SUBSTRATE REQUIREMENTS OF SPAWNING CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*) ARE DEPENDENT ON LOCAL CHANNEL HYDRAULICS

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ABSTRACT

Micro-scale (<0.1 channel widths) physical conditions within channels ultimately exert a strong control on habitat selection by fish species. Data are presented demonstrating that micro-habitat requirements of spawning Chinook salmon (*Oncorhynchus tshawytscha*) are strongly inter-related; fish utilized coarser substrate if associated with faster flow velocities. This was not observed to be controlled through a hydraulic sorting mechanism but, rather, related to the physical processes of spawning. Failure to consider the 'elastic' nature of Chinook salmon spawning requirements resulting from links between the physical parameters may have implications for river management practices such as restoration or setting environmental flows. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: chinook salmon; spawning; micro-habitat; hydraulics; sediments; elastic habitat preference

INTRODUCTION

There are many scale-dependent factors that may influence the location within a river that adult salmonids choose for spawning. At the basin scale, contributing basin area and local slope are the topographic controls on where channels occur, how much sediment may be transported, and the longitudinal distribution of reach types, including large-scale hydraulic sorting of sediment (Montgomery and Buffington, 1996; Buffington *et al*., 2004). At the reach-scale, discharge and sediment supply shape alluvial features to produce an interdependent set of physical variables (water depth and velocity, hyporheic flow conditions, substrate size) over a discernible landform known as a morphological unit (e.g., pool, riffle, glide, run; Tonina and Buffington, 2007; Moir and Pasternack, 2008). In aquatic ecology, this scale is termed 'mesohabitat'. Within a given mesohabitat, local topographic and roughness controls on hydraulics cause patterns in the same variables, which are termed 'microhabitat' at this scale.

In addition to these scale-dependent physical processes, there are a host of fish behavioural controls at the individual, population and community levels (e.g., in response to hiding/cover, social factors, competition, predation) that influence where adult salmonids spawn. Many factors at many scales affect spawning behaviour, but this study focuses on the smallest resolution factors (for an animal the size of an adult Chinook salmon) that control specific site selection. This study therefore describes the basic mechanistic controls on the micro-scale physical conditions required for the process of spawning by Chinook salmon; these controls remain relevant regardless of other larger scale factors that are thought to influence spawning behaviour.

The physical micro-habitat of spawning salmonids (typically local flow depth, velocity and substrate size) has been studied for many decades and there is a large literature describing requirements for a wide range of species and geographical locations (Kondolf and Wolman, 1993; Moir *et al*., 2002). Such information is required for defensible prescription of environmental flows (using habitat modelling procedures such as PHABSIM; Gibbins and Acornley, 2000), to guide river restoration design (Wheaton *et al*., 2004; Elkins *et al*., 2007) and in predicting ecological response to changes in physical channel conditions (e.g., due to river management, land-use, climate change etc). However,

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many studies assess micro-habitat variables in isolation (i.e., substrate, e.g., Kondolf and Wolman, 1993; hydraulics, e.g., Beland *et al.*, 1982) or consider them together but as mutually independent factors (e.g., Crisp and Carling, 1989; Moir *et al.*, 2002). Despite the issue of interdependence of micro-scale habitat variables having been raised some time ago (e.g. Mathur *et al.*, 1985), and other more recent studies employing an array of multivariate approaches in addressing the issue (Ahmadi-Nedushan *et al.*, 2006), there have been no published studies that provide empirical data explicitly examining these inter-relationships (i.e., integrating hydraulic and sedimentary variables) for spawning salmonids. Traditional approaches (that are still the mainstay of environmental flow assessment in many regions) that fail to consider micro-habitat inter-relationships assume fish preference for any given variable is 'inelastic', regardless of the value of other variables. In this respect they explicitly ignore the inter-dependent fluvial processes that control the variables, potentially resulting in misleading predictions of habitat availability in ecological assessments. For example, might a fish species that is thought to normally prefer spawning in small gravel be able to use larger material if aided by higher flow velocity? The aim of this paper is to evaluate the integrated hydraulic and sedimentary characteristics of micro-habitat utilized by spawning Chinook salmon (*O. tschawytscha*) in relation to the availability of these variables on a regulated but geomorphically dynamic gravel-bed river. Specific causal mechanisms that explain observed linkages in micro-habitat variables are discussed.

STUDY AREA

The Yuba River in the northern central valley of California drains $3480 \, km^2$ of the western Sierra Nevada range (Figure 1). Annual precipitation mostly falls between November and April ($\sim 85\%$) and increases with elevation from $\sim 500 \, mm$ at the Feather River junction to $> 1500 \, mm$ in the headwaters (Moir and Pasternack, 2008). The Yuba basin has been highly manipulated for hydropower, water supply, flood regulation, gold mining and sediment control (James, 2005). Although two small dams exist on the South and Middle Forks (Spaulding Dam and Jackson Meadows Reservoir respectively), they are situated high enough in the watershed that their effects on flows (particularly during floods) in lower river locations are minimal. In contrast, New Bullards Bar Dam (operational in 1969) captures nearly the entire runoff of the North Fork Yuba and has a large reservoir capacity of 1.2 billion m^3 (6.7 times the combined total capacity of Spaulding and Jackson Meadows). Englebright Dam is an older concrete arch dam built in 1941 on the mainstem Yuba $\sim 38 \, km$ upstream from the confluence with the Feather and $\sim 16 \, km$ downstream from New Bullards Bar. It primarily serves as a sediment barrier blocking export of hydraulically mined, gold-depleted sedimentary deposits and has a reservoir capacity of 86 million m^3 (Moir and Pasternack, 2008). The section from Englebright Dam to the Feather River confluence is defined as the Lower Yuba River (LYR, Figure 1).

