

Habitat connectivity as a metric for aquatic microhabitat quality: application to Chinook salmon spawning habitat

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ABSTRACT

Quality of fish habitat at the scale of a single fish, at the metre resolution, which we defined here as microhabitat, has been primarily evaluated on short reaches, and their results have been extended through long river segments with methods that do not account for connectivity, a measure of the spatial distribution of habitat patches. However, recent investigations of quality of aquatic habitat at the stream segment scale, at hundredth of metre resolution macrohabitat, indicate that the spatial distribution of aquatic habitat quality and size is an important factor at the network scale. Here, we hypothesize that aquatic habitat connectivity, quality and patch size are also important at the microhabitat scale. We test this hypothesis by modelling Chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat in a 6-km long reach of Bear Valley Creek (Idaho, USA) with microhabitat resolution of 1-m square. We use two-dimensional hydraulic numerical modelling coupled with suitability curves to predict the spatial distribution of spawning habitat quality. We quantify connectivity for each habitat patch with the ratio between the area of neighbouring patches and their squared hydrographic distances. Results from a logistic regression analysis comparing predicted with observed spawning locations indicate that habitat quality and patch size are important factors and connectivity among patches may have a secondary effect. Therefore, spatial distribution of aquatic habitat and size of habitat patches are important aspects of its quality, suggesting that composite metrics such as weighted usable area may not be sufficient in defining the condition of the river environment. Copyright © 2015 John Wiley & Sons, Ltd.

KEY WORDS aquatic habitat quality; habitat patch connectivity; Chinook salmon; numerical simulations; spawning habitat

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INTRODUCTION

Many traditional habitat assessment techniques for riverine environments focus on local measurements of attributes such as velocity, depth, and water temperature and quality (Bovee, 1978; Bovee, 1982; Capra *et al.*, 1995; Pasternack *et al.*, 2004; Wheaton *et al.*, 2004; Durance *et al.*, 2006; Roy *et al.*, 2009; Lancaster and Downes, 2010). For instance, the in-stream flow incremental methodology (IFIM) (Bovee, 1978; Bovee, 1982; Bovee *et al.*, 1998) uses the statistical distribution of the physical properties to generate flow-habitat relationships such as the weighted usable area (WUA) (Bovee, 1978; Bovee *et al.*, 1998; Payne, 2003; Payne and Allen, 2009). WUA is a composite value developed from point samples but does not account for the size and spatial connectivity of discrete habitats within a reach or river network. Areas where habitat conditions are similar are often considered discrete habitat

‘patches’ that serve different ecological functions and are used by different species and life stages of those species. The spatial distribution of habitat patches and their context relative to other types of habitat is also known to be important because individual organisms must move among patches to satisfy their needs (Wiens, 2002). The relationship among habitat patches can be quantified using connectivity metrics based on the size, arrangement and hydrographic distances of habitats to provide a compliment to traditional habitat measures (Le Pichon *et al.*, 2009).

The labor-intensity of traditional stream survey techniques has restricted their application to relatively short reaches of stream (0.1–1 km), which lack the geographical scope necessary to describe many types of stream impairments (Fausch *et al.*, 2002). Rapid assessment techniques have been applied at larger scales (Le Pichon *et al.*, 2006a; Rieman *et al.*, 2006; Isaak *et al.*, 2007), but these lack the precision needed to resolve microhabitat conditions (Le Pichon *et al.*, 2006a; Le Pichon *et al.*, 2009). Recent advances in remote sensing of riverine environments using LiDAR sensors, such as the Experimental Advanced Airborne Research LIDAR (EAARL)

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(McKean *et al.*, 2009a; McKean *et al.*, 2009c), can provide detailed stream topography with resolution relevant to aquatic microhabitat along hundreds of kilometres of river networks (Tonina *et al.*, 2011; Walther *et al.*, 2011). For instance, EAARL surveys result in stream bathymetry with resolution of between 2×2 m and 1×1 m and vertical errors often in the range of ± 8 – 13 cm (McKean *et al.*, 2014). These survey methods may support two-dimensional (2D) fluid dynamic models at a resolution adequate to define fish microhabitat (Leclerc *et al.*, 1995; Leclerc *et al.*, 1996; Crowder and Diplas, 2000; Kondolf *et al.*, 2000; Pasternack *et al.*, 2004; Tonina *et al.*, 2011). The coupling of accurate topography with 2D numerical hydraulic and biological models can be used to describe traditional microhabitat characteristics like depth, substrate and flow conditions but also a broader array of conditions associated with connectivity or habitat trends associated with phenomenon like climate change. Here, we demonstrate the use of these technologies to describe the locations of Chinook salmon (*Oncorhynchus tshawytscha*) nests. Spawning salmon are an ideal study organism because they home to specific natal reaches, but females are also territorial nest builders that force other nesting females into adjacent habitats. Both behaviours increase the odds that better connected habitats will be important, and we assess that importance relative to other factors like habitat size and quality.

To address our goal, we quantified salmonid spawning habitat patches over a 6-km long reach of Bear Valley Creek (Idaho, USA) (Figure 1), one of the most important salmon spawning tributaries of the Salmon River (McKean *et al.*, 2009c). We used a 2D hydraulic model supported by an accurate and high-resolution 1×1 m topographical survey conducted with the EAARL system to predict flow properties. We used field data to describe streambed sediment patches. This information coupled with suitability index curves of local depth, velocity, percentage of sand coverage and substrate size were used to quantify spawning habitat quality at the microhabitat scale of approximate 1 m^2 streambed area (Hampton, 1988; Bjornn and Reiser, 1991; Tonina and McKean, 2010). We used statistical analysis to quantify the importance of habitat connectivity for spawning site selection by comparing model predictions with the locations of field surveyed redds in the study reach.

