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Effects of habitat quality and ambient hyporheic flows on salmon spawning site selection

Rohan Benjankar[1], Daniele Tonina[1], Alessandra Marzadri[2], Jim McKean[3], and Daniel J. Isaak[3]

[1]Center for Ecohydraulics Research, University of Idaho, Boise, Idaho, USA, [2]Department of Civil, Environmental and Mechanical Engineering, University of Trento, Trento, Italy, [3]Rocky Mountain Research Station, U.S. Forest Service, Boise, Idaho, USA

Key Points:
- Channel hydraulics and morphological features are cues for spawning site selection
- Bed form-induced hyporheic fluxes are not a significant predictor of spawning site selection
- Aquatic habitat distribution from 2-D models supported by bathymetric lidar survey

Correspondence to:
R. Benjankar,
rohanb@uidaho.edu

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Abstract Understanding the role of stream hydrologic and morphologic variables on the selection of spawning sites by salmonid fishes at high resolution across broad scales is needed for effective habitat restoration and protection. Here we used remotely sensed meter-scale channel bathymetry for a 13.5 km reach of Chinook salmon spawning stream in central Idaho to describe habitat quality and set boundary conditions for a two-dimensional surface water model coupled with a three-dimensional hyporheic flux model. Metrics describing ambient hyporheic flow intensity and habitat quality, which is quantified as a function of stream hydraulics and morphology, were compared to the locations of nests built by female salmon. Nest locations were predicted most accurately by habitat quality followed by channel morphology (i.e., riffles location). As a lesser degree than habitat quality, water surface curvature was also a good indicator of spawning location because its intensity can identify riffle morphology. The ambient hyporheic flow predicted at meter-scale resolution was not a strong predictor of redd site selection. Furthermore, the study suggests direct morphological measurements obtained from easily measured channel bathymetry data could enable effective and rapid assessments of salmon spawning channels across broad areas.

1. Introduction

Salmon famously return to their natal streams [*Bjornn and Reiser*, 1991] where females dig nests (hereafter referred to as redds) in gravel substrates and deposit their eggs during the act of spawning [*DeVries*, 1997]. Completed redds have a distinctive shape characterized by a pit and a hump that resembles a dune-like bed form [*Crisp and Carling*, 1989] and range in size from tenths of a meter to several meters depending on the size and species of salmon. Habitat conditions in spawning streams are a key determinant of salmon population productivity, so understanding the factors that affect salmon redd site selection is important for management and habitat conservation [*Burnett et al.*, 2007]. It is assumed that female fish will select the highest-quality spawning habitat areas to lay their eggs [*Milhous et al.*, 1989], and previous studies showed that microscale (tenths of meters or $10^{-1}W$, where W is the channel width) habitat quality information on gravel size, percentage of sand, and hydraulic variables, such as water depth and stream velocity, may be primary predictors of salmonid spawning site selection [*Bernier-Bourgault and Magnan*, 2002; *Bjornn and Reiser*, 1991; *Gard*, 1998, 2009; *Geist and Dauble*, 1998; *Geist et al.*, 2000; *Isaak et al.*, 2007; *Mull*, 2005]. Habitat quality assessments have traditionally been done using costly and labor intensive in-stream hydromorphologic measurements [*Bovee*, 1978; *Bovee et al.*, 1998; *Leclerc et al.*, 1995, 1996].

Mesoscale habitat variables are also sometimes related to spawning sites [*Geist and Dauble*, 1998]. These variables include factors such as reach-averaged water depth, velocity, Froude number, velocity-depth ratio, water surface slope [*Hauer et al.*, 2009; *Jowett*, 1993; *Schweizer et al.*, 2007], and bed material size [*Montgomery and Buffington*, 1997] and are predicted with hydrodynamic models [*Brown and Pasternack*, 2009; *Gard*, 2009] or measured in the field [e.g., *Knapp and Preisler*, 1999; *Muhlfeld*, 2002; *Mull*, 2005]. Hydrodynamic models can be used to distinguish between specific geomorphologic and hydraulic patterns, such as pool, riffle, and run, and also employed to define different fish habitat units for habitat modeling at the mesoscale (tens of meters or $10^{1}W$) [*Hauer et al.*, 2009; *Pasternack*, 2011]. However, as highlighted in several studies, many other additional factors such as the presence of woody debris and vegetation cover, undercut banks, overhanging vegetation [e.g., *Merz*, 2001; *Witzel and Maccrimmon*, 1983], water temperature, dissolved oxygen concentration, hyporheic flow, and substrate conductivity [see *Geist and Dauble*, 1998; *Mull*, 2005] also influence spawning site selection.

It has been suggested that hyporheic flow and distinct areas of upwelling or downwelling should be important variables for spawning site selection [e.g., *Baxter and Hauer*, 2000; *Geist and Dauble*, 1998;

Shirvell, 1989; *Stuart*, 1953, 1954] because salmon embryos depend so strongly on the streambed environment [*Coble*, 1961; *Cooper*, 1965]. Hyporheic flows are the main process to deliver stream water constituents, including heat, nutrients, solutes, and particulates to the bed sediment environment, where biogeochemical reactions may occur [*Edwards*, 1998; *Harvey and Gooseff*, 2015; *Marzadri et al*., 2012, 2013; *Zarnetske et al*., 2011]. In particular, downwelling hyporheic flow forces oxygen-rich surface water to the incubating salmonid embryos and returning flows remove biological waste products [*Cooper*, 1965; *Tonina and Buffington*, 2009b; *Tonina et al*., 2015]. Hyporheic flow intensity is determined by several mechanisms, which include the interaction between stream flow and streambed morphology, sediment hydraulic conductivity heterogeneity, and lateral alluvial width and depth variations [*Boano et al*., 2014; *Tonina and Buffington*, 2009a; *Tonina*, 2012]. Here we define this exchange as *ambient* hyporheic flow to distinguish it from that generated by the change in bed morphology caused by construction of the redds themselves [*Cooper*, 1965; *Tonina and Buffington*, 2009b].

