



2 Salmon-driven bed load transport and bed morphology in mountain 3 streams

4 Marwan A. Hassan,¹ Allen S. Gottesfeld,² David R. Montgomery,³ Jon F. Tunncliffe,⁴
5 Garry K. C. Clarke,⁵ Graeme Wynn,¹ Hale Jones-Cox,¹ Ronald Poirier,¹ Erland MacIsaac,⁶
6 Herb Herunter,⁶ and Steve J. Macdonald⁷

7 Received 13 December 2007; revised 10 January 2008; accepted 18 January 2008; published XX Month 2008.

9 [1] Analyses of bed load transport data from four streams
10 in British Columbia show that the activity of mass spawning
11 salmon moved an average of almost half of the annual bed
12 load yield. Spawning-generated changes in bed surface
13 topography persisted from August through May due to lack
14 of floods during the winter season, defining the bed surface
15 morphology for most of the year. Hence, salmon-driven bed
16 load transport can substantially influence total sediment
17 transport rates, and alters typical alluvial reach morphology.
18 The finding that mass-spawning fish can dominate sediment
19 transport in mountain drainage basins has fundamental
20 implications for understanding controls on channel
21 morphology and aquatic ecosystem dynamics, as well as
22 stream responses to environmental change and designing
23 river restoration programs for channels that have, or
24 historically had large spawning runs. **Citation:** Hassan,
25 M. A., et al. (2008), Salmon-driven bed load transport and bed
26 morphology in mountain streams, *Geophys. Res. Lett.*, 35,
27 LXXXXX, doi:10.1029/2007GL032997.

29 1. Introduction

30 [2] Physiographic change has been long regarded as a
31 primary determinant of evolutionary change in biological
32 systems, but the influence of organisms on their habitat is
33 less well appreciated. At relatively fine scales, the role of
34 gophers [e.g., *Yoo et al.*, 2005], ants [*Butler*, 1995], and
35 termites [*Selby*, 1993; *Butler*, 1995] in hillslope sediment
36 transport is well known, as is how beavers can greatly alter
37 river systems [*Butler*, 1995], cattle cause bank erosion
38 [*Trimble*, 1994], and crayfish shape local bed morphology
39 [*Statzner et al.*, 2000]. Although the effects of fish on
40 sediment sorting of streambed gravels during the digging

of nests (redds) have been widely recognized [*Kondolf and* 41
Wolman, 1993; *Kondolf et al.*, 1993; *Montgomery et al.*, 42
1996], the role of fish on sediment transport remains little 43
explored due to the difficulty in both collecting bed load 44
transport data and in discriminating between hydrologic and 45
biologic transport. 46

[3] The localized geomorphic role of spawning salmon 47
involves both direct transport during redd excavation that 48
modifies streambeds and indirect effects through changes 49
in bed-surface grain size and packing [*Butler*, 1995; 50
Montgomery et al., 1996]. Specifically, the flexing action 51
of female salmon creates a series of water jets that mobilize 52
sediment to excavate a depression ~5–50 cm in depth (for 53
review, see *DeVries* [1997]). In the process, fine clay, silt 54
and sand are lifted into the water column and carried 55
downstream. Coarser pebbles and gravels accumulate in a 56
pile, called the tailspill, at the downstream edge of the redd. 57
The floor of a redd consists of large gravel or cobble 58
particles that the fish cannot move, and this is where the 59
eggs are deposited [e.g., *Chapman*, 1988]. Once the eggs 60
have been fertilized by the male, the female covers them 61
with fresh gravel excavated upstream. Again, bed materials 62
are disturbed, fine sediment is carried downstream, and the 63
eggs are covered with relatively coarse grains [*Kondolf and* 64
Wolman, 1993; *Kondolf et al.*, 1993; *Rennie and Millar*, 65
2000]. Salmon tend to spawn on the upstream and down- 66
stream ends of riffles, and the edges of bars [*Gottesfeld et* 67
al., 2004]. But in streams with high spawning densities their 68
redds may disturb the entire channel bed [*Montgomery et* 69
al., 1996; *Gottesfeld et al.*, 2004]. *Gottesfeld et al.* [2004] 70
documented coarse sediment dispersion by floods and fish, 71
and showed that although spawning salmon do not move 72
material particularly far, the burial depths achieved by fish 73
are of the same range as those yielded by floods. However, 74
Gottesfeld et al. [2004] did not evaluate the influence of 75
spawning salmon on net sediment yields. 76

