

Fish use of turbulence around wood in winter: physical experiments on hydraulic variability and habitat selection by juvenile coho salmon, *Oncorhynchus kisutch*

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Abstract Re-introduction of large wood for expanding hydraulic variability is an increasingly common practice, yet it is not yet known what elements of hydraulic variability are most beneficial to fish. In an experiment designed to emphasize the minimization of energy expenditure through controlled predation and drift, we investigated whether juvenile coho, under winter conditions, discriminated between microhabitats based primarily on flow strength, depth, distance to wood, or based on temporal or spatial variability of the flow field, with the hypothesis that turbulence would be a strong factor in habitat selection. We conducted physical experiments in a 1:1 scale model of a large wood jam at the Oregon Hatchery Research Center in Alsea, Oregon. We conducted high resolution (0.1 m) mapping of the flow field using an acoustic Doppler velocimeter array and underwater videogrammetry of fish locations. Results indicated that discrimination of microhabitats by juvenile coho salmon in cold, low flows emphasized depth and distance to wood over any hydraulic measures of the flow field. Correlations between hydraulic parameters and distance to wood limited our ability to distinguish the importance of turbulence measures relative to velocities, but highlighted the positive relationships between velocity and turbulence measures and the negative relationships between hydraulics and distance from the roughness elements. Findings suggest areas of further

study including potential thresholds of temperature and flow intensity on the importance of turbulence in habitat selection.

Keywords Bioenergetics · Physical model · Acoustic Doppler velocimeter · Large woody debris · River restoration · Woody debris habitat · Velocity refuge

Introduction

Following decades of removal of wood from rivers for navigation, log drives, fish passage, and water quality (Sedell and Luchessa 1982; Bryant 1985; Stednick 2010), reintroduction of large woody debris (LWD) is now one of most common restoration practices in the Pacific Northwest (Katz et al. 2007) and is widely practiced elsewhere (Bernhardt et al. 2005; Nagayama and Nakamura 2009). In recognition of the important benefits of large wood to river morphology (Robinson and Beschta 1990; Abbe and Montgomery 1996; Hogan et al. 1996) and ecology (Bustard and Narver 1975; Swanson and Lienkaemper 1978; Harmon et al. 1986; Hicks et al. 1991; Thomson 1991; Koski 1992), objectives of reintroducing large wood into rivers often include sediment and wood retention, increased hydraulic variability, and increased habitat heterogeneity (Brooks et al. 2006). Observational evidence (e.g. Cederholm et al. 1997; Roni and Quinn 2001; Pess et al. 2012) has indicated that reintroducing wood may be effective in the recovery of salmonids, with higher densities in

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reaches treated with large wood relative to untreated reaches.

A growing body of research has contributed to identifying the mechanisms for salmonid recovery following the reintroduction of wood. For fish bioenergetics in particular, large wood can provide: 1) areas of reduced velocity that are used by fish (Shirvell 1990), referred to as velocity shelters (*sensu* Fausch 1993); 2) increases in pool frequency and cover (Hilderbrand et al. 1997; Keim et al. 2002); 3) potentially improved foraging conditions through establishing beneficial stream positions for foraging (*cf* Fausch 1984; but see Giannico 2000 and Gustafsson et al. 2012 for negative impacts on foraging); 3) visual isolation from predators and conspecifics (Wilzbach 1985; Sundbaum and Näslund 1998; Crook and Robertson 1999; Harvey et al. 1999; Allouche 2002; Nagayama and Nakamura 2009; Kawai et al. 2014); and 5) a substrate for macroinvertebrate biomass (Spänhoff et al. 2000; Hernandez et al. 2005). In particular, the contribution of large wood to establishing low-velocity shelters adjacent to high velocity areas with high drift densities, which are especially important to maximizing energy gain (Fausch 1984), may be a potentially critical element in the recovery of salmonids.

While it appears that, for much of the year, the swimming costs associated with active foraging attempts outweigh the importance of maintaining position (Boisclair and Tang 1993; Hill and Grossman 1993), the importance in bioenergetics for juveniles may shift from maximizing energy gain to minimizing expenditure in winter when temperatures are cold (Heggenes et al. 1993; Garvey et al. 2004; Huusko et al. 2007). Even at the lower activity levels and metabolic rates associated with low winter temperatures, juvenile salmonids often enter winter with low initial energy stores and accumulate a net metabolic deficit over the winter, which appears to reduce their survival (see Huusko et al. 2007 for details and references). The velocity shelters (*cf* Fausch 1993) selected by juvenile fish during winter (Rimmer et al. 1984; Heggenes et al. 1993) presumably improve survival through decreasing juvenile's use of energy stores. Given the importance of winter habitats as a bottleneck for juvenile coho survival (Nickelson et al. 1992; Solazzi et al. 2000), the benefit of introducing wood to support minimizing energy expenditure should be large.

The application of the concept of velocity shelters in bioenergetics models and in habitat design has thus far

assumed that areas of low velocity are consistent with areas where fish can minimize energy expenditure (Fausch and White 1981). However, turbulence is known to influence energy dynamics of the flow field and is not always correlated with velocity, particularly in pools (MacVicar and Roy 2007a; MacVicar and Roy 2007b) and around roughness elements (Papanicolaou et al. 2012), features that define the hydraulics around LWD. Turbulence describes the temporally and spatially fluctuating features of fluid flow that are characterized by randomness, diffusivity, three-dimensional vorticity, and energy dissipation (Tennekes and Lumley 1972). These fluctuations are generated by the shearing of flow across simple velocity gradients from the bed to the channel surface, and from the separation and convergence of flow around roughness elements (Roy et al. 2004; Smith et al. 2005). Thus, it is the case that areas of similar velocity can have both high and low turbulence intensities, depending on the mechanism responsible for the shearing of flow that generates turbulence.