Despite the basin's dams, historic analyses have determined that the LYR still experiences a dynamic geomorphic regime (Moir and Pasternack, 2008). The statistical 'bankfull' discharges (often defined as the 1.5 year return interval of the annual peak series) recorded at the U.S. Geological Survey (USGS) Smartville gauge (#11418000) located 0.5 km downstream of Englebright Dam for the periods 1941–2004 and for 1971–2004 are 330 and $160 \, m^3 \, s^{-1}$, respectively, illustrating the significant impact to hydrology of New Bullards Bar. Independently, several geomorphic and hydraulic indicators of bankfull channel dimensions and floodplain geometry support these statistical estimates. Englebright Dam has a controlled flow release maximum of $135 \, m^3 \, s^{-1}$, although uncontrolled flows over Englebright Dam occur frequently. One hundred flow events have exceeded bankfull discharge and overtopped Englebright Dam between the construction of New Bullards Bar Dam in 1970 and the beginning of October 2005, suggesting the channel is presently undersized. Over the 1971–2004 period, the median daily discharge at the Smartville gauge was $43.6 \, m^3 \, s^{-1}$. The 5, 10 and 50 year return interval discharge for 1971–2004 are 1050, 1450 and $4025 \, m^3 \, s^{-1}$, respectively. Therefore, despite some flow regulation, the Yuba River below Englebright Dam experiences a dynamic winter flood regime. The combination of a near-natural flood hydrology and a plentiful supply of locally stored sediment in the LYR provides a dynamic geomorphic environment that produces a sequence of active bar complexes and a heterogeneous channel and floodplain morphology normally associated with a wandering gravel-bed river (Pasternack, 2008).

The specific site (Figure 1) examined in the present study was selected because it was the most heavily spawned area by Chinook salmon on the LYR in recent years. It is 6.3 km downstream from Englebright in 'Timbuctoo Bend' (39°13'56''N, 121°18'48''W), has a well-connected floodplain, active gravel bars and a non-uniform
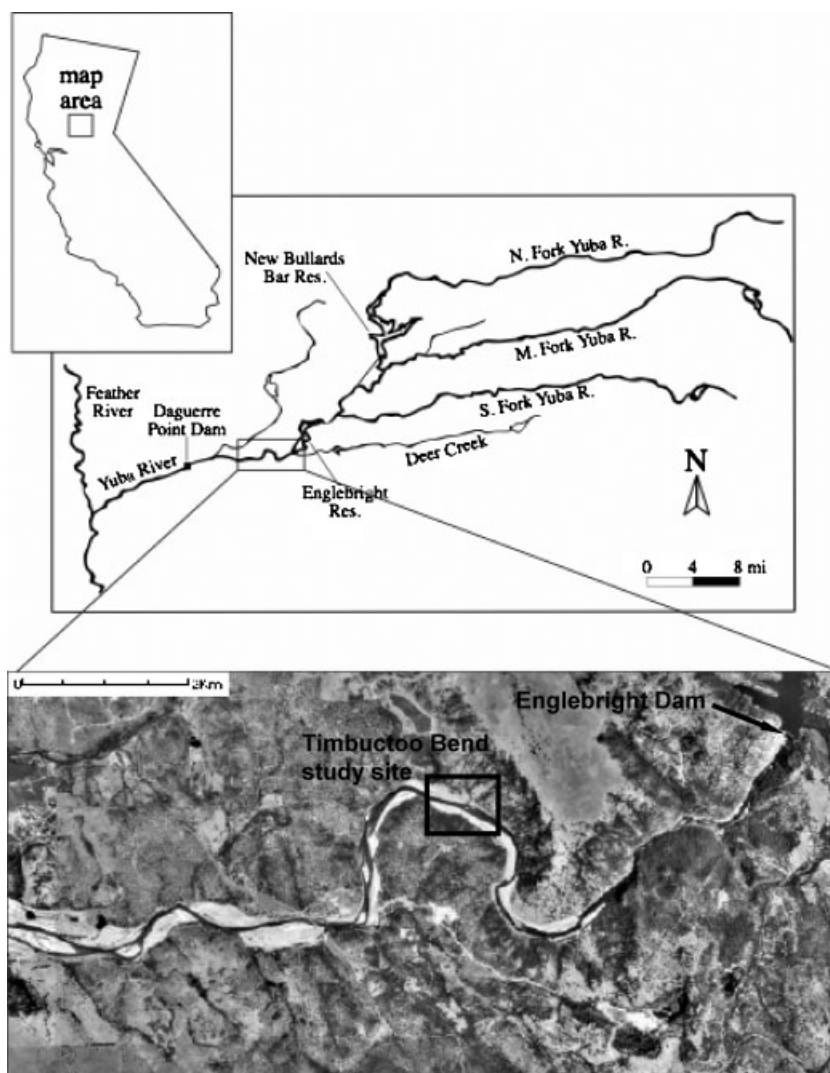
Figure 1. Study area. Yuba River watershed and Timbuctoo Bend study site