[4] Here we expand and further analyze this unique data 77
set to show that the mass spawning activity of salmon can 78
be a primary control on the transport of coarse sediment 79
(bed load) and sub-reach scale morphology. Specifically, we 80
calculate sediment yield to assess the relative influence of 81
snowmelt (nival), summer storm floods, and spawning 82
salmon on rates of bed load transport. The extent to which 83
we find that mass spawning salmon shape their environment 84
is particularly significant because originally abundant and 85
widely distributed runs of native salmon in Europe, northern 86
Asia, and North America have been massively reduced 87
historically and are now the focus of substantial river resto- 88

¹Department of Geography, University of British Columbia, Vancouver, British Columbia, Canada.

²Skeena Fisheries Commission, Hazelton, British Columbia, Canada.

³Earth and Space Sciences, University of Washington, Seattle, Washington, USA.

⁴National Institute of Water and Atmospheric Research, Christchurch, New Zealand.

⁵Department of Earth and Ocean Sciences, University of British Columbia, Vancouver, British Columbia, Canada.

⁶Fisheries and Oceans Canada, Co-operative Resource Management Institute, Burnaby, British Columbia, Canada.

⁷Department of Fisheries and Oceans, Centre for Aquaculture and Ecological Research, West Vancouver, British Columbia, Canada.

