Geomorphology, Hyporheic Exchange, and Selection of Spawning Habitat by Bull Trout (Salvelinus Confluentus)

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Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*)

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Abstract: The distribution and abundance of bull trout (*Salvelinus confluentus*) spawning were affected by geomorphology and hyporheic groundwater – stream water exchange across multiple spatial scales in streams of the Swan River basin, northwestern Montana. Among spawning tributary streams, the abundance of bull trout redds increased with increased area of alluvial valley segments that were longitudinally confined by geomorphic knickpoints. Among all valley segment types, bull trout redds were primarily found in these bounded alluvial valley segments, which possessed complex patterns of hyporheic exchange and extensive upwelling zones. Bull trout used stream reaches for spawning that were strongly influenced by upwelling. However, within these selected reaches, bull trout redds were primarily located in transitional bedforms that possessed strong localized downwelling and high intragravel flow rates. The changing relationship of spawning habitat selection, in which bull trout selected upwelling zones at one spatial scale and downwelling zones at another spatial scale, emphasizes the importance of considering multiple spatial scales within a hierarchical geomorphic context when considering the ecology of this species or plans for bull trout conservation and restoration.

Résumé : La distribution et l'abondance de l'omble à tête plate (*Salvelinus confluentus*) en phase de reproduction étaient affectées par la géomorphologie et par l'échange d'eau entre la nappe sous-terraine hyporhéique et les cours d'eau à des échelles spatiales multiples dans les cours d'eau du bassin de la Swan, nord-ouest du Montana. Parmi les affluents de fraye, l'abondance des nids d'omble à tête plate augmentait avec la superficie des portions de vallées alluviales qui étaient longitudinalement confinées par des ruptures de pente. Parmi tous les types de portions de vallée, les nids d'omble à tête plate se retrouvaient principalement dans ces portions confinées, qui présentaient des régimes complexes d'échange hyporhéique et de vastes zones de remontée d'eau. L'omble à tête plate recherchait pour la fraye des tronçons fortement influencés par les remontées d'eau. Toutefois, à l'intérieur de ces tronçons sélectionnés, les nids se retrouvaient principalement dans des types de lit de transition qui présentaient une forte remontée d'eau localisée et des taux élevés d'écoulement à l'intérieur du gravier. La relation changeante régissant le mode de sélection de l'habitat de fraye – l'omble de fontaine choisissait les zones de remontée d'eau à une échelle spatiale et les zones d'enfoncement des eaux à une autre échelle spatiale – fait ressortir qu'il est important de considérer des échelles spatiales multiples à l'intérieur d'un contexte géomorphologique hiérarchique lorsqu'on étudie l'écologie de cette espèce ou qu'on fait des plans pour sa conservation et son rétablissement.

[Traduit par la Rédaction]

Introduction

Stream ecologists have long recognized the interactive relationship between a stream and its valley (Hynes 1975). Patterns and processes of stream ecosystems are closely tied to the surrounding terrestrial environment (Junk et al. 1989; Gregory et al. 1991), longitudinal gradients (Vannote et al. 1980; Minshall et al. 1985), and groundwater – stream water exchange (Grimm and Fisher 1984; Stanford and Ward 1993). Because of these interactions, it is essential that stream ecosystems be examined holistically within the context of their landscapes (Frissell et al. 1986; Swanson et al. 1988).

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The flow of water over land shapes the geomorphology of stream systems. Geomorphic change, combined with the interactive response of the stream environment, results in alternating erosion and deposition. This dynamic process of cut and fill creates spatial heterogeneity in physical habitat for stream organisms. Stream habitat can be classified hierarchically into drainages, valley segments, stream reaches, and channel bedform units (pool–riffle) (Frissell et al. 1986). Each level of the stream habitat hierarchy corresponds to a distinct spatial scale, from kilometres to metres to centimetres, etc.

At the drainage spatial scale, alluvial river systems of the northern Rocky Mountains are characterized by confined and unconfined valley segments occurring in alternating series along the stream gradient. In unconfined alluvial segments, streams flow across deposits of gravel and cobble associated with alluvial floodplains (Church 1992). These reaches commonly have a vertical dimension of groundwater – surface water interaction extending tens of metres into the alluvium

(Stanford and Ward 1988, 1993). The size and arrangement of particles contained in vertical and lateral profiles of an alluvial segment vary with geomorphic surface. Differences in substrate porosity lead to the formation of preferential hyporheic flow pathways in longitudinal, lateral, and vertical dimensions. In contrast, confined valley segments are generally characterized by narrow valley walls, near-surface bedrock, absence of a floodplain, and relatively high stream gradient (Montgomery et al. 1996).

The response of stream organisms to habitat is scale dependent. Habitat-use patterns for any organism in an ecosystem can be related to many environmental factors. The variation of a habitat factor may be perceived by an organism as information at certain scales, while at another scale, it may be perceived as noise (Dutilleul and Legendre 1993). Consequently, understanding the distribution and abundance of species relative to habitat factors may require a multiscale approach (Wiens 1989). Relationships between fish and their habitat have been primarily examined at fine spatial scales (Bayley and Li 1992). However, there is increasing recognition of the importance of a multiscale approach (e.g., Poizat and Pont 1996; Torgersen et al. 1999) and inclusion of critical landscape features such as zones of process interaction (e.g., land–water ecotones) (Schlosser 1995).

The hyporheic zone is an ecotone that links ground and surface water processes in streams (Brunke and Gonser 1997). The boundaries of groundwater – stream water interactions are spatially and temporally dynamic because of fluctuating hydrographic regimes. Although hyporheic exchange has been hypothesized to occur at multiple spatial scales (e.g., drainage, valley segment, reach, and channel unit scales; Stanford and Ward 1993), few efforts have been made to quantify hyporheic exchange extensively within a spatial hierarchy (Boulton et al. 1998). Most investigations of groundwater – surface water interaction in streams have focused at the channel bedform scale (i.e., pool–riffle, which includes local, shallow exchange). Hyporheic exchange at this spatial scale is known to vary with discharge, gradient, bedform, sediment permeability, and water surface slope (Vaux 1968; Thibodeaux and Boyle 1987; Harvey and Bencala 1993). Few studies of hyporheic exchange have been conducted at anything larger than the reach scale; however, theoretical models predicting how the hyporheic zone changes within a drainage have recently been proposed (e.g., Stanford and Ward 1993; White 1993).

For decades, fisheries research involving groundwater – stream water exchange has primarily focused on the importance of intragravel flow to the incubation of fish embryos (e.g., Terhune 1958; Curry and Noakes 1995). Upwelling water often differs from surface water in numerous ways (e.g., dissolved oxygen, nutrients), but perhaps none more important than temperature regime. Upwelling waters in temperate climates are generally cooler in summer and warmer in winter and may provide thermal refugia for stenothermic fish species (e.g., Gibson 1966; Nielson et al. 1994).

