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GEOMORPHIC CONTROLS, RIFFLE SUBSTRATE QUALITY, AND SPAWNING SITE SELECTION IN TWO SEMI-ALLUVIAL SALMON RIVERS IN THE GASPÉ PENINSULA, CANADA[†]

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ABSTRACT

The relationships between valley and channel morphology, spawning substrate quality (content of fine sediment <2 mm) and the selection of spawning sites by Atlantic salmon (*Salmo salar*) were investigated along 45 km of two semi-alluvial, valley-confined rivers in the Gaspé Peninsula, Canada. Linear and logistic regressions confirm that Atlantic salmon prefer spawning at riffles providing good rather than mediocre or poor spawning substrate, as defined by the percentage sand and the Sand Index of Peterson and Metcalfe. However, exceptionally large concentrations of redds were observed on the few riffles located at island heads, with sub-optimal substrate quality. This observation suggests that, in addition to content of fine material in the substrate, the morphology of spawning reaches may be a significant factor controlling the intensity of inter-gravel flow through redds and the consequent selection of spawning sites. In the study systems, the quality of spawning substrate was controlled by 'large-scale' geomorphic attributes at the scale of valley segments (1–5 km here): segments located within a wide valley were actively meandering, had higher sinuosity and bank erosion rates, generally lower shear stresses and presented somewhat higher sand content than segments confined by a narrow valley. Although sand contents were significantly higher, laterally unstable segments in wide valleys still harboured good to excellent spawning substrate overall. The study data do not allow the roles of variations in levels of riffle-zone shear stress to be distinguished from those of cut bank fines input, to explain the observed inter-segment association between valley width and riffle fines content. Copyright © 2004 John Wiley & Sons, Ltd.

KEY WORDS: fluvial geomorphology; Atlantic salmon; fish habitat; substrate quality; spawning; gravel-bed river; redd; fine sediment

INTRODUCTION

Assessing the quality of spawning habitat is of great importance for the management of salmonid populations in natural rivers. The detrimental effects of fine sediment on the survival of salmonid embryos/sac-fry have been documented in numerous laboratory studies (Wickett, 1954; McNeil and Ahnell, 1964; Lotspeich and Everest, 1981; Peterson and Metcalfe, 1981; Tappel and Bjornn, 1983; Chapman, 1988; Young *et al.*, 1991). However, successful salmonid reproduction depends on multiple physical controls. Reproductive success at a redd site fundamentally depends on the intensity of interstitial water flow through spawning gravel as well as on physical factors that minimize the vulnerability of redds to freezing, scouring and entombment (Sowden and Power, 1985; Walsh and Calkins, 1986; Kondolf *et al.*, 1991; Montgomery *et al.*, 1999; Baxter and Hauer, 2000; Lapointe *et al.*, 2000). The intensity of intergranular flow through the spawning gravel is a function of its permeability, controlled by substrate sedimentology, but equally of the riffle-zone gradients in hydraulic head, partly controlled by local channel and bedform morphology (Geist and Dauble, 1998; Geist, 2000). Considering all the factors affecting spawning habitat quality, and because redd excavation by spawners is known to reduce the amount of fine sediment in redds compared to that of the original bed material (Kondolf *et al.*, 1993), one can question how strongly riffle substrate size composition, typically sampled at low flows rather than during the reproductive season, can act as a predictor of spawning site selection by Atlantic salmon. To the authors' knowledge, no large-scale field study has

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investigated statistically the relationship between riffle sedimentology and the probability of redd occurrence during spawning season. This paper begins by testing this relation along 45 km of two semi-alluvial, valley-confined fifth-order river main stems in the Gaspé Peninsula, Canada. Semi-alluvial systems refer here to river systems where streams flow within their alluvium while constrained locally by a range of bedrock outcrops and confining valley walls acting as lateral and vertical controls.

The second aspect of this study addresses how differences in valley morphology (particularly variations in valley to channel width ratio) at the valley segment scale (1–5 km here) affect the quality of spawning habitat. The sedimentology of riverbeds is known to vary strongly at the basin scale, as a function of stream slope and order, from coarse-bed mountain headwaters to sandy lowland reaches. Within stream segments of a given order, bed sedimentology should vary locally as a reflection of (1) sediment inputs from tributary, valley side and channel bank erosion and (2) local changes in stream competence controlled by the geomorphic configuration of the channel and valley (Bull, 1997; Payne and Lapointe, 1997; Rice and Church, 1998; Buffington and Montgomery, 1999a,b; Hoey and Bluck, 1999). In semi-alluvial mountain valley systems, differences in degree of lateral valley confinement at the segment scale may affect both the grain size of lateral sediment inputs and the channel competence: in particular fine sediment input from channel bank erosion and channel competence may be inversely related, in cases where lateral channel shifting is hindered within steeper, high shear stress, river segments laterally confined by a narrow valley. This study investigates the effects of contrasting patterns in valley confinement and lateral channel stability on the quality of spawning substrate in the two study systems, along which sediment input from tributaries is negligible overall.

The first objective of this research is thus to test the usefulness of a simple index of abundance of fine material applied to riffle substrate sampled prior to the reproductive season as a predictor of probability of Atlantic salmon redd construction. The second objective is to test the hypothesis that, within the study systems, when compared to segments experiencing a greater degree of lateral confinement, segments where the river freely meanders within a wide valley exhibit greater bank erosion rates, lower overall channel competence, greater substrate fines content and thus somewhat poorer spawning habitat on average.

STUDY SITES

The Petite Cascapédia and Bonaventure Rivers are adjacent gravel–cobble systems in the Gaspe Peninsula of Quebec, Canada. The study was carried out along the fifth-order (based on 1: 250 000 maps) main stems of both rivers, along which Atlantic salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) reproduction and juvenile rearing as well as world class salmon and sea trout sport fishing occur. Despite broadly similar geology and land use, large variations in valley widths, channel shear stress regimes and lateral instability conditions occur within and between the two rivers.