The importance of hyporheic flows is reinforced by the observation that salmonids prefer transitional areas between pools. These areas, which include the pool-tail [*Baxter and Hauer*, 2000], the riffle-crest [*Vronskii and Leman*, 1991], and the zones downstream of the riffle-crest [*Geist and Dauble*, 1998; *Hanrahan*, 2007], are characterized by abrupt changes in water surface elevations over short distances [*Marzadri et al*., 2010; *Trauth et al*., 2013]. Such water surface curvature is probably the primary driver for hyporheic flows in pool-riffle systems [*Tonina and Buffington*, 2007, 2009a; *Vaux*, 1968], although other mechanisms such as variations of near-bed pressure due to dynamic heads, alluvial volume, and sediment hydraulic conductivity may also affect hyporheic flow [*Boano et al*., 2009; *Elliott and Brooks*, 1997; *Marzadri et al*., 2014; *Stonedahl et al*., 2010, 2013; *Tonina and Buffington*, 2009a]. Consequently, riffle crests have been assumed to be a proxy for high-intensity hyporheic flows due to high gradients of the stream water surface [*Marzadri et al*., 2010; *Tonina and Buffington*, 2007].

Modeling the hyporheic fluxes along stream reaches requires coupling surface water and groundwater predictions [*Kasahara and Hill*, 2006; *Lautz and Siegel*, 2006; *Marzadri et al*., 2013]. Whereas this is feasible at the reach scale (10^2W, few kilometers), it is less viable at the river segment (10^3W, tens of kilometers) and river network (10^4W, hundreds of kilometers) scales. At the river segment, 2-D surface models can accurately predict the water surface elevation [*Lane and Ferguson*, 2005; *Pasternack et al*., 2004; *Pasternack and Senter*, 2011; *Tonina and Jorde*, 2013]. Therefore, we hypothesize that location of high water surface curvature, the second derivative of the water surface elevation, could be an effective index for hyporheic flow intensity [*Vaux*, 1962, 1968]. Convex-upward water surfaces indicate upwelling water, where sediment pore water exits the streambed, whereas concave water surfaces suggest downwelling areas, where stream water enters the streambed sediment [*Anderson et al*., 2005; *Tonina and Buffington*, 2009a; *Vaux*, 1962, 1968]. Thus, the intensity and shape of water surface curvature may be used to select areas with highly convex and concave bed form shapes, which should indicate strong upwelling or downwelling areas potentially preferred by female salmonids to construct redds [*Baxter and Hauer*, 2000].

In this study, we test the hypothesis that ambient hyporheic flow intensity, which is due to streambed-flow interaction, and habitat quality, which is quantified as a function of stream hydraulics and morphology, are important indexes of salmonid spawning site selection in rivers with pool-riffle morphology. Because water surface curvature, hereafter curvature, can be measured or predicted easier than hyporheic flows, we test whether curvature could be used as a surrogate of hyporheic flow. Additionally, curvature can be a proxy for the pool-tail and riffle-crest, where water surface slope changes abruptly in pool-riffle streams. We suggest that spawning site selection by Chinook salmon depends on habitat quality, which includes stream flow properties and bed morphology, and hyporheic flux intensity, and that curvature can be used to map areas of high hyporheic fluxes and/or location of riffles.

2. Methodology

To test our hypotheses, we developed a two-dimensional (2-D) depth-averaged surface water hydrodynamic model supported by high-resolution accurate bathymetry surveyed with the Experimental Advanced Airborne Research Lidar (EAARL) [*McKean et al*., 2009]. We numerically simulated water surface elevations, depth, and velocity at the microhabitat scale (meter scale) for a 13.5 km long reach of the Bear Valley Creek (Idaho, USA), an important Chinook salmon and Steelhead spawning stream. By coupling the predicted surface hydraulic variables of depth and velocity with biological habitat suitability curves, we quantified the habitat quality for Chinook spawners at the meter scale. We used the predicted water surface elevations as piezometric heads for the upper boundary of a three-dimensional (3-D) hyporheic flow model, which we

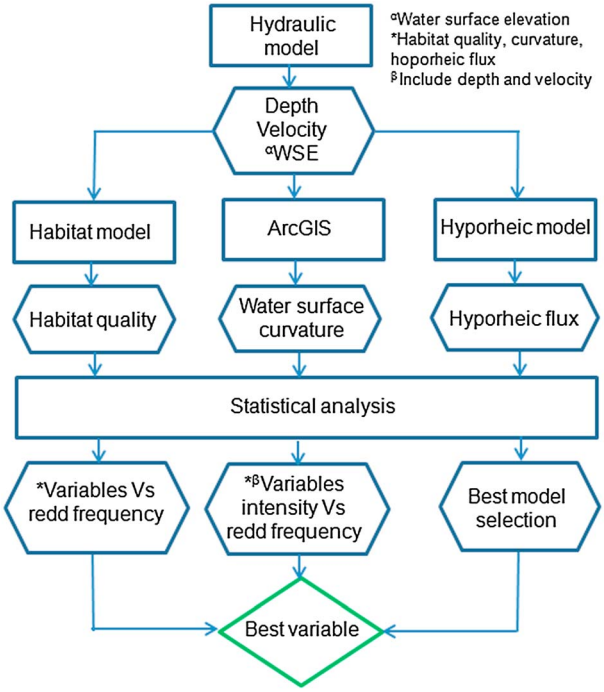

Figure 1. Flow chart showing model development, output variables, and statistical analyses to study important physical variables for redd site selection.

developed to quantify near-bed hyporheic flux intensities for selected reaches of the study area. We then statistically examined the relative contributions of ambient hyporheic flow intensity, spawning habitat quality and water surface curvature, to salmonid redd locations (Figure 1). We also tested whether these variables have similar values in locations with and without redds.

2.1. Study Area

Bear Valley Creek is a tributary of the Middle Fork Salmon River and is one of the most important Chinook salmon and Steelhead spawning streams in that river basin (Figure 2) [*McKean and Tonina*, 2013]. The watershed area upstream of the study site is approximately 161 km^2, and the elevation ranges from 1966 m to 2660 m. The watershed hydrology is snowmelt dominated with average annual precipitation of 767 mm. Base flows vary between 0.8 and 1.3 m^3/s during the fall and winter, and bankfull discharge is approximately 7 m^3/s [*Gariglio et al*., 2013; *McKean and Tonina*, 2013]. The flow hydrograph during the spawning period has been similar in the last 15 years with a discharge of about 1.15 m^3/s.