STUDY SITE

Bear Valley Creek is a tributary of the Middle Fork Salmon River with a mean watershed elevation of 2158 m (McKean *et al.*, 2009b; McKean *et al.*, 2009c; Gariglio *et al.*, 2013), contributing drainage basin of approximately 497 km^2 and annual mean precipitation of 762 mm (Mabe, 2011) (Figure 1). It is a snowmelt dominated system with peak flow

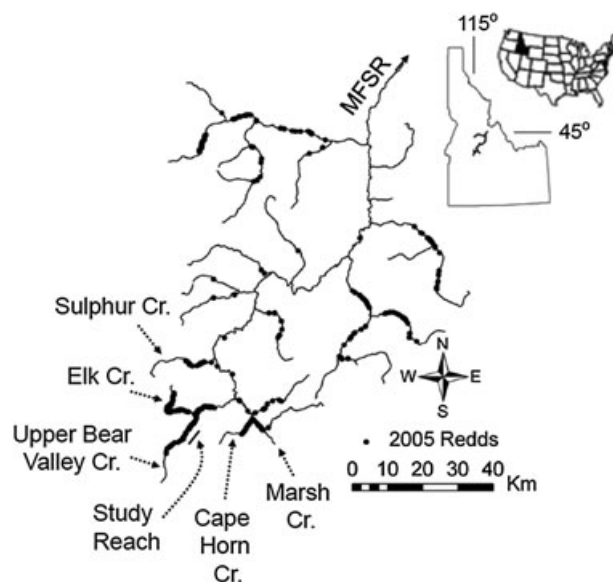


Figure 1. Vicinity map of Bear Valley Creek and the Study Site [modified from McKean and Tonina (2013)].

occurring between late May and early June (Mabe, 2011). Bear Valley Creek is primarily a gravel bed stream with localized areas of sand and cobbles and an average median grain diameter, D_{50} , of 0.054 m (McKean *et al.*, 2008). The study reach consists of a meandering pool-riffle segment within a wide alluvial valley, with mean channel width of 15 m and mean longitudinal slope of 0.3%. The channel morphology is stable with limited sediment transport of mostly fine-grained material only during high flows (Maturana *et al.*, 2013; McKean and Tonina, 2013).

The study reach in Bear Valley Creek consists of prime spawning habitat that was heavily used by Chinook salmon before population abundance declined considerably during the 20th century (Isaak *et al.* 2003). Populations have stabilized in recent decades and tens to hundreds of salmon still return most years to spawn in Bear Valley Creek. The salmon construct redds by laying their eggs in the bottom of a pit dug in the streambed gravel and then covering them with the sediment dislodged from an adjacent upstream pit (Crisp and Carling, 1989). This results in a characteristic highly permeable dune-shape bedform, which enhances the transfer of oxygen-rich surface water to the egg pocket during incubation (Pyper and Vernon, 1955; Coble, 1961; Cooper, 1965; Tonina and Buffington, 2009). Chinook salmon redd construction typically occurs between late July and early September in Bear Valley (Isaak *et al.*, 2007). After hatching in February/March the following year, the young fish reside within streambed gravels for several weeks as they absorb their yolk sacs. The young fish then emerge and live near channel margins or in side channels until most migrate downstream to the Pacific Ocean one year later (Bjornn and Reiser, 1991).

METHODS

Topographical survey

The EAARL system surveyed Bear Valley Creek and its surrounding floodplain in October of 2004 during low flow with clear water conditions (McKean *et al.*, 2008; McKean *et al.*, 2009b; McKean *et al.*, 2009a). The raw data were processed using the Airborne Lidar Processing Software resulting in a digital elevation model (DEM) with 1-m pixel resolution with average vertical root mean square (RMS) errors of ± 13 cm relative to real-time kinematic GPS ground surveys (McKean *et al.*, 2009c; McKean *et al.*, 2014). The 1-m resolution DEM was used to support the 2D hydraulic model, Multi-dimensional Surface Water Modeling System (MD-SWMS) (McDonald *et al.*, 2005; McKean *et al.*, 2009c; Maturana *et al.*, 2013; McKean and Tonina, 2013; McKean *et al.*, 2014).

Redd location and substrate survey

We surveyed 29 Chinook redds within the 6 km study reach at the end of the 2005 spawning season with a horizontal precision of approximately 0.3–0.5 m. The streambed is very stable with few changes in river morphology between the bathymetric and redd surveys, which were performed 12 months apart (McKean and Tonina, 2013). Our experience with the site also suggests that river morphology and surface texture, resulting in grain size patch distribution, have been stable since 2005 (Maturana *et al.*, 2013).

In August of 2011, we field-identified and mapped substrate grain size patches. For each patch, we quantified the representative median grain size, D_{50} , and the sand percentage following the work of Buffington and Montgomery (1999). We visually identified each patch and then we characterized its associated D_{50} by collecting and measuring the b -axis of a set of grains (approximately 5), which were visually considered the most common. The mean value of those diameters for each patch was recorded as the D_{50} . We tested our performance to identify the D_{50} by comparing the visually-predicted D_{50} with those quantified with the pebble count technique at four locations within our study reach. Differences were less than 15 mm from D_{50} of

22, 54, 77 and 122 mm, which were quantified with the pebble count technique. The substrate grain sizes range from a D_{50} of 2 to 305 mm. The sand percentages were grouped into four percentage categories that included: greater than 75, 50–75, 30–50 and less than 30%. Patches with 2 mm D_{50} were considered sand and categorized as being greater than 75% sand coverage. Using these categories, the field survey identified 249 sediment texture patches. The substrate patch areas were used for the habitat modelling and to define a spatially variable hydraulic roughness in the hydrodynamic model (Legleiter and Kyriakidis, 2008).

Hydrology

The US Geological Survey (USGS) gage 13309000 is on Bear Valley Creek near Cape Horn, at the confluence with Fir Creek, about 12 km downstream from the study reach. However, its records, started in 1921, stopped in 1960 (USGS, 2012) (Gariglio *et al.*, 2013; Luce *et al.*, 2013). The USGS gage station 13295000, is approximately 40 km away in Valley Creek, which is a neighbouring stream with hydrologic characteristics that are similar to Bear Valley Creek, is currently active. Its record covers the periods between 1921–1971 and 1993–2010. The overlapping period for the two gage stations between 1929 and 1960 was used to define a mean monthly ratio to predict the daily discharge at Bear Valley gage station. We then divided the discharge of Bear Valley gage station by 3 to predict those at the study site because a third of the station drainage area contributes discharge to the study site (Table I). Differences between discharges estimated with this scaling method and measured with velocity transects at the study site between 2006 and 2011 are around 10%, which is similar to typical errors associated with discharge estimated with the cross-section velocity technique (McKean and Tonina, 2013). Also observed in the gage record was a long-term decline in average summer flows of 8.8% that is probably related to warming climate conditions and earlier snowmelt runoff (Luce and Holden, 2009). To understand the potential role of discharge on habitat quality and connectivity, we compared the spatial distribution of patch size at discharges of 1, 2, and 3 m³ s^{−1}, which cover the range of summer low flows during spawning period.

Table I. Bear Valley Creek and Valley Creek USGS gage summary information.