The rivers drain southward into Chaleurs Bay from the dominantly igneous Shickshock Highlands of the Appalachian mountain belt in the Gaspé Peninsula (Figure 1). Within the middle and lower drainage basins, bedrock is mainly composed of folded and faulted Palaeozoic sandstone, mudstone and limestone. The study focuses on a total channel length of about 30 km in the Petite Cascapédia River and 15 km in the Bonaventure River (Figure 1). These main-stem valleys are incised into low plateaus (300 m of local relief) of a Cenozoic age Appalachian peneplain and tend to be either narrow and V-shaped or have flat bottoms bordered by discontinuous terraces of fluvio-glacial origin. Smaller tributary watersheds along the main-stem study reaches are mostly forested. Large-scale logging occurs near the head of the basins, but this activity occurs too far upstream to cause inter-reach differences in substrate quality in the study area.

Although cobble supply is abundant in these incised valleys, the mountain river systems are best described as semi-alluvial since their courses are partially constrained by valley walls. While most of the channel perimeter is cobble–gravel alluvium, large boulders and bedrock outcrops are abundant along the channel perimeter in the more confined reaches (especially along the Bonaventure river). Valley walls limit lateral migration in narrower valley sections (<0.5 km). In sections where the valley is locally wider (0.5 to 1 km), channels can meander relatively freely through their floodplain.

While local geomorphic conditions vary within and between the rivers, the two study systems are of comparable scale. In the middle of the study sections mean annual discharge is 33.3 m^3/s for the Petite Cascapédia River, at the

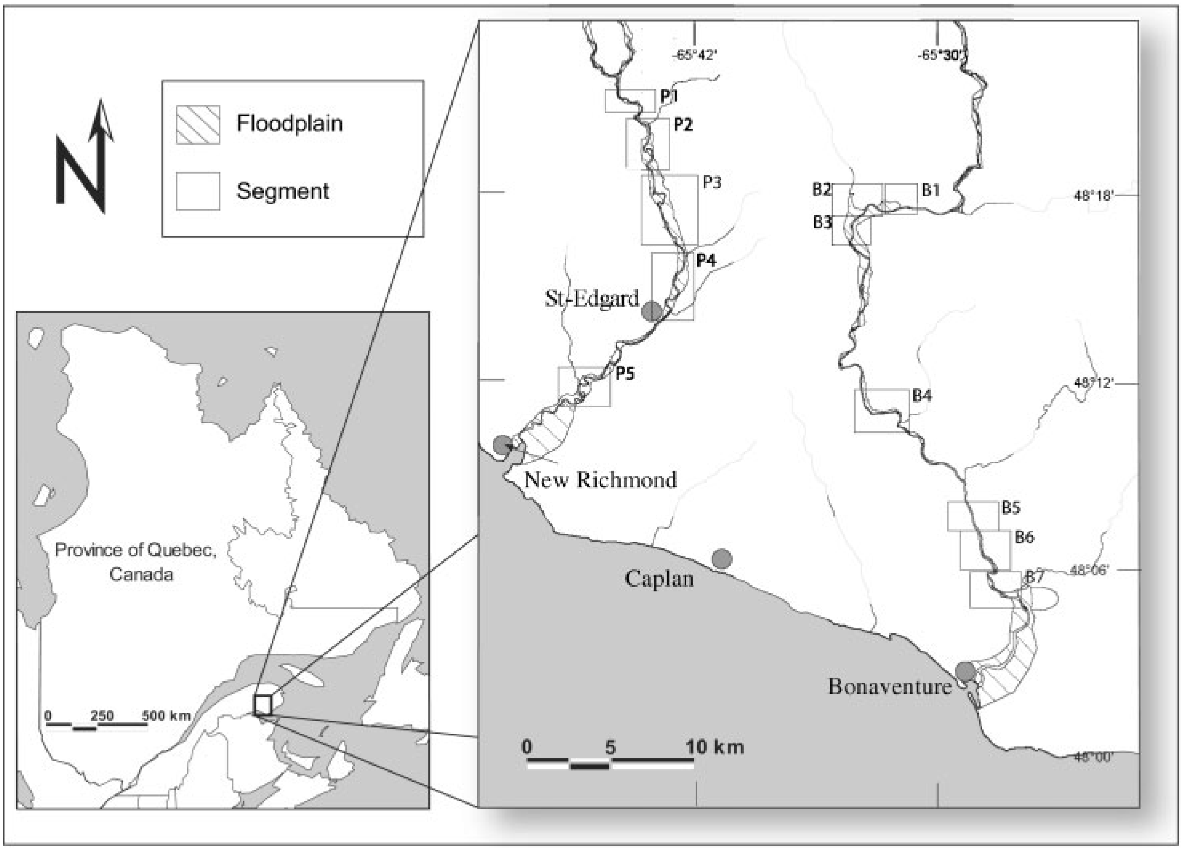

Figure 1. Location of rivers and limits of river segments

town of St-Edgard, and 51.3 m^3/s for the Bonaventure River, 25 km upstream of its mouth (Figure 1). Unit bankfull stream power (ω), a measure of energy dissipated at bankfull discharge by flowing water on a unit area of channel boundary ($\omega = \rho gQS/W$) ranges from 90 to 140 W/m^2 in the Petite Cascapédia study reaches and 80 to 170 W/m^2 in the Bonaventure River reaches. According to Ferguson (1987), such rivers are classified as high-energy streams. Typical bankfull widths and mean channel gradients in the study reaches are similar: 60 m and 0.20% for the Petite Cascapédia River and 73 m and 0.23% for the Bonaventure River.

METHODS

Sediment sampling of potential spawning beds

Bulk sampling of the sub-pavement bed material (Church *et al.*, 1987), was performed systematically at each riffle along the study sections. In total, 44 riffles were sampled along the Petite Cascapédia River and 22 along the Bonaventure River. Significant small-scale heterogeneity in substrate composition is usually observed over riffles (Adams and Beschta, 1980; Lisle, 1989; Payne, 1995). However samples from geomorphically comparable zones within successive riffles can provide meaningful information about along-river trends in spawning substrate quality (Payne and Lapointe, 1997). To standardize sampling location, bulk samples were collected at approximately one channel width upstream of the riffle crest, halfway between the thalweg and the channel bank and in the 'high velocity zone' of the riffle (*sensu* Payne and Lapointe, 1997; Lapointe *et al.*, 2000) (Figure 2). Spawning by Atlantic salmon is considered most likely to be observed upstream of the riffle crest, where down-welling of stream water typically occurs. Within the riffle cross-section, bulk samples were collected on the high-velocity side or within the thalweg, where bed material tends to be coarsest and lowest in sands and consequently more suitable