The distinction between velocity refuges with varying turbulence levels is of significance to fish bioenergetics because studies indicate that fish typically expend more energy in higher turbulence environments (Boisclair and Tang 1993; Krohn and Boisclair 1994; McLaughlin and Noakes 1998; Enders et al. 2003; Tritico and Cotel 2010; plus see Liao 2007 for comprehensive review of fish use of turbulence). Meanwhile, fish have a diminished ability to swim, accelerate, and maintain position during winter conditions when temperature is low (Rimmer et al. 1985; McMahon and Hartman 1989; Graham et al. 1996). Thus, avoiding turbulence could be particularly important to the bioenergetics of juvenile fish in the winter. Knowledge on how fish perceive and utilize the spatial and temporal variability of flow fields around large wood is not well developed, though this information seems particularly important for understanding the importance of velocity shelters for juvenile fish seeking to minimize energy expenditure in winter.

To begin investigating the use and benefit of flow field variability around wood for juvenile coho, we conducted a mensurative, 1:1 scale experiment in outdoor stream channels with high-resolution observations of the three-dimensional velocities and fish locations around a full-channel log jam. Generally, our interest was in investigating the bioenergetic benefits of wood for minimizing the energy expenditure of juvenile coho in winter. More specifically, we hypothesized that a)

based on contour plots and reach-scale correlations, the flow field around the log jam would include two types of velocity refuges: areas of higher turbulence due to flow divergence and convergence around the obstruction of the wood and areas of lower turbulence in the pool downstream of the wood, b) under the assumption that fish were selecting habitats to minimize energy expenditure, distributions of available and observed locations of fish would indicate that fish selected habitats in areas of the lowest turbulence and velocity. By replicating the habitat and flow of a natural channel but restricting foraging opportunities and predation, we sought to identify the hydraulic habitat fish would most often and most reliably select to minimize energy expenditure.

Materials and methods

Experimental design

We conducted the experiment as a 1:1 scale physical model of a full channel jam and related channel topography in one of the outdoor experimental channels (Fig. 1) at the Oregon Hatchery Research Center near Alsea, Oregon (Noakes and Corrarino 2010). The concrete channels are each 7.6 m wide and 61 m long, filled with gravel to wetted widths of 1.3–4.7 m and depths of 0.1–0.3 m for our experiments. We restricted observations of hydraulics and fish to 4.6 m longitudinally to focus on the areas immediately surrounding the large wood. We used three logs of 0.25 to 0.8 m diameter to replicate the prototype full channel jam on Canal Creek, a tributary of the Alsea River near Tidewater, OR. For the experimental channels, water flow is diverted from Fall Creek, also a tributary of the Alsea



Fig. 1 Physical model and ADV instrumentation at the experimental channels at Oregon Hatchery Research Center

River, through a settling basin and was held at a discharge of $0.045 \text{ m}^3 \text{ s}^{-1}$ for the duration of the experiments, representative of baseflow conditions at the prototype jam. Hydraulic conditions during the experiments were subcritical, with a mean Froude number of 0.1, and fully turbulent, with a mean Reynolds number of 9×10^5 .

Given that the state of the fish can influence its behavioral decisions (Houston and McNamara 1999), we deliberately constrained the experiments to emphasize state variables that relate to a fish's selection of hydraulic microhabitat. We limited our experiment to wild juvenile coho salmon (*Oncorhynchus kisutch*), approximately 10 cm fork length, kept at consistent energy reserves maintained through controlled feeding, at a constant temperature of $7 (+/- 1) \text{ }^\circ\text{C}$. Furthermore, we screened drift from the channels and installed an overhead shade cloth. The shade cloth both eliminated actual predation as well as the visibility of predators by reducing ambient light to 30 % of incident natural daylight. We did not directly measure drift in the channels during the experiment, though it was previously measured to be "essentially zero" (Ron Griffiths, personal communication). Thus, by eliminating both the presence and visibility of predators, eliminating drift, and conducting the experiments during the winter, we expected that fish selection of habitats would emphasize minimization of energy expenditure over foraging.

Observations of fish

Juvenile wild coho were collected by seine from Fall Creek November 30, 2012 for observation in the experimental channels. Fish were held in a single 6' shaded circular fiberglass tank with Fall Creek water running at an exchange rate of 26 min. Fish were provided 1.5 mm pellets and salmon roe 2–3 times daily during the time they were held. Fish were observed over 2-h periods, one morning and one afternoon, on February 1, 19, and 20, 2013 in two groups: first as a group of 12 on February 1st and then as a group of five February 19th and 20th. The channels were cleared of fish by electroshocking at the end of all observations. Recovered fish were euthanized using tricaine methanesulfonate (MS-222) and analyzed for weight, fork length, and preserved (10 % formalin, 70 % alcohol) for analysis of gut contents.

The two observed group sizes represent fish densities of 0.3 and 0.6 fish/m^2 , which are similar to juvenile

coho densities (0.15–0.66 fish/m²) found by Ebersole et al. (2006) in the Oregon Coast Range. These two group sizes reflected a much smaller difference in group size than was intended with the original experimental design. Unfortunately, unusually high flows reduced our intended collection of 120 fish to 33 individuals, and difficulties retrieving fish from the experimental channels during trial observations reduced our observed individuals. Thus, while we observed fish in two group sizes, due to the small differences in densities, we chose to pool the observations because the differences in densities are so similar that it would be difficult to conclude that any differences between groups would be due to group size.

Fish were observed using underwater videogrammetry (Fig. 2) initially with three pairs of cameras, then with six pairs of cameras for the second set of observations starting February 19th. Paired videos were calibrated and analyzed in VidSync (Neuswanger 2013; Leitshuh et al. 2014). We subsampled the videos by recording fish coordinates every 20 s, resulting in over 800 observations of exact focal position coordinates and orientations of the juvenile salmonids, with each fish observed multiple times. For each camera pair, the coordinates of fish observations were transformed via translation and rotation from the coordinate system established in VidSync to match the coordinate system of the velocity measurement locations using at least three control points in Cyclone (Leica Geosystems Inc 2012).