Gage ID	Gage name	Period of record	Watershed area (km ²)	Mean basin elevation (m)
13309000	Bear Valley Creek nr Cape Horn, Idaho	1921–1928 (summer months) WY 1929–WY 1960	443	2146
13295000	Valley Creek near Stanley, Idaho	June 1911 to October 1913 May 1921 to November 1971 May 1972 to September 1972 WY 1993 to WY 2010	381	2256

Hydraulic analysis

The USGS MD-SWMS was used to perform 2D hydraulic modelling and to quantify the spawning habitat suitability values at the cell size. MD-SWMS uses the Flow and Sediment Transport Morphological Evolution of Channels model (McDonald *et al.*, 2005; McKean and Tonina, 2013), which solves the depth averaged Reynolds Averaged Navier–Stokes equations with finite differences over a curvilinear grid.

The study segment was modelled as six discrete reaches because the computational burden of processing the entire study reach simultaneously was beyond the performance of a typical desktop computer. The grid size was developed to match the resolution of the topographic information, which was approximately 1×1 m (Lane and Richards, 1998). Figure 2 shows an example of the grid layout over the topographic surface created in MD-SWMS. Each model reach overlapped its neighbours by a distance of approximately 5 channel widths. We checked that water surface elevations predicted at the ends of the consecutive model reach agreed within 0.02 m when we combined them into a composite stream model.

MD-SWMS requires the specification of two parameters: the streambed resistance and lateral eddy viscosity. The former is quantified with a drag coefficient, C_d , which accounts for cell-size energy losses (Morvan *et al.*, 2008; Tonina and Jorde, 2013). We selected the MD-SWMS option to define a spatially variable drag coefficient, dependent on both z_0 , which is the height above the

streambed where the velocity drops to zero in the logarithmic velocity profile, and the local water depth, h :

$$C_d(s, n) = \int_{z_0(s, n)}^{h(s, n)} f(z, z_0) dz \quad (1)$$

Here f is the logarithmic velocity vertical profile function, z is the dummy variable of integration and s and n are the longitudinal and transverse coordinates along the curvilinear grid. Turbulence is solved with a zero-equation model based on a constant lateral eddy viscosity, whose value can be quantified with the equation $\nu = 0.011 UH$, where U and H are the mean flow velocity and depth at the reach scale (Tonina and Jorde, 2013). Previous published studies tested and validated C_d and ν values on a shorter 1.6-km long reach within our study site (Tonina and McKean, 2010; Tonina *et al.*, 2011; Maturana *et al.*, 2013; McKean and Tonina, 2013). The best results from these investigations, which used a single reach-averaged grain size distribution, were $z_0 = 0.15 D_{50}$ and $\nu = 0.05 \text{ m}^2 \text{ s}^{-1}$.

In this study, the model was first run with the values used by the previous research of a spatially constant lateral eddy viscosity of $0.05 \text{ m}^2 \text{ s}^{-1}$ and a uniform $z_0 = 0.006$ m to approximate the velocity and depth distribution (Tonina and McKean, 2010; Maturana *et al.*, 2013; McKean and Tonina, 2013). Then we varied the surface roughness with the mapped grain size patches based on the z_0 dependence

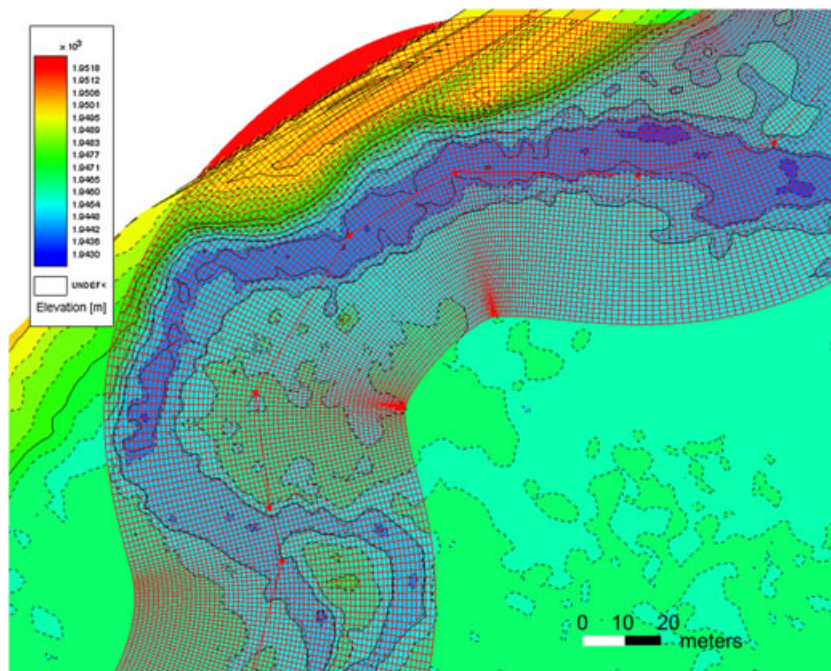


Figure 2. MD-SWMS Curvilinear grid, with centerline (red solid line) overlays the stream and floodplain topographical map.

on D_{50} . We checked the performance of the model with variable roughness by comparing measured and predicted water surface elevation along the entire 6 km reach at a discharge of $1.6 \text{ m}^3 \text{ s}^{-1}$ and velocity at two cross sections in the middle of the study site for a discharge of $1 \text{ m}^3 \text{ s}^{-1}$. Comparison between measured and predicted water surface elevations showed a RMS error of 0.054 m and a coefficient of determination, R^2 , of 0.99 (Figure 3a). The fit of the measured to modelled velocities had a RMS error of 0.06 m s^{-1} and a coefficient of determination, R^2 , of 0.81 (Figure 3b). These uncertainty values are within the ranges for velocity and water surface elevation reported for similar systems (Kondolf *et al.*, 2000; Pasternack *et al.*, 2006).

Habitat modelling

We quantified spawning habitat suitability by considering local fraction of sand, median grain size, depth and velocity (Hampton, 1988; Bjornn and Reiser, 1991; Tonina and McKean, 2010). Sand and small-grained sediments are considered unsuitable for spawning because they do not allow dissolved oxygen to be in contact with eggs (Bjornn and Reiser, 1991). Grain sizes that are too large are not easily moved by salmon during redd construction and therefore large grain sizes reduce suitability. The amount of dissolved oxygen exposed to salmonid eggs increases with increasing velocities (Schälchli, 1992; Schälchli, 1995; Tonina and Buffington, 2009). When velocity increases to a point where it mobilizes the gravels used in redd construction, there is a diminishing return on habitat suitability (Wu, 2000). Salmonids also require a minimum depth to swim in streams.