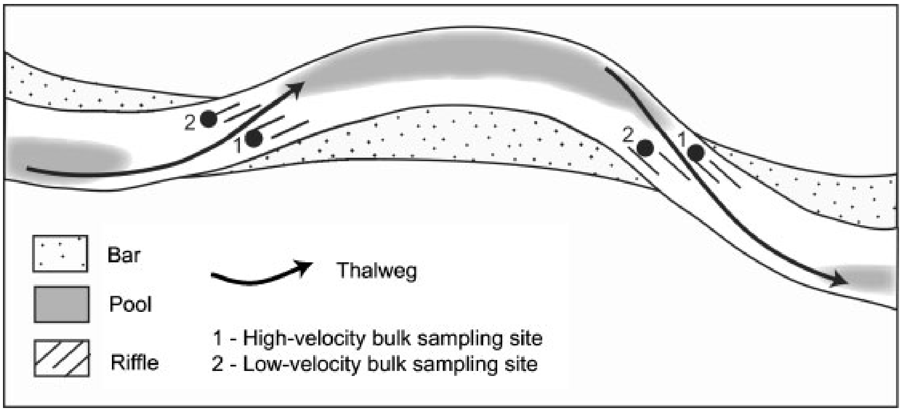

Figure 2. Location of bulk sampling sites within pool–riffle sequences

for spawning (Figure 2, sites 1). Identification of the high-velocity side was ambiguous at some riffles located in straighter reaches; in these cases the coarsest side of the thalweg was systematically sampled.

Conventional, small-volume freeze-core or McNeil samples are often truncated to various degrees at the coarse end of the size distribution, as these samplers often cannot efficiently collect coarser fractions within the natural spawning substrate. Moreover, the inferred percentage of fine sediment necessarily increases as the upper truncation size limit in the substrate sample decreases. Here, to avoid poorly controlled biases in fines contents due to site-dependent levels of undersampling of coarse fractions, large volumetric samples of the spawning substrate are collected and analysed using conventional bulk sampling techniques (Church *et al.*, 1987).

Pavement stones, the top layer of bed material, are removed from the 60 cm wide sampling area and excluded from the sample. A minimum of 100 kg of sub-surface material was sampled at each site. Sample holes were 20 to 30 cm deep, which is a typical depth for Atlantic salmon redds (DeVries, 1997). The coarser particles were then wet-sieved directly in the field at single phi-intervals ranging from 256 mm to 16 mm. Templates were used for particles greater than 45 mm and sieves for the smaller particles. Representative sub-samples of particles smaller than 16 mm (>30 g) were brought to the laboratory to be dry sieved down to 0.063 mm (silt) at single phi-intervals.

To minimize the loss of fine particles when bulk sampling riffle spawning zones at low flow under shallow water, we used a flow-isolation chamber similar to the sampling device described in Payne and Lapointe (1997). This device is composed of a pentagonal enclosure, measuring approximately 100 × 60 × 60 cm, with an open top and bottom, driven 5–10 cm into the substrate. After insertion, the perimeter is sealed with sandbags. The chamber has a mesh panel facing upstream and a conical mesh downstream made of 77 μm Nytex material. The permeable panel mesh allows water currents passing through the chamber to transport into the conical mesh the fines put in suspension during substrate extraction. Trapped particles are subsequently added to the sample.

Estimations of fine sediment lost for each grain-size class based on a concurrent freeze-core sample analysis done at seven sites indicate that an average of *c.* 5% of the total sample weight was lost using the isolation cell, mostly from the fine sand and silt fractions. Sampling efficiencies using this bulk technique range from 20% for the silt fraction (under 0.063 mm), 50% for 0.250 mm sands and 100% for coarse sands (greater than 0.5 mm). Our estimates of loss factors based on the seven replicates are not sufficiently consistent to apply to all 66 bulk samples along the two rivers and the grain size data presented below are uncorrected for these partial losses of some silts and fine sands. Sensitivity analyses show that while these sampling losses of very fine fractions will affect slightly the absolute values of substrate quality indices, these losses do not significantly affect the relative ranking of the samples nor the results of the present study. The errors due to these partial losses of very fine fractions are smaller than those commonly incurred due to variations in effective upper truncation limit when alternative sampling methods (such as freeze cores and McNeil samplers) are applied to coarse cobble salmon spawning substrate, often displaying >100 mm fractions of 10% or more.

Although numerous spawning substrate quality indices are proposed in the literature (Beschta, 1982; Crisp and Carling, 1989; Lotspeich and Everest, 1981; McNeil and Ahnell, 1964; Tappel and Bjornn, 1983), the percentage of fine material (<2 mm) was selected for this analysis because it relates more directly to sedimentation processes than do other indices (Witzel and MacCrimmon, 1983). Percentages of fine material in the samples were then compared to the Sand Index (*SI*) of Peterson and Metcalfe (1981). The Sand Index is defined as:

$$SI = Sc/16 + Sf/8 \tag{1}$$

where *Sc* is the percentage by weight of the coarse sand fraction (between 0.5 and 2 mm) and *Sf* is the percentage by weight of the fine and medium sand fraction (smaller than 0.5 mm). A Sand Index value is considered excellent if smaller than 1, mediocre if between 1 and 1.5 and poor if larger than 1.5 (Peterson and Metcalfe, 1981).

To facilitate comparisons with previous studies, cumulative distributions were then recalculated excluding particles larger than 64 mm (as in Payne and Lapointe, 1997), before estimating the sand content and spawning substrate indices. This procedure allowed us to meet the 1% precision criteria of Church *et al.* (1987) but also sets a consistent level of upper truncation of grain size curves at 64 mm across all environments. This approximately corresponds to the effective truncation of the coarse fractions (often explicit, due to limited sampler dimensions) in many published studies of spawning substrate. Most importantly, the truncation at 64 mm used here corresponds to the apparent truncation of the spawning substrate samples analysed by Peterson and Metcalfe (1981) in the definition of the Sand Index, tested in this study.