The bull trout (*Salvelinus confluentus*) is a native char in the Pacific Northwest whose populations are fragmented and declining throughout their range due to overharvest, displacement by exotic species, and habitat degradation (Rieman and McIntyre 1993). In 1997 the U.S. Fish and Wildlife Service recommended the bull trout for listing under the U.S. Endangered Species Act. The Swan basin in northwestern Montana (Fig. 1) has received attention as a refuge where many bull trout remain (Rieman and McIntyre 1993; Baxter et al. 1999). Consequently, this basin provides an opportunity for developing a better understanding of bull trout in a system where sufficient numbers exist for effective study.

Bull trout display migratory life histories that are associated with large lake and river systems. Migratory bull trout in the Swan basin spawn in second- to fourth-order streams from August through October. Embryos and alevins overwinter in spawning gravel for more than 200 days prior to fry emergence. Juveniles remain in the natal streams for 1–3 years prior to migrating to Swan Lake where they spend 2–4 years growing before sexual maturity (Fraley and Shepard 1989). Factors such as temperature, channel stability, and cover are known to be important spawning habitat characters (for a review, see Rieman and McIntyre 1993). However, researchers have long recognized that many stream segments of ostensibly suitable habitat (i.e., substrata, gradient, and cover) were never used by spawning bull trout. For example, over 75% of the spawning in the Swan basin occurs in less than 10% of the available stream length (Leathe and Enk 1985). Although studies have noted that stream habitats selected by bull trout for spawning are often influenced by groundwater (Graham et al. 1981; Weaver and White 1985), a quantitative spatial assessment of this habitat factor and its importance to bull trout has not yet been conducted. Furthermore, no studies have focused on a multiscale spatial assessment of hyporheic exchange and spawning habitat use patterns.

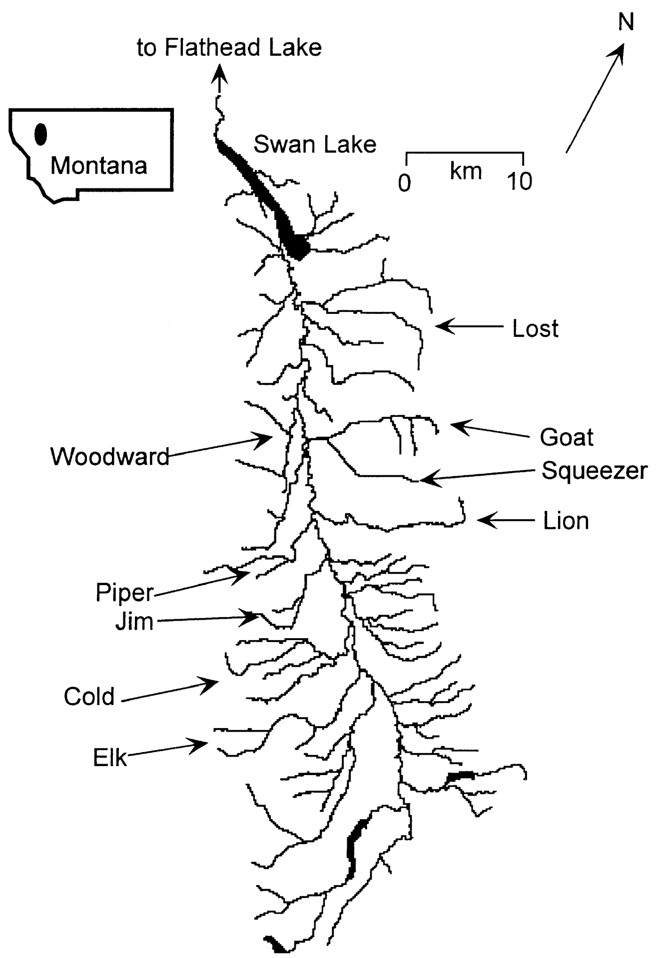
The objective of this study was to examine the relationships between geomorphology, groundwater – stream water exchange patterns, and the distribution and abundance of bull trout spawning sites. General observations of geomorphic structure at the landscape scale, recent study of hyporheic exchange in large, coarse-substratum alluvial floodplains (Stanford and Ward 1993), and patterns of bull trout spawning (e.g., Weaver and White 1985) led us to hypothesize that these biophysical variables were related. Our specific research objectives were to (*i*) quantify the process of hyporheic exchange at multiple spatial scales, (*ii*) identify geomorphic features associated with variation of hyporheic exchange at each spatial scale, and (*iii*) evaluate the influence of hyporheic exchange within the context of a geomorphic hierarchy (i.e., drainage, valley segment, reach, and bedform scales) on the distribution of bull trout spawning.

Materials and methods

Study area

The Swan basin (2070 km^2) is a densely forested, north–south trending, glaciated basin between the Swan and Mission fault-block mountain ranges in northwestern Montana. From peak elevations over 2500 m that are in excess of 1500 m above the valley floor, waters drain through tributary canyons carved in Precambrian metamorphic rock. Tributary streams reach their confluence with the sinuous Swan River as it flows across morainal and alluvial deposits of the broad Swan Valley north into Swan Lake (Fig. 1). The current geomorphic character of the Swan River and its tributaries was established during two major Pleistocene glacial advances, which led to a period of fluvial transport, mass wasting, and alluvial thickening by in-filling from glacial outwash (Kleinkopf et al. 1972). Streams in the Swan basin traverse valley

Fig. 1. Map of the Swan River basin (latitude 47°35′, longitude 113°45′). The nine primary bull trout spawning tributary streams are identified by name. The inset indicates the location of the Swan River in northwestern Montana.



floors dominated by mixed-conifer forest (e.g., *Abies*, *Pinus*, *Thuja*, *Pseudotsuga*, *Picea*, *Larix*), with deciduous trees and shrubs (e.g., *Betula*, *Populus*, *Salix*) concentrated along riparian areas and floodplains.

Our study area included nine third- and fourth-order (Strahler 1964) tributary streams, which constitute the principal bull trout spawning tributaries of the Swan River (Leathe and Enk 1985). The nine tributary drainages ranged in size from 32.9 km^2 (Piper Creek) to 81.8 km^2 (Lion Creek). These streams are typical of the northern Rocky Mountains, possessing a snowmelt-dominated hydrograph with peak flows in late May or June as much as three orders of magnitude greater than base flows. Streams are further characterized by large cobble substratum and waters that are generally very low in dissolved ions, nutrients, and suspended particulates.

Characterization of geomorphic features

At the drainage scale, we used standard U.S. Geological Survey topographic 7.5′ quadrangle maps (1 : 24 000 scale) and structural geological maps (1 : 250 000 scale) to identify and measure 28 geomorphic variables for each of the nine study drainages (Fig. 1; Table 1). We also used aerial photographs and field verification to aid in discrimination of specific features. In addition to traditional landscape-scale geomorphic metrics (Strahler 1964), we classified valley segments into three categories: (*i*) bounded alluvial valley segments, (*ii*) unbounded alluvial valley segments, and (*iii*) confined valley segments.