Observations of channel hydraulics

We made detailed observations of the flow field around the wood using an array of four Acoustic Doppler Velocimeters (ADVs: SonTek 16 MHz MicroADV) which we operated for 5 min at 50 Hz at each location. The ADV array was suspended from a free-standing instrumentation platform, which spanned the wetted

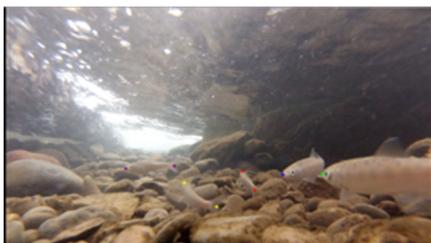


Fig. 2 Underwater videogrammetry

channel to avoid any hydraulic interference from the supports (Fig. 1). Each ADV measurement was spatially located by measurements of distances between the probes, instrument platform, and fixed channel structures. We used a Cartesian coordinate system, with u aligned longitudinally, v oriented across the channel, and w representing the vertical orientation. Three-dimensional velocities were measured on a three-dimensional grid at 0.1 m spacing. In addition, irregularly-spaced measurements were collected in the regions around the wood. This sampling program resulted in over 1500 measurement locations (Fig. 3) and nearly 17 million observations of velocities. Raw ADV velocities were filtered in WinADV (Wahl 2013) to remove data with low (<70 %) average correlation coefficients, low average signal to noise ratio (<15 dB), and despiked using phase-space thresholding (Wahl 2000; SonTek/YSI 2001; Goring and Nikora 2002; Wahl 2003).

The temporal and spatial variabilities that characterize turbulence can be summarized in a number of ways (see Nezu and Nakagawa 1993; Lacey et al. 2012 for review). In addition to the time-averaged longitudinal velocity, hydraulic variability may be defined over time by the turbulent fluctuations in velocities, represented herein by turbulent kinetic energy (TKE, Eq. 1). TKE, as a representation of energy extracted from the bulk flow by turbulent eddies (Bradshaw 1985), has been shown to influence fish swimming performance and

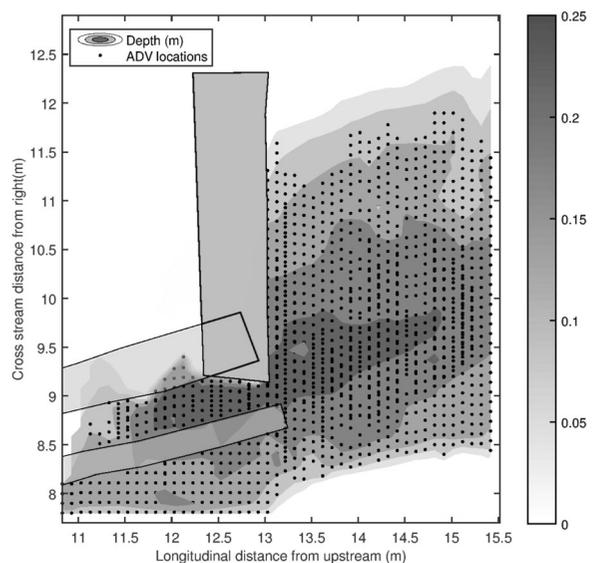


Fig. 3 Channel topography, location and orientation of wood, and location of velocity observations

holding position (Odeh et al. 2002; Silva et al. 2012) and increase swimming costs (Enders et al. 2003). Locations with high TKE values may be generally avoided by fish (Smith et al. 2005). Alternately, hydraulic variability may be defined in terms of spatial gradients in velocities, represented herein as a steady-state hydraulic strain (Eq. 2). Hydraulic strain reflects how the fluid field deforms across space, and can influence fish selection of hydraulic environment as they migrate (Goodwin et al. 2006; Nestler et al. 2008) and can be used in estimates of power expenditure by fish (Crowder and

Diplas 2002).

$$TKE = 0.5 * \left(RMS[u]^2 + RMS[v]^2 + RMS[w]^2 \right) \tag{1}$$

where u , v , and w represent the longitudinal, transverse, and vertical velocities, respectively, and RMS represents the standard deviation for each velocity component.

$$strain(e) \sqrt{\left(\frac{u_{i+1} - u_i}{x_{i+1} - x_i} + \frac{u_i - u_{i-1}}{x_i - x_{i-1}} \right)^2 + \left(\frac{v_{i+1} - v_i}{y_{i+1} - y_i} + \frac{v_i - v_{i-1}}{y_i - y_{i-1}} \right)^2 + \left(\frac{w_{i+1} - w_i}{z_{i+1} - z_i} + \frac{w_i - w_{i-1}}{z_i - z_{i-1}} \right)^2} \tag{2}$$