Suitability curves provided habitat preference values between zero and one for substrate median grain size, SI_{D50} , percentage of sand coverage, SI_{Sand} , velocity, SI_V , and depth, SI_D (Figure 4). These curves were consistent with research performed in similar streams located in the states of Washington and California as well as a previous study performed in Bear Valley Creek (Hampton, 1988; Washington Department of Fish and Wildlife (WDFW),

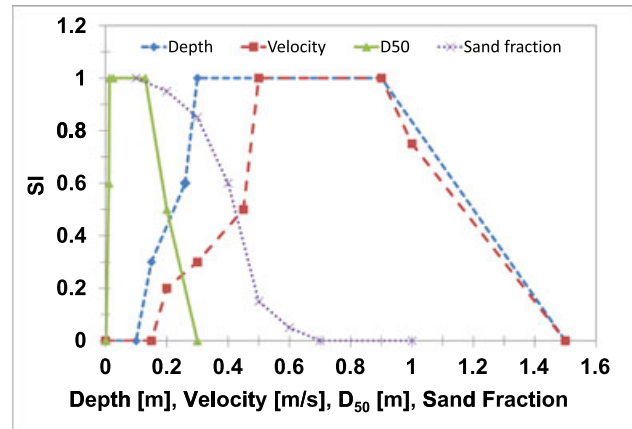


Figure 4. Suitability curves for depth, velocity median grain size, D_{50} , of streambed surface material and sand content of surface material for Chinook salmon spawning.

2004). We used the geometric mean method to define a cell spawning habitat suitability, CSI_i , as a combined value from each single suitability index:

$$CSI_i = \sqrt[4]{SI_{V,i} SI_{D,i} SI_{D50,i} SI_{Sand,i}} \quad (2)$$

Spawning habitat quality was then ranked in five categories from 1 to 5 (Table II) for each cell (Benjankar *et al.*, 2014).

Habitat spatial analysis

Habitat patches can influence the spatial structures of species populations (Isaak *et al.*, 2007). Patches were defined as the cumulative area of any contiguous cells with the same spawning habitat quality. Consequently, they can be as small as the study resolution, which in our case is $1 \times 1 \text{ m}$. We used Anaqualand®, freeware developed by Cemagref Inc., to define patches and calculate distance quantities associated with each patch from the habitat quality distribution (Cemagref, 2006; Le Pichon *et al.*, 2006b). Patches were created by connecting cells that share

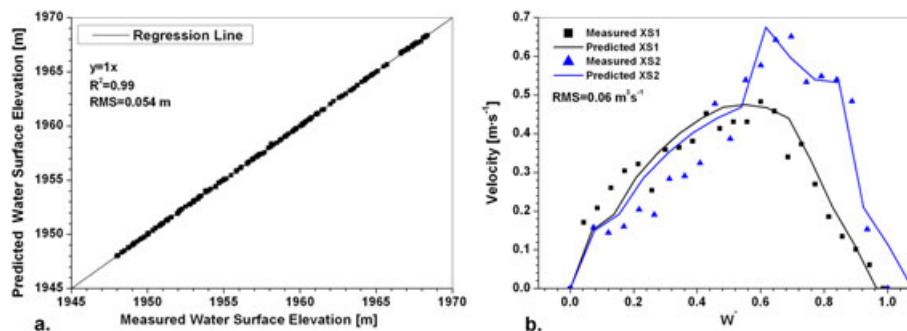


Figure 3. Comparison of (a) surveyed water surface elevation measurements compared with modelled water surface elevations at $Q = 1.6 \text{ m}^3 \text{ s}^{-1}$ and (b) velocity measurements with an ADV with modelled velocities with MD-SWMS at two cross-section (W^* dimensionless cross-sectional distance as the ratio between distance from right side and channel width) within the study site at $Q = 1 \text{ m}^3 \text{ s}^{-1}$.

Table II. Habitat quality designations.

Category	Suitability	Description
1	0–0.2	No habitat
2	0.2–0.4	Poor habitat
3	0.4–0.6	Fair habitat
4	0.6–0.8	Good habitat
5	0.8–1	Excellent habitat

either a side or corner. We restricted our spatial analysis to the spawning habitat class of excellent quality, category 5, because almost all redds, 24 out of 29 surveyed redds, were located in this highest quality class.

Connectivity describes the spatial relationships of habitat patches with their neighbours (Le Pichon *et al.*, 2006a; Le Pichon *et al.*, 2006b) and can be used to distinguish sparse distributions of small patches from clusters of large patches (Gustafson and Parker, 1994). Connectivity was determined for each spawning habitat patch using a proximity index calculation developed by Le Pichon *et al.* (2009). A subject patch is a habitat patch for which the proximity index calculation is performed and target patches are neighbouring habitat patches used in the proximity index equation. A proximity index, P_x , was calculated for each spawning habitat patch as

$$P_x = \sum_{i=1}^n \frac{Area_i}{D_{ix}^2} \quad (3)$$

where n is the number of spawning habitat patches contained in the subject reach and x is the subject spawning habitat patch. $Area_i$ is the area of i th patch located a hydrographic distance of D_{ix} from the subject patch. Equation 3 has been modified from Gustafson and Parker (1994) to replace the Euclidean distance with the hydrographic distance (Le Pichon *et al.*, 2009). Anaqualand® was used to calculate the hydrographic distance in both the upstream and downstream directions between patches using a sparse approximation technique appropriate for large raster data maps, in which only a small percentage of cells represent the river (Le Pichon *et al.*, 2009). The sparse approximation technique neglects the varying cell size from the curvilinear mesh from the 2D hydraulic model and we assigned a 1-m cell

dimension. Anaqualand's hydrographic distance calculator uses an eight-neighbour cell algorithm that eliminates cells with no data from the distance calculations. Cells with no data are dry cells from the hydraulic model and represent the edge of the stream channel. D_{ix} is calculated by selecting the shortest distance adding cell diagonals or sides within the stream boundary between the subject and target patches. The proximity index representing the connectivity value was calculated for each spawning habitat patch of excellent quality.