Bounded alluvial valley segments were characterized by unconfined stream sections at least 500 m in length and greater than 50 m in valley bottom width with a downstream geomorphic knickpoint. Generally, knickpoints were distinguished by steepening in channel slope, constriction in valley width, and a geologic formation near the surface, such as bedrock or terminal moraine deposits. By including measures of valley bottom width and the number of knickpoints, we were able to estimate the number, length, and area of bounded alluvial valley segments (Fig. 2). The area of bounded alluvial segments was examined because it helped describe the overall valley shape that we hypothesized was important to the structuring of hyporheic flow patterns (Fig. 2). Unbounded alluvial valley segments were similar to bounded alluvial valley segments but were always the furthest downstream segment of a tributary where the stream emerged onto the Swan Valley floor and flowed to the Swan River without encountering another knickpoint. We identified confined valley segments by their narrow valley bottoms (typically <50 m) and steep gradients (usually <0.05 m/m). Confined valley segments often were associated with canyons and near-surface bedrock with only a patchy, thin (<2 m) layer of cobble substratum.

Characterization of hyporheic exchange

We quantified hyporheic exchange by measuring vertical hydraulic gradient (VHG) and streambed hydraulic conductivity. We installed piezometers in the stream substratum and calculated VHG from the equation

$$\mathrm{VHG} = \mathrm{d}h/\mathrm{d}l$$

where dh is the difference in head between the water surface in the piezometer and the level of the stream surface (the hydraulic head differential, centimetres), and dl is the depth from the substratum surface to the first opening in the piezometer sidewall (the elevation head differential, centimetres). Thus, VHG is a unitless measure that is positive under upwelling conditions and negative under downwelling conditions.

Hydraulic conductivities (K) were estimated using falling head tests (Lee and Cherry 1978), which measure the rate of water-level equilibration between the piezometer and the surrounding groundwater. For some piezometers, we were able to estimate K using the Hvorslev (1951) equation:

$$K = \frac{(\pi)(D)}{(11)(T_0)}$$

where D is the inside diameter of the piezometer and T_0 is the basic time lag, a value derived from the construction of an equilibration curve (for summary of calculation, see Cedergren 1989). However, among many of the piezometers, equilibration took place so quickly that it was impossible to use the conventional falling head test to create a curve and acquire an accurate estimate of K. Thus, we derived an alternative equation:

$$K = \frac{(0.2501)(D)}{(d_t)}\left|\ln\frac{h_0}{h}\right|$$

where D is the inside diameter of the piezometer and d_t is the time it takes for the head level to drop from h_0 to h. In the situations where we were able to estimate K using the Hvorslev method as well as our modified equation, there was no appreciable difference between the two estimates. Therefore, for consistency, we used only the values obtained by the latter approach for all our analyses. Following the estimation of K, we were able to calculate the vertical component of flow using Darcy's equation for specific discharge (v, centimetres per second):

Table 1. Drainage-scale geomorphic variables that were examined as a part of this study.

Morphometric measure	Slope class	BAVS[a] related
Drainage area	% drainage <1% slope	Maximum valley bottom width
Stream order	% drainage 1–2% slope	Mean valley bottom width
Total stream length	% drainage 2–7% slope	Variation in valley bottom width
Accessible stream length	% drainage 7–20% slope	Number of gradient steps >10%
Drainage density	% drainage 20–40% slope	Number of BAVS
Drainage length	% drainage 40–55% slope	Total area of BAVS
Average stream gradient	% drainage >55% slope	Length of accessible BAVS
Gradient of accessible stream length	% drainage >55% slope	Area of accessible BAVS
Relief ratio		
Form ratio		
Elongation ratio		
Mean bedrock dip angle		

Note: Accessibility refers to whether migratory bull trout can navigate the stream.
[a]Bounded alluvial valley segment.

$$v = -K \times dh/dl$$

where dh and dl are as above for the calculation of VHG (Freeze and Cherry 1979).

We quantified hyporheic exchange at the drainage scale in four of the nine principal bull trout spawning streams: Elk, Lion, Cold, and Lost creeks (see Fig. 1). We installed more than 500 piezometers in alluvial valley segments of these drainages. We did not sample confined segments for VHG because generally, it was impossible to install piezometers in the large, boulder-dominated bed material typical of the confined segments, and frequently confined segments were characterized by near-surface bedrock.

Alluvial valley segments within each of the four tributary drainages were divided into upper, middle, and lower regions, and a reach of approximately 200 m length was sampled in each. Piezometers were spaced at 10- to 15-m intervals, and a minimum of 15 piezometers were installed in each reach. At this scale of sampling, we measured only VHG for each piezometer (no estimate of K). To examine the relative potential for upwelling at each piezometer site, we transformed these VHG data by changing all negative values to zero, while all positive values remained the same. For the sake of simplicity, we refer to these values as groundwater input, although they are actually only a measure of input potential.

We examined hyporheic exchange and streambed geomorphology at the bedform (pool–riffle) spatial scale through detailed analysis of two spawning reaches in Cold and Lion creeks. Following installation of an extensive network of more than 50 piezometers in 100 m of stream length, we measured VHG and K. We then used a Lietz TC600 Total Station to survey channel bedform, topographic complexity of the surrounding floodplain, and piezometer and bull trout redd locations by acquiring 600–700 individual point readings. We then constructed detailed planimetric maps of floodplain and channel morphometry, bull trout redds, and piezometer locations using SURFER™ mapping software. We also constructed topographic contour maps and interpolated isopleths of VHG and intragravel v. Channel morphometry maps were used to separate the streambed into three categories based on longitudinal bedslope character: (*i*) concave, (*ii*) convex, and (*iii*) transitional. Concave patches typically were associated with riffles and the head of pools and convex areas with pool tailouts, and transitional patches were located at the downstream edge of pool tailouts that merge into the head of a riffle. Because we did not want to disturb bull trout eggs, piezometers were not installed directly into redds.

Bull trout redds and stream temperature

Data on the distribution and abundance of bull trout redds were collected in two ways. In all nine principal spawning streams of the Swan basin, we obtained redd data from surveys conducted by the Montana Department of Fish, Wildlife and Parks in autumn 1995. The precision of these data was sufficient for drainage and valley segment scale analyses and allowed us to position bull trout redd locations on topographic 7.5′ quadrangle maps that had geomorphic variables delineated for landscape characterization. We also conducted our own redd surveys on Elk, Lion, Cold, and Lost creeks in order to map locations of redds with the greater precision required for reach and channel unit scale analyses.

We installed Onset™ data loggers to monitor water temperature within the four primary study drainages. We placed temperature loggers in stream reaches that our VHG data indicated to be reaches of groundwater discharge and in reaches known to be either VHG neutral or VHG negative. We also conducted several winter surveys of each creek to estimate the percent ice cover and document the occurrence or absence of anchor ice in proximity to positive or negative VHG readings from our piezometers.

