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Authors

Moir, HJ
Pasternack, GB

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1 **Manuscript for Rivers Research and Applications**

2
3 **Substrate requirements of spawning Chinook salmon (*Oncorhynchus tshawytscha*)**
4 **are dependent on local channel hydraulics.**

5
6 Hamish J. Moir¹ and Gregory B. Pasternack²

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8 1. Corresponding author. The Macaulay Institute, Craigiebuckler, Aberdeen, AB15 8QH,
9 U.K. Fax: +44 (0) 1224 311556; E-mail: h.moir@macaulay.ac.uk.

10
11 2. Department of Land, Air, and Water Resources, University of California, One Shields
12 Avenue, Davis, CA 95616-8626, U.S.A. E-mail: gpast@ucdavis.edu.

accepted manuscript

13 **Abstract**

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

23

24 Key words: Chinook salmon, spawning, micro-habitat, hydraulics, sediments, elastic
25 habitat preference.

accepted manuscript

26 **Introduction**

27 There are many scale-dependent factors that may influence the location within a river
28 that adult salmonids choose for spawning. At the basin scale, contributing basin area and
29 local slope are the topographic controls on where channels occur, how much sediment
30 may be transported, and the longitudinal distribution of reach types, including large-scale
31 hydraulic sorting of sediment (Montgomery and Buffington, 1996; Buffington et al.,
32 2004). At the reach-scale, discharge and sediment supply shape alluvial features to
33 produce an interdependent set of physical variables (water depth and velocity, hyporheic
34 flow conditions, substrate size) over a discernible landform known as a morphological
35 unit (e.g., pool, riffle, glide, run; Tonina and Buffington, 2007; Moir and Pasternack,
36 2008). In aquatic ecology, this scale is termed ‘mesohabitat’. Within a given
37 mesohabitat, local topographic and roughness controls on hydraulics cause patterns in the
38 same variables, which are termed ‘microhabitat’ at this scale.

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

48 The physical micro-habitat of spawning salmonids (typically local flow depth,
49 velocity and substrate size) has been studied for many decades and there is a large
50 literature describing requirements for a wide range of species and geographical locations
51 (Kondolf and Wolman, 1993; Moir *et al.*, 2002). Such information is required for
52 defensible prescription of environmental flows (using habitat modelling procedures such
53 as PHABSIM; Gibbins and Acornley, 2000), to guide river restoration design (Wheaton
54 *et al.*, 2004; Elkins *et al.*, 2007) and in predicting ecological response to changes in
55 physical channel conditions (e.g., due to river management, land-use, climate change
56 etc). However, many studies assess micro-habitat variables in isolation (i.e., substrate,
57 e.g., Kondolf and Wolman, 1993; hydraulics, e.g., Beland *et al.*, 1982) or consider them
58 together but as mutually independent factors (e.g., Crisp and Carling, 1989; Moir *et al.*,
59 2002). Despite the issue of interdependence of micro-scale habitat variables having been
60 raised some time ago (e.g., Mathur *et al.*, 1985), and other more recent studies employing
61 an array of multivariate approaches in addressing the issue (Ahmadi-Nedushan *et al.*,
62 2006), there have been no published studies that provide empirical data explicitly
63 examining these inter-relationships (i.e., integrating hydraulic and sedimentary variables)
64 for spawning salmonids. Traditional approaches (that are still the mainstay of
65 environmental flow assessment in many regions) that fail to consider micro-habitat inter-
66 relationships assume fish preference for any given variable is “inelastic”, regardless of
67 the value of other variables. In this respect they explicitly ignore the inter-dependent
68 fluvial processes that control the variables, potentially resulting in misleading predictions
69 of habitat availability in ecological assessments. For example, might a fish species that is
70 thought to normally prefer spawning in small gravel be able to use larger material if aided

71 by higher flow velocity? The aim of this paper is to evaluate the integrated hydraulic and
72 sedimentary characteristics of micro-habitat utilised by spawning Chinook salmon
73 (*Oncorhynchus tshawytscha*) in relation to the availability of these variables on a
74 regulated but geomorphically dynamic gravel-bed river. Specific causal mechanisms that
75 explain observed linkages in micro-habitat variables are discussed.