channel geometry (Moir and Pasternack, 2008). Between the Smartville gage and the study site, Deer Creek enters the river, contributing direct runoff during rain events and little otherwise. It drains ~220 km^2 on the southeast margins of the Yuba Basin and includes a small reservoir. The reservoir does not impede flood flows, but it does block the majority of sediment yield from reaching the Yuba. Therefore, flood hydrographs at the study site during rainstorm events reflect the combined flow of the mainstem Yuba and Deer Creek. A flow hydrograph covering the period of study is given in Figure 2. In the mainstem LYR, sediments were dominantly in the cobble (64–256 mm) and gravel (2–64 mm) sizes across the study site in 2005 and 2006 study seasons. Visually, there was no general change in bed composition apparent after a 24 year return interval flood in December 2005. However, available sediment characteristics were not sampled prior to the flood so a quantitative comparison was not possible. Sand and finer sized material (<2 mm) was generally absent from the sediment surface (although some lenses were observed in the lee of larger clasts). However, in upstream channel margin locations where flow velocities were lowest, sand and finer material was the dominant size class. The bed exhibited a degree of armouring, with subsurface material having a higher proportion of fine material (although generally not matrix supported). However, there was no evidence across the study site of a well-imbricated substrate surface that would have indicated a high degree of armouring.
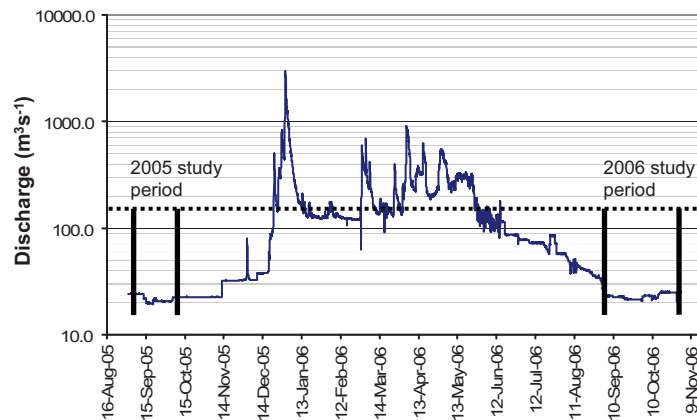
Figure 2. Study period hydrograph (Sept 1 2005–Nov 1 2006) identifying 2005 and 2006 study periods. The horizontal dashed line represents the 1971–2004 statistical bankfull discharge ($160 \, m^3 \, s^{-1}$). This figure is available in colour online at www.interscience.wiley.com/journal/rra

METHODS

To characterize micro-scale spawning habitat, hydraulic and sedimentary data were gathered to represent available and utilized conditions. The null hypothesis of utilization inelasticity was that any fish preference for spawning in a certain range of sediment particle sizes would be independent of local velocity (mean column or near-bed) or Froude number. A possible confounding condition in the form of a pre-existing relation between sedimentary and hydraulic conditions caused by hydraulic sorting was accounted for. Thus, to deny the null hypothesis would require not only the presence of a functional relation, but one that is distinct from any hydraulic sorting function.

Quantifying available conditions

Available habitat was represented by joint pebble counts (Wolman, 1954) and hydraulic measurements that were taken prior to spawning between Sept 3 and 12, 2006 at 81 locations on the main spawning riffle. At the time of the available conditions survey, the study site exhibited a 'fresh' morphology due to 24 year return interval flood that occurred on December 31, 2005. It has been observed that spawning by large numbers of Chinook salmon can significantly alter the morphological characteristics of a channel, influencing the location of suitable sedimentary and hydraulic conditions for spawning in subsequent seasons (Hassan *et al.*, 2008). However, due to the morphology re-setting flood of December 2005, this was not an issue at this study site.

The 81 sampling locations were selected to represent areas of visually consistent sedimentary and hydraulic conditions on an approximate grid across the study site (total area of $\sim 100 \times 80 \, m^2$, individual sampling locations were ~ 10–$20 \, m$ apart laterally and longitudinally). At each location, >100 particles (mean = 109.9, range = 100–130) were sampled using a standard gravel template (i.e., measuring b-axis dimensions of clasts) over a $\sim 3 \times 3 \, m^2$ section of the bed. Less than 1% of particles within the $\sim 3 \times 3 \, m^2$ area were removed from the bed during sampling; thus, there was negligible alteration to substrate texture as a result of sampling. From these data, the sediment sizes of which 50 and 84% of the samples were finer (i.e., D_{50}, D_{84}). Hydraulic measurements were taken at points $\sim 1 \, m$ inside the vertices of the sample square and at its centre (i.e., $n = 5$ per sample square). Velocity was measured with a Marsh-McBirney Flo-Mate, 2000 at 30 Hz and averaged over 30 sec at 0.2 and $0.8 \times$ depth from water surface. The $0.2 \times$ depth measurement represented the near bed interface where fish spawn. The mean of the 0.2 and $0.8 \times$ depth velocity measurements were used to approximate mean column velocity, as per Byrd *et al.* (2000). Measurement errors were $\pm 1 \, cm$ for depth using a stadia rod and $\pm 33 \, mm \, s^{-1}$ for velocity.

To account for the 'hydraulic noise' typical of high resolution velocity measurements in gravel-bed rivers, mean hydraulic conditions over the $\sim 3 \times 3 \, m^2$ sampling area were obtained by averaging the five individual measurement locations. Since the sampling squares were selected on the basis of displaying approximately consistent hydraulic and sedimentary conditions, this averaging process was considered appropriate. The centre position of each

sampling square was therefore assigned the average hydraulic and sedimentary characteristics measured within the $\sim 3 \times 3\,\mathrm{m}^2$ area. The geographic coordinates of this location was surveyed using a Leica 1200 total station.

Quantifying utilized conditions

Two methods were employed to characterize utilized habitat. Firstly, hydraulics and sediment were characterized at specific redds concurrently with spawning activity in the 2005 season (Sept 9 to Oct 7, 2005). It is important to note that this was not undertaken to characterize the sedimentary conditions that fish were selecting but to determine the relationship between hydraulic conditions as spawning occurred and the sediment that fish were able to mobilize from the substrate. Discharge was relatively stable during this period, varying between 19.5 and $22.4\,\mathrm{m}^3\,\mathrm{s}^{-1}$ (12.2 and 14.0% of the 1971–2004 statistical bankfull discharge, respectively). Individual redds ($n = 104$) were identified by an experienced observer based on diagnostic macro-topography and freshly turned sediment that was distinct from the algae-covered, undisturbed bed material. Any redd lacking a distinct tail-spill or that had evidence of super-imposition was not sampled. Pebble counts were taken in the redd tail-spill to characterize the size distribution of particles mobilized by spawners (rather than the substrate conditions selected by Chinook). Within each tail-spill >50 particles (mean = 64.0, range = 50–81) were sampled, because of their relatively small area. The tailspills of individual redds (i.e., not composite features) varied in length ~ 1–4 m and width ~ 0.5–2 m). The standard Wolman (1954) procedure was employed, particles sampled on an approximate grid across the tail spill with one or two (generally two in smaller features) complete passes over the feature to obtain the minimum sample size (i.e., $n = 50$). Since a truncated particle size distribution is present in tailspills (due to sorting by fish i.e., fine material being carried downstream and inability of fish to mobilize largest clasts; Crisp and Carling, 1989), these relatively small sample sizes were considered adequate to representatively characterize redd sediments. Because the 2005 data is from tailspills, it is not possible to compare it with the 2006 bed surface grain size dataset to evaluate flood-induced changes in the bed surface, such as possibly increased bed armouring. Whereas sustained low flows within the bankfull channel on the LYR have been observed to cause local bed armouring on riffles (Pasternack, 2008), large overbank floods such as occurred in December 2005 have been observed to cause significant channel incision, exhuming the underlying hydraulic mining debris that is finer and well mixed.