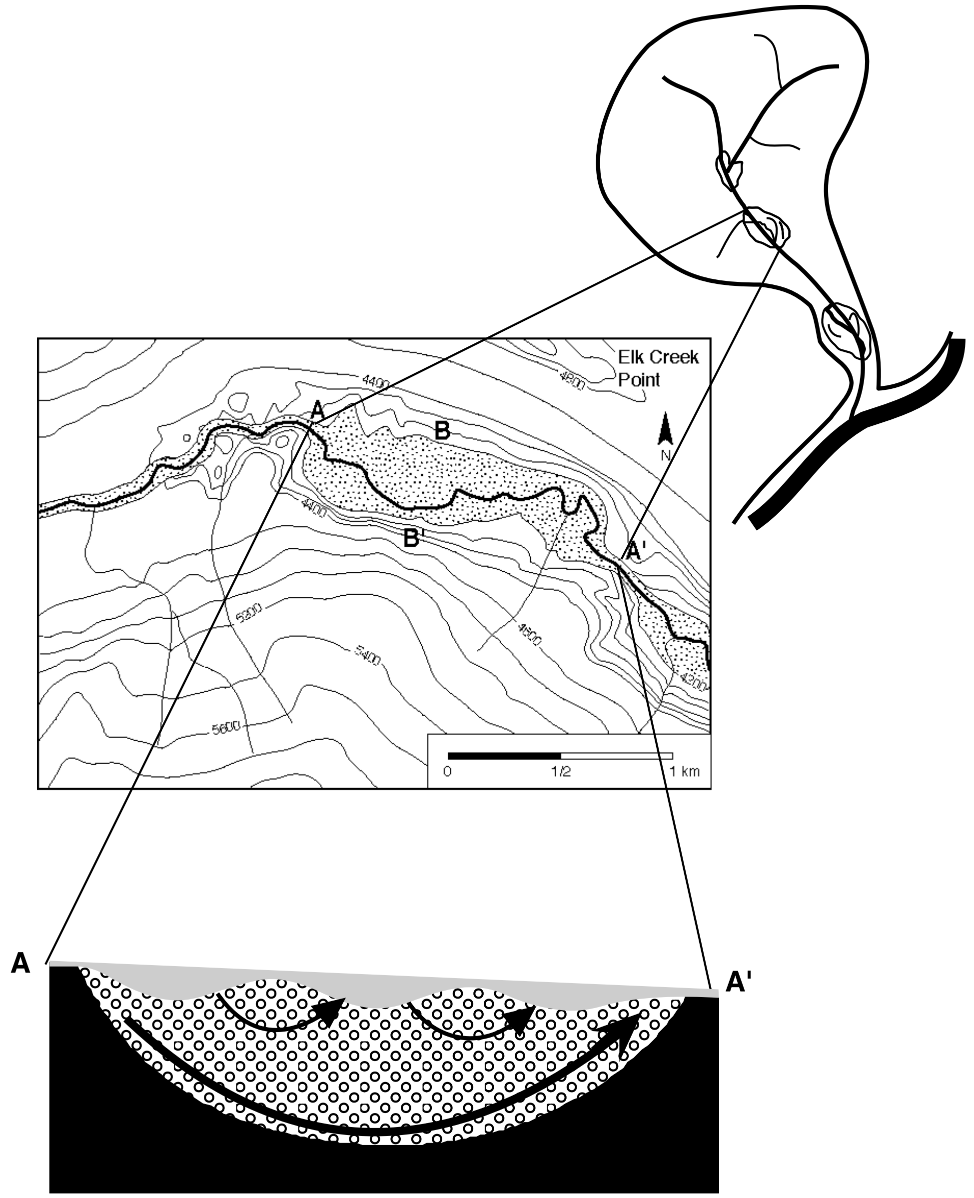
Data analysis

We utilized an empirical approach to assess the distribution of bull trout spawning with respect to geomorphology and hyporheic exchange. At each spatial scale (i.e., drainage, valley segment, reach, and channel unit), we expected that the distribution of bull trout redds would take one of two theoretical forms: (*i*) a uniform, even distribution or (*ii*) a discontinuous or patchy distribution. Our working hypothesis was that bull trout redds would be patchily distributed, with specific habitat preference regarding geomorphic and hyporheic exchange variables occurring at each spatial scale. The null hypothesis was that the distribution of bull trout redds is independent of geomorphic or hyporheic exchange variables.

We examined all combinations of dependent and independent variables. At the drainage scale, two correlation matrices were constructed, one that included geomorphic features and bull trout redd numbers for the nine principal bull trout spawning drainages and another that included only the four streams that were sampled for VHG. Similarly, at valley segment and reach scales, one matrix was constructed for all segments and reaches in the nine basins and another for those in which we collected VHG data. These matrices allowed us to examine individual associations between bull trout spawning and landscape-scale geomorphic variables as well as groundwater – surface water exchange variables. They also allowed us to assess covariation among variables. Where we detected significant correlations, we applied linear regression to assess the relationship between dependent and independent variables.

We used nonparametric χ^2 analysis to determine differences between expected and observed patterns of bull trout redd distribu-

Fig. 2. One of the bounded alluvial valley segments (BAVS) in the Elk Creek drainage (latitude 47°30′, longitude 113°48′). The dimensions of the BAVS were measured directly from U.S. Geological Survey topographic 7.5′ quadrangle maps (1 : 24 000 scale) (*A–A′* = length, *B–B′* = maximum valley bottom width). The cross-sectional diagram (*A–A′*) illustrates how reach-scale (large arrow) and bedform-scale (small arrows) hyporheic exchange typically occurs within a BAVS. The stippling denotes the alluvial valley fill.



tion. We also applied nearest-neighbor analysis and Mann–Whitney *U* tests to assess spatial association between bull trout redds and VHGs. When χ^2 tests resulted in significant differences between used and available habitat, we used Jacobs' *D*, a modification of Ivlev's electivity index, as a nonstatistical indication of where differences between use and availability of habitat types occurred (Jacobs 1974). We considered statistical test results to be significant at $\alpha = 0.05$.

Results

Drainage scale

Among the four tributary streams sampled for VHG, the groundwater input, measured as the mean of positive VHG readings and as maximum positive VHG reading, was positively correlated with the area of bounded alluvial valley segments ($P < 0.05$ and $P < 0.01$, respectively). The mean of all VHG values, positive and negative, was significantly associated with only one geomorphic variable, the number of bounded alluvial valley segments ($P < 0.05$) per stream. Drainages with large and frequent bounded alluvial valley segments possessed more stream habitat that was thermally moderated by groundwater discharge than drainages dominated by confined stream segments and unbounded alluvial floodplain segments.

Among the nine principle spawning streams, the abundance of bull trout redds per tributary drainage was not associated with any of the traditional geomorphic metrics, such as drainage area or accessible stream length (Table 1). The distribution and abundance of redds were, however, posi-

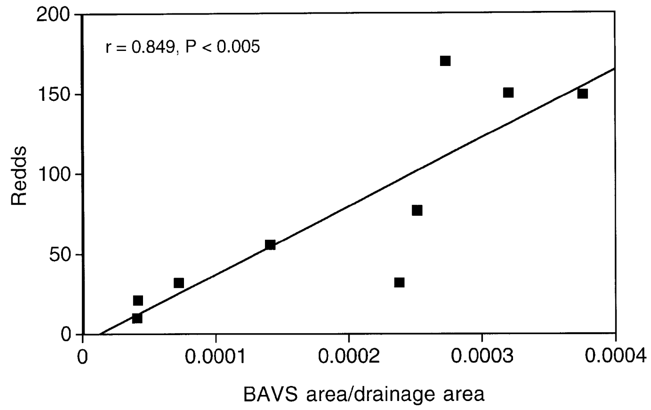


Fig. 3. Number of bull trout redds versus the proportion of the total drainage area that was bounded alluvial valley segment (BAVS) for the nine tributary spawning streams in the Swan River basin.