The average channel width and slope is approximately 15 m and 0.35%, respectively. Bed sediment is dominated by gravel with median grain size for the entire reach of $d_{50} = 54$ mm. The stream is sinuous, with a sinuosity index = 1.5 [*McKean and Tonina*, 2013] and flows through an extensive low-gradient meadow system. Streambed sediment has very low mobility even at and above bankfull flows, such as the 25 year return period flow, resulting in stable morphology and sediment patch distribution at the decadal time scale [*Maturana et al*., 2013; *McKean and Tonina*, 2013].

2.2. Redd Survey and Study Design

Salmon redd surveys were conducted in the spawning season (end of August and beginning of September) between 2005 and 2012 by using handheld GPS devices and located 68 redds within the study area (Figure 2). We surveyed redds by identifying the center of the redd, and in several instances we also mapped the perimeters of their occupied areas denoted by disturbed sediment overturned by spawning fish. Sediment mobility analysis showed that streambed morphology is stable and changes between years of redd surveys are negligible because coarse gravel particles are not mobile at bankfull flows in this meadow system where higher than bankfull discharges flood the nearby floodplain keeping shear stresses in the channel below those mobilizing the coarse sediment [*Maturana et al*., 2013; *McKean and Tonina*, 2013]. We extended the redd location by randomly selecting 67 additional locations without redds within the channel using the ArcGIS® tool "Create random points" without any constraint [see *Gard*, 2009; *Hanrahan*, 2007; *Isaak et al*., 2007]. This allowed us to quantify whether physical values such as habitat quality, water surface curvature, and hyporheic fluxes are similar in locations with and without redds (see example in Figure 2). We averaged the water depth, velocity, habitat quality, curvature, and hyporheic flux values within a 3 m-by-3 m cell window around each cell of interest. The spatial averaging was done because large salmonid redds occupy an area larger than a single 1 m-by-1 m cell and an average single Chinook redd area is between 6 and 9 m^2 [*Crisp and Carling*, 1989].

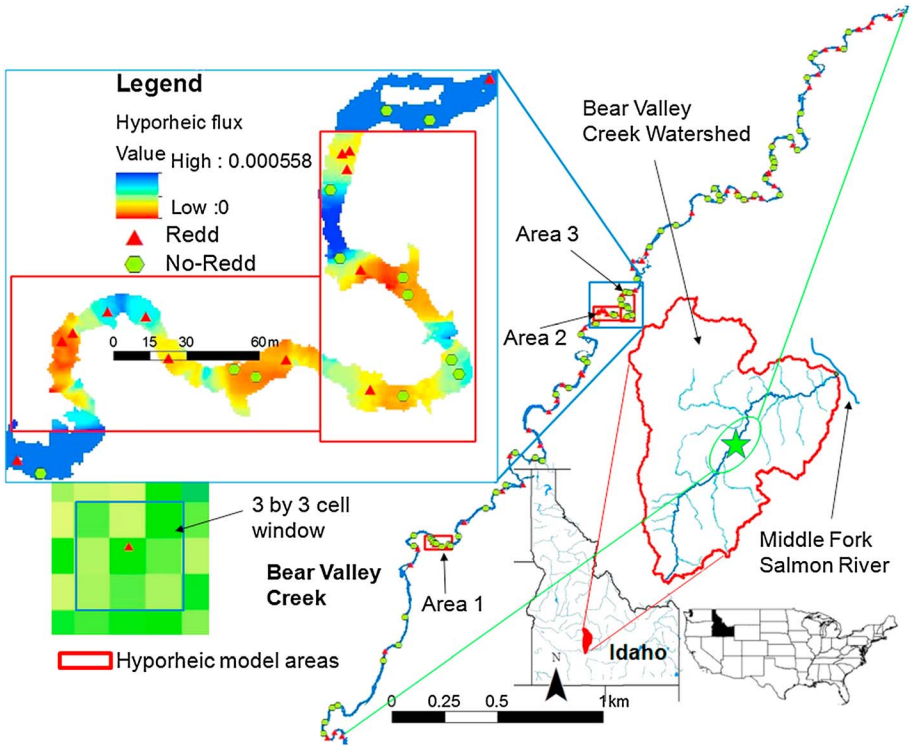

Figure 2. Bear Valley Creek study area with redd and no-redd locations and three subreaches, indicated by Areas 1, 2, and 3, where the hyporheic flow model is applied.

2.3. Model Development

2.3.1. Hydraulic Model Setup

We used MIKE21 software for the 2-D hydraulic model [*Danish Hydraulics Institute (DHI)*, 2011]. The model solves the time-dependent, vertically integrated Reynolds Averaged Navier-Stokes (RANS) equations of mass and momentum conservation in the two horizontal directions with a finite difference algorithm [*DHI*, 2011]. It simulates unsteady two-dimensional hydraulic variables based on channel bathymetry, bed resistance, and lateral eddy (turbulence closure) coefficients [*Tonina and Jorde*, 2013].

We set up the 2-D model for a 13.5 km of Bear Valley Creek between Cache and Elk Creeks by using a high-resolution (1 m grid cell) digital elevation model generated from airborne bathymetric lidar data acquired with the Experimental Advanced Airborne Research Lidar (EAARL) [*McKean et al*., 2009, 2014]. The EAARL sensor provides a relatively high density of bathymetric measurements (~1 m spacing) with vertical accuracy (0.10–0.15 m) adequate to support two-dimensional numerical modeling [*McKean et al*., 2014]. The bathymetry is the same used in previous publications where we tested its accuracy, ability to support 2-D numerical modeling [*McKean et al*., 2014], and investigate grain mobility [*McKean and Tonina*, 2013] and sediment transport [*Maturana et al*., 2013]. Similarly, we used the uniform Manning's roughness value calibrated and validated in those previous published works [*Maturana et al*., 2013; *McKean and Tonina*, 2013; *McKean et al*., 2014] for the entire study reach. We modeled a low flow condition of 1.15 m^3/s appropriate for the spawning period of Chinook salmon in the last decades. Comparison between observed and simulated water surface elevation shows a root-mean-square error of 0.11 m.