Redd distribution data

Data on redd locations were available from field surveys conducted by the Société de la Faune et des Parcs du Québec (FAPAQ) right after the spawning period in 1998 and 1999 on the Petite Cascapédia River and for 1999 and 2000 on the Bonaventure River. Redd locations were surveyed with a GPS and then repositioned on georeferenced aerial photos using a GIS. In the study systems, inter-riffle separation averages 300 m, so that redd positions were unambiguously linked to specific riffle zones. The distribution of within-riffle redd locations were not available from this database however. The presence or absence of redds was recorded at each of the 44 sampled riffles along the Petite Cascapédia River but at only 11 of the 22 sampled riffles along the Bonaventure River because of missing data on redd locations.

Geomorphic variables at the channel segment scales

Channel segments are defined as relatively homogeneous river sections, here including a minimum of three to ten pool–riffle sequences (1–5 km), with relatively uniform channel slope, valley morphology and bank erosion rates. A pool–riffle unit sequence refers here to a shorter river section including one pool and the next downstream riffle. Bank erosion rates and the percentage of fine material (<2 mm) at riffles were measured at the scale of pool–riffle units and then averaged per river segment. Valley width as well as bankfull shear stresses were measured at the segment scale. In total, five segments were defined in the Petite Cascapédia River and seven in the Bonaventure River (Figure 1).

Bank erosion rates were measured using a Baush and Lomb Zoom-Transferscope, an optical rectifying device, from two aerial photograph series separated by a 28-year time span (1964–1992). Lateral movement of the channel was measured at the apex of meander bends with a 0.3 mm precision ruler, where the magnitude of channel migration is greatest. To control for the general scaling of migration rates with channel width, these rates were then expressed as a percentage of the bankfull channel width (Hickin and Nanson, 1984). Percentages of river width eroded per year range from 0% to 4.3% (±0.12%). For each river segment, the degree of lateral channel confinement by valley walls was expressed as the ratio between the valley bottom (floodplain) width and bankfull channel width, as measured from georeferenced aerial photos within a GIS. Valley width was estimated as the total valley bottom area (determined through stereo air photo analysis and excluding boulder-rich fluvio-glacial terraces) divided by valley-segment length.

Mean bankfull shear stress for each river segment is the average force per unit area dissipated on bed surfaces and bed forms by flowing water at bankfull discharge. Segment-average shear stress estimates (τ_0) were obtained according to a method similar to that of Lapointe *et al.* (2002) and Talbot and Lapointe (2002) using the Du Boys equation for steady uniform flow:

$$\tau_0 = \rho g D S \tag{2}$$

where ρ is water density, g is the gravitational acceleration, D is the mean bankfull depth at the thalweg and S is the bankfull energy slope. For each river segment, a total station survey referenced by a high precision differential GPS yielded a longitudinal profile of the floodplain elevation as well as the thalweg elevation at riffle crests. Linear trend lines were then fitted through both the floodplain and the thalweg profiles within the 1–5 km long segments. The elevation difference between both best-fit lines approximated mean bankfull channel depth at riffles (D) and the best-fit slope of the floodplain elevation approximated bankfull energy slope (S) over the segments. The segment P5 was not surveyed, hence shear stress estimates are not available for this section.

RESULTS

Spawning site selection

Given the relatively constrained fine to coarse sand ratios within the study systems, a tight correspondence exists between the percentage of fine sediment (<2 mm) and the Sand Index for samples truncated at 64 mm; thus, sand content is a meaningful index within the Petite Cascapédia and Bonaventure Rivers for ranking sedimentological quality of spawning substrate (Figure 3; $R^2 = 0.96$). Substrate quality is, overall, slightly better in the Bonaventure River than in the Petite Cascapédia River (t-test, $p < 0.05$).

A univariate logistic regression model (Equations 3 and 4, below) fitted to the 1998–2000 redd survey data demonstrates that the probability (f) of observing at least one redd at a given riffle significantly increases with substrate quality (with X = sand content for each riffle) within the Petite Cascapédia and for both rivers pooled together (Table I and Figure 4). Based on our data, the estimated probability of finding a redd at a site with

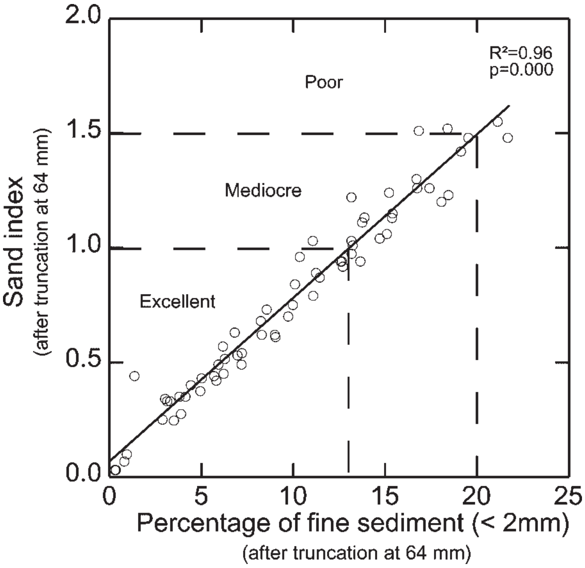

Figure 3. Relationship between the Sand Index and the percentage of fine sediment (<2 mm) for samples of sub-surface bed material taken along the Petite Cascapédia and Bonaventure rivers. Samples are truncated at 64 mm. Correspondences between Sand Index criteria for excellent, mediocre and poor substrate (Peterson and Metcalfe, 1981) and the percentage of fine sediment (<2 mm) are presented

Table I. Output of the logistic regression between percentage of sand and the presence/absence of redds at riffles. Bold values significant at 5% level.