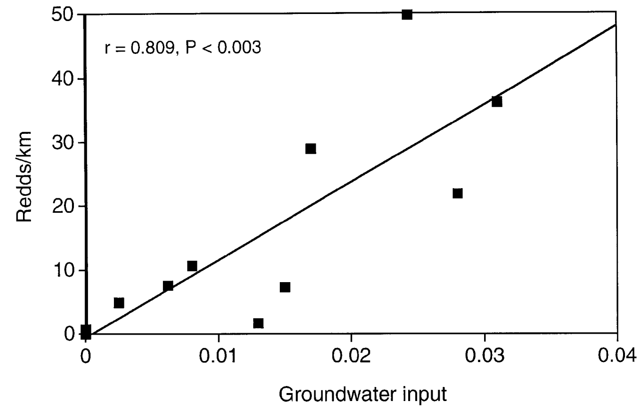


Fig. 4. Number of bull trout redds per stream kilometre in each of the alluvial valley segments sampled for VHG versus the relative strength of groundwater input (mean of transformed VHG readings, unitless) for each valley segment.

tively correlated with geomorphic measures of bounded alluvial valley segments. In particular, the number of redds was positively correlated with bounded alluvial valley area (P < 0.005) as well with as the proportion of the drainage area that was bounded alluvial valley (P < 0.005) (Fig. 3). In addition, the number of redds was associated with the total area of all bounded alluvial valley segments including those above fish barriers (P < 0.05) and with the proportion of the accessible stream length found within bounded alluvial valley segments (P < 0.05). Among the four streams sampled for VHG, we found that the relative strength of groundwater input and maximum positive VHG were positively associated with redd counts (P < 0.05 and P < 0.01, respectively).

Valley segment scale

Within the four streams sampled for VHG, alluvial valley segment types differed significantly in hyporheic exchange depending on whether they were bounded or unbounded by a downstream knickpoint (Mann–Whitney U, P < 0.010). All bounded alluvial valley segments possessed large and significant upwelling zones, while three of the four unbounded alluvial valley segments were exclusively losing or neutral and the fourth showed only weak zones of positive VHG in isolated sites. We also observed a close association between bounded alluvial valley segment area and the relative strength of groundwater input to a segment (P < 0.01). Likewise, bounded alluvial valley segments possessed more stream length that was thermally moderated by groundwater discharge than either unbounded alluvial valley segments or confined segments. They also had the greatest amount of ice-free habitat in the winter.

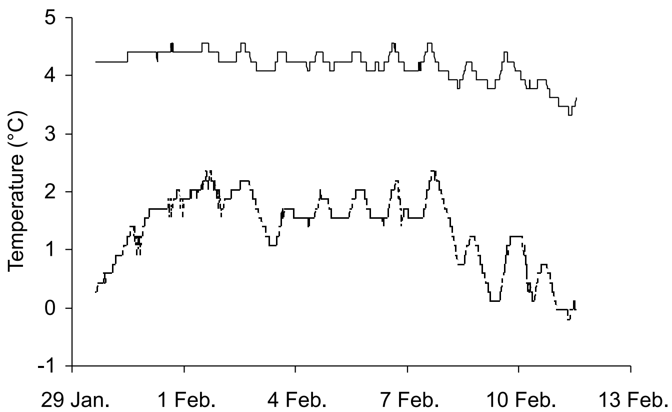
Among all valley segments in the nine principal spawning streams, bull trout redds were positively associated with bounded alluvial valley segments (χ^2 = 917, P < 0.0001). Of the redds observed, 88.5% were located in bounded alluvial valley segments, whereas 8% were found in unbounded alluvial floodplain segments and only 3.5% were observed in confined valley segments. Of the available stream length, 38% was located in bounded alluvial valley segments, 56% in unbounded alluvial valley segments, and 5% in confined segments. The availability of bounded alluvial valley segments relative to their usage suggested a positive selection (Jacobs' D = 0.450). Additionally, among the valley segments of the four VHG-sampled tributaries, the relative strength of groundwater input in a segment was positively associated with both the number of redds (P < 0.05) and the redd density (P < 0.005) (Fig. 4). When only bounded alluvial valley segments were considered, the number of redds was weakly correlated with groundwater input (P < 0.1).

Reach scale

Within bounded alluvial valley segments, the geomorphic context of a reach along the longitudinal gradient was often indicative of whether it was a gaining, losing, or neutral reach. Reaches at the upstream end of a bounded alluvial valley segment were usually downwelling, those in the middle were often neutral, and those at the downstream end, just upstream of the bounding knickpoint or valley constriction, were always upwelling. The mean VHG per reach was negatively associated with the mean valley bottom width at each reach (P < 0.005). Reaches in the middle of bounded alluvial valley segments had very wide valley bottom widths and were typically neutral or slightly negative in VHG. In addition, several reaches located in the unbounded alluvial valley segments of the four streams had wide valley bottom widths and were strongly downwelling. The thermal regimes of gaining reaches were significantly moderated by the groundwater effect (Fig. 5). Gaining reaches possessed the least ice cover even when the reaches were exposed to extremely cold winter air temperatures. These moderating effects dissipated with increasing downstream distance from the upwelling zone.

Reaches that were gaining water (mean VHG = 0.0169) had the highest number of observed bull trout redds (n = 94). Among the reaches sampled, there were no significant differences in redd distribution associated with geomorphic variables (e.g., reach gradient, valley bottom width) other than the proximity to a downstream knickpoint. The number of bull trout redds per reach was positively correlated (P < 0.001) with the relative strength of groundwater input per reach (Fig. 6). Furthermore, since the scatter of points on this graph was somewhat clustered, we broke the reaches into categories of low (<0.03) and high (≥0.03) groundwater input and tested the observed versus random distribution of redds among reaches. We found the difference to be highly

Fig. 5. Thermal profiles for two winter weeks from a gaining (solid line) and a losing (broken line) reach of Lion Creek clearly show the moderating effects (both seasonal and diel) of groundwater. The supercooled temperature of the losing reach at the end of the profile corresponded to anchor ice formation. Twenty-three bull trout redds were counted in the gaining reach, while none were found in the losing reach.



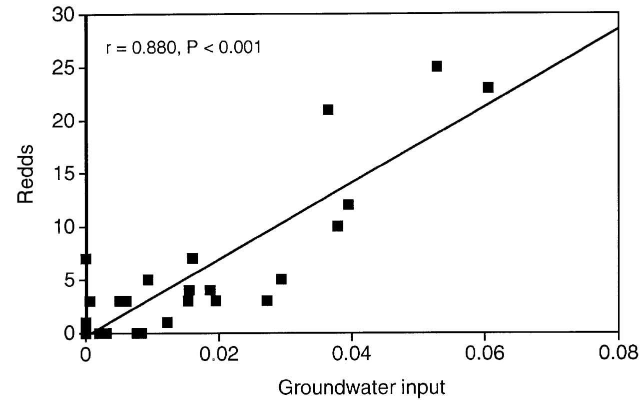
significant (χ^2 = 215, P < 0.0001), and reaches with strongly positive groundwater input were selected for spawning based on their availability (Jacobs' D = 0.795).