76

77 **Study Area**

78 The Yuba River in the northern central valley of California drains 3480 km² of the
79 western Sierra Nevada range (Figure 1). Annual precipitation mostly falls between
80 November and April (~85%) and increases with elevation from ~500 mm at the Feather
81 River junction to >1500 mm in the headwaters (Moir and Pasternack, 2008). The Yuba
82 basin has been highly manipulated for hydropower, water supply, flood regulation, gold
83 mining, and sediment control (James, 2005). Although two small dams exist on the
84 South and Middle Forks (Spaulding Dam and Jackson Meadows Reservoir respectively),
85 they are situated high enough in the watershed that their effects on flows (particularly
86 during floods) in lower river locations are minimal. In contrast, New Bullards Bar Dam
87 (operational in 1969) captures nearly the entire runoff of the North Fork Yuba and has a
88 large reservoir capacity of 1.2 billion m³ (6.7 times combined total capacity of Spaulding
89 and Jackson Meadows). Englebright Dam is an older concrete arch dam built in 1941 on
90 the mainstem Yuba ~38 km upstream from the confluence with the Feather and ~16 km
91 downstream from New Bullards Bar. It primarily serves as a sediment barrier blocking
92 export of hydraulically mined, gold-depleted sedimentary deposits and has a reservoir
93 capacity of 86 million m³ (Moir and Pasternack, 2008). The section from Englebright

94 Dam to the Feather River confluence is defined as the Lower Yuba River (LYR, Figure
95 1).

96 Despite the basin's dams, historic analyses have determined that the LYR still
97 experiences a dynamic geomorphic regime (Moir and Pasternack, 2008). The statistical
98 "bankfull" discharges (often defined as the 1.5 yr return interval of the annual peak
99 series) recorded at the U.S. Geological Survey (USGS) Smartville gauge (#11418000)
100 located 0.5 km downstream of Englebright Dam for the periods 1941-2004 and for 1971-
101 2004 are 330 and 160 m^3s^{-1} , respectively, illustrating the significant impact to hydrology
102 of New Bullards Bar. Independently, several geomorphic and hydraulic indicators of
103 bankfull channel dimensions and floodplain geometry support these statistical estimates.
104 Englebright Dam has a controlled flow release maximum of 135 m^3s^{-1} , although
105 uncontrolled flows over Englebright Dam occur frequently. One hundred flow events
106 have exceeded bankfull discharge and overtopped Englebright Dam between the
107 construction of New Bullards Bar Dam in 1970 and the beginning of October 2005,
108 suggesting the channel is presently undersized. Over the 1971-2004 period, the median
109 daily discharge at the Smartville gauge was 43.6 m^3s^{-1} . The 5-, 10-, and 50-yr return
110 interval discharge for 1971-2004 are 1050, 1450, and 4025 m^3s^{-1} , respectively.
111 Therefore, despite some flow regulation, the Yuba River below Englebright Dam
112 experiences a dynamic winter flood regime. The combination of a near-natural flood
113 hydrology and a plentiful supply of locally stored sediment in the LYR provides a
114 dynamic geomorphic environment that produces a sequence of active bar complexes and
115 a heterogeneous channel and floodplain morphology normally associated with a
116 wandering gravel-bed river (Pasternack, 2008).

117 The specific site (Figure 1) examined in the present study was selected because it was
118 the most heavily spawned area by Chinook salmon on the LYR in recent years. It is 6.3
119 km downstream from Englebright in ‘Timbuctoo Bend’ (39°13'56"N, 121°18'48"W), has
120 a well-connected floodplain, active gravel bars, and a non-uniform channel geometry
121 (Moir and Pasternack, 2008). Between the Smartville gage and the study site, Deer Creek
122 enters the river, contributing direct runoff during rain events and little otherwise. It
123 drains ~220 km² on the southeast margins of the Yuba Basin and includes a small
124 reservoir. The reservoir does not impede flood flows, but it does block the majority of
125 sediment yield from reaching the Yuba. Therefore, flood hydrographs at the study site
126 during rainstorm events reflect the combined flow of the mainstem Yuba and Deer Creek.
127 A flow hydrograph covering the period of study is given in Figure 2. In the mainstem
128 LYR, sediments were dominantly in the cobble (64 – 256 mm) and gravel (2 – 64 mm)
129 sizes across the study site in 2005 and 2006 study seasons. Visually, there was no
130 general change in bed composition apparent after a ~24-yr return interval flood in
131 December 2005. However, available sediment characteristics were not sampled prior to
132 the flood so a quantitative comparison was not possible. Sand and finer sized material
133 (<2 mm) was generally absent from the sediment surface (although some lenses were
134 observed in the lee of larger clasts). However, in upstream channel margin locations
135 where flow velocities were lowest, sand and finer material was the dominant size class.
136 The bed exhibited a degree of armouring, with subsurface material having a higher
137 proportion of fine material (although generally not matrix supported). However, there
138 was no evidence across the study site of a well imbricated substrate surface that would
139 have indicated a high degree of armouring.