River	n	p	β_0	β_1
Petite Cascapédia	44	**0.003**	2.57	−0.24
Bonaventure	11	0.085	2.01	−0.24
Both rivers	55	**0.001**	2.44	−0.23

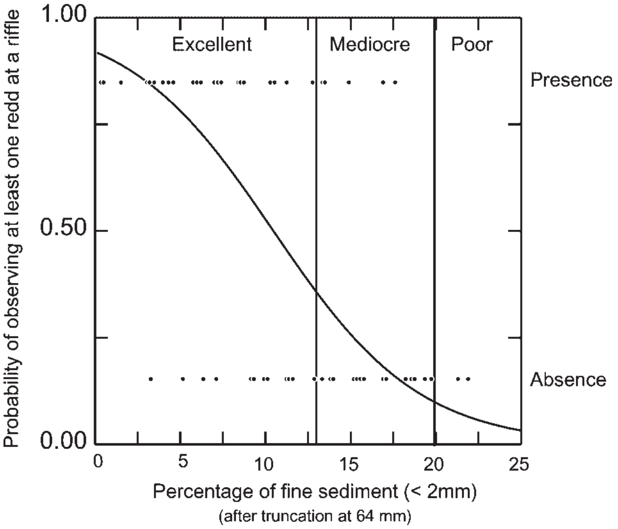

Figure 4. Logistic regression between the probability of observing at least one redd at a riffle and the percentage of fine sediment (<2 mm) in sub-surface material observed at low flow season. Observations were made between 1998 and 2000. Sediment samples were truncated at 64 mm. Dots illustrate the presence or absence of redds at each riffle. Substrate quality classes are derived from the Sand Index for excellent, mediocre and poor substrate (Peterson and Metcalfe, 1981)

mediocre or poor sediment quality (Sand Index greater than 1; Figures 3 and 4) is under 30% for the period 1998–2000 in the study systems. The relation was not significant at a 5% level for the Bonaventure River because of the small number of data points (11 sites). Interestingly, the regression parameters (β_0 and β_1) are similar for both rivers when fitted individually (Table I).

$$f(Z) = \frac{1}{1 + e^{-Z}} \tag{3}$$

$$\mathrm{Z_i} = \beta_0 + \beta_1 X_I \tag{4}$$

Not only does the probability of a riffle being spawned increase with substrate quality, but the number of redds at a riffle also tends to increase (Figure 5). The latter linear regressions have low predictive power but are significant at a 5% level for the Bonaventure River and for both rivers pooled together (Table II). No significant relation is observed in the Petite Cascapédia River because of three outlier riffles: each of these had had an unusually high number of redds (Figure 5: 62, 24 and 11 redds, while 80% of riffles had less than five redds) but substrate quality that was borderline between good and mediocre. Closer investigation reveals that these sites are the only riffles located at the head of alluvial islands along the study reaches of the Petite Cascapédia River. In addition to these three sites, a fourth island located outside of the study area, 1 km upstream of segment P5, bore 27 redds. This site would rank second according to the number of redds if compared to the 44 riffles studied on Petite Cascapédia River. Except for these particular riffles, discussed later, most of the spawning occurred at riffles with content of fine sediment in the substrate classified as excellent, with the number of redds clearly decreasing as substrate quality decreases (Figure 5).

Controls on percentage of sand at the segment scale

Within the study segments, the Petite Cascapédia River has, overall, slightly higher percentages of sand, higher sinuosity and bank erosion rates, lower formative shear stresses and a larger ratio of valley to channel widths than the Bonaventure River ($p < 0.10$) (Table III). Here, channel migration corresponds mostly to the normal erosion of the floodplain at outer banks in meander bends although undermining of high terraces was also observed at a few locations along both rivers.

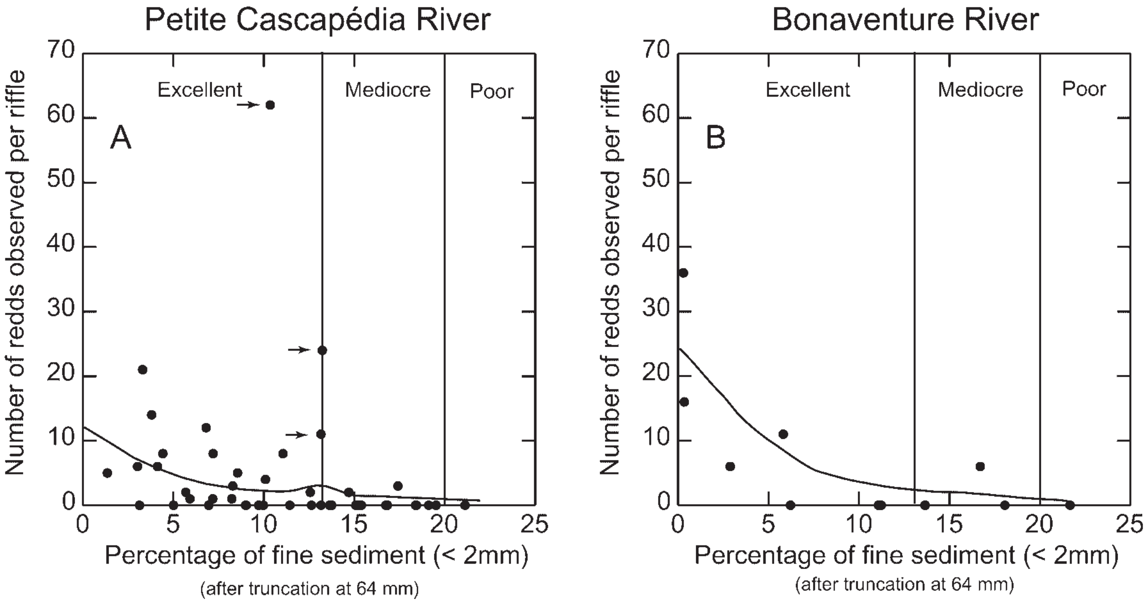

Figure 5. Number of redds observed per riffle over two years plotted against the percentage of fine material in the substrate of the Petite Cascapédia (A) and Bonaventure (B) rivers. Samples were truncated at 64 mm. Redd locations were surveyed in 1998–1999 in the Petite Cascapédia River and 1999–2000 in the Bonaventure River. Lowess trend lines are fitted to the data. Sites marked with arrows correspond to anomalous riffles situated at the head of alluvial islands

Table II. Correlation between the percentage of fine sediment and the number of redds observed on riffles. Samples are truncated at 64 mm. Relationships significant at a 5% level are printed in bold

River	*n*	R^2	*p*
Petite Cascapédia River	44	0.04	0.191
Bonaventure River	11	0.44	**0.026**
Both rivers	55	0.10	**0.017**

Table III. Geomorphic variables measured along river segments. Values are averages per river section. Dashes represent missing data