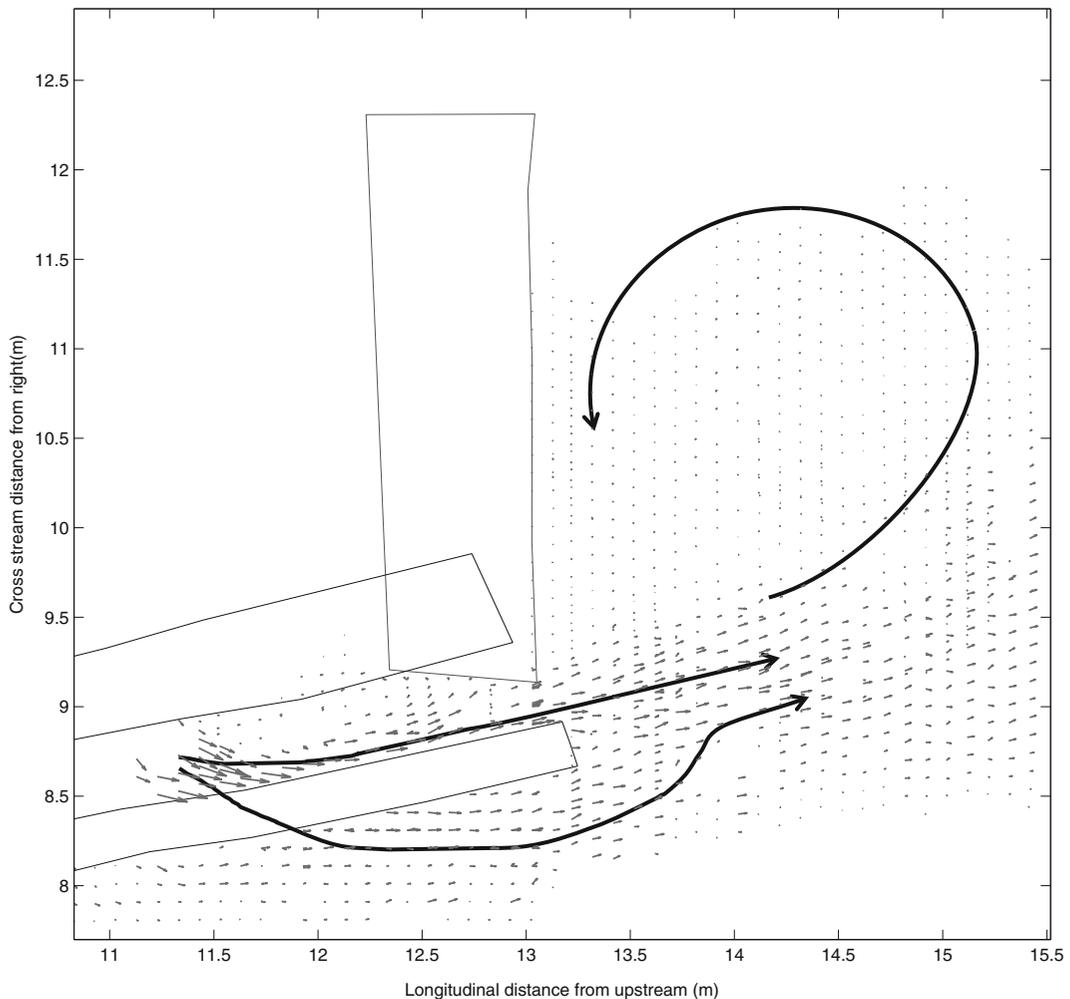


Fig. 4 Horizontal velocity vectors for bulk flow. *Bold lines* represent flow paths

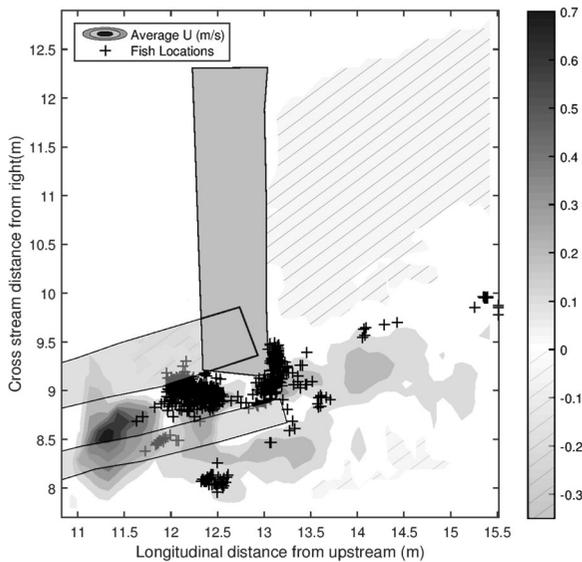


Fig. 5 Longitudinal velocities and fish locations 0.04 m above the channel bottom

where i represents each location, $i+1$ represents the closest adjacent location in the positive direction, and $i-1$ represents the closest adjacent location in the negative direction.

The three hydraulic metrics were each linearly interpolated (Clunie et al. 2007; Enders et al. 2009) to two

surfaces at 0.04 and 0.13 m above the channel bottom. These surfaces were used to plot contours over space, derive values at observed fish locations, and derive values of available hydraulics at a 0.01 m horizontal and 0.02 m vertical spacing.

Analysis of hydraulic habitat selection

Given that this was a mensurative experiment (cf Hurlbert 1984) and no treatment effects were evaluated, we interpreted our results qualitatively to identify evidence of strong or weak selection of habitats relative to what habitat was available to the fish. We generated a null model, where the mechanism being evaluated was deliberately excluded (Gotelli 2001), based on a distribution of hydraulic habitat conditions in proportions equal to their availability, in order to evaluate whether fish selection was expressed in our observations. We applied the chi-square goodness of fit test to evaluate the null hypothesis that fish choose the range of hydraulic habitats in proportion of their availability. This test involves comparing the distribution of hydraulic values at locations where fish were observed to the distribution of hydraulic values of available locations. For each metric, we evaluated the distribution of values in ten bins spanning the range of the values at available

Fig. 6 TKE and fish locations 0.04 m above the channel bottom

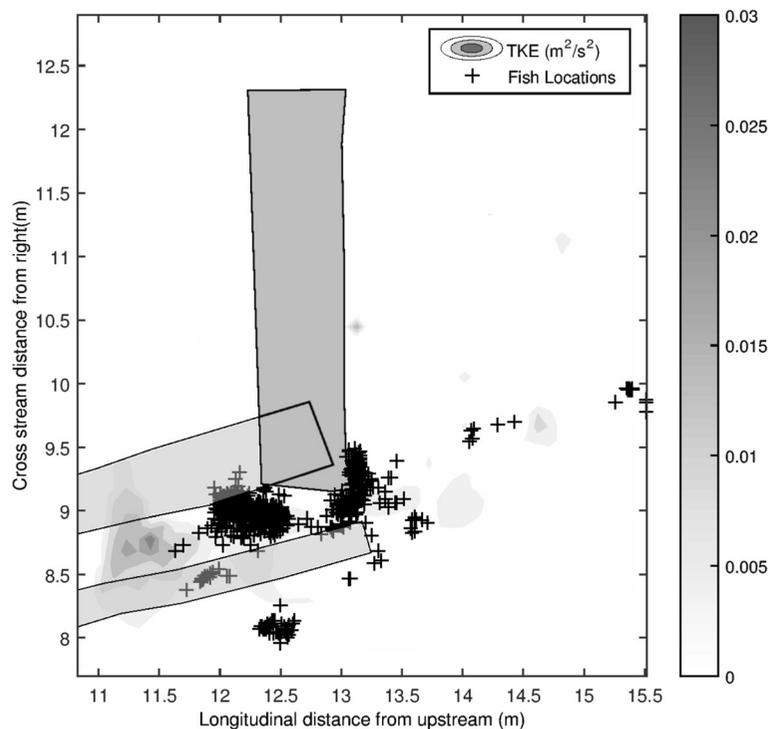
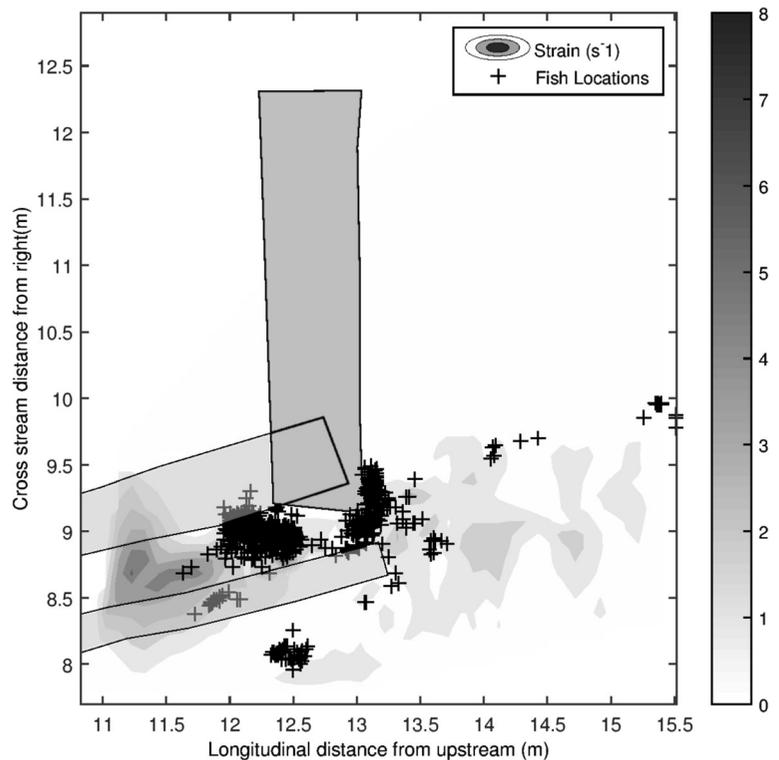


