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# 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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- 1 Fish use of turbulence around wood in winter: Physical experiments on hydraulic
- 2 variability and habitat selection by juvenile coho salmon, Oncorhynchus kisutch
- 3
- 4 Desirée Tullos, PhD, PE
- 5 Biological and Ecological Engineering, Oregon State University, 116 Gilmore Hall,
- 6 Corvallis, OR 97330 USA
- 7 Email: desiree.tullos@oregonstate.edu
- 8 Phone: 541.737.2038; Fax: 541.737.2082
- 9
- 10 Cara Walter
- 11 Biological and Ecological, Oregon State University, 116 Gilmore Hall, Corvallis, OR
- 12 97330 USA
- 13 Email: walterc@onid.oregonstate.edu
- 14 Phone: 541.737.8612; Fax: 541.737.2082
- 15

#### 16 Abstract

- 17 Re-introduction of large wood for expanding hydraulic variability is an
- 18 increasingly common practice, yet it is not yet known what elements of hydraulic
- 19 variability are most beneficial to fish. In an experiment designed to emphasize the
- 20 minimization of energy expenditure through controlled predation and drift, we
- 21 investigated whether juvenile coho, under winter conditions, discriminated
- 22 between microhabitats based primarily on flow strength, depth, distance to wood,
- 23 or based on temporal or spatial variability of the flow field, with the hypothesis
- 24 that turbulence would be a strong factor in habitat selection. We conducted
- 25 physical experiments in a 1:1 scale model of a large wood jam at the Oregon
- 26 Hatchery Research Center in Alsea, Oregon. We conducted high resolution (0.1
- 27 m) mapping of the flow field using an acoustic Doppler velocimeter array and
- 28 underwater videogrammetry of fish locations. Results indicated that discrimination
- 29 of microhabitats by juvenile coho salmon in cold, low flows emphasized depth and
- 30 distance to wood over any hydraulic measures of the flow field. Correlations
- 31 between hydraulic parameters and distance to wood limited our ability to 32
- distinguish the importance of turbulence measures relative to velocities, but 33
- highlighted the positive relationships between velocity and turbulence measures 34 and the negative relationships between hydraulics and distance from the roughness
- 35
- elements. Findings suggest areas of further study including potential thresholds of
- 36 temperature and flow intensity on the importance of turbulence in habitat
- 37 selection.
- 38
- 39

#### 40 Kev words

- 41 Bioenergetics; Physical model; Acoustic Doppler velocimeter; Large woody
- 42 debris, River restoration; Woody debris habitat; velocity refuge
- 43
- 44

## 46 Introduction

47

48 Following decades of removal of wood from rivers for navigation, log drives, fish 49 passage, and water quality (Sedell and Luchessa 1982; Bryant 1985; Stednick 2010), 50 reintroduction of large woody debris (LWD) is now one of most common restoration 51 practices in the Pacific Northwest (Katz et al. 2007) and is widely practiced elsewhere 52 (Bernhardt et al. 2005; Nagayama and Nakamura 2009). In recognition of the important 53 benefits of large wood to river morphology (Robinson and Beschta 1990; Abbe and 54 Montgomery 1996; Hogan et al. 1996) and ecology (Bustard and Narver 1975; Swanson 55 and Lienkaemper 1978; Harmon et al. 1986; Hicks et al. 1991; Thomson 1991; Koski 56 1992), objectives of reintroducing large wood into rivers often include sediment and 57 wood retention, increased hydraulic variability, and increased habitat heterogeneity 58 (Brooks et al. 2006). Observational evidence (e.g. Cederholm et al. 1997; Roni and Quinn 59 2001; Pess et al. 2012) has indicated that reintroducing wood may be effective in the 60 recovery of salmonids, with higher densities in reaches treated with large wood relative to 61 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 Gustaffson et al. 2012 for negative impacts on

69 foraging); 3) visual isolation from predators and conspecifics (Wilzbach 1985; Sundbaum 70 and Näslund 1998; Crook and Robertson 1999; Harvey et al. 1999; Allouche 2002; 71 Nagayama and Nakamura 2009; Kawai et al. 2014); and 5) a substrate for 72 macroinvertebrate biomass (Spänhoff et al. 2000; Hernandez et al. 2005). In particular, 73 the contribution of large wood to establishing low-velocity shelters adjacent to high 74 velocity areas with high drift densities, which are especially important to maximizing 75 energy gain (Fausch 1984), may be a potentially critical element in the recovery of 76 salmonids.