140

141 **Methods**

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

150 A. Quantifying available conditions

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

160 The 81 sampling locations were selected to represent areas of visually consistent
161 sedimentary and hydraulic conditions on an approximate grid across the study site (total
162 area of ~100x80 m², individual sampling locations were ~10-20m apart laterally and

163 longitudinally). At each location, >100 particles (mean = 109.9, range = 100-130) were
164 sampled using a standard gravel template (i.e., measuring b-axis dimensions of clasts)
165 over a ~3m×3m section of the bed. Less than 1% of particles within the ~3m×3m area
166 were removed from the bed during sampling; thus, there was negligible alteration to
167 substrate texture as a result of sampling. From these data, the sediment sizes of which
168 50% and 84% of the samples were finer (i.e., D_{50} , D_{84}). Hydraulic measurements were
169 taken at points ~1 m inside the vertices of the sample square and at its centre (i.e., n = 5
170 per sample square). Velocity was measured with a Marsh-McBirney Flo-Mate 2000 at 30
171 Hz and averaged over 30 sec at 0.2 and 0.8 × depth from water surface. The 0.2 × depth
172 measurement represented the near bed interface where fish spawn. The mean of the 0.2
173 and 0.8 × depth velocity measurements were used to approximate mean column velocity,
174 as per Byrd *et al.* (2000). Measurement errors were ±1 cm for depth using a stadia rod
175 and ±33 mm s⁻¹ for velocity.

176 To account for the ‘hydraulic noise’ typical of high resolution velocity measurements
177 in gravel-bed rivers, mean hydraulic conditions over the ~3×3m sampling area were
178 obtained by averaging the five individual measurement locations. Since the sampling
179 squares were selected on the basis of displaying approximately consistent hydraulic and
180 sedimentary conditions, this averaging process was considered appropriate. The centre
181 position of each sampling square was therefore assigned the average hydraulic and
182 sedimentary characteristics measured within the ~3×3m area. The geographic coordinates
183 of this location was surveyed using a Leica 1200 total station.

184 B. Quantifying utilised conditions

185 Two methods were employed to characterize utilized habitat. Firstly, hydraulics and
186 sediment were characterised at specific redds concurrently with spawning activity in the
187 2005 season (Sept 9 to Oct 7, 2005). It is important to note that this was not undertaken
188 to characterise the sedimentary conditions that fish were selecting but to determine the
189 relationship between hydraulic conditions as spawning occurred and the sediment that
190 fish were able to mobilise from the substrate. Discharge was relatively stable during this
191 period, varying between 19.5 and 22.4 m³s⁻¹ (12.2% and 14.0% of the 1971-2004
192 statistical bankfull discharge, respectively). Individual redds (n=104) were identified by
193 an experienced observer based on diagnostic macro-topography and freshly turned
194 sediment that was distinct from the algae-covered, undisturbed bed material. Any redd
195 lacking a distinct tail-spill or that had evidence of super-imposition was not sampled.
196 Pebble counts were taken in the redd tail-spill to characterise the size distribution of
197 particles mobilised by spawners (rather than the substrate conditions selected by
198 Chinook). Within each tail-spill >50 particles (mean = 64.0, range = 50-81) were
199 sampled, because of their relatively small area. The tailspills of individual redds (i.e., not
200 composite features) varied in length ~1-4 m and width ~0.5-2m). The standard Wolman
201 (1954) procedure was employed, particles sampled on an approximate grid across the tail
202 spill with one or two (generally two in smaller features) complete passes over the feature
203 to obtain the minimum sample size (n=50). Since a truncated particle size distribution is
204 present in tailspills (due to sorting by fish i.e., fine material being carried downstream
205 and inability of fish to mobilize largest clasts; Crisp and Carling, 1989), these relatively
206 small sample sizes were considered adequate to representatively characterize redd
207 sediments. Because the 2005 data is from tailspills, it is not possible to compare it with

208 the 2006 bed surface grain size dataset to evaluate flood-induced changes in the bed
209 surface, such as possibly increased bed armouring. Whereas sustained low flows within
210 the bankfull channel on the LYR have been observed to cause local bed armouring on
211 riffles (Pasternack, 2008), large overbank floods such as occurred in December 2005
212 have been observed to cause significant channel incision, exhuming the underlying
213 hydraulic mining debris that is finer and well mixed.