Fig. 7 Hydraulic strain and fish locations 0.04 m above the channel bottom



locations and sized such that there was approximately the same number of available locations per bin. The observed frequency was calculated as the number of fish observed at locations with values in each bin. We tested at the 95 % confidence level with nine degrees of freedom for a significance level of $p < 0.05$, where the p value represents the probability that the deviation of the observed from the expected distribution is due to chance alone.

Results

Hydraulics around the full channel jam

The orientation of the flow field varies as flow moves through the jam. Upstream of the log jam, flow is shallow, wide, and oriented downstream. As flow moves through the log jam (Figs. 4 and 5), it encounters areas of contraction, expansion, acceleration and resistance, generating a variety of hydraulic conditions over the short 4.6 m study reach, which can generally be organized into two primary regions downstream of the jam. First, flow was constricted and rapidly dropped into an approximately 1.3 m wide, 2.2 m long, turbulent jet through the jam, which was split by a log in contact with

the bed only at the bottom of the jet (Figs. 4 and 5). Flow moved laterally underneath this downstream-oriented log then converged with the primary jet just downstream of the jam. The second primary flow region reflects flow through the pool downstream of the jam. In this region, flow advected downstream, with mostly parallel streamlines, through a 0.3 m deep pool. In addition to these two primary flow regions, a large, shallow, low velocity eddy was generated on the left, looking downstream, downstream of the jam which fish appeared to avoid (Fig. 5). The wood thus generated a turbulent, three-dimensional flow field in the area immediately around the jam and an area of more downstream-oriented flow in the pool below the jam, the strength and variability of which are represented by the observed velocities (Fig. 5), turbulence kinetic energy (Fig. 6), and hydraulic strain (Fig. 7).

The magnitude of velocities were generally low (Fig. 5), primarily in the range of $0\text{--}0.3\text{ m s}^{-1}$, which is consistent with other studies on the ranges of 1D velocities used by juvenile coho around wood (e.g. Huusko et al. 2007, $<0.4\text{ m s}^{-1}$). The highest values were represented by downstream-oriented velocities in the jet within the jam (Fig. 5). Near bed velocities attenuated approximately 1 m downstream of the jam, diminishing with distance downstream through the pool (Figs. 4 and 5).

Peak values for TKE were concentrated in similar locations to velocity, primarily at the top of the jam where the bed rapidly drops and flow splits around the log in the jet (Fig. 6). Detectable values of TKE were primarily located in the jet within and immediately downstream of the jam. The magnitude of hydraulic strain, representing the spatial velocity gradients and the deformation of the flow field, was also highest at the top of and within the jet (Fig. 7). Detectable values of strain extended downstream through the pool, due in part to variability in the vertical velocity component (data not presented).

Observed locations of fish

Of the available hydraulic habitats, fish were consistently observed in three primary regions across the channel: 1) adjacent to the wood and in the jet within the jam, 2) adjacent to the wood and in the jet downstream of the jam, and 3) within the flow between the jam and the right bank. The velocity contours (Fig. 5) indicate that these regions represent a wide range of velocities, with fish observed both within and adjacent to areas of high and low velocities. These regions also encompassed a range of turbulent fluctuations (Fig. 6) and hydraulic strain (Fig. 7). Though fish were commonly observed in areas of low velocity, TKE, and strain, they were not exclusively found in low energy environments.

Selectivity of habitats based on focal position coordinates

Chi-square goodness of fit tests indicated that distributions of values for observed and available locations were significantly different at the 95 % confidence level, with $p < 0.001$, for all metrics. Because we included multiple observations per fish, each data point was not independent and pseudoreplication was introduced by applying the chi-squared goodness of fit test to non-independent data (Hurlbert 1984). Thus, the chi-squared p-values were artificially small. While the pseudoreplication means that our p-values were artificially small, since the p-values values from the tests were all much smaller ($p < 0.001$) than the typical threshold for significance ($p < 0.05$), it was reasonable to conclude that the observed distributions were significantly different from the available distributions for all hydraulic parameters. However, due to the issues with pseudoreplication, we did not attempt to interpret the relative differences in fit across the hydraulic parameters based on chi-square

values, which could otherwise have been used to evaluate the relative importance of the hydraulic parameters in the selection of habitats by the fish.