Segment	River	% fine <2mm truncation at 64 mm	D50 (mm) pavement untruncated	D50 (mm) Sub-pavement untruncated	Bank erosion rates (% of width/y)	Bankfull ι_0 (Pa)	Sinuosity	Valley to channel width ratio
1	P. Cascapédia	6.4	80	52	0.5	51	1.14	2.6
2	P. Cascapédia	10.8	82	43	1.9	55	1.35	8.0
3	P. Cascapédia	12.6	74	22	4.3	38	1.36	12.5
4	P. Cascapédia	12.2	66	37	2.5	53	1.25	9.1
5	P. Cascapédia	13.4	—	21	3.6	—	1.54	12.4
Average	P. Cascapédia	11.1	75	35	2.6	49	1.33	8.9
1	Bonaventure	8.9	79	34	0.5	46	1.04	6.4
2	Bonaventure	5.2	97	36	0.1	56	1.31	6.3
3	Bonaventure	17.3	76	42	1.4	53	1.07	8.9
4	Bonaventure	8.4	114	32	0.0	72	1.08	3.5
5	Bonaventure	8.7	125	28	0.0	89	1.01	1.0
6	Bonaventure	5.7	84	30	0.0	60	1.00	1.9
7	Bonaventure	6.7	69	31	0.1	50	1.05	2.4
Average	Bonaventure	8.7	92	33	0.3	61	1.08	4.3

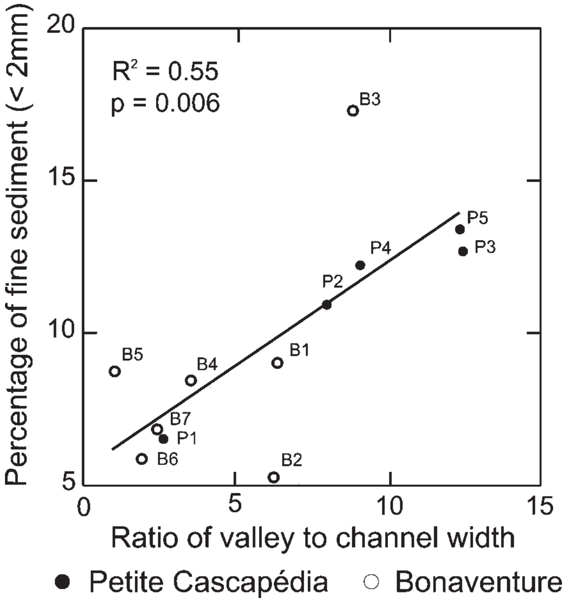

Figure 6. Segment-average percentage of fine material (<2 mm) at riffles plotted against the valley-to-channel-width ratio. Segments from the Petite Cascapédia River are plotted as black circles while those from the Bonaventure River are shown as white circles

For each river individually as well as across both systems, a significant increase in the percentage of fine material in sampled riffles was observed with an increase in the valley-to-channel-width ratio at segment scale ($p = 0.006$) (Figure 6). It is important to note however, that despite generally higher sand contents, spawning substrate quality remains generally excellent even in the widest valley segments in the study systems (cf. Figures 3, 4 and 6). Streams in wider valley segments tend to be more sinuous ($p = 0.003$), experience greater meander migration rates

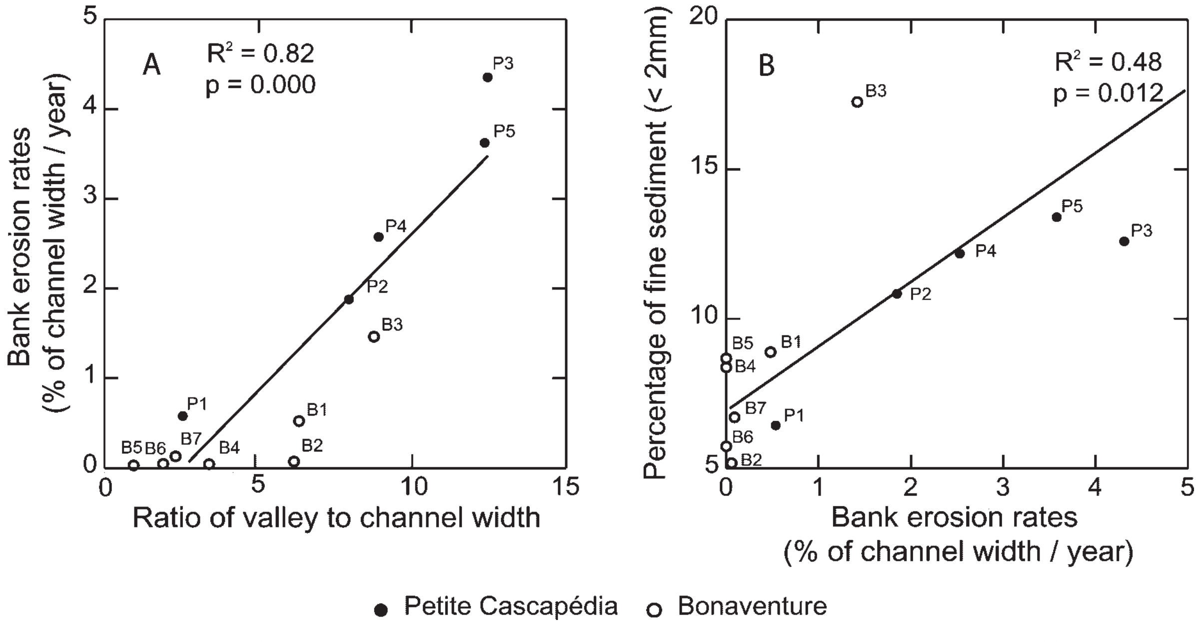

Figure 7. Segment-scale empirical relationships between valley-to-channel-width ratio, bank erosion rates and percentage of fine material in the substrate. (A) Linear regression between valley-to-channel-width ratio and segment-averaged bank erosion rates. (B) Linear regression between segment-average bank erosion rates and the segment-average percentage of fine material in the substrate (<2 mm). Segments from the Petite Cascapédia River are plotted as black circles while those from the Bonaventure River are shown as white circles