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

224 The second method to characterise utilised habitat involved relating the position of
225 2006 redds to the physical conditions of the site that had been sampled immediately prior
226 to spawning (i.e., the available data described above). Physical (i.e., hydraulics and
227 sediments) characterisation of the site and spawning in the 2006 season both took place
228 under a relatively static flow regime compared with previous autumnal spawning seasons
229 that had greater water deliveries to downstream users and as dictated by the operations
230 schedule. During the period September 3, 2006 to November 1, 2006 (the entire period

231 over which available and utilised conditions were sampled in 2006), Englebright Dam
232 flow releases ranged between 20.8 to 25.1 m³s⁻¹ (13.0% and 15.7% of the 1971-2004
233 statistical bankfull discharge, respectively) to meet water delivery schedules. This
234 variation in discharge was not observed to result in significant changes in the magnitude
235 and pattern of hydraulics across the site. Also, there was not a systematic change in
236 discharge between 2006 availability and utilisation surveys; flows slightly increased and
237 decreased a number of times over the entire study period due to downstream water
238 demands (Figure 2). Therefore, the physical conditions that the fish had available to
239 them in the 2006 season were representatively sampled immediately prior to the
240 commencement of spawning activity. Redds constructed in the 2006 spawning season
241 were identified on a daily basis between September 9 and November 1 by a skilled
242 observer and their position (i.e., the center of the redd pit) recorded using a Leica 1200
243 total station. This yielded a total sample size of 140 redds. Although fall spawning in the
244 LYR is regarded to continue until December 31 (Moir and Pasternack, 2008), there had
245 been sufficient spawning activity by November 1 that it was very difficult to distinguish
246 between new and previously constructed redds due to super-imposition, despite the use of
247 markers to identify previously sampled features. Therefore, to avoid bias through re-
248 sampling, the final redd survey was conducted on November 1. The number of redds
249 surveyed by that date (i.e., 140) was sufficient to conduct statistical analyses. Subsequent
250 visits to the study site after November 1 revealed that no new locations on the riffle had
251 been utilized so that the spatial cover of the surveys conducted was representative. Redd
252 surveys overlapped with pebble counts on four days (Sept. 9-12) in the 2006 sampling
253 season. However, over these days there were relatively few fish present on the study site

254 and their locations were determined prior to sediment sampling commencing. Pebble
255 counts were then carried out as far away as possible from fish spawning within the study
256 site on those days.

257 C. Statistical analyses

258 As described earlier, 81 micro-habitat point measurements of 2006 available
259 conditions prior to spawning were made on an approximate grid over an area of $\sim 100 \times 80$
260 m^2 . This spatial sampling scheme is suitable for interpolation to estimate conditions
261 between observation points. The data were interpolated using the radial basis functions
262 in the Geostatistical Analyst toolbox of ArcGIS 9.2 to create continuous surfaces of
263 hydraulic (depth, d ; mean column velocity, v_m ; near-bed velocity, v_b ; Froude number, Fr)
264 and sedimentary (D_{50} , D_{84}) conditions at the site. Hydraulic variables were interpolated
265 using multiquadratic surface fitting kernel functions, whereas sedimentary variables were
266 interpolated using spline with tension kernel functions. These different approaches
267 helped reduce error to obtain the best surface characterization possible given the
268 relatively low density of surface sampling compared with the common procedure for
269 topographic mapping that uses much more dense data and simpler TIN-based
270 interpolation. To obtain the micro-habitat conditions that characterized the points fish
271 selected for spawning, the position of each surveyed redd pit was projected onto the
272 surface and values for the hydraulic and sedimentary variables were interpolated.