Instead, visual interpretation of the distributions provided some qualitative evidence of which parameters were of importance in selection of habitat. Across the range of hydraulic parameters, fish were most clearly over-represented in areas of greater depths relative to the available depths (Fig. 8a) and shorter distances to wood relative to the available distances to wood, suggesting depth and distance to wood were important factors in the fish's selection of habitats. In contrast, for all the hydraulic parameters (Fig. 8b–d), fish were observed in distributions more similar to the distributions of available hydraulic conditions, indicating weaker selection by the fish based on the flow field than on depth. Fish were most commonly found and slightly overrepresented in the lowest velocities (Fig. 8b). In contrast, fish were observed to be slightly overrepresented in locations of higher TKE and hydraulic strain, relative to the available turbulence environments. Thus, the observed-available distributions suggested that, during winter conditions and without foraging opportunities, fish selected areas of greater depth, low velocities, and low but not minimum turbulence intensity and flow field deformation, and close to wood. Qualitatively, the distinction between the distributions did indicate some discrimination based on distance to wood and depth, with weaker discrimination based on velocity, turbulence, and strain.

Relationships among hydraulic parameters

Locations of peak magnitudes for the hydraulic parameters were correlated in this experiment as indicated by Pearson correlation coefficients (Table 1). The downstream-oriented velocity was correlated with TKE and hydraulic strain, and TKE and strain were correlated to each other. To a lesser degree, distance to wood was negatively correlated with the hydraulic parameters (Table 1). Notably, most of the hydraulic parameters were not correlated with water depth. Only strain had a moderately weak correlation with water depth.

The nature of the relationships between hydraulic parameters was highlighted by scatter plots (Fig. 9), which further illustrated the range of available habitats selected by the fish. From the values of coefficient of variability for available habitat parameters, the velocities, TKE, strain values, and wood distances generally occurred over a wider range (Fig. 8b–f) than the

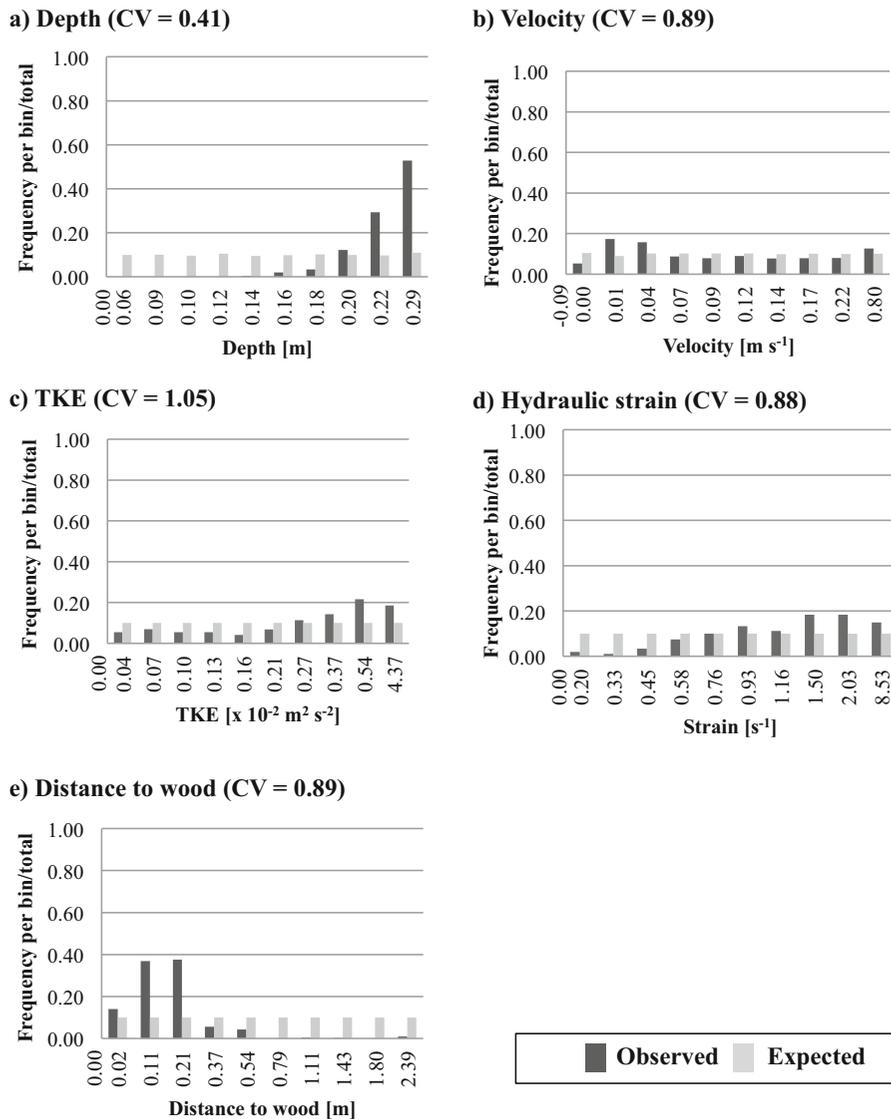


Fig. 8 Proportion of occurrence for: **a** depth ($\chi^2=2255$; $p<0.001$), **b** longitudinal velocities ($\chi^2=135$; $p<0.001$), **c** TKE ($\chi^2=285$; $p<0.001$), **d** hydraulic strain ($\chi^2=307$; $p<0.001$), and **e**

distance to wood ($\chi^2=1678$; $p<0.001$) based on observations and expected proportions under a no-preference null model. Values given for the bins are the upper value for each bin

relatively narrow ranges of available depth (Fig. 8a). However, while the net CV values for hydraulic

parameters were higher than depths, the range of hydraulic conditions did vary over space. As expected for a turbulent environment, velocities and turbulence measures generally fell into a wide range near the wood (<~0.2 m away from the wood) and a narrower range outside of the jet area (Fig. 9b, e, h). In addition, the positive relationships between velocity and TKE (Fig. 9f) and velocity and strain (Fig. 9i) for both used and available locations were evident, whereas the lack of relationship between other parameters was also clear (Fig. 9a–e, g–h). The most notable finding from the scatterplots is the observation of fish within a narrow depth range that

Table 1 Pearson correlation coefficients for hydraulics and cover parameters in the experimental channel

	Velocity	Depth	TKE	Strain
Depth	0.01			
TKE	0.51	-0.08		
Strain	0.51	-0.17	0.45	
Distance to wood	-0.21	-0.02	-0.22	-0.30