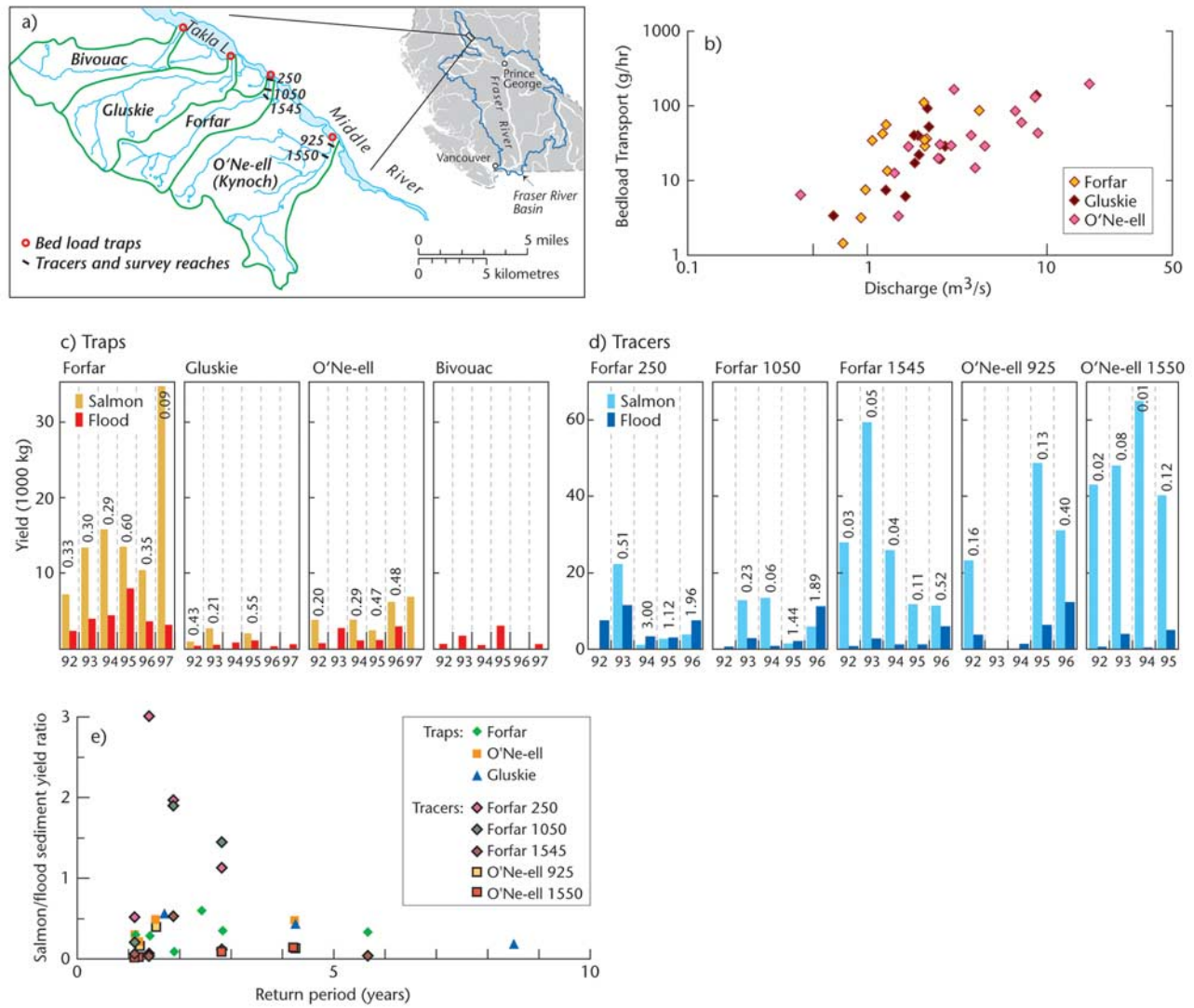


Figure 1. (a) Location map of the study streams. (b) Rating curve between sediment transport rate and discharge as measured using pit traps (Forfar $g = 9.54Q^{2.00}$, $r^2 = 0.56$; O'Ne-ell $g = 8.31Q^{0.96}$, $r^2 = 0.71$; and Gluskie $g = 8.32Q^{1.56}$, $r^2 = 0.60$; g is transport rate and Q is discharge). Sediment yield as estimated for floods and fish spawning for the years 1992–1997 using (c) pit traps and (d) tracer data; annual yield for tracers was estimated using the mean depth, width, and distance of travel data. Numbers presented for each year indicate the fish/flood bed load yield ratio (note that no flood data are available for Bivouac Creek). (e) Relationship between the fish/flood annual yield ratio and flood return period (calculated using data from 1991–2007) for the three creeks for which data on transport by both fish and floods were available.

89 ration programs in Europe and North America [Montgomery,
90 2003].

91 **2. Study Creeks and Methods**

92 [5] We analyzed repeated bed surface surveys and bed
93 load transport data from four watersheds in the Fraser River
94 basin, British Columbia, Canada (Figure 1a). These data
95 provide a unique opportunity to evaluate the role of mass
96 spawning salmon on sediment transport and channel morpho-
97 logy because repeated sub-annual monitoring allows
98 quantification of the relative influence of floods and spawn-
99 ing activity on channel morphology and sediment transport.
100 The watersheds are between 36 and 77 km², stream gradient
101 of the study reaches range between 0.2 and 1.7%, median

particle size ranged between 20 and 40 mm, and stream
width ranged from 5 to 20 m. These gravel-bed, pool-riffle
channels represent highly productive habitat for sockeye
salmon, as well as resident salmonids [Scrivener and
Macdonald, 1998]. Spawning densities are greatest within
two to three km of the river mouth and spawning occurs
when discharge is well below the threshold discharge for
initiating sediment transport, making it possible to unam-
biguously distinguish between flood and fish-induced
transport.