2.3.2. Habitat Model Development

Habitat quality is a dimensionless index that ranges from 0 (poor quality) to 1 (excellent quality). It indicates whether physical variables such as depth and velocity are within the range required by the selected species for a particular life stage at the local scale [*Bovee*, 1978]. We used the geometric mean of individual suitability indexes to determine the overall combined cell habitat quality [*Moir et al*., 2005; *Tonina et al*., 2011]. We represent the habitat quality as a function of depth and velocity, two commonly used variables in aquatic habitat modeling [see *Hanrahan et al*., 2004a]. We did not include substrate size in our analysis because median gravel

size of 35 mm, suitable for spawning, is ubiquitous throughout the study reach [*McKean and Tonina*, 2013]. We quantified the habitat quality from spatially distributed numerically predicted depths and velocities and univariate spawning habitat preference curves adopted from previous studies [*Bjornn and Reiser*, 1991; *Carnie et al*., 2015; *Groves and Chandler*, 1999; *Hampton*, 1988; *Raleigh et al*., 1984; *Smith*, 1973; *Tonina et al*., 2011].

2.3.3. Water Surface Curvature

We calculated curvature in the direction of the maximum slope from numerically predicted water surface elevations using the "Curvature" tool in ArcGIS®. The geographic information system (GIS) program computes the curvature at a cell by fitting the surface through that cell and its eight surrounding neighbors. A nine-term fourth-order polynomial equation was fitted to a surface composed of a three-by-three cell moving window for each cell [*Moore et al*., 1991; *Zevenbergen and Thorne*, 1987]. A positive second derivative corresponds to a locally convex-upward water surface, whereas a negative value corresponds to a concave surface. We computed curvature on a cell-by-cell (1 m grid cell) basis. We calculated the absolute values of curvature because salmonids spawned in both convex and concave zones, so intensity is the important characteristic, rather than direction.

2.3.4. Hyporheic Flux Model

The analysis of the hyporheic flow was focused on three subreaches of the study area characterized by a high concentration of redds (Figure 2). One of these, Area 2, was previously analyzed both in terms of spatial and temporal changes in hyporheic fluxes [*Gariglio et al*., 2013] and in terms of the role that stream morphodynamics plays in controlling the hyporheic zone thermal regime [*Marzadri et al*., 2013]. Here, we took advantage of these previous studies, and in particular, we extended the model proposed and validated by *Marzadri et al*. [2013] to Area 1 and Area 3 (Figure 2). The hyporheic model of *Marzadri et al*. [2013] performed very well in matching measured temperature fluctuations within the streambed sediment. Comparisons between Gariglio's temperature-derived velocities and those predicted by the hyporheic model show differences within 10% for all 17 locations at both 10 and 20 cm below the original streambed with a root-mean-square error of 5.14 10^{-5} m/s.

The hyporheic flow intensity in each cell was obtained by solving the equations of Laplace (equation (1)) and Darcy (equation (2)):

$$\nabla^2 h = 0 \tag{1}$$

$$\mathbf{u} = -\frac{K}{n}\cdot\nabla h \tag{2}$$

where **u** is the seepage velocity, K is the hydraulic conductivity, n is the sediment porosity, and h is the energy head [*Elliott and Brooks*, 1997; *Marion et al*., 2002], under the assumption of homogeneous and isotropic porous media [*Marzadri et al*., 2010]. We used the following boundary conditions: (i) a predicted water surface elevation represented in terms of a Fourier transform at the upper boundary, (ii) an impervious layer mimicking the behavior at the bottom of the alluvial sediment, and (iii) lateral boundary conditions obtained by interpolating the value of piezometric head along the banks to the adjacent floodplain. Following the work of *Tonina and Buffington* [2007, 2009b] and *Trauth et al*. [2013], water surface elevation expresses the portion of the total head inducing hyporheic flows for large bed forms. This implies that dynamic head associated with velocity losses has negligible effect at the pool-riffle scale [*Gomez-Velez and Harvey*, 2014]. For this study, the simulated water surface was extended in the floodplain by interpolation between meanders to provide the lateral boundary conditions of the system. This last approximation should be considered adequate for late summer periods, as supported by the analysis of the hyporheic flow time series performed by *Gariglio et al*. [2013] in Area 2.

2.4. Statistical Analysis

2.4.1. Correlations Between Physical Variables and Redd Frequency

Water surface curvature intensity and hyporheic fluxes were distributed into 10 classes based on their percentage distribution using a quantile method that assigns an equal number of cells to each class (equal probability). Thus, class 1 contains 10% of curvature cells that have lowest intensity, whereas class 10 contains 10% of curvature cells with highest intensity. We also classified habitat quality (0–1) into 10 classes using a 0.1 increment. Habitat quality 0–0.1 was assigned class 1, whereas quality 0.9–1.0 was class 10. Finally, we calculated the number of redds in each variable class in order to analyze correlations between variable intensity and redd frequency. The null hypothesis is no correlation between variables and frequency of redd and no-redd locations. We also compared curvature and hyporheic flux at the cell-by-cell resolution to examine correlation between these two variables. The null hypothesis of this analysis is no correlation between