Depth and velocity were measured at 3–6 points (using the same procedure as described above) adjacent to and upstream of redds over undisturbed sediment (as per Moir *et al.*, 2002); the number of sample points depended on the size of the redd. Sampling hydraulics at the time of spawning activity meant the conditions selected by fish were accurately characterized. Although previous spawning activity may significantly modify bed sedimentology and topography and therefore influencing local hydraulics, our sampling approach still characterized the conditions that the fish were selecting. Nevertheless, areas of the bed most modified by spawners were not sampled given our criterion of avoiding features that suggested superimposition (i.e., redd complexes).

The second method to characterize utilized habitat involved relating the position of 2006 redds to the physical conditions of the site that had been sampled immediately prior to spawning (i.e., the available data described above). Physical (i.e., hydraulics and sediments) characterisation of the site and spawning in the 2006 season both took place under a relatively static flow regime compared with previous autumnal spawning seasons that had greater water deliveries to downstream users and as dictated by the operations schedule. During the period September 3, 2006 to November 1, 2006 (the entire period over which available and utilized conditions were sampled in 2006), Englebright Dam flow releases ranged between 20.8 to $25.1\,\mathrm{m}^3\,\mathrm{s}^{-1}$ (13.0 and 15.7% of the 1971–2004 statistical bankfull discharge, respectively) to meet water delivery schedules. This variation in discharge was not observed to result in significant changes in the magnitude and pattern of hydraulics across the site. Also, there was not a systematic change in discharge between 2006 availability and utilisation surveys; flows slightly increased and decreased a number of times over the entire study period due to downstream water demands (Figure 2). Therefore, the physical conditions that the fish had available to them in the 2006 season were representatively sampled immediately prior to the commencement of spawning activity. Redds constructed in the 2006 spawning season were identified on a daily basis between September 9 and November 1 by a skilled observer and their position (i.e., the centre of the redd pit) recorded using a Leica 1200 total station. This yielded a total sample size of 140 redds. Although fall spawning in the LYR is regarded to continue until December 31 (Moir and Pasternack,

2008), there had been sufficient spawning activity by November 1 that it was very difficult to distinguish between new and previously constructed redds due to super-imposition, despite the use of markers to identify previously sampled features. Therefore, to avoid bias through re-sampling, the final redd survey was conducted on November 1. The number of redds surveyed by that date (i.e., 140) was sufficient to conduct statistical analyses. Subsequent visits to the study site after November 1 revealed that no new locations on the riffle had been utilized so that the spatial cover of the surveys conducted was representative. Redd surveys overlapped with pebble counts on four days (Sept. 9–12) in the 2006 sampling season. However, over these days there were relatively few fish present on the study site and their locations were determined prior to sediment sampling commencing. Pebble counts were then carried out as far away as possible from fish spawning within the study site on those days.

Statistical analyses

As described earlier, 81 micro-habitat point measurements of 2006 available conditions prior to spawning were made on an approximate grid over an area of $\sim100 \times 80\,\text{m}^2$. This spatial sampling scheme is suitable for interpolation to estimate conditions between observation points. The data were interpolated using the radial basis functions in the Geostatistical Analyst toolbox of ArcGIS 9.2 to create continuous surfaces of hydraulic (depth, d; mean column velocity, v_m; near-bed velocity, v_b; Froude number, Fr) and sedimentary (D_{50}, D_{84}) conditions at the site. Hydraulic variables were interpolated using multiquadratic surface fitting kernal functions, whereas sedimentary variables were interpolated using spline with tension kernal functions. These different approaches helped reduce error to obtain the best surface characterization possible given the relatively low density of surface sampling compared with the common procedure for topographic mapping that uses much more dense data and simpler TIN-based interpolation. To obtain the micro-habitat conditions that characterized the points fish selected for spawning, the position of each surveyed redd pit was projected onto the surfaces and values for the hydraulic and sedimentary variables were interpolated.

If hydraulic sorting played a significant role in causing spatial patterns of bed surface grain size at the study site, then that could interfere with the assessment of the inter-dependence of utilized micro-habitat conditions. Between the recession of overbank flows in the early summer of 2006 and the measurements made in autumn 2006, there was insufficient time for low-flow hydraulic patterns to sort the bed in the study area. Such hydraulic bed sorting was subsequently monitored in relation to riffle knickpoint propagation (Pasternack, 2008). Multiple regression analysis was performed between sedimentary and hydraulic variables for the 2006 available condition to objectively determine if low-flow hydraulic sorting had occurred at the study site. If the test revealed that a high level of variation in the substrate size parameters was explained by the hydraulic variables, then hydraulic sorting would be viewed as likely. In the absence of those relations, then hydraulic sorting was unlikely to have occurred in relation to survey period flow magnitudes.