Pool–riffle scale

Within reaches in Lion and Cold creeks, we observed an association between bedform morphology, hyporheic exchange, and redd distribution. These reaches possessed significant sources of groundwater discharge, had moderated thermal regimes, and were free of ice throughout the winter. However, VHG varied significantly with local bedform character (Fig. 7). Convex and transitional bedforms were significantly different in VHG from concave bedforms (Mann–Whitney U = 64, P < 0.0001), in that areas of the streambed that were transitional or convex possessed negative VHG with means of –0.099 and –0.042, respectively, while concave streambed displayed upwelling VHG (mean = 0.038). In each reach, we observed several instances in which large wood contributed to local variation in bed topography and heterogeneity in the magnitude and direction of VHG. For logs that were positioned perpendicular to the current and that created a pool, shallow downwelling occurred above the logs and upwelling occurred in the pools below the logs. Estimated K ranged from 2.32 × 10^{-6} cm/s to a maximum of 3.37 × 10^{-1} cm/s, a difference of more than five orders of magnitude. Falling head test data indicated that transitional bedforms possessed significantly higher intragravel v than either convex or concave bedforms (Mann–Whitney U, P < 0.0001).

Bull trout redds were located most frequently in transitional as opposed to convex or concave bedform classes (χ^2 = 54, P < 0.0001) (Fig. 7). Of the 15 redds found in the Lion Creek and Cold Creek reaches, only one of these was located in a concave bedform unit. There were two transitional units where no redds were constructed; however, the availability of transitional areas relative to their usage was suggestive of positive selection (Jacobs' D = 0.895). Examination of individual redds revealed that spawning sites were

Fig. 6. Number of bull trout redds observed in each of the reaches sampled for VHG versus the groundwater input (mean of transformed VHG readings) for each reach.



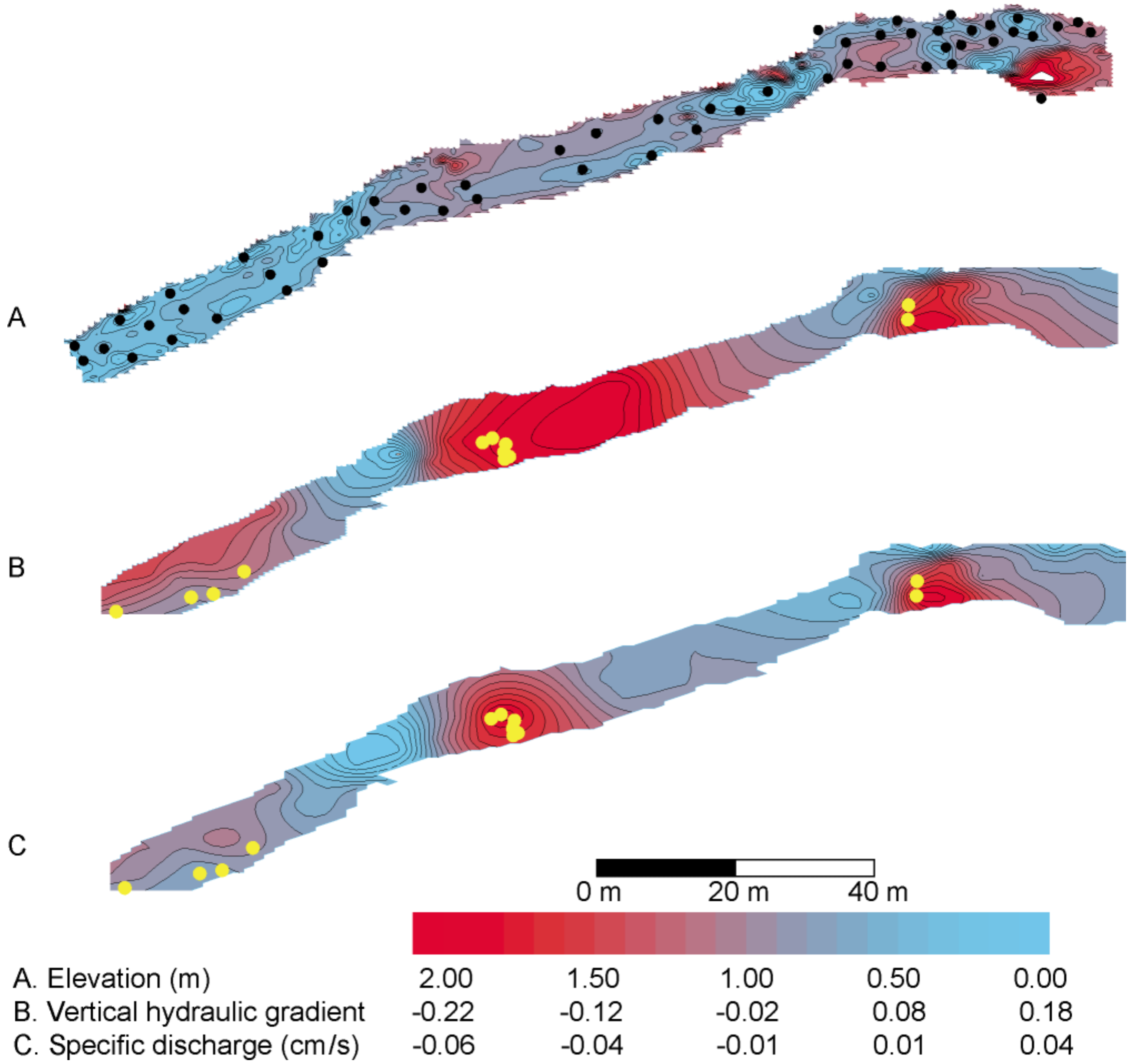
strongly associated with piezometers having a negative VHG to the second nearest neighbor (Mann–Whitney U = 32, P < 0.001). The median distance from redds to the nearest downwelling piezometer was only 2.1 m, while the median distance to the nearest upwelling piezometer was 14.6 m. Furthermore, after accounting for the relative availability of downwelling versus upwelling habitat within these reaches, we found a significant difference between the expected and the observed distributions of redds (χ^2 = 8.99, P < 0.005), suggesting positive selection of transitional bedforms that are also downwelling areas (Jacobs' D = 0.751) (Fig. 7).

The distribution of redds was also associated with the magnitude of intragravel v. Redds were located in areas with the highest flow (indicated by piezometric falling head tests), while those with the weakest flow were never used (Fig. 7). We separated the estimates of v (i.e., v using Darcy's equation) in the two mapped reaches into three categories of low (<0.001 cm/s), medium (0.001–0.01 cm/s), and high (>0.01 cm/s). After accounting for the relative availability of habitat in each intragravel flow category, we found a significant difference between the expected and the observed distributions of redds (χ^2 = 17.98, P < 0.0001), suggesting positive selection of areas with high intragravel v (Jacobs' D = 0.727).