273 If hydraulic sorting played a significant role in causing spatial patterns of bed surface
274 grain size at the study site, then that could interfere with the assessment of the inter-
275 dependence of utilized micro-habitat conditions. Between the recession of overbank
276 flows in the early summer of 2006 and the measurements made in autumn 2006, there

277 was insufficient time for low-flow hydraulic patterns to sort the bed in the study area.
278 Such hydraulic bed sorting was subsequently monitored in relation to riffle knickpoint
279 propagation (Pasternack, 2008). Multiple regression analysis was performed between
280 sedimentary and hydraulic variables for the 2006 available condition to objectively
281 determine if low-flow hydraulic sorting had occurred at the study site. If the test revealed
282 that a high level of variation in the substrate size parameters was explained by the
283 hydraulic variables, then hydraulic sorting would be viewed as likely. In the absence of
284 those relations, then hydraulic sorting was unlikely to have occurred in relation to survey
285 period flow magnitudes.

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

299

300 **Results**

301 The values of hydraulic (d , v_m , v_b , Fr) and sedimentary (D_{50} , D_{84}) data for 2005
302 surveyed redds, 2006 availability and 2006 interpolated utilised are given in Table 1.
303 Sediment sizes for a given flow velocity tended to be smaller in the 2005 redd tailspill
304 sites than on the bed surface for 2006 available and interpolated utilised spawning
305 conditions. The 2006 interpolated utilised data-set represented the surface sediment that
306 the fish dug into, while the 2005 redd tailspill data-set represents the material mobilised
307 by the fish during spawning. Thus, the difference cannot be attributed to flood-induced
308 bed armouring.

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

314 No evidence of low-flow hydraulic sorting was identified at the study site. Multiple
315 regression analysis showed that the variation in the sedimentary variables (D_{50} , D_{84}) was
316 not explained well by any combination of the hydraulic variables (d , v_m , v_b , Fr) (Table 2).
317 No more than 20 or 30% of the variation in D_{50} or D_{84} was explained by hydraulics,
318 respectively. Thus, prior to spawning in 2006, the texture of the bed surface was
319 independent of overlying hydraulic conditions. If fish selected sedimentary conditions
320 independently from hydraulic conditions, then that would yield a similar lack of
321 statistically significant relation in the utilization data.

322 Conversely, multiple regression analysis revealed a high level of the variation in
323 sedimentary characteristics was explained by hydraulic variables at the sub-set of
324 locations associated with fish utilisation in 2006 and for 2005 redds (Table 2). The fact
325 that some of the single covariate models explained almost the same variability as larger
326 models demonstrates the importance of these variables. For example, Fr explained 51.3
327 % of the variation in the 2006 utilised data. Adding in as many other variables as
328 available only explained an additional 5.9% of variance. Therefore, simple univariate
329 linear regressions were valid in showing the nature of sediment-hydraulic relationships.
330 These tests revealed that there were no significant relationships identified in the 2006
331 availability dataset, while both the 2005 redd and 2006 interpolated utilisation datasets
332 exhibited strong positive relationships between hydraulic (v_m , v_b , Fr) and sediment
333 variables (Figure 4). 2005 redd hydraulics tended to be best related to the coarse
334 sediment fraction (i.e., D_{84}) while 2006 interpolated utilisation regressions were
335 inconsistent in this regard. Near-bed velocity (i.e., $0.2 \times \text{depth}$) had consistently higher R^2
336 values than mean column velocity for 2005 redds while the opposite was the case for
337 2006 interpolated utilisation. The highest individual R^2 value was obtained between D_{84}
338 and near-bed velocity for the 2005 redd data set although this relationship was associated
339 with much greater scatter for 2006 interpolated utilisation.

340

341 **Discussion**

342 Although fluvial geomorphologists have quantified the interdependence of channel
343 sediments and hydraulics in general, these parameters have not been integrated to
344 properly characterise Chinook salmon spawning micro-habitat requirements. This is