Dependence of fish selection of sedimentary conditions on co-varying hydraulic conditions was similarly assessed using multiple regression analysis. For dependence to be indicated, there would have to be a high amount of variability in sediment characteristics explained by hydraulic variables at spawning locations. Simple univariate linear regressions were also carried out to determine the nature of inter-relationships between sedimentary and hydraulic variables. This proved difficult with multiple regression due to the high correlation between co-variates meaning that and any effect shown by the estimated coefficients was conditional on everything else in the model. Further evidence of the explicit dependence of fish selection of substrate on over-lying hydraulic conditions (i.e., independent of a hydraulic sorting mechanism) would be provided if both the 2005 redd and the 2006 interpolated utilization data-sets showed statistically significant univariate linear regressions with similar slopes, and for those to be much higher than that for any hydraulic sorting relationship.

RESULTS

The values of hydraulic (d, v_m, v_b, and Fr) and sedimentary (D_{50}, D_{84}) data for 2005 surveyed redds, 2006 availability and 2006 interpolated utilized are given in Table I. Sediment sizes for a given flow velocity tended to be smaller in the 2005 redd tailspill sites than on the bed surface for 2006 available and interpolated utilized spawning conditions. The 2006 interpolated utilized data-set represented the surface sediment that the fish dug into, while the

Table I. Summary statistics for sedimentary and hydraulic variables providing ranges and means (in parentheses)

Descriptor	2005 Redds	2006 Availability	2006 Utilisation
Median grain size, D_{50} (mm)	29.2–79.9 (49.2)	45.3–119.4 (71.6)	58.3–93.7 (76.1)
D_{84} (mm)	47.5–128.0 (82.9)	73.5–222.9 (137.9)	121.4–182.2 (155.0)
Depth, d (m)	0.17–0.75 (0.37)	0.20–0.92 (0.46)	0.21–0.81 (0.55)
Mean column velocity, v_m (ms^{-1})	0.20–1.34 (0.66)	0.11–1.23 (0.52)	0.28–0.92 (0.63)
Near-bed velocity, v_b (ms^{-1})	0.15–1.03 (0.52)	0.06–0.91 (0.39)	0.21–0.71 (0.46)
Froude number, Fr	0.07–0.73 (0.36)	0.05–0.72 (0.26)	0.14–0.39 (0.27)

2005 redd tailspill data-set represents the material mobilized by the fish during spawning. Thus, the difference cannot be attributed to flood-induced bed armouring.

Contoured hydraulic and sedimentary surfaces produced from the 2006 availability data with 2006 surveyed redd locations included are provided in Figure 3. These spatial plots show a non-random, tight clustering of redds in the centre of the channel near the riffle crest, even though all other wetted areas were easily accessible to fish. This implies that specific conditions existed in this area that spawning fish were responding to.

No evidence of low-flow hydraulic sorting was identified at the study site. Multiple regression analysis showed that the variation in the sedimentary variables (D_{50}, D_{84}) was not explained well by any combination of the hydraulic variables (d, v_m, v_b, and Fr) (Table II). No more than 20 or 30% of the variation in D_{50} or D_{84} was explained by hydraulics, respectively. Thus, prior to spawning in 2006, the texture of the bed surface was independent of overlying hydraulic conditions. If fish selected sedimentary conditions independently from hydraulic conditions, then that would yield a similar lack of statistically significant relation in the utilization data.
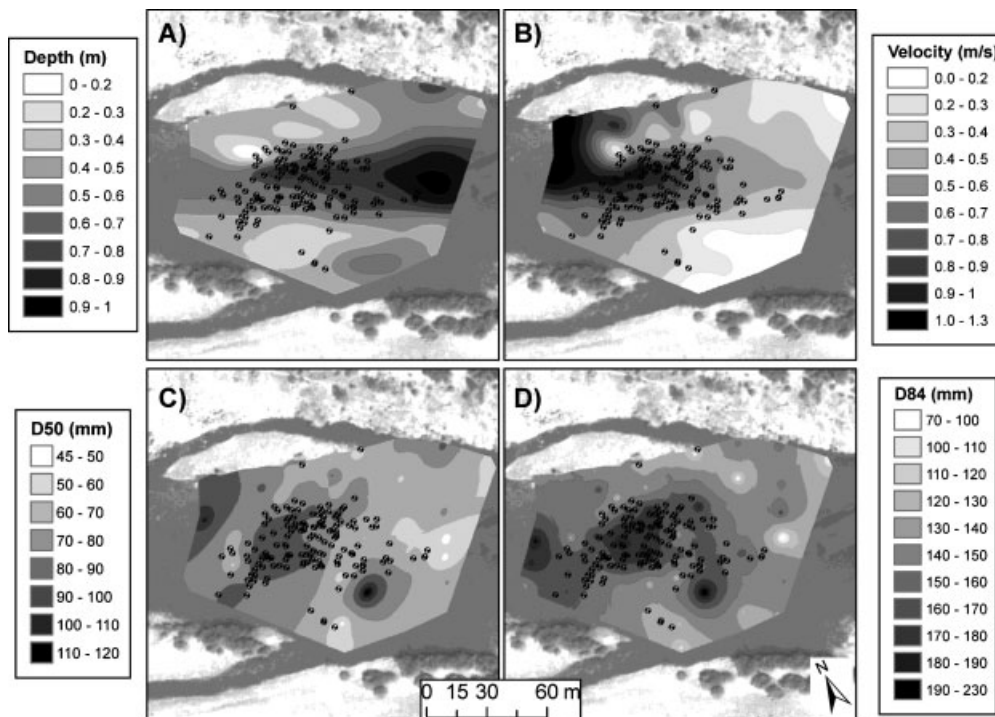

Figure 3. Sedimentary and hydraulic surfaces interpolated from 2006 availability surveys with 2006 surveyed redd positions included (segmented circles). A) depth, d; B) mean column velocity, v_m; C) median sediment size, D_{50} and D) D_{84}

Table II. Results of multiple regression analysis. A. Regressions with D_{50} as dependent variable, B. Regressions with D_{84} as dependent variable. * - Residual variance exceeds that of response variate

