. State of California Resources Agency Department of Fish and Game. 17 p.

- Clay CH. 1995. *Design of Fishways and other Fish Facilities*, 2nd edn. Lewis Publishers, CRC Press (imprint): Boca Raton, FL; 248 p.
- Coutant CC. 1998. *Turbulent attraction flows for juvenile salmonid passage at dams*. ORNL/TM-13608. Oak Ridge National Laboratory, Oak Ridge, TN. 28 p.
- Coutant CC, Whitney RR. 2000. Fish behavior in relation to passage through hydropower turbines: a review. *Transactions of the American Fisheries Society* **129**: 351–380.
- Ebbin SA. 2002. Enhanced fit through institutional interplay in the Pacific Northwest salmon co-management regime. *Marine Policy* **26**: 253–259.
- Everest FH, Chapman DW. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. *Journal of Fisheries Research Board of Canada* **29**: 91–100.
- Gessel MH, Williams JG, Brege DA, Krcma RF, Chambers DR. 1991. Juvenile salmonid guidance at the Bonneville Dam second powerhouse, Columbia River, 1983–1989. *North American Journal of Fisheries Management* **11**: 400–412.
- Goodwin RA, Nestler JM, Anderson JJ, Weber LJ, Loucks DP. 2006. Forecasting 3-D fish movement behavior using a Eulerian-Lagrangian-agent method (ELAM). *Ecological Modelling* **192**: 197–223.
- Hendry K, Cragg-Hine D, O'Grady M, Sambrook H, Stephen A. 2003. Management of habitat for rehabilitation and enhancement of salmonid stocks. *Fisheries Research* **62**: 171–192.
- Hinch SG, Rand PS. 2000. Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 2470–2478.
- Kemp PS, Gessel MH, Williams JG. 2005a. Seaward migrating subyearling Chinook salmon avoid overhead cover. *Journal of Fish Biology* **67**: 1381–1391.
- Kemp PS, Gessel MH, Williams JG. 2005b. Fine-scale behavioral response of Pacific salmonid smolts as they encounter divergence and acceleration of flow. *Transactions of the American Fisheries Society* **134**: 390–398.
- Liao JC, Beal DN, Lauder GV, Triantafyllou MS. 2003. Fish exploiting vortices decrease muscle activity. *Science* **302**: 1566–1569.
- Matthews GM, Swann GA, Smith JR. 1977. Improved bypass and collection system for protection of juvenile salmon and steelhead trout at Lower Granite Dam. *Marine Fisheries Review* **39**: 10–14.
- McKinnon GA, Hnytka FN. 1985. Fish passage assessment of culverts constructed to simulate stream conditions on the Liard River tributaries. Winnipeg, Manitoba, Canada: Western Region, Department of Fisheries and Oceans. *Canadian Technical Report of Fisheries and Aquatic Sciences* **1255**: 1–121.
- Morantz DL, Sweeney RK, Shirvell CS, Longard DA. 1987. Selection of microhabitat in summer by juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **44**: 120–129.
- ODFW. 2004. *Fish passage criteria*. Oregon Department of Fish and Wildlife. 6 p.
- Rajaratnam N, Katopodis C, McQuitty N. 1989. Hydraulics of culvert fishways II: slotted weir culvert fishways. *Canadian Journal of Civil Engineering* **16**: 375–383.
- Rajaratnam N, Katopodis C, Fairbairn MA. 1990. Hydraulics of culvert fishways V: Alberta fish weirs and baffles. *Canadian Journal of Civil Engineering* **17**: 1015–1021.
- Robson BJ, Chester ET, Davis JA. 1999. Manipulating the intensity of near-bed turbulence in rivers: effects on benthic invertebrates. *Freshwater Biology* **42**: 645–653.
- Stone M, Tritico H, Hotchkiss R, Flanagan P. 2003. Turbulence characteristics in obstructed gravel bed flow. *16th ASCE Engineering Mechanics Conference*, July 16–18 2003, University of Washington, Seattle.
- WDFW. 2003. Design of road culverts for fish passage. Washington Department of Fish and Wildlife publication. 111 p.