345 despite the issue of the likely inter-dependence of physical habitat variables having been
346 raised over two decades ago (Mathur *et al.*, 1985). This helps explain inconsistent data
347 on physical requirements for a given species from different rivers, one of the factors
348 responsible for 'ex-situ' inelastic suitability curves often not predicting observed
349 salmonid spawning patterns well (e.g., Shirvell, 1989; Knapp and Priestler, 1999; Moir *et*
350 *al.*, 2005). Multi-variate techniques are now increasingly being adopted to describe the
351 habitat requirements of and utilization by instream species (see Ahmadi-Nedushan *et al.*,
352 2006 for a recent review). However, no study to date has provided fully integrated field-
353 derived data (i.e., explicitly linking sedimentary and hydraulic habitat requirements) that
354 permits such analysis for spawning Chinook salmon, a globally important and
355 endangered species (Yoshiyamaa *et al.*, 1998). The data presented here demonstrate that
356 such information is necessary in order that the micro-habitat requirements of this species
357 are characterized representatively. The LYR data demonstrated that Chinook salmon
358 have elastic preferences for individual habitat components (i.e., depth, velocity and
359 substrate size) governed by the relations among all characterized habitat components;
360 spawning fish select a sub-set of combinations of micro-scale hydraulic and sedimentary
361 variables available to them. Despite employing multiple regression analysis, single
362 univariate models (v_m , v_b , Fr) explained very similar levels of variability in the dependent
363 (sedimentary) variable as multivariate models in some cases (Table 2); this identified the
364 dominant hydraulic variables influencing substrate utilization. Specifically, the results
365 showed that fish tended to select coarser substrate in faster flow and finer substrate if
366 associated with velocities sufficiently low to permit the maintenance of that substrate
367 caliber. The latter condition provided low values for velocity and sediment size relative

368 to the utilization ranges quoted in the literature for spawning Chinook (Kondolf and
369 Wolman, 1993; Geist and Dauble, 1998; Groves and Chandler, 1999; Hanrahan *et al.*,
370 2004), particularly within one relatively small (i.e., ~2 channel widths in length) study
371 site. It is stressed that the micro-habitat utilization ranges quoted here are unlikely to
372 represent the full range of conditions that spawning Chinook salmon can use. Sampling
373 in 2006 (habitat availability and subsequent redd locations) only took place within one
374 riffle unit. Moir and Pasternack (2008) demonstrated that spawning Chinook will spawn
375 in different types of morphological unit (i.e., riffle, riffle entrance, lateral bar) that exhibit
376 contrasting joint depth-velocity relationships. Indeed, the generally broader ranges of
377 micro-habitat utilization apparent for 2005 redds compared to 2006 interpolated
378 utilization may reflect the former data-set incorporating redds sampled over a number of
379 morphological units (riffle entrance, lateral bar and secondary channel as well as riffle).
380 Compared to available conditions, 2006 interpolated utilisation data showed that fish
381 tended to spawn in sediment somewhat coarser and in marginally deeper and faster
382 flowing water. Regardless of these differences in details, the fact that both utilization
383 data-sets showed statistically significant relations whereas the availability data did not
384 leads to the conclusion that fish actively selected a subset of sedimentary conditions
385 predicated on what the hydraulic conditions were.

386 The data further showed that relationships between micro-habitat variables did not
387 simply reflect available joint sedimentary-hydraulic conditions (i.e., through a hydraulic
388 sorting mechanism); pre-spawning surveys across the entire study site showed that little
389 of the variation in sedimentary conditions was explained by any combination of hydraulic
390 characteristics. Although the 2005 redd utilization and 2006 availability data-sets were

391 from consecutive spawning seasons separated by a major flood, the 2006 interpolated
392 utilization data revealed similar hydraulic-sedimentary relationships to those for 2005
393 redds (Figure 4). Furthermore, despite flood-induced morphological change at the study
394 riffle between 2005 and 2006, aerial photographs since 1937 suggested a dynamic
395 equilibrium condition with a quasi-stable island/bar morphology that would have
396 provided a similar range of hydraulic and sediment conditions over time. The process of
397 spawning is known to truncate the particle size distribution of redd tailspills compared to
398 that from the undisturbed bed (sorting by spawning fish reduces the proportion of the
399 finest and coarsest material in redd tailspills; Crisp and Carling, 1989). However, in the
400 present study, the generally smaller sediment size at a given velocity for 2005 redds
401 compared to 2006 available and interpolated utilization conditions implies that the
402 inability of spawning fish to mobilize large clasts from the bed was the dominant process
403 controlling the size of material in the tailspill (Figure 4). Indeed, during both the 2005
404 and 2006 field seasons, large clasts were observed within redd pits that were not present
405 in the associated tail spills. These large clasts that remain within the ‘pit’ are an
406 important element of redd structure, providing hydraulic ‘dead zones’ for deposited eggs
407 to settle between prior to burial (as per Jones, 1959). A small proportion of immobile
408 clasts within the substrate may therefore be an important component of spawning habitat,
409 particularly in locations where more energetic flow conditions could displace eggs out of
410 the pit prior to burial. Despite the fact that wide ranges in the micro-scale physical
411 conditions (i.e., depth, velocity and substrate) were utilized by fish, inter-relations
412 between these variables meant that relatively limited ranges of suitable joint conditions
413 were available within the study site; failure to consider this will significantly over-