A. Model	% Variance in D_{50} explained		
	2005 Redds	2006 Utilized	2006 Available
Fr, d, v_m, $v_{0.2}$, $d.v_m$, $d.v_{0.2}$	35.1	57.2	18.3
d, v_m, $v_{0.2}$, $d.v_m$, $d.v_{0.2}$	35.8	57.4	19.4
Fr, v_m, $v_{0.2}$	33.2	54.8	14.8
Fr, d, $v_{0.2}$, $d.v_{0.2}$	33.2	51.4	11.9
Fr, d, v_m, $d.v_m$	21.0	52.7	15.1
d, v_m, $d.v_m$	21.8	52.7	12.9
d, $v_{0.2}$, $d.v_{0.2}$	31.54	43.7	7.4
Fr, d	20.7	51.0	1.3
Fr, $v_{0.2}$	33.2	51.2	1.3
Fr, v_m	22.5	51.0	5.2
v_m, $v_{0.2}$	33.7	52.4	14.6
Fr	17.4	51.3	2.7
v_m	23.1	39.5	5.3
$v_{0.2}$	32.7	23.8	2.4
d	*	*	*

B. Model	% Variance in D_{84} explained		
	2005 Redds	2006 Utilized	2006 Available
Fr, d, v_m, $v_{0.2}$, $d.v_m$, $d.v_{0.2}$	62.5	45.4	28.1
d, v_m, $v_{0.2}$, $d.v_m$, $d.v_{0.2}$	60.9	45.4	29.2
Fr, v_m, $v_{0.2}$	61.2	46.4	28.5
Fr, d, $v_{0.2}$, $d.v_{0.2}$	61.8	41.4	18.2
Fr, d, v_m, $d.v_m$	44.6	44.4	18.4
d, v_m, $d.v_m$	44.1	43.2	15.1
d, $v_{0.2}$, $d.v_{0.2}$	59.0	38.7	10.7
Fr, d	39.3	41.8	5.0
Fr, $v_{0.2}$	61.3	35.1	1.9
Fr, v_m	44.8	44.2	16.4
v_m, $v_{0.2}$	61.1	38.2	11.2
Fr	32.3	16.4	*
v_m	44.7	38.6	0.1
$v_{0.2}$	59.7	35.5	*
d	0.1	22.7	6.3

Conversely, multiple regression analysis revealed a high level of the variation in sedimentary characteristics was explained by hydraulic variables at the sub-set of locations associated with fish utilisation in 2006 and for 2005 redds (Table II). The fact that some of the single covariate models explained almost the same variability as larger models demonstrates the importance of these variables. For example, Fr explained 51.3% of the variation in the 2006 utilized data. Adding in as many other variables as available only explained an additional 5.9% of variance. Therefore, simple univariate linear regressions were valid in showing the nature of sediment-hydraulic relationships. These tests revealed that there were no significant relationships identified in the 2006 availability dataset, while both the 2005 redd and 2006 interpolated utilisation datasets exhibited strong positive relationships between hydraulic (v_m, v_b, and Fr) and sediment variables (Figure 4). 2005 redd hydraulics tended to be best related to the coarse sediment fraction (i.e., D_{84}) while 2006 interpolated utilisation regressions were inconsistent in this regard. Near-bed velocity (i.e., $0.2 \times$ depth) had consistently higher R^2 values than mean column velocity for 2005 redds while the opposite was the case for 2006 interpolated utilisation. The highest individual R^2 value was obtained between D_{84} and near-bed velocity for the 2005 redd data set although this relationship was associated with much greater scatter for 2006 interpolated utilisation.
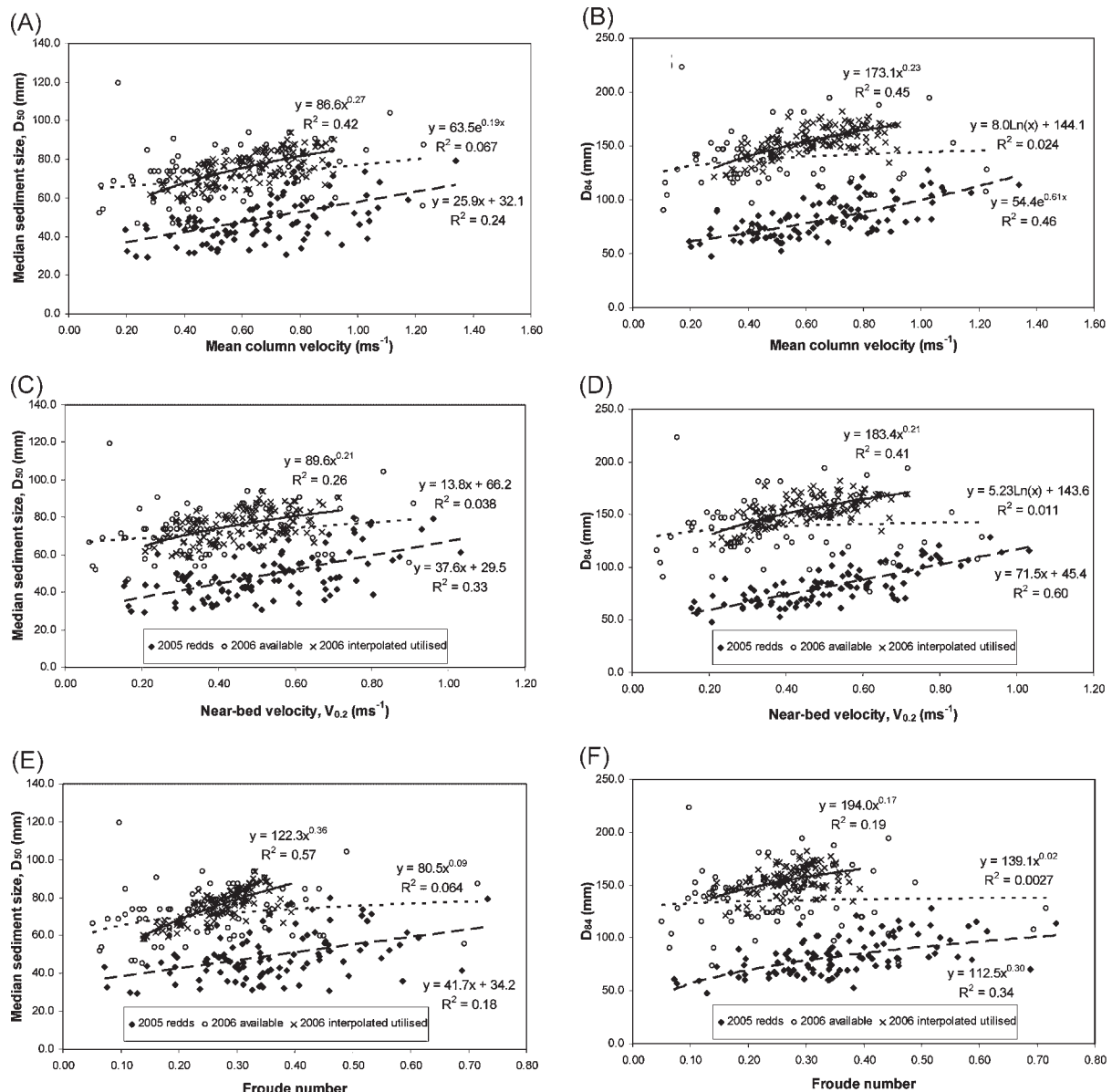
Figure 4. Example data from 2005 redd sampling, 2006 available and 2006 interpolated utilized habitat surveys linking, A) v_m and D_{50}, B) v_m and D_{84}, C) v_b and D_{50}, D) v_b and D_{84}, E) Fr and D_{50} and F) Fr and D_{84}.