Data analysis

The LOGISTIC procedure in SAS (Allison, 1999) was used to develop logistic regression models for describing the effects that patch attributes had on the probability of redd occurrence. Four models were evaluated including a global model that included patch area, connectivity among excellent quality patches and the interaction between these factors. Also considered were models representing subsets of the global model (Table III). An adjusted Akaike information criterion for small sample sizes, AIC_c , was used to compare the relative fit of the models (Hurvich and Tsai, 1989).

$$AIC_c = -2\ln(\text{likelihood}) + 2K + \frac{2K(K+1)}{n-K-1} \quad (4)$$

K represents the number of parameters in the model and n represents the sample size, which is the number of habitat patches. The ranking of the models involves a comparison between the highest ranking model, with the lowest AIC_c , and other candidate models. This ranking metric, referred to as the ΔAIC_c is the difference between the lowest AIC_c and the candidate model AIC_c (Isaak *et al.*, 2007). Akaike weights, w_i , and Akaike ratios, w_i/w_1 were calculated. These Akaike weights represent the strength of evidence for the i th model being the best model. Values of AIC_c less than 3 among models indicate that those models have similar likelihood to be correct (Burnham and Anderson, 2002). The best model was then used to predict the probability of occupancy of a patch with the following equation (Allison, 1999)

Table III. Logistic regression results of five models including the parameters affecting Chinook salmon spawning patch occupancy.

Model no.	Candidate model	P	ΔAIC_c	Akaike weight (w_i)	w_i/w_1
1	Connectivity, area, interaction	4	4.05	9.22437E+30	7.6
2	Connectivity, area	3	2.02	2.55177E+31	2.7
3	Area	2	0.00	7.00588E+31	1.0
4	Connectivity	2	22.67	8.38694E+26	83533.2

$$pi = \frac{\exp(\alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)}{1 + \exp(\alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_k x_k)} \quad (5)$$

where β is the coefficient to be estimated for the parameter x and pi represents the probability of occupancy after selecting the most likely model.

RESULTS

Anaqualand[®] delineated 563 patches of excellent spawning habitat quality varying in size from 1 to 298 m² for the discharge of $Q = 1 \text{ m}^3 \text{ s}^{-1}$ present during the 2005 spawning season when the redd survey was conducted. All observed redds were located within the excellent-habitat class except for 4, which were in the good habitat near an excellent class. This indicates that habitat quality is a key element for spawning habitat selection. Individual patches with small areas were fewer for the excellent habitat relative to the other categories, except for the no-habitat group (Figure 5). The number of high-quality patches less than the redd minimum size, which is approximately 6 m², were 256, resulting in 317 patches

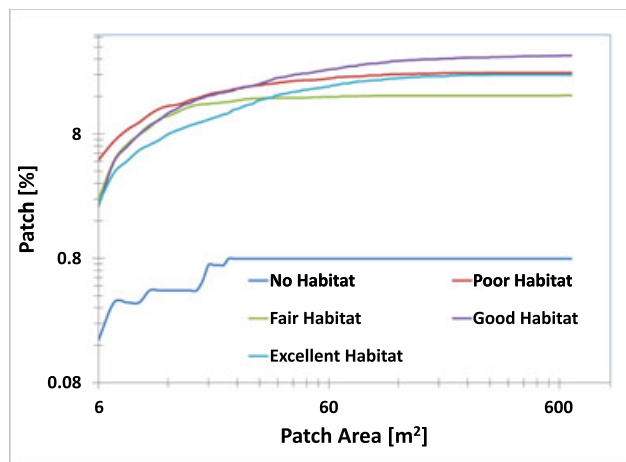


Figure 5. Cumulative frequency, defined as the number of patches of equal or smaller size than a given area divided by the total number of patches, as a function of patch area. The analysis is for discharge of $1 \text{ m}^3 \text{ s}^{-1}$ and restricted to patches with minimum area equal to or larger than the smaller redd area of 6 m². The total number of patches with the 6 m² size cut-off were 1134; the number of patches with areas less than 6 m² were 3880 of which 54, 1531, 1278, 725 and 292 were for the no, poor, fair, good and excellent habitat classes respectively.

with size too small to be used by fish. The location of the small high-quality patches did not coincide with or was not present predominantly in any specific morphological unit, like riffles, pools or bars. Similarly, the large patches extended over several morphological units, which included pools, riffle and the submerged portion of bars. Conversely, patches with size near the average excellent habitat patch size of 20 m² were mostly localized at the riffles (Table IV). Consequently, most of the good habitat of adequate patch size was located at riffle. The spawning season flow rate of $Q = 1 \text{ m}^3 \text{ s}^{-1}$ creates relatively large patches of good and excellent habitat near the centre of the channel and most low-quality habitat along the stream margins (Figure 6), where it formed mostly small patches. For instance, the average patch for the no-habitat class was almost an order of magnitude smaller, 3 m², than that of the excellent habitat quality.

Effects of hydrologic variation

Analysis of the flow records indicated that the approximate average discharge during the spawning season of 2005 was $1 \text{ m}^3 \text{ s}^{-1}$. Results also showed the discharge during the spawning period has fluctuated annually varying between 1 and $3 \text{ m}^3 \text{ s}^{-1}$ with an average value of $2 \text{ m}^3 \text{ s}^{-1}$ (Figure 7). The spawning period average discharge has been declining since 1939 and has been below $2 \text{ m}^3 \text{ s}^{-1}$ since 2000 with a mean value of $1.2 \text{ m}^3 \text{ s}^{-1}$ in the last decade. This reduction in discharge between 2 to $1.2 \text{ m}^3 \text{ s}^{-1}$ corresponds to a 32% decrease in WUA; WUA reduction is 45% when discharge decreases from 3 to $1.2 \text{ m}^3 \text{ s}^{-1}$. At the local scale, the number of patches in all categories generally declined with increasing flow and the decline was much greater in the excellent category (Table IV). The average patch size declined or stayed relatively constant in the 'no-habitat' through 'good-habitat' categories. In strong contrast, the patch size increased in the excellent-habitat category. This is because of two contributing processes: reduction of low quality patches and merging of high quality patches into larger contiguous areas. High-quality habitat at 2 and $3 \text{ m}^3 \text{ s}^{-1}$ is present also within pools connecting the medium size patches, which were isolated at riffles for the low discharge of $1 \text{ m}^3 \text{ s}^{-1}$ (Figure 8). The percentage of wetted area covered by the no-habitat category was constant with increasing flow, but declined with increasing flow in the 'poor-' through good-habitat catego-

Table IV. The habitat patch size and quantity metrics.