414 estimate habitat availability. Generally, characterizing physical habitat of spawning
415 Chinook salmon by independently considering depth, velocity and substrate size
416 requirements (i.e., still common in habitat modeling exercises) could lead to considerable
417 error propagation.

418 A small number of studies have examined bivariate hydraulic habitat requirements/
419 utilization (i.e., joint depth-velocity distributions) for freshwater fish species (e.g., Le
420 Coarer, 2007). For gravel-bed rivers, velocity and depth are generally inversely related at
421 low discharge when hydraulics are strongly controlled by the longitudinal distribution of
422 morphological units (e.g. riffles, pools, glides, and runs) and directly related at high
423 discharge when the above morphological units are relatively submerged and thus
424 hydraulics are strongly controlled by the lateral shape of a channel (Stewardson and
425 MacMahon, 2002; Brown and Pasternack, 2008). Because salmon tend to avoid high
426 flows for spawning (Moir et al., 2006), the velocity-depth environment of the channel
427 when fish are spawning will typically exhibit the inverse relation. In this condition,
428 velocity exhibits a wide range for low depth and a narrow range for high depth (Brown
429 and Pasternack, 2008). Thus, when one considers that a riffle is generally defined as an
430 area of low depth, it may be expected that there would be both relatively high velocity
431 and high variation in velocity. As a result, there is an opportunity for adults to choose
432 among a range of velocity and substrate options within a riffle of relatively uniform
433 depth. This reasoning is supported by the results of the present study in that univariate
434 models incorporating flow depth explained little of the variability of utilized substrate
435 size within the riffle, whereas those incorporating flow velocity explained very similar
436 amounts to larger multivariate models. Therefore, in terms of the mechanical hydraulic

437 requirements of spawning, although depth was a component in habitat selected at the the
438 meso-scale (i.e. riffles versus pools or glides) within the riffle it was only directly
439 important in providing access for fish to a specific location of the channel bed, flow
440 velocity was the dominant control on the process of substrate excavation.

441 Many studies conclude that spawning salmonids select for depth beyond the simple
442 access criterion described here and without considering mesohabitat-scale variation (e.g.,
443 Burner, 1952; Beland *et al.*, 1982; Deverall *et al.*, 1993). In the absence of sedimentary
444 requirements, we propose that this apparent ‘selection’ within riffles is auto-correlative
445 and an artifact of the implicit inverse-relationship between depth and velocity in channels
446 as dictated by open channel flow mechanics. Thus, the apparent avoidance of high depth
447 points in riffles is not due to these conditions being unsuitable per se but more likely
448 related to insufficiently high velocities to mobilize the substrate and carry the dislodged
449 material downstream to construct a redd. However, the sedimentary-hydraulic
450 relationships presented here suggest that such locations could be utilized if they were
451 associated with sediment of sufficiently small caliber to permit the process of redd
452 excavation in low velocity areas. At the study site, redds were observed to occur in
453 relatively high depth, low velocity points in the riffle that were also associated with small
454 substrate sizes (mean depth = 0.71m, mean column velocity = 0.20ms^{-1} , tailspill D_{50} =
455 32.4mm at one sampled redd). Velocity must be sufficient to carry the majority of
456 sediment particles loosened from the channel bed during ‘cutting’ by the spawning
457 female (vigorous vertical flexing of the tail over the substrate surface while lying on her
458 side; Jones, 1959) to excavate a sufficiently large ‘pit’ to deposit eggs in. The coarser the
459 sediment, the faster the overlying flow velocity must be to allow completion of this