77 While it appears that, for much of the year, the swimming costs associated with 78 active foraging attempts outweigh the importance of maintaining position (Boisclair and 79 Tang 1993; Hill and Grossman 1993), the importance in bioenergetics for juveniles may 80 shift from maximizing energy gain to minimizing expenditure in winter when 81 temperatures are cold (Heggenes et al. 1993; Garvey et al. 2004; Huusko et al. 2007). 82 Even at the lower activity levels and metabolic rates associated with low winter 83 temperatures, juvenile salmonids often enter winter with low initial energy stores and 84 accumulate a net metabolic deficit over the winter, which appears to reduce their survival 85 (see Huusko et al. 2007 for details and references). The velocity shelters (cf Fausch 1993) 86 selected by juvenile fish during winter (Rimmer et al. 1984; Heggenes et al. 1993) 87 presumably improve survival through decreasing juvenile's use of energy stores. Given 88 the importance of winter habitats as a bottleneck for juvenile coho survival (Nickelson et 89 al. 1992; Solazzi et al. 2000), the benefit of introducing wood to support minimizing 90 energy expenditure should be large.

91	The application of the concept of velocity shelters in bioenergetics models and in
92	habitat design has thus far assumed that areas of low velocity are consistent with areas
93	where fish can minimize energy expenditure (Fausch and White 1981). However,
94	turbulence is known to influence energy dynamics of the flow field and is not always
95	correlated with velocity, particularly in pools (MacVicar and Roy 2007a; MacVicar and
96	Roy 2007b) and around roughness elements (Papanicolaou et al. 2012), features that
97	define the hydraulics around LWD. Turbulence describes the temporally and spatially
98	fluctuating features of fluid flow that are characterized by randomness, diffusivity, three-
99	dimensional vorticity, and energy dissipation (Tennekes and Lumey 1972). These
100	fluctuations are generated by the shearing of flow across simple velocity gradients from
101	the bed to the channel surface, and from the separation and convergence of flow around
102	roughness elements (Roy et al. 2004; Smith et al. 2005). Thus, it is the case that areas of
103	similar velocity can have both high and low turbulence intensities, depending on the
104	mechanism responsible for the shearing of flow that generates turbulence.
105	The distinction between velocity refuges with varying turbulence levels is of
106	significance to fish bioenergetics because studies indicate that fish typically expend more
107	energy in higher turbulence environments (Boisclair and Tang 1993; Krohn and Boisclair
108	1994; McLaughlin and Noakes 1998; Enders et al. 2003; Tritico and Cotel 2010; plus see
109	Liao 2007 for comprehensive review of fish use of turbulence). Meanwhile, fish have a
110	diminished ability to swim, accelerate, and maintain position during winter conditions
111	when temperature is low (Rimmer et al. 1985; McMahon and Hartman 1989; Graham et
112	al. 1996). Thus, avoiding turbulence could be particularly important to the bioenergetics
113	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.

117 To begin investigating the use and benefit of flow field variability around wood for 118 juvenile coho, we conducted a mensurative, 1:1 scale experiment in outdoor stream 119 channels with high-resolution observations of the three-dimensional velocities and fish 120 locations around a full-channel log jam. Generally, our interest was in investigating the 121 bioenergetic benefits of wood for minimizing the energy expenditure of juvenile coho in 122 winter. More specifically, we hypothesized that a) based on contour plots and reach-scale 123 correlations, the flow field around the log jam would include two types of velocity 124 refuges: areas of higher turbulence due to flow divergence and convergence around the 125 obstruction of the wood and areas of lower turbulence in the pool downstream of the 126 wood, b) under the assumption that fish were selecting habitats to minimize energy 127 expenditure, distributions of available and observed locations of fish would indicate that 128 fish selected habitats in areas of the lowest turbulence and velocity. By replicating the 129 habitat and flow of a natural channel but restricting foraging opportunities and predation, 130 we sought to identify the hydraulic habitat fish would most often and most reliably select 131 to minimize energy expenditure.