	$Q=1$	$Q=2$	$Q=3$	$Q=1$	$Q=2$	$Q=3$	$Q=1$	$Q=2$	$Q=3$
No habitat	63	56	56	3	5	5	0.4%	0.4%	0.3%
Poor habitat	1813	1505	1081	5	5	8	19.9%	10.3%	9.7%
Fair habitat	1463	909	477	4	3	6	10.7%	4.4%	3.1%
Good habitat	1113	1476	1339	21	15	14	46.6%	33.5%	22.00%
Excellent habitat	563	250	79	20	140	705	22.4%	51.4%	64.9%

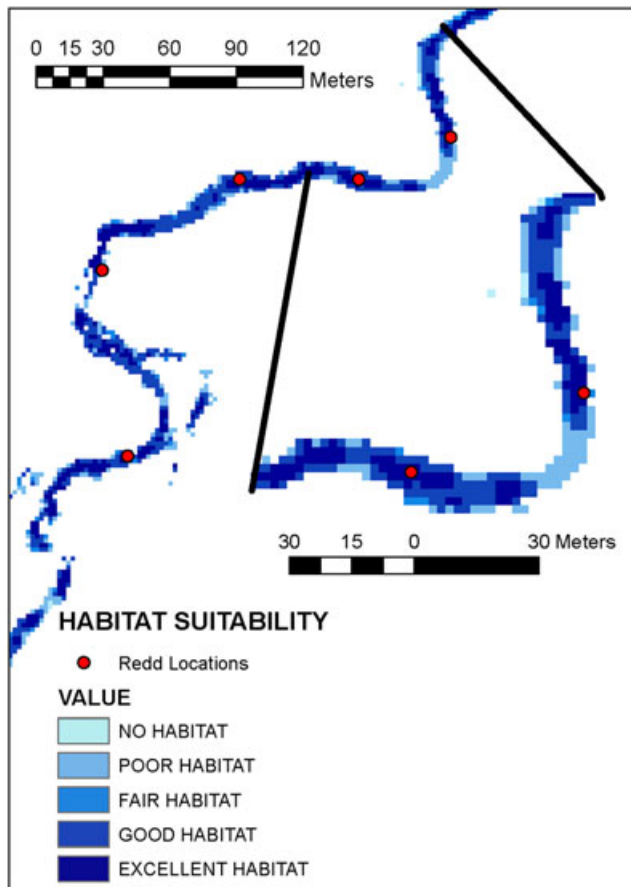


Figure 6. A raster map of suitability illustrates the spatial distribution of spawning habitat throughout the channel for $Q = 1 \text{ m}^3/\text{s}$. White colour denotes emerged topography.

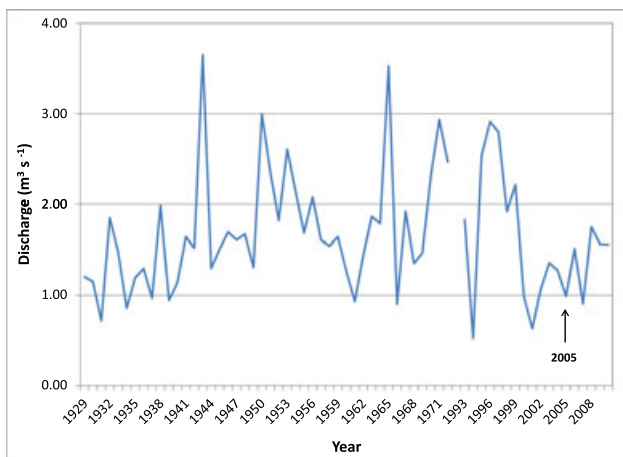


Figure 7. Average discharge in Bear Valley Creek during spawning season between 1929 and 2010.

ries. In contrast, the percentage that was excellent-habitat increased. Consequently, poorer quality habitats improved with discharge. The no-habitat class was not very numerous and mostly occurred on the margins of flow.

Figure 8 shows the increase of excellent habitat quality patch with discharge for a representative section of the study site. The high-quality habitat for the $Q = 3 \text{ m}^3 \text{ s}^{-1}$ discharge seems to form a contiguous large quality patch, which extends along the centre of the stream. This trend suggests that historic conditions of higher discharges during the spawning season may have provided larger areas of spawning habitat than the present time low discharges ($1 \text{ m}^3 \text{ s}^{-1}$).

Logistic regression results

Results of the logistic regression evaluation indicate that the most likely model included patch size but that connectivity effects were also important (Table III). The most likely model is approximately 2.7 times more plausible than the next best model containing connectivity and area as indicated by the Akaike ratio (w_i/w_j). Consequently, these results suggest that Chinook salmon redd occupancy predictions depend on both patch area and connectivity (Table V) in addition to habitat quality, which is a key component as almost all spawners selected the excellent-habitat category to spawn. Probability of occupancy was predicted based on Model 2, which accounts for connectivity and area (Table VI) and is shown in Figure 9. Connectivity has a very small effect as shown by the small differences among the family of curves for different connectivity. We used these curves to create a map of habitat probabilities for the entire site. Figure 10 is a reach close up to show the spatial distribution probability of the year 2005 discharge of $1 \text{ m}^3 \text{ s}^{-1}$. For most of the reach the probability of redd occurrence is below 25% because of the size of the patch rather than connectivity.

DISCUSSION

Our analysis is the first attempt to understand the role of spatial distribution of aquatic habitat quality patches with microhabitat (1 m) resolution along rivers. Our analysis accounts for habitat quality and its spatial distribution via size of habitat patch and connectivity among patches. Previous studies of habitat connectivity have been limited to the network scale using the macro-scale habitat or to coarse (reach scale) physical information (Le Pichon *et al.*, 2006a; Isaak *et al.*, 2007; Le Pichon *et al.*, 2009). Isaak *et al.* (2007) investigated the spatial context of aquatic habitat over a large network using the reach scale. Their study delineated habitat patches with a combination of biological and physical descriptors including river morphological features such as pool and riffle sequences and the presence of salmon redds. Potential areas of suitable spawning habitat patches were identified from mean flow properties and stream morphology at the reach scale with

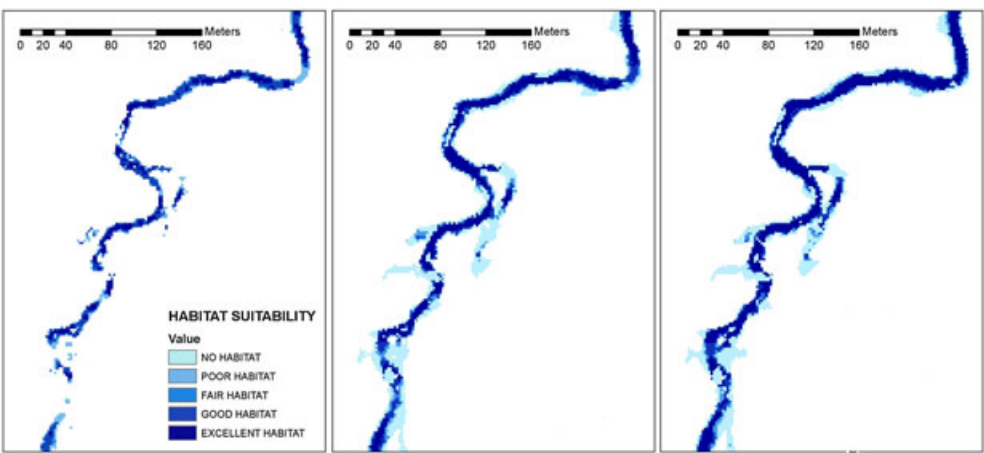


Figure 8. Comparison of spawning habitat patch distribution for a representative reach of the study site for 1, 2 and 3 m³/s discharge from left to right panel. White colour denotes emerged topography.