460 process. Faster flow velocities may also assist in the initial dislodging of substrate
461 particles during 'cutting' by providing a greater 'background' force that assists spawners
462 in mobilising larger clasts from the stream bed. The upper limits to spawning will be met
463 when a critical proportion of sediment particles become too large to initially liberate from
464 the bed and/or flow velocity is too high for the fish to maintain position long enough to
465 complete redd excavation; both these factors are related to fish size (Crisp and Carling,
466 1989; Kondolf and Wolman, 1993; Moir *et al.*, 2002). Therefore, species-specific
467 spawning micro-habitat requirements reflect the integration of available joint hydraulic-
468 sedimentary conditions (controlled by discharge, mesohabitat geometry and roughness
469 characteristics) with the ability of spawning fish to gain access to those conditions
470 (controlled by depth and, therefore, related to fish size), dislodge the substrate (controlled
471 by the combination of forces applied to the river bed by fish and hydraulics, the former
472 linked to fish size) and have it transported a small distance downstream (linked to
473 hydraulic forces).

474

475 **Conclusions**

476 The data demonstrated that substrate suitability can vary significantly for the same life
477 stage, species and river depending on the hydraulic conditions (particularly velocity) that
478 fish are spawning in. Moreover, since the proposed explanation for the observed pattern
479 of co-varying substrate-hydraulic utilisation is explicitly mechanism (i.e., the micro-scale
480 assessment of the ability of fish to mobilise sediment particles in relation to assisting
481 forces from local flow velocity), it should apply to all salmonid species that employ the
482 same 'cutting' behaviour for spawning (as per Jones, 1959). Understanding the

483 interaction of the key micro-scale physical variables is a prerequisite to monitoring the
484 spawning potential of streams. Failure to consider such inter-relationships could result in
485 significant over-prediction of suitable habitat. . Therefore, flow allocations (e.g., using
486 habitat models such as PHABSIM) or river restoration designs based on these inaccurate
487 predictions may well be sub-optimal for spawning Chinook (and likely other salmonid
488 species) and could propagate large errors through to setting and implementation of
489 environmental flows and the design of river management/ restoration projects.

490

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497

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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)

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

583 Figure 1. Study area. Yuba River watershed and Timbuctoo Bend study site.

584

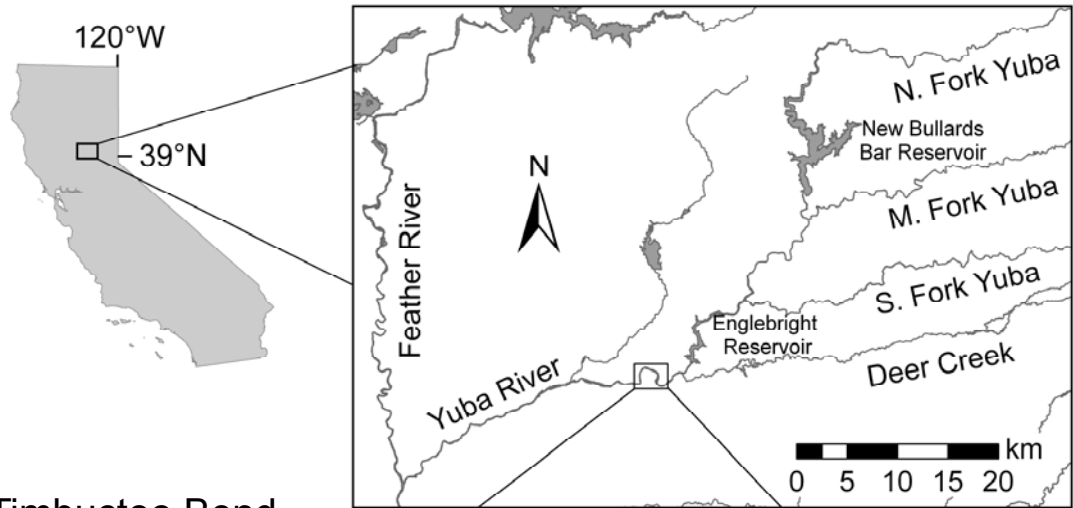
585 Figure 2. Study period hydrograph (Sept 1 2005 – Nov 1 2006) identifying 2005 and
586 2006 study periods. The horizontal dashed line represents the 1971-2004 statistical
587 bankfull discharge ($160\text{m}^3\text{s}^{-1}$).

588

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

592

593 Figure 4. Example data from 2005 redd sampling, 2006 available and 2006 interpolated
594 utilised 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
595 D_{84} , E) Fr and D_{50} , and F) Fr and D_{84} .



Timbuctoo Bend