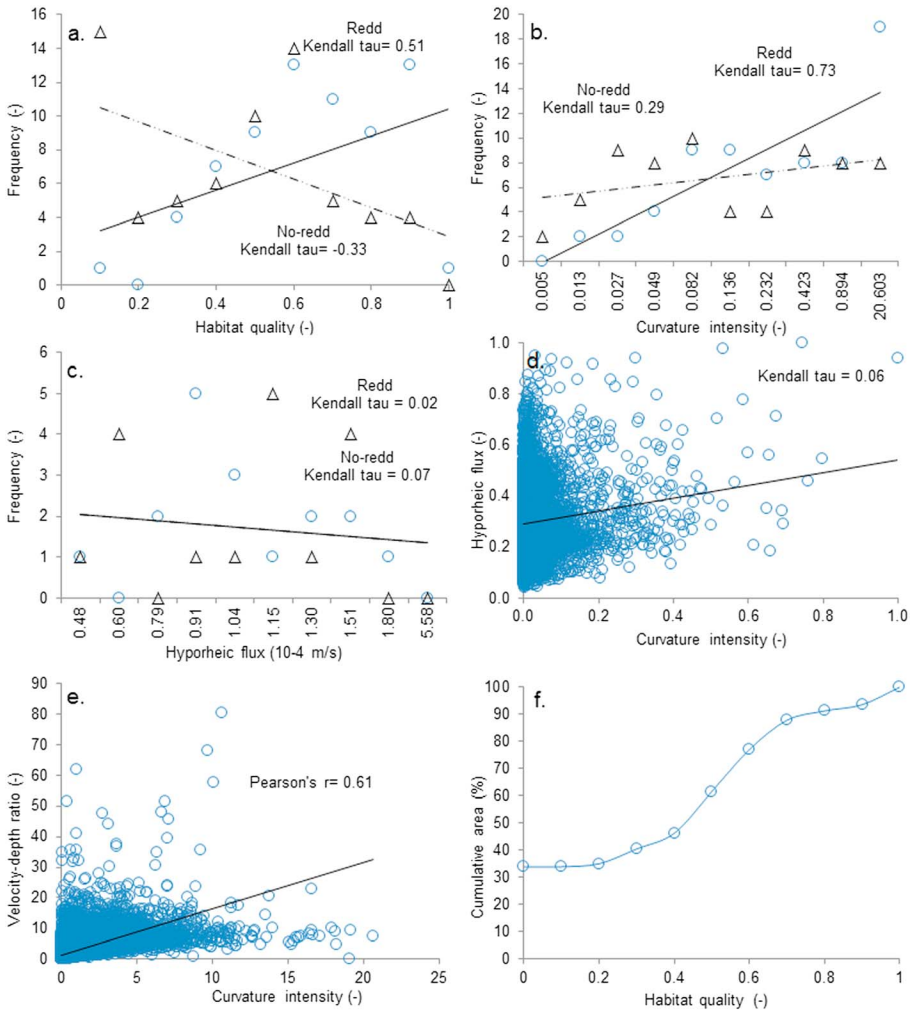

Figure 3. Number of redd (circle) and no-redd (triangle) locations with respect to (a) habitat quality, (b) curvature intensity, and (c) hyporheic flux. The solid and dotted trend lines are for redd and no-redd locations, respectively. (d) The correlation between curvature and hyporheic flux both normalized with their respective maximum values, (e) correlation between curvature and velocity-depth ratio, and (f) cumulative distribution function of aquatic habitat quality.

curvature and hyporheic flux intensity. We further analyzed the correlation between velocity-depth ratio and curvature, which is used to define mesohabitat types [*Hauer et al*., 2009; *Jowett*, 1993].

We used Kendall's τ [*Kendall*, 1955] method to test our hypotheses using the tool "Real Statistics Using Excel" (http://www.real-statistics.com/). This is a nonparametric statistical test appropriate for ordinal data [*Mrakovcich*, 1998]. The Kendall's τ can be interpreted as a difference between the probabilities that the observed data are in the same order against their not being in the same order [*Abdi*, 2007]. It is the most commonly used approach to test the hypothesis of no correlation between two sets of independent data.

2.4.2. Intensity of Physical Variables at Redd and No-Redd Locations

We used the Mann-Whitney test for two independent samples [*Mann and Whitney*, 1947] to test the hypothesis that differences in intensities of the variables water depth, velocity, habitat quality, curvature, and hyporheic fluxes are statistically greater (at $\alpha = 0.05$) at the redd versus no-redd locations. The Mann-Whitney test is one of the most well-known nonparametric significance tests, which examine if one of two samples from independent observations tends to have larger values than the other [see *Benjankar et al*., 2015; *Gard*, 2009]. The null hypothesis is no differences in variable intensities between redd and no-redd locations.

2.4.3. Best Model Selection

We used a logistic function to develop models that predict the probability of redd occurrence from each variable (i.e., habitat quality, curvature, and hyporheic flux) or their combination. We tested the hypothesis that

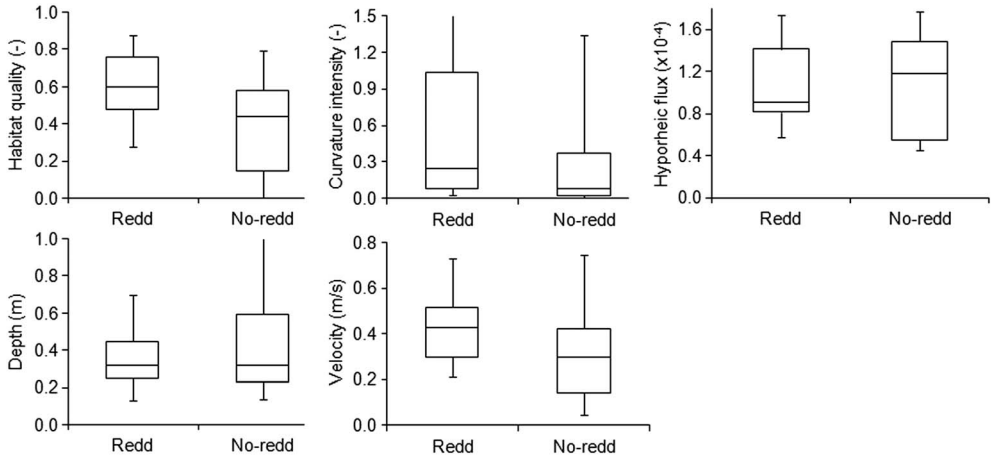

Figure 4. Box plots for habitat quality, curvature intensity, and hyporheic flux for redd and no-redd locations. The lower and upper whiskers correspond to the 5% and 95% percentiles, respectively. The lower and upper box sides correspond to the 25% and 75% quartiles and the middle line to the median.

the full model with all three variables would explain maximum variability for redd site selection compared to the model with each single variable and combination of two variables (e.g., habitat quality and curvature). We also tested a model that included an interaction between habitat quality and curvature to counter the potential spatial shifts of these variables [*Flather and Bevers*, 2002; *Isaak et al*., 2007]. We selected the best model among all by ranking them based on Akaike's Information Criterion (AIC) [*Akaike*, 1973] adjusted for small sample sizes (AIC_c) [*Hurvich and Tsai*, 1989]. The model with the lowest AIC_c was selected as the best model. Furthermore, prediction accuracy and significance of the Wald statistic were analyzed among different models in order to characterize model accuracy.