Table V. A summary of values comparing connectivity, area and the interaction between connectivity and area.

Patch description.	Average connectivity (dimensionless)	Average area (m ²)	Average interaction value (m ²)
Occupied	4.2	66.3	273.7
Entire sample	4.1	19.0	76.3

Table VI. Parameter estimate values for the most likely models to predict redd occupancy.

Model	Connectivity (x1)	Area (x2)	Interaction (x3)	Intercept (α)
1	—	0.0197	—	−3.5681
2	0.00332	0.0197	—	−3.5822
3	−0.000111	0.00205	0.0000178	0.0118

patch sizes ranging from 0.3 to 20 ha. Similarly, *Le Pichon, et al.* (2009) delineated habitat patches supporting feeding and resting stages based on mapping of river morphologic features. Patch areas averaged 176 m² for resting habitat and 1114 m² for feeding. These studies used reach scale information to delineate meso-macro habitat patches and concluded that habitat patch size and connectivity are important indexes with a positive trend on occupancy at the macro-scale.

In this study, the average area of redd occupied patches was three times larger than the average patches available within the stream (Table V). As in previous investigations, our results show that patch size is a key parameter in determining model performance. We suggest this may be the result of two effects. First, large patches simply cover a large percentage of the wetted surface and thus they tend to be occupied by more salmon redds. Secondly, salmon often display a territorial behaviour, and this requires patches to be larger than a single redd size, which varies from an approximate minimum of 2 m² up to 6 m² (Bjornn and Reiser, 1991; Healey, 1991). Consequently, we used the

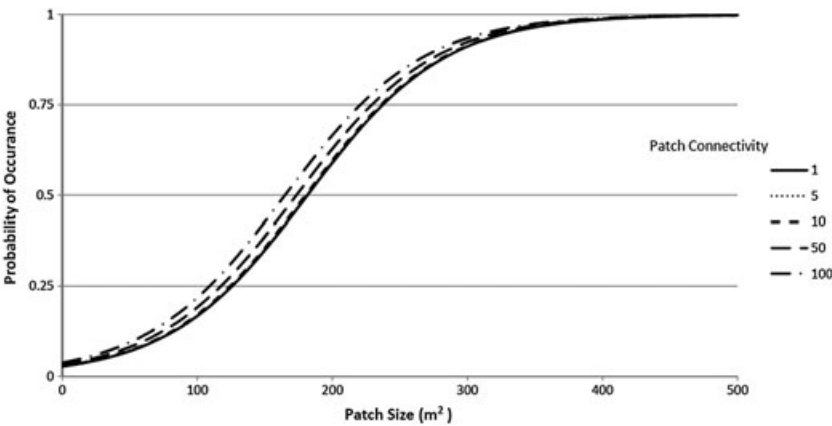


Figure 9. Response curves for the second most likely model of spawning habitat patches derived from the logistic regression analysis.

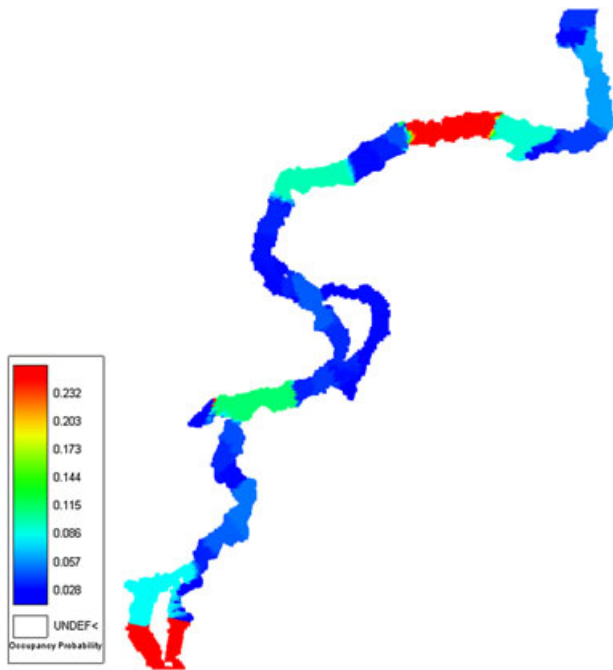


Figure 10. Distribution of probability of spawning patch occupancy by Chinook salmon in Bear Valley Creek.

patch size of 6 m^2 as a threshold size for usable spawning size. Salmon spawning partners defend an area up to about four times the redd size, or approximately 24 m^2 (Healey, 1991). Our results show an average spawning habitat patch that is approximately 3 times larger than a redd in this river environment, which has a depauperate salmon population and thus presumably less redd site competition. Our results also suggest that salmon will bypass excellent, but relatively smaller, patches of habitat in favour of larger habitat areas.

Although our results support the general idea that connectivity is potentially an important parameter, its importance is weaker than that quantified by the work of Isaak *et al.* (2007) at the stream network scale. These studies differed in reach scale and the spatial resolution of patch delineation. The resolution of this study was the microhabitat scale of 1 m^2 , and the predicted spawning habitat patches had an average area of 66 m^2 . In contrast, Isaak *et al.* (2007) used information at the reach average scale to directly delineate macrohabitat patches, which varied between 0.3 and 20 ha. Their analysis focused on a large salmon population in a drainage network, whereas our analysis considered the interaction between individual spawning salmon at the microhabitat scale. The territorial behaviour of a single Chinook salmon could potentially explain the secondary importance of connectivity for this species. The territorial behaviour may not affect the spawning reach selection at the population scale, where connectivity is at a larger scale than the single fish instinct to protect their egg nests. Consequently, we suggest that patch connectivity will

be a key factor for fish species with lower territorial instinct than the salmonids studied in this work.