[6] Gottesfeld *et al.* [2004] reported that the range and
median travel distances of tagged particles mobilized by
nival floods and spawning fish were comparable in areas of
high spawning return each year between 1992 and 1996.
Burial depths of tagged particles were typically shallow;

117 58% of tagged clasts transported in May and 43% of those
118 transported in August were recovered from within the
119 surface layer of the gravel. Average burial depths ranged
120 from $2D_{50}$ to $10D_{50}$ (where $D_{50} \sim 40$ mm, is the median
121 size of the bed material), and was approximately equivalent
122 after transport by either floods or salmon bioturbation.

123 [7] In addition to the data on particle burial depths and
124 travel distances reported by *Gottesfeld et al.* [2004], bed
125 load transport was measured over six years (1992–1997) at
126 six reaches in the four study watersheds. Bed load sediment
127 transport during flood and spawning periods was measured
128 using bed load traps (Forfar, O’Ne-ell, Gluskie, and Biv-
129 ouac, Figure 1a) and magnetically tagged particles (Forfar
130 and O’Ne-ell). Pit traps (20 L plastic buckets inserted flush
131 with the bed surface) were installed in the study reaches
132 roughly 200 m upstream of the channel mouth to collect
133 sediment and were monitored through the spring snowmelt,
134 summer storm, and salmon spawning seasons [*Scrivener*
135 *and Macdonald*, 1998]. During high flows bed load traps
136 can fill, resulting in underestimates of actual transport
137 [*Hassan and Church*, 2001]. Our estimated transport rates
138 for salmon spawning and summer floods are based on
139 measurements from bed load traps partially filled during
140 low to intermediate flows, and are therefore considered
141 reliable. However, our estimates for high flow events,
142 especially during the nival floods, may be biased by trap
143 filling and hence somewhat underestimate sediment trans-
144 port during these floods.

145 [8] Because of such concerns we compare the bed load
146 trap data with sediment transport rates estimated from tracer
147 data, which represent transport from the whole flood, in
148 order to provide additional data and evaluate the potential
149 magnitude of any such bias. As described by *Gottesfeld et*
150 *al.* [2004], particles 40–200 mm in diameter collected from
151 the surface of a riffle were magnetically tagged, marked for
152 identification, and replaced in lines across the channels (of
153 the same reaches in Forfar and O’Ne-ell). We extend
154 *Gottesfeld et al.*’s [2004] analysis to use the tracer data to
155 estimate sediment yield for the study reaches.

156 [9] Bed surface changes produced by floods and spawn-
157 ing activity were documented over two years (1996–1997)
158 by repeated, detailed topographic mapping of channel
159 morphology in five reaches with extensive salmon spawn-
160 ing activity from two of the watersheds (3 reaches in Forfar
161 and 2 reaches in O’Ne-ell). Using a total station, total reach
162 lengths ranging between 4 and 9 channel widths were
163 surveyed; with a survey data density range of between 4
164 and 9 points per m^2 of channel bed area. Seasonal measure-
165 ments allow calculation of the net changes in channel
166 elevation between transport episodes and independent eval-
167 uation of the erosional and morphological effects of both
168 floods and spawning fish. Changes in the frequency and
169 amplitude of bed forms created from flood and spawning
170 events were analyzed through repeated surveys of longitu-
171 dinal profiles of the stream bed topography. Specifically, for
172 each study area and time period, three longitudinal profiles
173 (one meter from each bank and one in the middle) were
174 extracted from bed survey data to analyze the wavelength,
175 amplitude and spatial frequency of the channel topography.