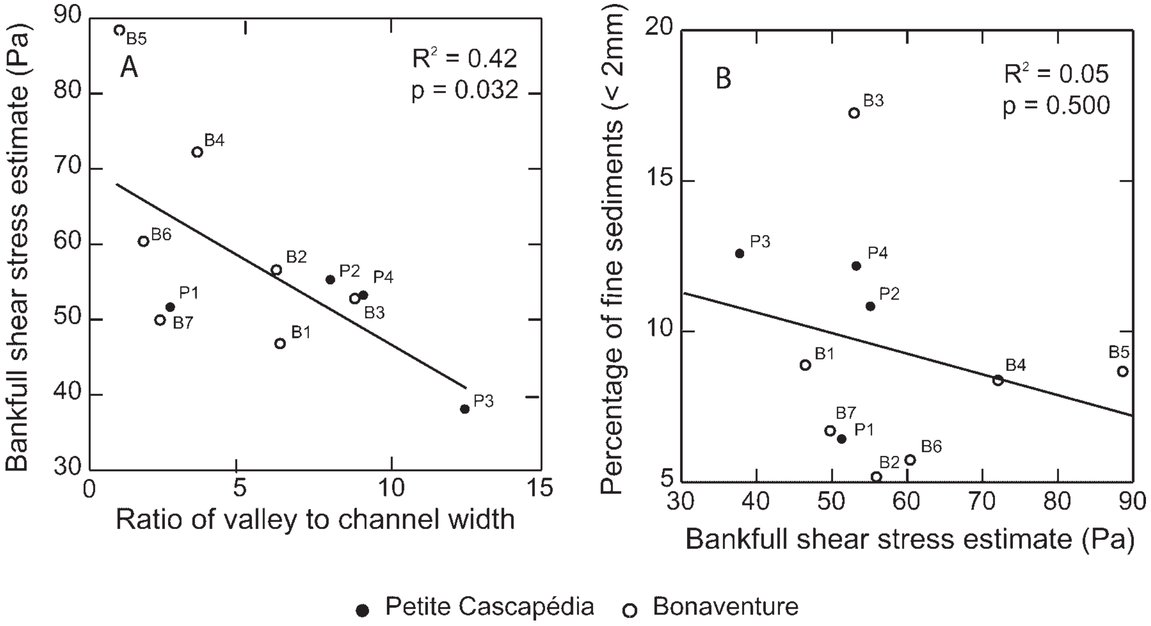

Figure 8. Segment-scale empirical relationships between valley-to-channel-width ratio, bankfull shear stresses and percentage of fine material in the substrate. (A) Linear regression between valley-to-channel-width ratio and segment-averaged bankfull shear stresses. (B) Linear regression between segment-average bankfull shear stresses and the segment-average percentage of fine material in the substrate (<2 mm). Segments from the Petite Cascapédia River are plotted as black circles while those from the Bonaventure River are shown as white circles

(Figure 7A, $p = 0.000$) and present somewhat lower bankfull shear stress values (Figure 8A, $p = 0.032$). Notably, only low shear stress values (40 to 55 Pa) are observed within laterally shifting channel segments occupying wider valleys (Figures 7B and 8: segments B3, P2, P3, P4. Missing stress data for P5). By contrast, a larger range of shear stress values is observed in laterally stable channels confined in narrow valleys (from 50 to 90 Pa, a 40 Pa range; segments P1, B1–7).

DISCUSSION

Spawning site selection

Based on data from the autumn 1998–2000 redd surveys and the summer sediment analyses conducted in 2000–2001, Atlantic salmon in the Petite Cascapédia and Bonaventure rivers demonstrate a significant preference for spawning at riffles with excellent substrate (percentage sand <13 or $SI < 1.0$) rather than poorer substrate. Despite the fact that abundance of fine particles in riffle substrate varies both spatially over a given riffle zone (Payne, 1995) and temporally (because of redd building itself as well as fines infiltration and evacuation associated with seasonal sediment transport events; Adams and Beschta, 1980; Kondolf *et al.*, 1993), these analyses support the assumption that limited sampling of potential spawning substrate in high-velocity riffle zones during late summer low flow stages can yield useful insights into the distribution of autumn spawning activity in these systems at the scale of channel segments. Since cleaning of substrate by spawning salmon and the subsequent re-infiltration of fine particles in redds affect substrate quality of redds only after the initial selection of spawning site in these systems, this is consistent with the hypothesis that environmental cues associated with substrate composition at the time of redd building are important to spawners at the time of site selection.

The large redd clusters observed at the occasional island heads in the study reaches suggest that, beyond the control exerted by riffle sedimentology, channel morphology also may directly influence selection of salmon spawning sites, possibly through its effects on hydraulic gradients in hyporheic zones. This is consistent with findings by Dauble and Watson (1990) and Geist and Dauble (1998) who noted that large clusters of chinook salmon (*Oncorhynchus tshawytscha*) redds in the Columbia River were associated with complex geomorphic forms such as anabranches and islands. Baxter and Hauer (2000) also showed that the selection of spawning sites by bull trout

(*Salvelinus confluentus*) along a stream was effectively controlled by patterns of hyporheic exchanges through bed material due to valley morphology and channel topography. Sowden and Power (1985) and Garrett *et al.* (1998) also observed that fry-sac survival of rainbow trout (*Salmo gairdneri*) and kokanee salmon (*Oncorhynchus nerka*) juveniles was not affected by substrate quality if strong hyporheic flow supplied sufficient oxygen to the egg pocket.

Our results also corroborate Geist (2000), who demonstrated the role of intense hyporheic discharge through bed material in spawning site selection by chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River, USA. Geist casts doubt that the higher hyporheic exchange observed at the spawning site was due solely to the cleaning action of spawners. Rather, he hypothesized that the general permeability of bed material, at the scale of large bed forms, was a major control of hyporheic flow intensity. As a corollary of this view, the occurrence of complex bed topography is likely to play a critical role for the availability of suitable spawning habitat in rivers where substrate quality is only mediocre.

In our study reaches, alluvial island heads were preferred areas for concentrated spawning activity. Theoretically, where a single channel splits to form an island, the two resulting channels develop greater total wetted perimeter and steeper slope (Leopold and Wolman, 1970) in order to maintain sediment transport capacity and mass-balance with conditions in the adjacent single-thread reaches. Along the Petite Cascapedia River, such a steepening of bed slope at anabranch channel entrances produces a steeper water slope at alluvial island heads. It is plausible that these unusually strong local hydraulic gradients trigger stronger hyporheic flow through redds and riffles located at island heads. The particular topography of island heads may thus promote the infiltration of hyporheic flow into the substrate even where substrate quality is mediocre (Brunke and Gonser, 1997).