Discussion

The results of this study describe how groundwater – stream water exchange is structured by geomorphic features at drainage, valley segment, stream reach, and channel unit scales. Our findings also show that the selection of spawning sites by bull trout is strongly associated with hyporheic exchange at all of these scales. The mechanisms governing bull trout spawning habitat selection may vary from one scale to another within the hierarchy. Furthermore, although we are unsure of the scale to which homing occurs in this species (Rieman and McIntyre 1993), there is a transition in process that occurs between homing and redd site selection (Northcote 1978). Spawning habitat selection is a complex function of the results of differential survival by embryos and rearing juvenile fish, along with fish sensory capabilities. Although our study does not explicitly determine causal mechanisms, we illustrate how hyporheic exchange may control a variety

Fig. 7. Three maps of a spawning reach on Lion Creek showing (A) channel bed topography and piezometer locations, (B) isopleths of VHG grading from positive VHG (blue) to negative VHG (red), and (C) isopleths of intragravel *v* grading from high (red) to low (blue) rates. Dots indicate piezometer locations in map A and bull trout redds in maps B and C. The direction of flow is from right to left.



of habitat factors (i.e., temperature, intragravel conditions, ice conditions) that may directly affect an integrated process of spawning habitat selection.

Geomorphic controls on hyporheic exchange

Our results demonstrate that the integration of hydrology and geomorphology across spatial scales plays a critical role in structuring hyporheic exchange patterns. Within a drainage, we observed that bounded alluvial valley segments and their associated hyporheic zones were structured longitudinally like beads on a string (sensu Stanford and Ward 1993). Among the study drainages, the amount of groundwater discharge to a stream appeared to vary closely with the size and frequency of bounded alluvial valley segments. The presence of knickpoints, particularly on the downstream end of alluvial valley segments, was critical to the constraining of hyporheic flow. The importance of alluvial floodplain segments and knickpoints to ecosystem structure and function has been observed in large montane rivers (Stanford and Ward 1993). Our results are consistent with the concept that these landforms play a significant role in structuring hyporheic exchange in small tributary systems as well.

Within tributary drainages of the Swan basin, we found that alluvial valley segment types differed in their hyporheic exchange character depending on whether they were bounded or unbounded by a downstream knickpoint. Bounded alluvial valley segments had the most variation in hyporheic exchange and the strongest upwelling zones. Moreover, the greater the spatial extent of a bounded alluvial valley segment, the greater the strength of groundwater input was within the segment. Unbounded alluvial valley segments were always associated with a tributary's confluence with the Swan River and were characterized by reaches with strongly negative VHG. These contrasts and associations are evidence that geomorphic constraint on the length, lateral complexity, volume of alluvial fill, and character of geomorphic knickpoints in alluvial valleys affects hyporheic exchange.

Reaches with upwelling hyporheic groundwater were almost exclusively located within bounded alluvial valley segments. Within a bounded alluvial valley segment, reaches at the upstream end were usually downwelling, and reaches at the downstream end of the floodplain just upstream of the confining knickpoint were upwelling. These sites were also marked by narrowing valley widths partly because the valley walls of bounded alluvial valley segments typically begin to pinch together as the downstream knickpoint is reached. These patterns are consistent with what might be expected based on the application of basic principles of hydrogeology (Freeze and Cherry 1979) at the scale of an alluvial valley segment. Although reaches located at the downstream ends of bounded alluvial valley segments were gaining subsurface water, these reaches were not the only ones with groundwater discharge. In part, we attribute this to nonhyporheic inputs (e.g., seeps from bedrock fissures) that were independent of hyporheic flow pathways. We also observed relatively impermeable clay layers that probably contributed to localized upwelling (i.e., positive VHG) measurements in some instances. In addition, in Cold Creek, we observed negative VHG above a large beaver dam complex and positive VHG for several hundred metres downstream, a phenomenon that has been observed by others (e.g., White 1990).

Within reaches, we also observed associations between geomorphology and hyporheic exchange. We observed that VHG varied significantly with bedform character, as has been shown by others (e.g., Vaux 1968; Thibodeaux and Boyle 1987; Harvey and Bencala 1993). Convex and transitional bedforms displayed localized, shallow downwelling, while concave areas possessed upwelling. In several instances, large wood appeared to create local variation in bed topography and heterogeneity in the magnitude and direction of VHG, where shallow downwelling occurred above logs and upwelling occurred in the pools below logs.

The K (as measured using falling head tests in piezometers) and intragravel v (estimated via Darcy's equation) were highly variable within stream reaches. Transitional bedforms located at the tailout of pools (i.e., just upstream of riffles) possessed the highest values of K and v. This observation concurs with laboratory flume experiments (Cooper 1965; Thibodeaux and Boyle 1987) in which the fastest intragravel flow rates were observed at the crests of waveforms as a consequence of pressure gradients. Qualitative observation of piezometer screens indicated the patchy distribution of clay or fine sediment at varying depths. Thus, both the shape of the stream bed and the structure of the stream substratum may contribute to the spatial variability in intragravel flow. In addition, although we did not investigate conditions within redds, the construction of redds may alter very localized patterns of VHG and may positively influence the K of the disturbed site (Cooper 1965).

At the drainage scale, the arrangement of bounded alluvial valley segments may influence the cumulative thermal and flow regimes of a stream. Although our study did not explicitly address this hypothesis, we did observe that drainages with larger, more frequent bounded alluvial valley segments possessed more stream habitat that was ice free during the winter. The strength and dissipation of the groundwater plume leaving the lower end of a bounded alluvial valley segment may affect the discharge and thermal regimes of areas downstream. We observed that areas influenced by groundwater discharge possessed relatively stable thermal regimes. Furthermore, reaches influenced by upwelling groundwater had less winter ice cover and experienced no anchor ice formation. This was in contrast with frequent occurrence of anchor ice in neutral and losing reaches that were not thermally buffered by upstream groundwater discharge.

Bull trout spawning patterns

The size and distribution of bounded alluvial valley segments on the landscape influence the distribution and abundance of bull trout spawning. In the Swan basin, bull trout redds were most abundant in drainages with extensive bounded alluvial valley segments. Previous landscape-scale analyses of bull trout spawning have suggested there is a significant association between redd frequency and drainage area and (or) stream order (Graham et al. 1981). These conventional drainage metrics may be important discriminators for presence–absence of bull trout spawning at broad spatial scales, as was suggested by Rieman and McIntyre (1995). However, they do not appear to be useful predictors of between-tributary variation in distribution or abundance among the principle spawning streams of the Swan basin.

We found that bull trout selected reaches for spawning with zones of hyporheic groundwater discharge. We also observed that these reaches consistently occurred within bounded alluvial valley segments. Various reach-scale geomorphic factors, such as stream gradient, have been identified as important factors affecting bull trout spawning habitat (Graham et al. 1981; Fraley and Shepard 1989). We found that low stream gradient was a character of both bounded and unbounded alluvial valley segments. Consequently, it was not a direct indicator of spawning reach selection. Rather, bull trout used reaches with hyporheic groundwater discharge that also possessed low stream gradient as a covariate.