176 [10] Flow data near the river mouth were measured
177 between 1991 and 2007. Based on this record, our obser-
178 vations cover flows with return periods ranging from 1.3 to

9 years. Due to the short length of the record we addition- 179
ally used nearby long-term gauge stations to estimate the 180
return period of the observed events (Environment Canada 181
Stations 08JA014 and 08EE008). The return period of the 182
largest measured event is between 10 and 20 years. We used 183
a rating curve to evaluate the relationship between flow 184
discharge and sediment accumulated in pit traps. The 185
amount of sediment moved during spawning was estimated 186
using trap data and tagged particles. The trap data were 187
combined to estimate total bed load transport for the 188
spawning season. For the tagged particles, the mobilized 189
sediment for the spawning season was estimated using a 190
combination of mean travel distance, mean burial depth and 191
channel width. 192

[11] Repeated sampling of freeze-cores [*Scrivener and* 193
Macdonald, 1998] collected from all four watersheds over 194
the study period to assess modification of bed material by 195
floods and fish, indicates that frequent disturbance of the 196
bed surface by fish reduces the vertical sorting and hence 197
the degree of surface armouring. In order to avoid problems 198
arising from the small sample size from individual freeze 199
cores [see *Zimmermann et al.*, 2005], we combined cores 200
into composite samples of about 100 kg taken before and 201
after the spawning period in both spawned and undisturbed 202
areas. Before aggregating the samples each core was divided 203
into surface and sub-surface material for separate analysis. 204
Hence, any systematic error introduced by the sampling 205
methodology will equally affect data from floods and spawn- 206
ing activity. 207

3. Results 208

[12] As in other sediment transport studies [e.g., *Hassan* 209
and Church, 2001], our data display substantial variance 210
around a trend of increased sediment transport with in- 211
creased discharge (Figure 1b). Due to gaps in flow record 212
from Bivouac Creek we could not develop a rating curve 213
and hence did not estimate bed load yield by floods. The 214
amount of total sediment mobilized by fish also is weakly 215
correlated ($r^2 = 0.20$ for all data) with the total number of 216
returning salmon. 217

[13] At Forfar 250 (near the river’s mouth), annual 218
sediment trap data show that fish mobilized between 9 219
and 60% of the amount of sediment annually moved by 220
floods (Figure 1c). Similar trends were obtained for O’Ne- 221
ell and Gluskie, where trap data indicate that fish mobilized 222
between 20 and 48% (O’Ne-ell), and 21 and 55% (Gluski). 223
In Bivouac Creek, where rating curve problems prevented 224
estimating the amount of flood-induced transport, the 225
amount of sediment mobilized by fish is of the same 226
magnitude as the amount moved by fish in O’Ne-ell. Hence, 227
averaged across all years for the three creeks, trap data 228
indicate fish mobilized about 35% of the net transport. 229
Tracer data from Forfar and O’Ne-ell indicate that fish 230
mobilized between 1 and 40% (O’Ne-ell – two reaches) 231
and 4 and 300% (Forfar – three reaches) of the material 232
moved by floods (Figure 1d). Averaged across all years for 233
both creeks, fish mobilized nearly half (55%) of the sedi- 234
ment moved by floods during the study period (see fish/ 235
flood ratios in Figure 1e). The ratio of bed load transport by 236
fish to that by floods declines for increasingly large floods 237
from an average of 47% (all available data, with a range of 238