Finally, it is important to emphasize that the parameters of any predictive relation between substrate quality and the probability of observing redds at a riffle, as presented in Table I and Figures 4 and 5 for the study rivers, should vary across rivers. Firstly, a higher ratio between the number of spawning salmon and the number of available spawning sites may force some individuals to spawn at riffles having poorer substrate quality. Secondly, the apparent preference of salmon for complex channel topography may also decrease the predicting power of sediment quality on its own. Thirdly, in two watersheds where differences in bedrock lithology produce different proportions of fine sediments, the same percentage of total fines (<2 mm) may actually represent different substrate permeability, depending on the ratio between sand and silt in the sample. Note finally that some sediment samplers (such as the freeze cores and small McNeil samplers) used by salmonid ecologists are physically too small to representatively sample the coarser particle sizes within typical spawning substrate for many salmonids. Consequently published sand content values for spawning substrate are hard to interpret in the absence of details on sampling technique and effective upper truncation limit set in grain-size analysis. Any literature-based comparisons of substrate quality based on reported abundance of fine material thus need to explicitly control for the effects of sampling technique and coarse end truncation in the size analysis.

Geomorphic controls over sand content at the valley segment scale

Observed, along-valley variations in fines content reflect different levels of restriction exerted by valley walls as these control the texture (size distribution) of sediment inputs from valley sides, the degree of lateral channel migration, associated channel sinuosity and rate of floodplain sediment recycling as well as the resultant adjustments of overall channel competence and shear stresses levels (Hoey and Ferguson, 1994; Rice and Church, 1998, 2001; Rice, 1999; Hoey and Bluck, 1999). As hypothesized, river segments with a greater degree of valley confinement provided spawning substrate of greater overall quality within the two study semi-alluvial systems (Figure 6). These confined segments were also characterized by lower average sinuosity, laterally more stable channels and generally higher but quite variable shear stress values (Figures 7A, 8A)

Cobble–gravel supply and transport capacity are strong in these incised mountain valleys, and streams develop actively shifting meanders wherever valley width allows. Where the normal development of meanders is inhibited, such as in narrow valley segments, the stream is often forced by bedrock controls to adopt steeper slopes and higher shear stresses. In addition, confined channels may also develop steep slopes and high shear stresses as a means to provide the transport capacity necessary to evacuate the coarse sediment that may be supplied by valley walls, terrace erosion and tributaries (Gilbert, 1917; Coulombe-Pontbriand, 2001). Note, however, that some of the valley-confined study segments (segments B6, B7 and P1; Figure 1) are controlled downstream by proximity to base (sea) level or a bedrock outcrop forming a weir across the channel bed (P1): these segments have relatively lower slope and bankfull shear stresses (Figure 8A).

In study segments where valley-to-channel-width ratios and channel shifting rates are higher (Figure 7A), coarse cobble or boulder sediment supply was lower, mean bankfull shear stresses were somewhat reduced (Figure 8A), and fine sediment accumulation in the substrate was somewhat stronger overall than in confined segments (Figure 6). The inverse relation in the study systems between rate of lateral shifting activity and shear stress levels (compare Figures 7A and 8A) appears to reflect a notable characteristic of such valley-confined mountain river systems (compared to lowland systems): here cobble–gravel transport rates and formative shear stress levels are relatively high everywhere and shifting activity is mainly limited by degree of lateral confinement rather than by formative stress levels. Segments flowing within wide valleys have generally fewer boulder inputs, lower median substrate calibre and lower shear stress levels (Coulombe-Pontbriand, 2001).

Along-river variations in fines content within gravel substrate can reflect direct supply controls (for example the effects of logging in some parts of the watershed) in combination with longer-term, geomorphically controlled, inter-reach differences in channel competence. In this study, an empirical link between higher bank erosion rates in wider valley segments and the percentage of fine material in the substrate is clearly evident (Figure 7B, $p = 0.012$). The unexpected high percentage of fine material measured in the substrate in section B3 appears to be due to fine sediment input from a sand-rich tributary discharging in the section (Figure 1). The data fail to indicate a similarly strong statistical link between lower segment-average bankfull shear stresses in larger valleys and higher percentages of fine material in the substrate, as these variables show weak negative correlation (Figure 8B, $p = 0.500$).

All other factors being equal, one would expect lower shear stress segments to display higher fines content. Two possible explanations can be advanced for the lack of strong relationship in our data between the segment-average percentage of fine material and the estimated bankfull shear stresses. Firstly, the effects of bank erosion rates and segment-average shear stresses on substrate composition are confounded in the study systems, as the two variables show opposing dependencies on valley width (Figures 7A and 8A). This illustrates a classic difficulty in empirically testing causal hypotheses that aim to separate the effects of environmental variables measured *in situ*. Secondly, it is possible that segment-scale shear stresses are inadequate to reveal differences in mean shear stress levels at the scale of riffle zones, because of systematic differences in channel morphology between confined and sinuous reaches.

Overall, spawning substrate, although somewhat finer, remains excellent overall even in the study segments with relatively high meander shifting rates (with segment averages up to 4% of width or 2.5 m per year; Figure 7B), although some riffles downstream of very rapidly shifting individual cut banks (over 5% per year) displayed mediocre substrate (sand contents between 13 and 21%; Figure 4). Given the generally acceptable quality of substrate even in highly shifting reaches, our findings do not support any compunction of fisheries habitat managers to artificially stabilize eroding banks, interventions with high capital and maintenance costs that can have serious side-effects for the morphology of pool–riffle habitat (Thorne, 1992; Payne and Lapointe, 1997).

The relation between the spawning substrate quality and the degree of lateral confinement (Figure 6) described in the study systems could be modified in other contexts by several factors. Large quantities of sand may deposit even in laterally confined reaches if external factors, such as the control of a base level, impose gentle channel slopes. Conversely, in river sections where valley slopes and shear stresses are too strong, the pavement of bed material may be too coarse for spawning to occur. Moreover, in some confined valleys with large sediment supply, excessive mobility of bed material may also limit spawning success as redds are washed away during peak floods. The relation between increased lateral confinement and spawning habitat quality also breaks down for bedrock-dominated channels as they offer little, if any, alluvium where spawning can occur. Finally, differences in land use and basin lithology in tributary basins can affect the quantity of fine sediment supply and the resulting bed material composition in two streams with similar degree of lateral confinement.

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