At drainage and valley segment scales, the importance of hyporheic exchange and its influence on bull trout spawning may be related to temperature and flow regimes. Numerous researchers have identified alluvial valley segments as critical spawning habitat for many fish species (e.g., Copp 1989; Montgomery et al. 1999). In addition to habitat influenced by groundwater discharge, these segments contain large, stable expanses of well-sorted gravel and cobble. Furthermore, the presence of floodplain surfaces in these segments allows overbank flow, which moderates sediment scour associated with flooding. In contrast, suitable spawning gravel is sparse and individual patches are often small in confined valley segments where floodwaters are not attenuated by a floodplain.

Habitat-use and spawning patterns of bull trout are influenced by the geologic legacy of a basin. Longitudinally stepped drainage forms, bowl-like floodplain shapes, deep alluvial fill, high gravel porosity, and position of knickpoints are features influenced by glaciation. These features create deep hyporheic flow pathways and influence bull trout spawning habitat in the Swan basin. In contrast, hyporheic exchange in similar-sized, nonglaciated stream systems of northeastern Oregon appears to occur only at shallow, small spatial scales (C. Baxter, Oregon State University, Corvallis, Oreg., unpublished data). Thus, many bull trout streams lack the deep, extensive flow pathways typical of glaciated basins and their floodplains. As a consequence of these differences, it is important to consider groundwater – surface water interactions (Creuze des Chatelliers et al. 1994) and bull trout habitat-use patterns in their biogeoclimatic context.

Reaches influenced by groundwater discharge possess relatively stable thermal and flow regimes that may be important for bull trout egg incubation, emergence success, and the survival of juvenile bull trout. Differential survival at any of these stages could influence the distribution of adult spawning. In addition, homing by bull trout may be guided by cues that are related to the unique chemical signature of groundwater. Although little is known about groundwater effects on bull trout, numerous studies have demonstrated the importance of groundwater discharge zones to a related species, the brook trout (*Salvelinus fontinalis*), and other salmonids. For example, our observations of bull trout reflect Benson's (1953) finding that groundwater-influenced reaches of the Pigeon River in Michigan had less ice cover and appeared to be selected as spawning reaches by brook trout. In general, groundwater discharge sources provide cold-water refugia for fish in summer (Gibson 1966; Nielson et al. 1994) and warmwater refugia in winter (Craig and Poulin 1975; Cunjak and Power 1986). In addition, warm groundwater temperatures in winter inhibit the formation of anchor ice, which would otherwise cause high mortality in postemergent salmonids (Benson 1955).

At the pool–riffle spatial scale, we found that bull trout redds were associated with transitional bedforms at the tailouts of pools that formed at the heads of riffles. These sites also possessed localized downwelling (i.e., negative VHG) and high intragravel flow rates. Similarly, in a spawning tributary of the North Fork of the Flathead River, Weaver and White (1985) detected greater permeability in a bull trout spawning area than in a nonspawning area. Whether it is the direction or the magnitude of hyporheic exchange, or both, that is actually involved in redd site selection, we are unsure. Intragravel flow has long been recognized by fisheries biologists as important to the growth, development, and survival of salmonid eggs and fry. Numerous salmonid species tend to spawn in the transitional zone between pools and riffles where intragravel flow rates are high, and percolation through the redd is thought to provide a constant supply of oxygen to the eggs and effectively remove metabolic waste materials (Bjornn and Reiser 1991). Finer spatial resolution in measures of VHG and intragravel flow rate, along with quantification of other factors such as substrate character and intragravel dissolved oxygen levels, would further delineate the relative importance of hyporheic exchange to spawning site selection at the microhabitat scale. Study of bull trout sensory capabilities, along with their growth and survival to emergence and the success of rearing juveniles in habitats possessing variable hyporheic exchange characters, could shed more light on the underlying biological mechanisms of these habitat-use patterns.

It appears that there is a spatially nested relationship between hyporheic exchange and bull trout spawning habitat use. Although we found at the larger spatial scales that bull trout spawning was associated with zones of positive VHG, at the pool–riffle scale, we found bull trout redd distributions associated with localized downwelling (i.e., negative VHG) and transitional bedforms between pools and riffles. Without a hierarchical approach to the interaction between hyporheic exchange and bull trout spawning, we would have obtained an erroneous picture of spawning habitat selection. For example, if we had only examined hyporheic exchange in the immediate vicinity of redds, we might have concluded that spawning habitat selection occurred within downwelling areas and had nothing to do with upwelling groundwater. Alternatively, had we ignored the smaller scale, the unique associations that we observed between VHG, transitional bedforms, intragravel flow, and specific redd placement would have been missed.

Much of the fisheries research on groundwater effects has focused on characteristics of the environment in and immediately surrounding redds (e.g., Webster and Eriksdottir 1976; Curry and Noakes 1995) and the consequences for growth and survival to emergence in redds with varying rates of subsurface flow (e.g., Sowden and Power 1985). The findings of this study suggest the drainage and valley segment scale context of a spawning site or a spawning reach are important considerations. Variation of some habitat factors may not be detectable or important to bull trout at all scales. Hyporheic exchange, however, appears to be important to spawning habitat selection processes at each of the spatial scales examined. In much of the fisheries research attempting to characterize habitat use, habitat variables have been considered as describing local conditions, regardless of their primary scales of heterogeneity. As we and other authors (e.g., Poizat and Pont 1996; Torgersen et al. 1999) have observed, this approach may obscure meaningful patterns by mixing specific organismal responses to habitat factors that vary differently at different scales.

The findings of this study emphasize the importance of considering local geomorphic context and spatial scale when describing stream processes. These factors are treated incompletely within the existing paradigm of the river continuum concept (Vannote et al. 1980; Minshall et al. 1985). Rather, our observations of the importance of local variability in hydrogeomorphic processes to habitat use by spawning bull trout may represent an example of the applicability of Montgomery's (1999) process domain concept. A landscape context is important to a better understanding of hyporheic processes, as geomorphology plays a scale-specific role in patterning variation of hyporheic exchange. Many studies of hyporheic processes have been done within a single, short stream reach (e.g., Harvey and Bencala 1993). Our observations demonstrate that the valley segment and drainage scale context of a reach could influence the findings of such a study and that quantifying hyporheic exchange in a spatially extensive manner is both critical and feasible.

Conserving the bull trout and other fish species that possess complex migratory life histories demands a landscape perspective (Schlosser 1995). Our findings demonstrate that the conservation of bull trout and the maintenance and (or) restoration of spawning habitat will require consideration of groundwater – surface water exchange within a hierarchical, geomorphic context. For example, the distribution of bounded alluvial valley segments on the landscape may be significant to bull trout restoration plans in this region because of the importance of this distribution to understanding the spatial geometry of bull trout habitat (e.g., Rieman and McIntyre 1995; Dunham and Rieman 1998). This study has helped to identify one component of the functional combination of habitats in the landscape mosaic required by this species. Finally, these findings have contributed to the growing body of research demonstrating the importance of hyporheic processes to the structure and function of stream ecosystems.

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