3. Results

3.1. Correlation Between Variable and Redd Frequency

Habitat quality and redd locations have a moderate (>0.5) [*Mukaka*, 2012], significant (at $\alpha = 0.05$), and positive correlation (Kendall's $\tau = 0.51$, $p = 0.04$, $N = 68$) (Figure 3a). Similar to habitat quality, our analysis shows a high (>0.7) and significant (at $\alpha = 0.05$) correlation between curvature and redd locations (Kendall's $\tau = 0.73$, $p = 0.003$, $N = 68$) (Figure 3b). The correlation between hyporheic flux and redd location was negligible (<0.3) and not significant at $\alpha = 0.05$ (Kendall's $\tau = 0.02$, $p = 0.93$, $N = 17$). Furthermore, contrary to our hypothesis, the number of redd locations decreased as hyporheic flux intensity increased (Figure 3c). About 65% of redds were observed in areas with hyporheic fluxes less than $1.04 \cdot 10^{-4}$m/s, which is the median flux of the modeled area. The correlation between curvature intensities and hyporheic flux was also negligible (<0.3) (Kendall's $\tau = 0.06$, $p = 0.000$, $N = 5399$) but positive and significant at $\alpha = 0.05$ (Figure 3d). The correlation between no-redd locations and all three variables, habitat quality (Kendall's $\tau = -0.33$, $p = 0.18$, $N = 67$), curvature (Kendall's $\tau = 0.29$, $p = 0.25$, $N = 67$), and hyporheic flux (Kendall's $\tau = 0.07$, $p = 0.79$, $N = 17$), was not statistically significant.

Habitat quality ($U = 1249$, $p = 0.000$ and $\alpha = 0.05$) and water surface curvature intensity ($U = 1570$, $p = 0.002$ and $\alpha = 0.05$) were significantly different between redd and no-redd locations (Figure 4). The median value of habitat quality was 0.60 and 0.44 at redd and no-redd locations, respectively, whereas curvature was 0.25 and 0.08 at redd and no-redd sites. Conversely, hyporheic flux ($U = 134$, $p = 0.72$, $\alpha = 0.05$) was not significantly different between redd and no-redd locations (Figure 4). Similarly, stream water depths were not significantly different ($U = 2184$, $p = 0.68$, $\alpha = 0.05$), but depth-averaged flow velocities were significantly different ($U = 1453$, $p = 0.000$, $\alpha = 0.05$) between redd and no-redd locations.

Curvature intensity had a strong correlation with the flow velocity-depth ratio (Pearson's, $r = 0.61$, $N = 88854$) (Figure 3e). The velocity-depth ratios were 2.01 ± 1.69 (mean $\pm$ standard deviation) for redd locations. This value is within the range of reported values for pool (0.15 ± 0.02–0.66 ± 0.83) and riffle (4.69 ± 3.98–5.14 ± 3.38) for low

Table 1. Logistic Regression Models to Predict Chinook Salmon Spawning Locations[a]

Nos.	Model	Test[b]	*p* Value[c]				ΔAIC_c	Accuracy	Rank
			HQ	CI	HQ · CI	HF			
1	D	no	0.095*				26.2	0.54	7
2	V	yes	0.001**				17.3	0.63	5
3	HQ	yes	0.000				5.6	0.64	4
4	CI	yes		0.025			24.3	0.57	6
5[d]	HF[e]	no				0.907	30.5	0.49	8
6[d]	HQ + CI + HF[e]	yes	0.000	0.062		0.485	5.4	0.64	3
7	HQ + CI	yes	0.000	0.061			3.7	0.64	2
8	**HQ + CI + HQ · CI**	**yes**	**0.000**	**0.009**	**0.021**		**0.0**	**0.67**	**1**

[a]HQ: habitat quality, CI: curvature intensity, and HF: hyporheic flux. Bold fonts indicate best model.
[b]Chi-square test, if the model is better than intercept-only model (null model).
[c]Significance test of Wald statistics.
[d]Model excluded for selecting best model based on ΔAIC_c criteria.
[e]Model developed based on a sample size of total 34 for redd and no-redd.
**p* value for depth.
***p* value for velocity.

flows ranging from 1.9 to 3.6 m^3/s [*Hauer et al.*, 2009; *Jowett*, 1993]. This shows that redds are located at transitions between pool and riffles. Furthermore, higher curvature is an indicative of strong velocity, which could carry away fine particles that diminish survival rate of embryos [see *Bernier-Bourgault and Magnan*, 2002; *Bowerman et al.*, 2014; *Maturana et al.*, 2013].

3.2. Spawning Site Selection Model

We developed eight logistic regression models (Table 1). The χ^2 test showed that models with the single variable for velocity, habitat quality, and curvature are significantly (at $\alpha = 0.05$) better than the intercept-only model. However, the model with the single variable for depth and hyporheic flux was not significant (Table 1). Similarly, Wald's statistical test, which quantifies the significance as a predictor of individual variables, showed that habitat quality and curvature are significant (at $\alpha = 0.05$) predictors but not hyporheic flux. One of our candidate models includes all three variables habitat quality, curvature, and hyporheic flux (model# 6). Although, this model was significantly better than the intercept-only model, Wald's statistical test showed that none of the individual (except for habitat quality) regression coefficient are significant ($p > 0.05$) at $\alpha = 0.05$ (Table 1).

Model# 8, which includes habitat quality, curvature, and their interaction expressed as their product presents the minimum ΔAIC_c and largest accuracy (0.67) and is the best model (Table 1). The second best model included habitat quality and curvature (model# 7), but curvature was not significant at $\alpha = 0.05$. Single-variable models of habitat quality (significant based on Wald statistics) were as good as model# 7 based on accuracy (Table 1). *Burhnah and Anderson* [2002] criteria suggest similar likelihood of being the correct model for models with differences in AIC_c (ΔAIC_c) of less than 3.