DISCUSSION

Although fluvial geomorphologists have quantified the interdependence of channel sediments and hydraulics in general, these parameters have not been integrated to properly characterize Chinook salmon spawning micro-habitat requirements. This is despite the issue of the likely inter-dependence of physical habitat variables having been raised over two decades ago (Mathur *et al.*, 1985). This helps explain inconsistent data on physical requirements for a given species from different rivers, one of the factors responsible for 'ex-situ' inelastic suitability curves often not predicting observed salmonid spawning patterns well (e.g., Shirvell, 1989; Knapp and Preisler, 1999; Moir *et al.*, 2005). Multi-variate techniques are now increasingly being adopted to describe the habitat

requirements of and utilization by instream species (see Ahmadi-Nedushan *et al.*, 2006 for a recent review). However, no study to date has provided fully integrated field-derived data (i.e., explicitly linking sedimentary and hydraulic habitat requirements) that permits such analysis for spawning Chinook salmon, a globally important and endangered species (Yoshiyamaa *et al.*, 1998). The data presented here demonstrate that such information is necessary in order that the micro-habitat requirements of this species are characterized representatively. The LYR data demonstrated that Chinook salmon have elastic preferences for individual habitat components (i.e., depth, velocity and substrate size) governed by the relations among all characterized habitat components; spawning fish select a sub-set of combinations of micro-scale hydraulic and sedimentary variables available to them. Despite employing multiple regression analysis, single univariate models (v_m, v_b and Fr) explained very similar levels of variability in the dependent (sedimentary) variable as multivariate models in some cases (Table II); this identified the dominant hydraulic variables influencing substrate utilization. Specifically, the results showed that fish tended to select coarser substrate in faster flow and finer substrate if associated with velocities sufficiently low to permit the maintenance of that substrate caliber. The latter condition provided low values for velocity and sediment size relative to the utilization ranges quoted in the literature for spawning Chinook (Kondolf and Wolman, 1993; Geist and Dauble, 1998; Groves and Chandler, 1999; Hanrahan *et al.*, 2004), particularly within one relatively small (i.e., ~2 channel widths in length) study site. It is stressed that the micro-habitat utilization ranges quoted here are unlikely to represent the full range of conditions that spawning Chinook salmon can use. Sampling in 2006 (habitat availability and subsequent redd locations) only took place within one riffle unit. Moir and Pasternack (2008) demonstrated that spawning Chinook will spawn in different types of morphological unit (i.e., riffle, riffle entrance, lateral bar) that exhibit contrasting joint depth-velocity relationships. Indeed, the generally broader ranges of micro-habitat utilization apparent for 2005 redds compared to 2006 interpolated utilization may reflect the former data-set incorporating redds sampled over a number of morphological units (riffle entrance, lateral bar and secondary channel as well as riffle). Compared to available conditions, 2006 interpolated utilisation data showed that fish tended to spawn in sediment somewhat coarser and in marginally deeper and faster flowing water. Regardless of these differences in details, the fact that both utilization data-sets showed statistically significant relations whereas the availability data did not leads to the conclusion that fish actively selected a subset of sedimentary conditions predicated on what the hydraulic conditions were.