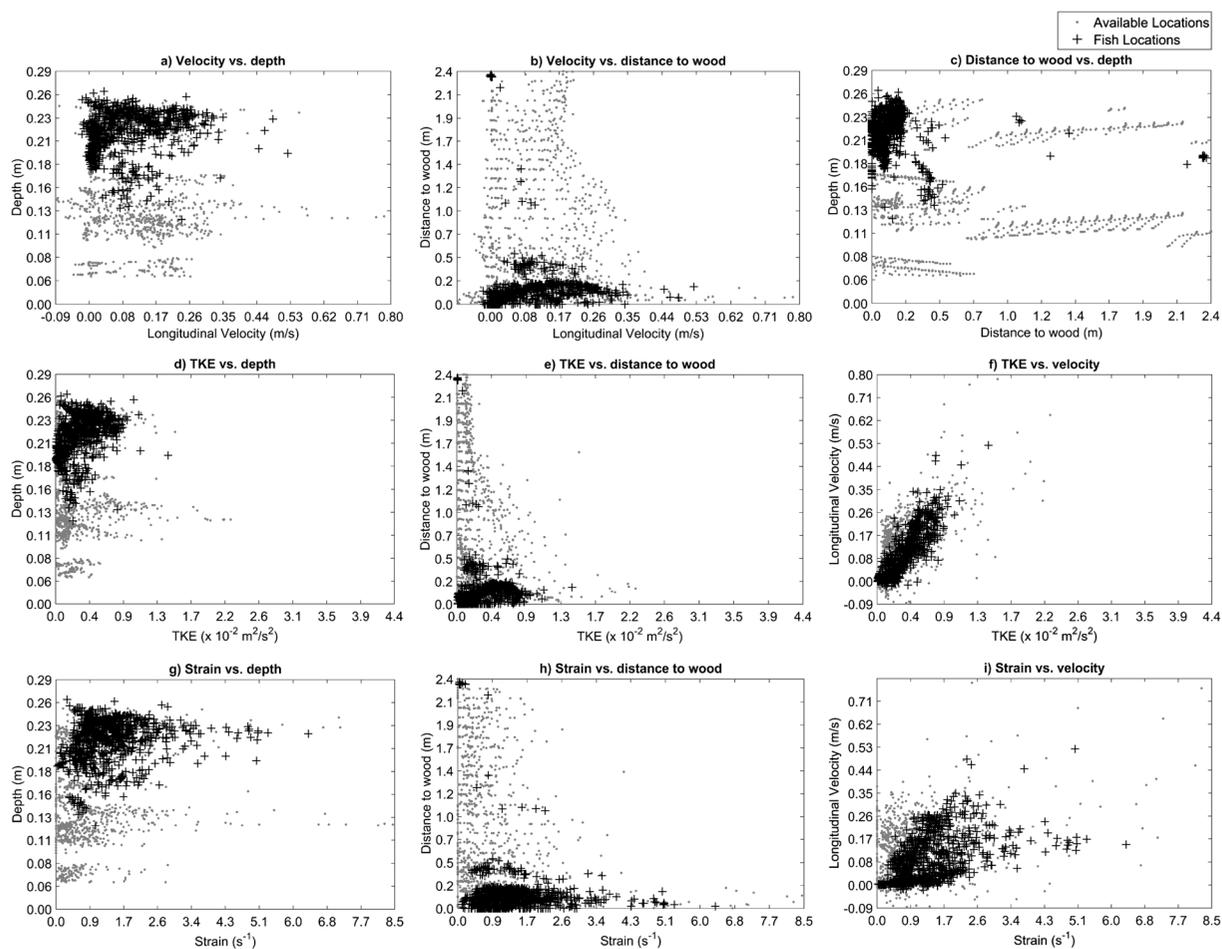


Fig. 9 Scatter plots of relationships between hydraulic parameters: **a** velocity and depth, **b** velocity and distance to wood, **c** distance to wood and depth, **d** TKE and depth, **e** TKE and distance

to wood, **f** TKE and velocity, **g** Strain and depth, **h** Strain and distance to wood, **i** Strain and velocity

emphasized the largest values (Figs. 8a and 9a, c, d, g), within the relatively narrow range of available depths, which provided evidence that depth was the strongest factor in the selection of habitats. The lack of correlation for depth and relatively wide range of available hydraulic parameters indicated that, if fish selected for depth, they were not necessarily eliminating other hydraulic conditions (e.g. velocity, TKE, strain) from their selection criteria, as there was a range of hydraulic conditions for each depth.

Discussion and conclusions

It is clear that the reintroduction of wood into rivers has many benefits for fish, including beneficial impacts on velocities, foraging, and predation that can help

maximize net energy intake (see review in Gustafsson et al. 2012). However, the details of how wood impacts the flow field, and potentially the energy expenditure of overwintering juvenile salmonids, are not well understood. We thus attempted to investigate how juvenile coho perceived the potential benefits of large wood, using a physical model to examine fish selection of hydraulic refuge around a large wood jam. This study included a comprehensive investigation of the hydraulic environment, in terms of the spatial resolution of the measurements and the characterization of the flow field, around a commonly-implemented type of log jam to investigate which elements of the flow field were the strongest cues for fish in minimizing energy expenditure. This study also included a detailed set of observations on the selection of habitat by juvenile coho during the winter, which were

unique both due to the high-resolution of the location observations and given that most studies of fish selection of habitat have been conducted during warmer months (Huusko et al. 2007).

We found that the flow field was generally characterized by the two hypothesized regions of hydrodynamics, including a more turbulent region near the wood associated with flow divergence and convergence, and a second region of more parallel streamlines that resulted in lower variability in velocities over space and time downstream of the wood. Broadly, fish primarily selected microhabitats near the bed and the wood, in regions of minimum velocities, consistent with observations of juvenile coho in summer (Fausch 1993) and salmonids generally in winter (Huusko et al. 2007), but also in areas of non-minimum TKE and strain.