132

133 Materials and Methods

134

135 Experimental design

136	We conducted the experiment as a 1:1 scale physical model of a full channel jam
137	and related channel topography in one of the outdoor experimental channels (Fig.
138	1) at the Oregon Hatchery Research Center near Alsea, Oregon (Noakes &
139	Corrarino 2010). The concrete channels are each 7.6 m wide and 61 m long, filled
140	with gravel to wetted widths of 1.3-4.7 m and depths of 0.1-0.3 m for our
141	experiments. We restricted observations of hydraulics and fish to 4.6 m
142	longitudinally to focus on the areas immediately surrounding the large wood. We
143	used three logs of 0.25 to 0.8 m diameter to replicate the prototype full channel
144	jam on Canal Creek, a tributary of the Alsea River near Tidewater, OR. For the
145	experimental channels, water flow is diverted from Fall Creek, also a tributary of
146	the Alsea River, through a settling basin and was held at a discharge of 0.045 $m^3 s^{-1}$
147	for the duration of the experiments, representative of baseflow conditions at the
148	prototype jam. Hydraulic conditions during the experiments were subcritical, with
149	a mean Froude number of 0.1, and fully turbulent, with a mean Reynolds number
150	of 9 x $10^5$ .
4 2 4	

151 Given that the state of the fish can influence its behavioral decisions 152 (Houston and McNamara 1999), we deliberately constrained the experiments to 153 emphasize state variables that relate to a fish's selection of hydraulic microhabitat. 154 We limited our experiment to wild juvenile coho salmon (Oncorhynchus kisutch), 155 approximately 10 cm fork length, kept at consistent energy reserves maintained 156 through controlled feeding, at a constant temperature of 7 (+/- 1) °C. Furthermore, 157 we screened drift from the channels and installed an overhead shade cloth. The 158 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.

165

166 Observations of fish

167 Juvenile wild coho were collected by seine from Fall Creek November 30, 168 2012 for observation in the experimental channels. Fish were held in a single 6' 169 shaded circular fiberglass tank with Fall Creek water running at an exchange rate 170 of 26 minutes. Fish were provided 1.5mm pellets and salmon roe 2-3 times daily 171 during the time they were held. Fish were observed over 2-hour periods, one 172 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 20<sup>th</sup>. 173 174 The channels were cleared of fish by electroshocking at the end of all 175 observations. Recovered fish were euthanized using tricaine methanesulfonate 176 (MS-222) and analyzed for weight, fork length, and preserved (10% formalin, 177 70% alcohol) for analysis of gut contents. The two observed group sizes represent fish densities of  $0.3 \text{ fish/m}^2$  and 178 179 0.6 fish/m<sup>2</sup>, which are similar to juvenile coho densities  $(0.15-0.66 \text{ fish/m}^2)$  found 180 by Ebersole et al. (2006) in the Oregon Coast Range. These two group sizes 181 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.

189 Fish were observed using underwater videogrammetry (Fig. 2) initially 190 with three pairs of cameras, then with six pairs of cameras for the second set of 191 observations starting February 19th. Paired videos were calibrated and analyzed in 192 VidSync (Neuswanger 2013; Leitshuh et al. 2014). We subsampled the videos by 193 recording fish coordinates every 20 seconds, resulting in over 800 observations of 194 exact focal position coordinates and orientations of the juvenile salmonids, with 195 each fish observed multiple times. For each camera pair, the coordinates of fish 196 observations were transformed via translation and rotation from the coordinate 197 system established in VidSync to match the coordinate system of the velocity 198 measurement locations using at least three control points in Cyclone (Leica 199 Geosystems 2012).