4. Discussion

Contrary to our initial hypothesis, results show that ambient hyporheic flows induced by bed forms are not a significant cue for spawning salmonids; intensity of hyporheic flux was not found to be a significant predictor in any of our analyses. Published literature is divided on the role of hyporheic exchange on salmonid spawning site selection. For example, *Baxter and Hauer* [2000] and *Geist and Dauble* [1998] argued that hyporheic exchange is important, while *Curry and Noakes* [1995] and *Mull* [2005] found that it was not. *Curry and Noakes* [1995] speculated that Brook trout may select the site based on visual or tactile stimuli such as substrate type, if other physical, thermal, and chemical variables are within the range used by the fish. *Baxter and Hauer* [2000] found a significant role for ambient hyporheic flows in spawning sites in Montana where hyporheic flows were defined in three classes: class 1 "$>10^{-4}$ m/s," class 2 between "10^{-5} and 10^{-4} m/s," and class 3 "$<10^{-5}$ m/s." *Curry and Noakes* [1995] reported hyporheic flows generally larger than 10^{-4} m/s, while *Geist and Dauble* [1998] and *Mull* [2005] do not report hyporheic flow velocity, but rather hydraulic gradients. The ambient hyporheic fluxes predicted by our modeling and measured by *Gariglio et al.* [2013] in our study site are all $>5 \cdot 10^{-5}$ m/s during the

spawning season. These values span between the two upper flow classes measured by *Baxter and Hauer* [2000], and those of *Curry and Noakes* [1995]. Differently from our and the *Curry and Noakes* [1995] analyses, hyporheic fluxes changed over several orders of magnitude in the investigation of *Baxter and Hauer* [2000]. This may suggest that spawning female salmonids are not sensitive to ambient hyporheic fluxes once they are above a certain threshold, which could be near 10^{-4} m/s.

Stream water temperature is not a limiting factor in Bear Valley Creek, such that the cooling effect of hyporheic exchange is not important in our case. However, hyporheic flow intensity may be important in reaches with stream water temperatures close to the upper limit of the temperature range used by salmonids. In that case, exchange between streams and sediment may provide an important cooling effect and areas with intense upwelling waters may provide near-bed water temperatures that are cooler than other portion of the streambed. Consequently, the suggested threshold of 10^{-4} m/s could be higher in those streams.

Earlier studies have also shown that a redd modifies streambed topography sufficiently to cause its own hyporheic flow [e.g., *Bowerman et al*., 2014; *Kondolf*, 2000a; *Stuart*, 1953, 1954; *Tonina and Buffington*, 2009b]. The numerical simulations of *Tonina and Buffington* [2009b] show that redd-induced hyporheic flows are often superimposed over the bed form-induced hyporheic flows. Redd-induced hyporheic flows could be 1 order of magnitude larger than those caused by bed forms (here ambient hyporheic flows) and so could dominate the local exchange within the redd environment. Consequently, we argue that ambient hyporheic exchange, which is present in streambeds without redds, is not a significant cue for salmonid spawning site selection. Instead, salmonids construct redds that produce their own hyporheic exchange, as long as the hydraulic conductivity of the streambed material is appropriate. This last requirement, adequate hydraulic conductivity, is further ensured by the fish, because during redd construction they winnow away fine particles and loosen the large particles, thus increasing the conductivity of the streambed material within redds [*Hassan et al*., 2008; *Montgomery et al*., 1996; *Tonina and Buffington*, 2009b].

Salmonids preferred locations with habitat quality ($>$0.5), although these habitat quality areas are limited to 38% of the total available area (Figure 3f). The highest number of redds (13) were observed at the habitat quality class 0.8–0.9, despite occupying only 2% of the total study area. Our results showed that habitat quality, characterized by surface water depth and velocity, is the primary predictor of site selection for salmonid spawning. This is in agreement with previous results on the importance of surface hydraulics and conditions that are used to quantify habitat quality [*Bjornn and Reiser*, 1991; *Bovee*, 1978; *Carnie et al*., 2015; *Kondolf*, 2000b; *Waddle*, 2009].

Based on our results and previous investigations, we suggest the following scenario for spawning site selection. Female salmonids return to their natal streams where they stop in staging areas with features that allow them to conserve energy and that provide refugia from predators; locations such as undercut banks, deep pools, and areas with overhanging vegetation [*Lapointe et al*., 2003; *Spence et al*., 1996]. They look nearby for flows with suitable depths and velocities and sites that avoid competition from other fish [cf. *Schuett-Hames and Pleus*, 1996]. Adequate flows are also necessary to move the gravel because females redirect the flow with their tails to build redds. Additionally, they may select areas with lower shear stresses than those necessary to move the particles, thus reducing the risk of scouring the redd, during the period of embryo incubation [*Lapointe et al*., 2000; *May et al*., 2009; *McKean and Tonina*, 2013]. It is also an advantage to have nearby downstream rearing areas to improve the survival of their eventual emergent fry [cf. *Schuett-Hames and Pleus*, 1996]. Then they test for suitable gravel sizes which allow excavation and adequate hydraulic conductivity. This process may require several trials until they select the final site. Finally, during redd construction, the fish alter the local head distribution and sediment hydraulic properties and enhance the hyporheic exchange in the redd [*Buxton et al*., 2015]. Suitable combinations of flows and depths are typically found at transition areas, riffles, which are important spawning areas based on surface rather than hyporheic hydraulics. The deeper and slower flows in the adjacent pools provide rearing areas for the alevins and refugia from predators for the spawners.

Because density of redds is currently low in this stream compared to historic data or, e.g., Alaskan streams, which offer relatively unobstructed migration corridors, our results may be conservative. In Bear Valley Creek, returning fish are able to select the best available spawning site in their natal area with little competition. Thus, if hyporheic flow was a very important selection cue, we would have found most redds where the hyporheic flux was high. However, we recognize that because of the low number of returning fish it may be that not all the best spawning areas are used. Consequently, some locations with high hyporheic flows may not have been selected, potentially

resulting in some bias in our results. In the other extreme case of streams with very large populations of spawning fish [*Buxton et al*., 2015; *Hassan et al*., 2008], spawning activities tend to subdue large bed forms thus decreasing the ambient hyporheic flows [*Hassan et al*., 2008]. In these cases the entire streambed is utilized regardless of bedforms [*Buxton et al*., 2015].

Another potential limitation of our analysis could be the numerical cell size, which is 1 m by 1 m. Finer cell sizes could provide higher resolution with potentially higher local values than those resolved on our grid. They could also resolve the hyporheic fluxes induced by smaller topographical features. However, finer mesh cells would require a higher survey resolution than was available to be able to predict fluxes. Mesh cell sizes smaller than that of the available topographic survey may predict quantities that are affected by interpolation, as described by *Lane and Richards* [1998]. Consequently, our mesh size was consistent with the topographic survey, which for the present standard is unique at the scale of our study site.