The results emphasized two primary findings. First, depth, and distance to wood to a lesser extent, appeared to dominate selection of habitats over the hydraulics of the flow field. This result is consistent with knowledge that juvenile coho generally use slow, deep pools (Hartman 1965), and that juvenile coho aggregate near the bed during winter when stream temperatures are low (Mason 1966). The strength of selection for depth was underscored by the correlations between and the ranges of hydraulic parameters around the wood. In the regions selected by fish, the flow field was of similar intensity, regardless of whether measured as the velocity magnitudes, or the temporal or spatial variability in those velocities. Furthermore, particularly for the flow field located farther from the wood, the range of velocities and turbulence was much narrower than the range of depth. As such, fish appeared to be selecting habitats based on depths, given that similar hydraulic conditions were available at other depths.

While studies have demonstrated the importance of turbulence on swimming activity and costs (McLaughlin and Noakes 1998; Enders et al. 2003; Tritico and Cotel 2010), habitat selection (Vehanen et al. 2000; Smith et al. 2005; Enders et al. 2009) and behavior of fish (Lupandin and Pavlov 1996; Pavlov et al. 2000), the correlated nature of the flow field and the clear importance of depth made it infeasible for us to confirm our hypothesis that TKE and strain were important to juvenile coho in the selection of habitats during winter conditions at low flows. Instead, fish were observed in regions of non-minimal turbulence, which indicated that fish were not selecting their positions to minimize turbulence but instead prioritized depth in

selection of habitats. These results led us to the hypothesis that thresholds exist in water temperature and velocities below which velocity and turbulence are of limited importance relative to the cover of depth and wood. Regarding temperature, Chapman and Bjorn's (1969) work suggested that 4 °C was a threshold temperature below which salmonids display cover-seeking behavior, whereas Taylor (1988) found in preliminary work that temperatures below 5 °C impacted juvenile salmonid locations. Regarding velocity and turbulence thresholds, Smith et al. (2005) found that rainbow trout differentially selected habitats in areas of contrasting velocity and turbulence as discharge increased, choosing a high velocity, low turbulence environment at lower flows and a low velocity, higher turbulence environment at higher flows. The potential for temperature and velocity to act as thresholds in habitat selection requires further and detailed investigation, with important impacts on the design of habitats to aid in juvenile salmon winter survival. If fish prioritize depth and cover in winter, at the expense of minimizing energy expenditure, not all LWD structures would be equally beneficial. The interactions between cover and hydraulics may thus be an important element of LWD structure design.

Study limitations and further work

In this experiment, we deliberately eliminated foraging opportunities and visibly screened predators using shade cloth in order to reduce the variability in state conditions that may influence a fish's decision on habitat selection (Houston and McNamara 1999) and to emphasize the impact of hydrodynamics on a juvenile coho's decision around minimizing energy expenditure during winter conditions. However, we acknowledge that eliminating foraging opportunities oversimplified the problem of detecting decision processes of the fish. Fish select microhabitats based on a wide range of behavioral and evolutionary compromises to balance energy intake and expenditure, including intraspecific hierarchies (Fausch 1984), competition and predation (Facey and Grossman 1992), cover (Kawai et al. 2014) and the interactions between turbulence and cover (Smith et al. 2005). In addition, and potentially of most importance to the bioenergetics of fish (Boisclair and Tang 1993; Hill and Grossman 1993), the energetic costs of detecting and capturing prey may be impacted by large wood. These foraging activities are correlated to velocity (Hughes and Dill 1990; Hughes et al. 2003) and its

variability (Piccolo et al. 2008). However, despite the growing body of literature on the bioenergetics of foraging (see 2014 special issue of *Environmental Biology of Fishes* for recent review), these relationships are complex and not well understood (Hughes et al. 2003; Piccolo et al. 2008). For example, the rate of encountering prey may increase with increasing velocity (Nislow et al. 1999; Hayes et al. 2000), while the probability of capturing prey decreases with increasing velocity (Hill and Grossman 1993; Nislow et al. 1999; Piccolo et al. 2008). Furthermore, cover has been shown to reduce activity and aggression (Sundbaum and Näslund 1998; Harvey et al. 1999; plus see reference within Gustafsson et al. 2012), but also can reduce foraging success (Gustafsson et al. 2012), due to shading (Wilzbach et al. 1986) or to a reduction in the search window size (O'Brien and Showalter 1993; Giannico 2000). Thus, in light of these complex interactions between the flow field, cover, energy expenditure, and foraging activities, we attempted to eliminate the latter to gain simple, and simplified, understanding on the potential impact of turbulence on the selection of resting habitats.

Thus, like habitat-preference models, with their known limitation of eliminating foraging (Nislow et al. 1998; Giannico 2000; Imre et al. 2004), this study does not include energetic costs or benefits of foraging. The transferability of the results is thus similar to laboratory experiments that lack the complexity of natural systems (Lawton 1996). However, despite being a 1:1 scale model, the goal of the experiments was not to be a complete replicate of the field site. The intent was to better understand the impacts of large wood on the selection of habitats by juvenile coho during winter, a bottleneck in their life cycle. The results indicated that depth was of primary importance to the juvenile coho under the conditions of our study.

This study represented a highly focused analysis of a very rich dataset that is limited in scope and points to needs for further investigation. First, regarding limitations, while habitat suitability appears to be transferrable in some circumstances (Mäki-Petäys et al. 2002), the selectivity of hydraulic habitats around wood will likely vary with jam architecture, discharge, temperature (Watz et al. 2014), as well as fish species and life stage. Second, regarding further investigation, the study of interactions between velocity, turbulence, and especially foraging activities is likely to be an important advancement in understanding fish bioenergetics but will require enormously complex experiments. Finally, we believe

that a primary goal of studies such as this, which use high-resolution instrumentation and datasets to re-evaluate relationships established by coarse observations of ecosystems, should be to determine the context and management goals for which high-resolution observations are warranted. In the case of juvenile coho selection of habitats in winter conditions with low flow, it appears that both the magnitude and variability of the flow field may be of limited importance relative to depth and cover. Thus, evaluation of and management for juvenile coho winter habitat that are based on the turbulent environment may not be warranted. However, the importance of turbulence may be dependent on water temperature and flow intensity. Thus, future investigations should evaluate the role of turbulence around roughness element in warmer conditions and at higher flows to evaluate how the tradeoffs that fish make between cover and minimizing energy expenditure vary across potential thresholds of water temperature and flow intensity.

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