200

201 Observations of channel hydraulics

202 We made detailed observations of the flow field around the wood using an array

203 of four Acoustic Doppler Velocimeters (ADVs: SonTek 16 MHz MicroADV)

which we operated for 5 minutes at 50 Hz at each location. The ADV array was

205	suspended from a free-standing instrumentation platform, which spanned the
206	wetted channel to avoid any hydraulic interference from the supports (Fig. 1).
207	Each ADV measurement was spatially located by measurements of distances
208	between the probes, instrument platform, and fixed channel structures. We used a
209	Cartesian coordinate system, with $u$ aligned longitudinally, $v$ oriented across the
210	channel, and w representing the vertical orientation. Three-dimensional velocities
211	were measured on a three-dimensional grid at 0.1m spacing. In addition,
212	irregularly-spaced measurements were collected in the regions around the wood.
213	This sampling program resulted in over 1500 measurement locations (Fig. 3) and
214	nearly 17 million observations of velocities. Raw ADV velocities were filtered in
215	WinADV (Wahl 2013) to remove data with low (<70%) average correlation
216	coefficients, low average signal to noise ratio (< 15 dB), and despiked using
217	phase-space thresholding (Wahl 2000; SonTek/YSI, 2001; Goring and Nikora
218	2002; Wahl 2003).
219	The temporal and spatial variabilities that characterize turbulence can be
220	summarized in a number of ways (see Nezu and Nakagawa 1993; Lacey et al.
221	2012 for review). In addition to the time-averaged longitudinal velocity (Eq. 1),
222	hydraulic variability may be defined over time by the turbulent fluctuations in
223	velocities, represented herein by turbulent kinetic energy (TKE, Eq. 2). TKE, as a
224	representation of energy extracted from the bulk flow by turbulent eddies
225	(Bradshaw 1985), has been shown to influence fish swimming performance and
226	holding position (Odeh et al. 2002; Silva et al. 2012) and increase swimming costs
227	(Enders et al. 2003). Locations with high TKE values may be generally avoided by

of spatial gradients in velocities, represented herein as a steady-state hydraulic

strain (Eq. 3). 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 2000).

234

 $uv - vu^2 + v^2$  Eq. 1

 $\overline{uv} = \sqrt{\overline{u}^2 + \overline{v}^2}$ 

where *u* and *v* represent the longitudinal and transverse velocities, respectively,

and the overbar represents time averaging.

238

239

240 
$$TKE = 0.5 * (RMS[u']^2 + RMS[v']^2 + RMS[w']^2)$$
 Eq. 2

241

242 where RMS represents the standard deviation for each velocity component.

 $strain(e) = \sqrt{\left(\frac{u_{i+1} - u_i}{x_{i+1} - x_i} + \frac{u_i - u_{i-1}}{x_i - x_{i-1}}\right)^2 + \left(\frac{v_{i+1} - v_i}{y_{i+1} - y_i} + \frac{v_i - v_{i-1}}{y_i - y_{i-1}}\right)^2 + \left(\frac{w_{i+1} - w_i}{z_{i+1} - z_i} + \frac{w_i - w_{i-1}}{z_i - z_{i-1}}\right)^2}{Eq. 3}$ 

245 where *w* represents the vertical velocity, i represents each location, i+1 represents

the closest adjacent location in the positive direction, i-1 represents the closest

adjacent location in the negative direction.

249 The three hydraulic metrics were each linearly interpolated (Clunie et al. 2007;

Enders et al. 2009) to two surfaces at 0.044 m and 0.129 m above the channel

251 bottom. These surfaces were used to plot contours over space, derive values at

252 observed fish locations, and derive values of available hydraulics at a 0.01m

- 253 horizontal and 0.02m vertical spacing.
- 254
- 255 Analysis of hydraulic habitat selection