One limitation of our analysis is fish spawning density. The impact of density on spawning site selection for salmon species has been the topic of many studies (Van den Berghe and Gross, 1989; Blanchet *et al.*, 2006; Moore *et al.*, 2008). Suitable spawning can be a limiting resource because of competition for spawning space (Moore *et al.*, 2008). The spatial distribution of salmon spawning has also been related to density in a drainage-basin scale study (Isaak and Thurow, 2006). Isaak and Thurow (2006) evaluated the spatial distribution of salmon redds throughout the Middle Fork of the Salmon River in Idaho. They found that as spawning salmon densities increased, redds were more evenly distributed throughout the region. They also indicated stream reaches previously unused for spawning were rapidly replenished when density increased (Isaak and Thurow, 2006). Thus, our analysis may be biased by the locally low redd density compared with similar systems with larger returns of spawning fish, such as in some Alaskan streams. However, it provides a first attempt to evaluate the effect of local spatial distribution of habitat patches. Although our analysis was performed at the microhabitat scale and with low fish densities, the positive correlation between redd occupancy and patch area determined in this study is significant. We suggest that more research should be devoted to understanding the interaction between fish habitat selection and the spatial distribution of the habitat.

As tools such as EAARL and efficient numerical modelling become broadly available, they will allow us to improve our understanding of the connection between physical habitat and use by biota. Our results show that use of suitability curves, detailed bathymetry and 2D numerical modelling provide a set of tools, which allow us to characterize the spatial distribution of aquatic habitat quality. Fast and accurate survey techniques such as, RTK GPS (Brasington *et al.*, 2000), sonar (Stewart, 2000), optical sensors (Fonstad and Marcus, 2005), and more recently remote sensing techniques, such as the bathymetric lidar EAARL system, are available tools that will provide high-resolution stream and floodplain survey. These techniques will help us address the need of 'quasi-census' of river morphology, which is the detailed survey of stream morphological features at the fish scale, advocated by Pasternack and Senter (2011). This will allow us to develop probability map distribution of presence absence of fish besides redd location. The probability map developed in this study can be extended to other life stages or fish behaviour. Overlay probability maps of different life stages and fish species will allow us to understand fish behaviour in ways not available earlier.

Whereas these techniques let us characterize the physical domain of the aquatic habitat well, biological models for

different life stages and aquatic organisms are difficult to find and sometime lacking. Consequently research on aquatic organisms behaviour is necessary to perform analysis like ours and develop probability maps, which could be performed because of well define spawning habitat requirements for the selected species and study site. Development of biological models could benefits from coupling hydraulic modelling and high-resolution bathymetry with monitoring fish or the aquatic organism of interest. Non-intrusive tracing of organisms within their environment, such as fish tagging, allow us to place monitored organisms within their physical domain, which we can simulate as we did in this study. This analysis will help us understand when and which zones of the stream and flow characteristics organisms use and consequently we will understand their ecological functions.

As in previous analyses, our results also support the importance of habitat spatial distribution via habitat patch size and connectivity. This suggests that defining habitat quality via WUAs only is not sufficient because fragmented high quality habitats may be less valuable than well connected habitats but still have the same WUA. Consequently, we suggest that the definition of WUA should be modified to account for a minimum size patch. This new definition would provide a better representation of the effective condition of the habitat quality at the reach scale, because it would partially account for habitat fragmentation.

Our results indicate that habitat quality is very important, as observed by previous research (Le Pichon *et al.*, 2006a; Isaak *et al.*, 2007; Le Pichon *et al.*, 2009), and also patch size is a key factor. Spatial analysis of aquatic habitat, which identifies quality, size and connectivity of habitat can strengthen the description of habitat quality developed from suitability curves. However, our result on the importance of habitat connectivity may be different for other fish species, which are more opportunistic and may use smaller habitat, less territorial and smaller. For instance, bull trout (*Salvelinus confluentus*) has been found spawning in small isolated areas and thus fragmentation at the micro-scale could be negligible whereas that at the macro-scale (network) is very important (Rieman and McIntyre, 1996).

Recent studies have evaluated some impacts that climate change may have on the spawning habitat of Chinook salmon in Bear Valley Creek (Tonina and McKean, 2010; Tonina *et al.*, 2011). These studies employed the variable infiltration capacity model to predict impacts to the annual hydrograph for Bear Valley Creek (Tonina and McKean, 2010; Tonina *et al.*, 2011; McKean and Tonina, 2013). The peak flow rate was anticipated to occur approximately one month earlier than current conditions, and the average annual peak flow rates were predicted to decline. The impact to the anticipated discharge during the July to September spawning season is an approximate average reduction from 2 to 1 m³ s⁻¹.

Changes in flow rates create different habitat patches with different connectivity. The 1 m³ s⁻¹ flow rate used to evaluate salmon spawning habitat patches in this study matched the 2005 conditions. The average flow rate for this reach over the entire gage record is approximately twice the rate of 2005 during salmon spawning season. This means that historically spawning flows were around 2 m³ s⁻¹ and earlier spawners experienced a flow of about 3 m³ s⁻¹. Variations in flow rates produce significantly different patch area, connectivity and habitat quality (Figure 7). During spawning period flows of 2 and 3 m³ s⁻¹, spawning patches were larger and more connected than in discharges of 1 m³ s⁻¹. As flows are expected to continue to decrease over time during the spawning season (Luce and Holden, 2009), connectivity among patches could become more important in future climate scenarios as larger patches become scarcer.

CONCLUSION

Our results confirm that habitat quality is the main factor along with patch size that characterize of redd occupancy. Our statistical analysis shows that connectivity has a smaller impact on spawning site selection at the micro-habitat scale than at the network scale for the fish species selected in this work. The low spawning density of the reach and the territorial behaviour of the selected species, Chinook salmon, could have biased this result, and thus, more research is needed to understand the effect of habitat spatial distribution at the microhabitat scale.

Our analysis demonstrate how a 2D numerical model, supported by metre -scale resolution and accurate stream bathymetry, can be used with biological surveys and predictive models to quantify spatial distributions and trends in spawning habitat. Moreover, these tools can be used to provide information about traditional measures of habitat quality like WUAs, while also providing new types of information about the sizes and spatial configuration of habitats within reaches and longer river segments. Further development of these tools could be used to quantify and assess stream habitats at scales and resolution sufficient for detecting and describing subtle changes associated with habitat restoration, local habitat use, climate change or other environmental trends.

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