The data further showed that relationships between micro-habitat variables did not simply reflect available joint sedimentary-hydraulic conditions (i.e., through a hydraulic sorting mechanism); pre-spawning surveys across the entire study site showed that little of the variation in sedimentary conditions was explained by any combination of hydraulic characteristics. Although the 2005 redd utilization and 2006 availability data-sets were from consecutive spawning seasons separated by a major flood, the 2006 interpolated utilization data revealed similar hydraulic-sedimentary relationships to those for 2005 redds (Figure 4). Furthermore, despite flood-induced morphological change at the study riffle between 2005 and 2006, aerial photographs since 1937 suggested a dynamic equilibrium condition with a quasi-stable island/bar morphology that would have provided a similar range of hydraulic and sediment conditions over time. The process of spawning is known to truncate the particle size distribution of redd tailspills compared to that from the undisturbed bed (sorting by spawning fish reduces the proportion of the finest and coarsest material in redd taillspills; Crisp and Carling, 1989), However, in the present study, the generally smaller sediment size at a given velocity for 2005 redds compared to 2006 available and interpolated utilization conditions implies that the inability of spawning fish to mobilize large clasts from the bed was the dominant process controlling the size of material in the tailspill (Figure 4). Indeed, during both the 2005 and 2006 field seasons, large clasts were observed within redd pits that were not present in the associated tail spills. These large clasts that remain within the 'pit' are an important element of redd structure, providing hydraulic 'dead zones' for deposited eggs to settle between prior to burial (as per Jones, 1959). A small proportion of immobile clasts within the substrate may therefore be an important component of spawning habitat, particularly in locations where more energetic flow conditions could displace eggs out of the pit prior to bulal. Despite the fact that wide ranges in the micro-scale physical conditions (i.e., depth, velocity and substrate) were utilized by fish, inter-relations between these variables meant that relatively limited ranges of suitable joint conditions were available within the study site; failure to consider this will significantly over-estimate habitat availability. Generally, characterizing physical habitat of spawning Chinook salmon by independently considering depth, velocity and substrate size requirements (i.e., still common in habitat modelling exercises) could lead to considerable error propagation.

A small number of studies have examined bivariate hydraulic habitat requirements/ utilization (i.e., joint depth-velocity distributions) for freshwater fish species (e.g., Le Coarer, 2007). For gravel-bed rivers, velocity and depth are generally inversely related at low discharge when hydraulics are strongly controlled by the longitudinal distribution of morphological units (e.g., riffles, pools, glides and runs) and directly related at high discharge when the above morphological units are relatively submerged and thus hydraulics are strongly controlled by the lateral shape of a channel (Stewardson and McMahon, 2002; Brown and Pasternack, 2008). Because salmon tend to avoid high flows for spawning (Moir *et al.*, 2006), the velocity-depth environment of the channel when fish are spawning will typically exhibit the inverse relation. In this condition, velocity exhibits a wide range for low depth and a narrow range for high depth (Brown and Pasternack, 2008). Thus, when one considers that a riffle is generally defined as an area of low depth, it may be expected that there would be both relatively high velocity and high variation in velocity. As a result, there is an opportunity for adults to choose among a range of velocity and substrate options within a riffle of relatively uniform depth. This reasoning is supported by the results of the present study in that univariate models incorporating flow depth explained little of the variability of utilized substrate size within the riffle, whereas those incorporating flow velocity explained very similar amounts to larger multivariate models. Therefore, in terms of the mechanical hydraulic requirements of spawning, although depth was a component in habitat selected at the meso-scale (i.e., riffles *versus* pools or glides) within the riffle it was only directly important in providing access for fish to a specific location of the channel bed, flow velocity was the dominant control on the process of substrate excavation.

Many studies conclude that spawning salmonids select for depth beyond the simple access criterion described here and without considering mesohabitat-scale variation (e.g., Burner, 1951; Beland *et al.*, 1982; Deverall *et al.*, 1993). In the absence of sedimentary requirements, we propose that this apparent 'selection' within riffles is auto-correlative and an artefact of the implicit inverse-relationship between depth and velocity in channels as dictated by open channel flow mechanics. Thus, the apparent avoidance of high depth points in riffles is not due to these conditions being unsuitable per se but more likely related to insufficiently high velocities to mobilize the substrate and carry the dislodged material downstream to construct a redd. However, the sedimentary-hydraulic relationships presented here suggest that such locations could be utilized if they were associated with sediment of sufficiently small caliber to permit the process of redd excavation in low velocity areas. At the study site, redds were observed to occur in relatively high depth, low velocity points in the riffle that were also associated with small substrate sizes (mean depth = 0.71 m, mean column velocity = 0.20 ms^{-1}, tailspill D_{50} = 32.4 mm at one sampled redd). Velocity must be sufficient to carry the majority of sediment particles loosened from the channel bed during 'cutting' by the spawning female (vigorous vertical flexing of the tail over the substrate surface while lying on her side; Jones, 1959) to excavate a sufficiently large 'pit' to deposit eggs in. The coarser the sediment, the faster the overlying flow velocity must be to allow completion of this process. Faster flow velocities may also assist in the initial dislodging of substrate particles during 'cutting' by providing a greater 'background' force that assists spawners in mobilising larger clasts from the stream bed. The upper limits to spawning will be met when a critical proportion of sediment particles become too large to initially liberate from the bed and/or flow velocity is too high for the fish to maintain position long enough to complete redd excavation; both these factors are related to fish size (Crisp and Carling, 1989; Kondolf and Wolman, 1993; Moir *et al.*, 2002). Therefore, species-specific spawning micro-habitat requirements reflect the integration of available joint hydraulic-sedimentary conditions (controlled by discharge, mesohabitat geometry and roughness characteristics) with the ability of spawning fish to gain access to those conditions (controlled by depth and, therefore, related to fish size), dislodge the substrate (controlled by the combination of forces applied to the river bed by fish and hydraulics, the former linked to fish size) and have it transported a small distance downstream (linked to hydraulic forces).

CONCLUSIONS

The data demonstrated that substrate suitability could vary significantly for the same life stage, species and river depending on the hydraulic conditions (particularly velocity) that fish are spawning in. Moreover, since the proposed explanation for the observed pattern of co-varying substrate-hydraulic utilisation is explicitly mechanistic (i.e., the micro-scale assessment of the ability of fish to mobilize sediment particles in relation to assisting forces

from local flow velocity), it should apply to all salmonid species that employ the same 'cutting' behaviour for spawning (as per Jones, 1959). Understanding the interaction of the key micro-scale physical variables is a prerequisite to monitoring the spawning potential of streams. Failure to consider such inter-relationships could result in significant over-prediction of suitable habitat. Therefore, flow allocations (e.g., using habitat models such as PHABSIM) or river restoration designs based on these inaccurate predictions may well be sub-optimal for spawning Chinook (and likely other salmonid species) and could propagate large errors through to setting and implementation of environmental flows and the design of river management/ restoration projects.

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