256 Given that this was a mensurative experiment (cf Hurlbert 1984) and no treatment effects 257 were evaluated, we interpreted our results qualitatively to identify evidence of strong or 258 weak selection of habitats relative to what habitat was available to the fish. We generated 259 a null model, where the mechanism being evaluated was deliberately excluded (Gotelli 260 2001), based on a distribution of hydraulic habitat conditions in proportions equal to their 261 availability, in order to evaluate whether fish selection was expressed in our observations. 262 We applied the chi-square goodness of fit test to evaluate the null hypothesis that fish 263 choose the range of hydraulic habitats in proportion of their availability. This test 264 involves comparing the distribution of hydraulic values at locations where fish were 265 observed to the distribution of hydraulic values of available locations. For each metric, 266 we evaluated the distribution of values in ten bins spanning the range of the values at 267 available locations and sized such that there was approximately the same number of 268 available locations per bin. The observed frequency was calculated as the number of fish 269 observed at locations with values in each bin. We tested at the 95% confidence level with 270 9 degrees of freedom for a significance level of p < 0.05, where the p value represents the 271 probability that the deviation of the observed from the expected distribution is due to

chance alone.

273	
274	Results
275	Hydraulics around the full channel jam
276	The orientation of the flow field varies as flow moves through the jam.
277	Upstream of the log jam, flow is shallow, wide, and oriented downstream. As flow
278	moves through the log jam (Fig. 4, Fig. 5), it encounters areas of contraction,
279	expansion, acceleration and resistance, generating a variety of hydraulic
280	conditions over the short 4.6 m study reach, which can generally be organized into
281	two primary regions downstream of the jam. First, flow was constricted and
282	rapidly dropped into an approximately 1.3 m wide, 2.2 m long, turbulent jet
283	through the jam, which was split by a log in contact with the bed only at the
284	bottom of the jet (Fig. 4, Fig. 5). Flow moved laterally underneath this
285	downstream-oriented log then converged with the primary jet just downstream of
286	the jam. The second primary flow region reflects flow through the pool
287	downstream of the jam. In this region, flow advected downstream, with mostly
288	parallel streamlines, through a 0.3 m deep pool. In addition to these two primary
289	flow regions, a large, shallow, low velocity eddy was generated on the left,
290	looking downstream, downstream of the jam which fish appeared to avoid (Fig. 5).
291	The wood thus generated a turbulent, three-dimensional flow field in the area
292	immediately around the jam and an area of more downstream-oriented flow in the
293	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).

296 The magnitude of velocities were generally low (Fig. 5), primarily in the range of 0-0.3ms<sup>-1</sup>, which is consistent with other studies on the ranges of 1D 297 298 velocities used by juvenile coho around wood (e.g. Huusko et al. 2007, <0.4 m s<sup>-</sup> 299 <sup>1</sup>). The highest values were represented by downstream-oriented velocities in the 300 jet within the jam (Fig. 5). Near bed velocities attenuated approximately 1 meter 301 downstream of the jam, diminishing with distance downstream through the pool 302 (Fig. 4, 5). Peak values for TKE were concentrated in similar locations to velocity, 303 primarily at the top of the jam where the bed rapidly drops and flow splits around 304 the log in the jet (Fig. 6). Detectable values of TKE were primarily located in the 305 jet within and immediately downstream of the jam. The magnitude of hydraulic 306 strain, representing the spatial velocity gradients and the deformation of the flow 307 field, was also highest at the top of and within the jet (Fig. 7). Detectable values of 308 strain extended downstream through the pool, due in part to variability in the 309 vertical velocity component (data not presented).

310

311 *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)

316 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

320 strain, they were not exclusively found in low energy environments.

321

322 Selectivity of habitats based on focal position coordinates

323 Chi-square goodness of fit tests indicated that distributions of values for 324 observed and available locations were significantly different at the 95% 325 confidence level, with p < 0.001, for all metrics. Because we included multiple 326 observations per fish, each data point was not independent and pseudoreplication 327 was introduced by applying the chi-squared goodness of fit test to non-328 independent data (Hurlbert 1984). Thus, the chi-squared p-values were artificially 329 small. While the pseudoreplication means that our p-values were artificially small, 330 since the p-values values from the tests were all much smaller (p < 0.001) than the 331 typical threshold for significance (p<0.05), it was reasonable to conclude that the 332 observed distributions were significantly different from the available distributions 333 for all hydraulic parameters. However, due to the issues with pseudoreplication, 334 we did not attempt to interpret the relative differences in fit across the hydraulic 335 parameters based on chi-square values, which could otherwise have been used to 336 evaluate the relative importance of the hydraulic parameters in the selection of 337 habitats by the fish.