This analysis is not only limited to Chinook salmon, but also extends to Steelhead trout because they spawn in the same locations selected by Chinook salmon in our study stream. Whereas, Chinook spawn in the late summer, Steelhead spawn in spring with their offspring hatching in the late summer, just as the Chinook salmon arrive at the stream. A potential risk associated with the high flows is the deposition of fine sediment (sand and finer particles), which are mobile at high flows in these systems [*Maturana et al*., 2013]. Fine sediment may deposit within coarse gravel particles and clog the gravel interstices [*Zimmermann and Lapointe*, 2005] reducing the hyporheic flow and the flux of dissolved oxygen and consequently impair embryo development [*Wu*, 2000].

Contrary to our hypothesis, our results identify only a weak correlation between water surface curvature and hyporheic flux. We anticipated that there would have been a strong correlation based on previous studies [e.g., *Anderson et al*., 2005; *Harvey and Bencala*, 1993; *Marzadri et al*., 2013; *Tonina and Buffington*, 2009a]. The lack of strong correlation between local curvature and local hyporheic fluxes could be explained by the dependence of the hyporheic flows on nearby heads, as encapsulated by the form of the Laplace equation (equation (1)), which describes the hyporheic flow field in the case of homogenous hydraulic properties, as we assumed in this study. Because the Laplace is an elliptical partial differential equation, the solution of the flux in one point in the domain is dependent on all the boundary conditions of the domain [*Anderson*, 1995], especially from the nearby cells. The complex topography of the study site generated complex water surface elevations including backwater effects. These phenomena may have smoothened curvature at riffles, and sinuosity-induced superelevations, which may have induced local high curvature [*Gariglio et al*., 2013; *Marzadri et al*., 2013]. Consequently, these effects may have formed a head distribution which may not correlate fluxes with curvature because of the interaction among the boundary conditions.

Our study found that water surface curvature could be used as an indicator for salmonid spawning site selection. As we anticipated, there is a positive, strong and statistically significant correlation between curvature and redd frequencies (Figure 3). Furthermore, there were statistically significant different curvature intensities between redd and no-redd locations (Figure 4). This reveals that salmonids prefer locations with high curvature intensity for site selection. Rather than identifying sites of accentuated hyporheic flow, curvature appears to be simply a proxy for morphologically transitional features such as pool-tail and riffle-crest, where redds are typically observed in pool-riffle systems [*Baxter and Hauer*, 2000; *Geist and Dauble*, 1998; *Hanrahan*, 2007; *Muhlfeld*, 2002; *Vronskii and Leman*, 1991]. Whereas, it is not surprising to find this strong correlation, we had hypothesized that this was due to hyporheic flux because studies on pool-riffle systems showed high near-bed fluxes at those morphologies [*Marzadri et al*., 2010; *Tonina and Buffington*, 2007, 2011; *Trauth et al*., 2013]. Instead, it is the high-quality habitat defined by the hydromorphologic properties of flow depth and velocity that characterize the riffle as preferred spawning locations.

A major difference of our investigation from previous studies is the extensive high-resolution survey of our study stream. The advent of accurate and high-density airborne surveys, such as EAARL, and of fast and accurate multidimensional numerical modeling [*Tonina and McKean*, 2010; *Tonina et al*., 2011] allowed us to predict the fish-scale habitat (meter-scale) distribution in an almost 14 km long reach. This allows us to include a much wider and fuller range of conditions in the analysis. The results of our meter-resolution modeling support the idea that habitat quality, which includes the interaction between water depth and velocity, is a major indicator of site selection for spawning habitat [*Brown and Pasternack*, 2009; *Gard*, 1998; *Hanrahan et al*., 2004b; *Thurow and King*, 1994]. Individual variables of depth [e.g., *Bernier-Bourgault and Magnan*, 2002; *Bjornn and Reiser*, 1991] and velocity [e.g., *Knapp and Preisler*, 1999; *Muhlfeld*, 2002; *Mull*, 2005] are not by

themselves major predictors. Previous studies of comparable stream lengths were performed with one-dimensional modeling, which may provide different habitat distributions than those predicted with a 2-D model mostly because of the lack of bathymetric resolution [*Benjankar et al*., 2014]. However, the effort and resources required to develop and evaluate 2-D models are less, compared to 1-D modeling [*Jackson et al*., 2015], once a detailed bathymetry is available [*Conner and Tonina*, 2013]. Water surface curvature can be simply calculated as the second derivative of water surface predicted from any depth-averaged hydraulic model. Therefore, our study underscores the capability and importance of spatially distributed 2-D models for management, conservation, and restoration of salmonid spawning habitat, as suggested by others [see *Pasternack et al*., 2004; *Pasternack and Senter*, 2011].

The fact that most salmonids spawn near riffle crests in systems with low numbers of fish suggests that this morphology could be a useful predictor for salmonid redd locations. However, it is a less accurate predictor of spawning site location than aquatic habitat quality. Thus, morphological analysis on high-resolution bathymetries using GIS tools such as the River Bathymetry Toolkit [*McKean et al*., 2009] could select riffle areas. This procedure would be quick and would avoid the need to run a two-dimensional numerical model to select areas with high curvature. It is important to notice that salmonids mostly spawn in transitional areas in pool-riffle systems, whereas in some systems they also spawn in plane-bed rivers where riffle morphology is not present [*Buxton et al*., 2015]. Thus, morphological analysis to select riffles is important only in pool-riffle streams and when the number of spawning fish is low to moderate.

5. Conclusion

Our analysis shows that surface hydraulics and conditions are the main cues for spawning site selection by salmonids. Habitat quality (water depth and velocity) is the main indicator followed by water surface curvature. The latter is a proxy for the riffle crest where redds are typically found in pool-riffle reaches. However, not all riffle crests have adequate stream hydraulics, and consequently, curvature is a less effective index than habitat quality. Riffles can be identified as a morphological feature using GIS tools such as the River Bathymetric Toolkit. This would avoid the need to run hydraulic models and have a first-order selection of those sites directly from the streambed bathymetry. Contrary to our expectations, magnitude of ambient hyporheic fluxes is not a significant index for spawning site selection as long as it is larger than 10^{-4} m/s. However, redd-induced hyporheic flow is vital for embryos survival and previous results show that redd shape and properties cause redd-induced hyporheic exchange to be even an order of magnitude stronger than and nested on top of the ambient hyporheic flow.

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