Instead, visual interpretation of the distributions provided some qualitativeevidence of which parameters were of importance in selection of habitat. Across

340 the range of hydraulic parameters, fish were most clearly over-represented in areas 341 of greater depths relative to the available depths (Fig. 8a) and shorter distances to 342 wood relative to the available distances to wood, suggesting depth and distance to 343 wood were important factors in the fish's selection of habitats. In contrast, for all 344 the hydraulic parameters (Figs. 8b-d), fish were observed in distributions more 345 similar to the distributions of available hydraulic conditions, indicating weaker 346 selection by the fish based on the flow field than on depth. Fish were most 347 commonly found and slightly overrepresented in the lowest velocities (Fig. 8b). In 348 contrast, fish were observed to be slightly overrepresented in locations of higher 349 TKE and hydraulic strain, relative to the available turbulence environments. Thus, 350 the observed-available distributions suggested that, during winter conditions and 351 without foraging opportunities, fish selected areas of greater depth, low velocities, 352 and low but not minimum turbulence intensity and flow field deformation, and 353 close to wood. Qualitatively, the distinction between the distributions did indicate 354 some discrimination based on distance to wood and depth, with weaker 355 discrimination based on velocity, turbulence, and strain. 356 *Relationships among hydraulic parameters* 357 Locations of peak magnitudes for the hydraulic parameters were correlated 358 in this experiment as indicated by Pearson correlation coefficients (Table 1). The

359 downstream-oriented velocity was correlated with TKE and hydraulic strain, and

- 360 TKE and strain were correlated to each other. To a lesser degree, distance to wood
- 361 was negatively correlated with the hydraulic parameters (Table 1). Notably, most

362 of the hydraulic parameters were not correlated with water depth. Only strain had363 a moderately weak correlation with water depth.

364 The nature of the relationships between hydraulic parameters was 365 highlighted by scatter plots (Fig. 9), which further illustrated the range of available 366 habitats selected by the fish. From the values of coefficient of variability for 367 available habitat parameters, the velocities, TKE and strain values, and wood 368 distances generally occurred over a wider range (Fig. 8b-f) than the relatively 369 narrow ranges of available depth (Fig. 8a). However, while the net CV values for 370 hydraulic parameters were higher than depths, the range of hydraulic conditions 371 did vary over space. As expected for a turbulent environment, velocities and 372 turbulence measures generally fell into a wide range near the wood ( $<\sim 0.2$  m away 373 from the wood) and a narrower range outside of the jet area (Fig. 9b, 9e, 9h). In 374 addition, the positive relationships between Vx and TKE (Fig. 9f) and Vx and 375 strain (Fig. 9i) for both used and available locations were evident, whereas the 376 lack of relationship between other parameters was also clear (Fig. 9a-e, Fig. g-h). 377 The most notable finding from the scatterplots is the observation of fish within a 378 narrow depth range that emphasized the largest values (Fig. 8a, Fig. 9a, 9c, 9d, 379 9g), within the relatively narrow range of available depths, which provided 380 evidence that depth was the strongest factor in the selection of habitats. The lack 381 of correlation for depth and relatively wide range of available hydraulic 382 parameters indicated that, if fish selected for depth, they were not necessarily 383 eliminating other hydraulic conditions (e.g. Vx, TKE, strain) from their selection 384 criteria, as there was a range of hydraulic conditions for each depth.

### 385 Discussion and Conclusions

386

387 It is clear that the reintroduction of wood into rivers has many benefits for fish, 388 including beneficial impacts on velocities, foraging, and predation that can help 389 maximize net energy intake (see review in Gustafsson et al. 2012). However, the details 390 of how wood impacts the flow field, and potentially the energy expenditure of 391 overwintering juvenile salmonids, are not well understood. We thus attempted to 392 investigate how juvenile coho perceived the potential benefits of large wood, using a 393 physical model to examine fish selection of hydraulic refuge around a large wood jam. 394 This study included a comprehensive investigation of the hydraulic environment, in terms 395 of the spatial resolution of the measurements and the characterization of the flow field, 396 around a commonly-implemented type of log jam to investigate which elements of the 397 flow field were the strongest cues for fish in minimizing energy expenditure. This study 398 also included a detailed set of observations on the selection of habitat by juvenile coho 399 during the winter, which were unique both due to the high-resolution of the location 400 observations and given that most studies of fish selection of habitat have been conducted 401 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

409 of non-minimum TKE and strain.

410 The results emphasized two primary findings. First, depth, and distance to wood to a 411 lesser extent, appeared to dominate selection of habitats over the hydraulics of the flow 412 field. This result is consistent with knowledge that juvenile coho generally use slow, deep 413 pools (Hartman 1965), and that juvenile coho aggregate near the bed during winter when 414 stream temperatures are low (Mason 1966). The strength of selection for depth was 415 underscored by the correlations between and the ranges of hydraulic parameters around 416 the wood. In the regions selected by fish, the flow field was of similar intensity, 417 regardless of whether measured as the velocity magnitudes, or the temporal or spatial 418 variability in those velocities. Furthermore, particularly for the flow field located farther 419 from the wood, the range of velocities and turbulence was much narrower than the range 420 of depth. As such, fish appeared to be selecting habitats based on depths, given that 421 similar hydraulic conditions were available at other depths. 422 While studies have demonstrated the importance of turbulence on swimming activity 423 and costs (McLaughlin and Noakes 1998; Enders et al. 2003; Tritico and Cotel 2010), 424 habitat selection (Vehanen et al. 2000; Smith et al. 2005; Enders et al. 2009) and behavior 425 of fish (Lupandin and Pavlov 1996; Pavlov et al. 2000), the correlated nature of the flow 426 field and the clear importance of depth made it infeasible for us to confirm our hypothesis 427 that TKE and strain were important to juvenile coho in the selection of habitats during 428 winter conditions at low flows. Instead, fish were observed in regions of non-minimal 429 turbulence, which indicated that fish were not selecting their positions to minimize 430 turbulence but instead prioritized depth in selection of habitats. These results led us to the 431 hypothesis that thresholds exist in water temperature and velocities below which velocity

432 and turbulence are of limited importance relative to the cover of depth and wood. 433 Regarding temperature, Chapman and Bjorn's (1969) work suggested that 4C was a 434 threshold temperature below which salmonids display cover-seeking behavior, whereas 435 Taylor (1988) found in preliminary work that temperatures below 5C impacted juvenile 436 salmonid locations. Regarding velocity and turbulence thresholds, Smith et al. (2005) 437 found that rainbow trout differentially selected habitats in areas of contrasting velocity 438 and turbulence as discharge increased, choosing a high velocity, low turbulence 439 environment at lower flows and a low velocity, higher turbulence environment at higher 440 flows. The potential for temperature and velocity to act as thresholds in habitat selection 441 requires further and detailed investigation, with important impacts on the design of 442 habitats to aid in juvenile salmon winter survival. If fish prioritize depth and cover in 443 winter, at the expense of minimizing energy expenditure, not all LWD structures would 444 be equally beneficial. The interactions between cover and hydraulics may thus be an 445 important element of LWD structure design.

446

#### 447 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

455	microhabitats based on a wide range of behavioral and evolutionary compromises
456	to balance energy intake and expenditure, including intraspecific hierarchies
457	(Fasuch 1984), competition and predation (Facey and Grossman 1992), cover
458	(Kawai et al. 2014) and the interactions between turbulence and cover (Smith et al.
459	2005). In addition, and potentially of most importance to the bioenergetics of fish
460	(Boisclair and Tang 1993; Hill and Grossman 1993), the energetic costs of
461	detecting and capturing prey may be impacted by large wood. These foraging
462	activities are correlated to velocity (Hughes and Dill 1990; Hughes et al. 2003)
463	and its variability (Piccolo et al. 2008). However, despite the growing body of
464	literature on the bioenergetics of foraging (see 2014 special issue of
465	Environmental Biology of Fishes for recent review), these relationships are
466	complex and not well understand (Hughes et al. 2003; Piccolo et al. 2008). For
467	example, the rate of encountering prey may increase with increasing velocity
468	(Nislow et al. 1999; Hayes et al. 2000), while the probability of capturing prey
469	decreases with increasing velocity (Hill and Grossman 1993; Nislow et al. 1999;
470	Piccolo et al. 2008). Furthermore, cover has been shown to reduce activity and
471	aggression (Sundbaum and Näslund 1998; Harvey et al. 1999; plus see reference
472	within Gustaffson et al. 2012), but also can reduce foraging success (Gustafsson et
473	al. 2012), due to shading (Wilzbach et al. 1986) or to a reduction in the search
474	window size (O'Brien and Showalter 1993; Giannico 2000). Thus, in light of these
475	complex interactions between the flow field, cover, energy expenditure, and
476	foraging activities, we attempted to eliminate the latter to gain simple, and

477 simplified, understanding on the potential impact of turbulence on the selection of478 resting habitats.

479 Thus, like habitat-preference models, with their known limitation of 480 eliminating foraging (Nislow et al. 1998; Giannico 2000; Imre et al. 2004), this 481 study does not include energetic costs or benefits of foraging. The transferability 482 of the results is thus similar to laboratory experiments that lack the complexity of 483 natural systems (Lawton, 1996). However, despite being a 1:1 scale model, the 484 goal of the experiments was not to be a complete replicate of the field site. The 485 intent was to better understand the impacts of large wood on the selection of 486 habitats by juvenile coho during winter, a bottleneck in their life cycle. The results 487 indicated that depth was of primary importance to the juvenile coho under the 488 conditions of our study.

489 This study represented a highly focused analysis of a very rich dataset that is 490 limited in scope and points to needs for further investigation. First, regarding limitations, 491 while habitat suitability appears to be transferrable in some circumstances (Mäki-Petäys 492 et al. 2002), the selectivity of hydraulic habitats around wood will likely vary with jam 493 architecture, discharge, temperature (Watz et al. 2014), as well as fish species and life 494 stage. Second, regarding further investigation, the study of interactions between velocity, 495 turbulence, and especially foraging activities is likely to be an important advancement in 496 understand fish bioenergetics but will require enormously complex experiments. Finally, 497 we believe that a primary goal of studies such as this, which use high-resolution 498 instrumentation and datasets to re-evaluate relationships established by coarse 499 observations of ecosystems, should be to determine the context and management goals

500	for which high-resolution observations are warranted. In the case of juvenile coho
501	selection of habitats in winter conditions with low flow, it appears that both the
502	magnitude and variability of the flow field may be of limited importance relative to depth
503	and cover. Thus, evaluation of and management for juvenile coho winter habitat that are
504	based on the turbulent environment may not be warranted. However, the importance of
505	turbulence may be dependent on water temperature and flow intensity. Thus, future
506	investigations should evaluate the role of turbulence around roughness element in warmer
507	conditions and at higher flows to evaluate how the tradeoffs that fish make between cover
508	and minimizing energy expenditure vary across potential thresholds of water temperature
509	and flow intensity.
510	

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Tables and Figures
<b>Table 1.</b> Pearson correlation coefficients for hydraulic parameters in the experimental
channel.
Fig. 1 Physical model and ADV instrumentation at the experimental channels at Oregon
Hatchery Research Center.
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Fig. 2 Underwater videogrammetry
Fig. 3 Channel topography, location and orientation of wood, and location of velocity
observations.
Fig. 4 Horizontal velocity vectors for bulk flow at 0.13m depth. Bold lines represent flow
paths.
Fig. 5 Longitudinal velocities at 0.13m depth and fish locations.
Fig. 6 TKE at 0.13m depth and fish locations.
Fig. 7 Hydraulic strain at 0.13m depth and fish locations.
<b>Fig. 8</b> 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.
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.