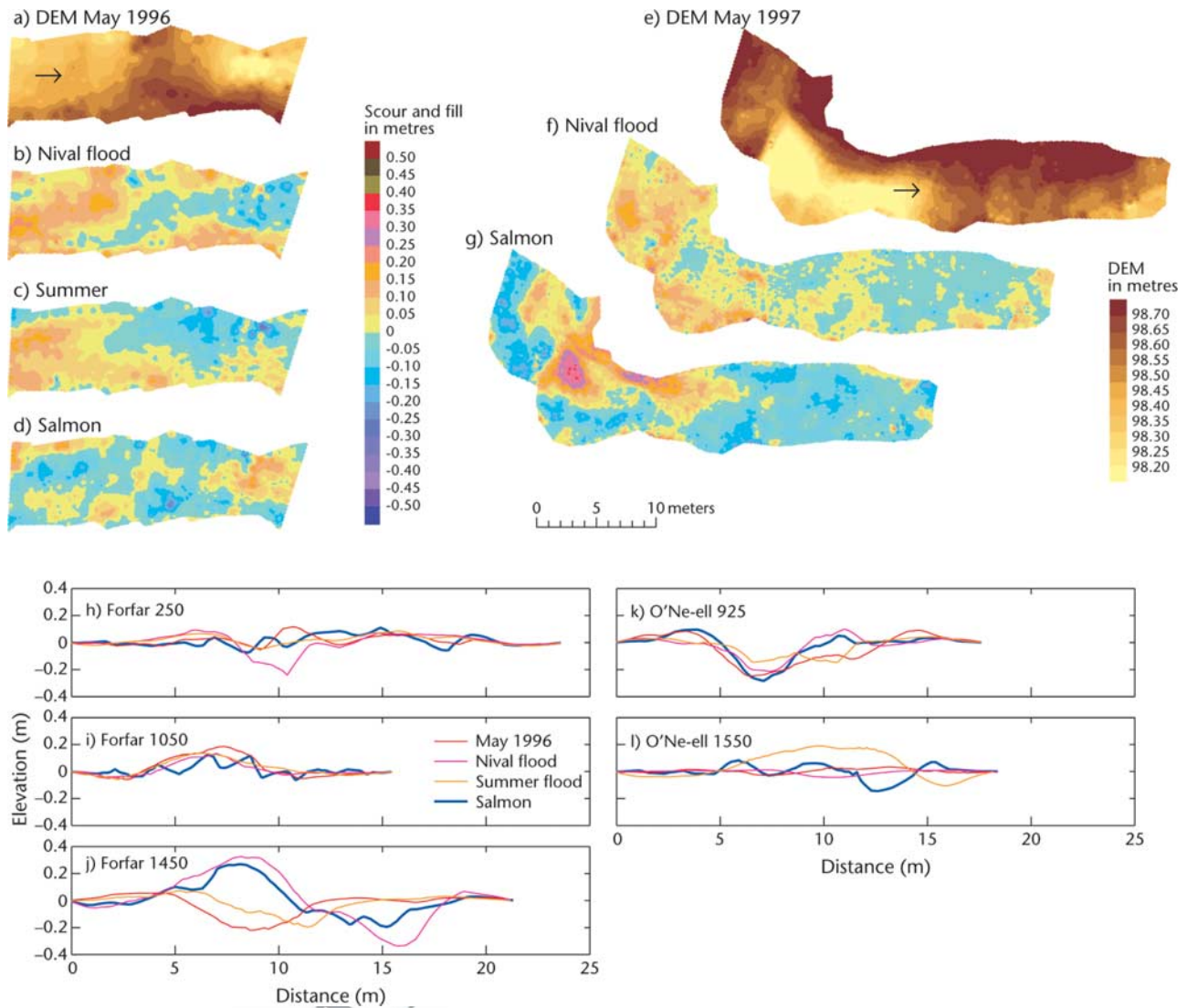


Figure 2. (a) Topographic map of Forfar 250 sub-reach prior to the 1996 nival flood. (b)–(d) Isopach diagrams from topographic surveys of Forfar 250 illustrating patterns of net cut and fill due to nival flood. (e) Topographic map of Forfar 1050 sub-reach prior to the 1997. (f) Isopach diagram of net scour and fill during nival floods. (g) Isopach diagram of net scour and fill during salmon transport. Blue areas indicate decreases in elevation; red areas indicate increases in elevation. (h)–(l) Bed surface profiles for study reaches in 1996 at times of pre-nival flood (May), nival flood, summer flood, and salmon spawning activity.

239 1–300%), for ≤ 2 yr recurrence interval events (Figure 1e).
 240 Hence, in years with low to intermediate magnitude flood
 241 events fish moved as much sediment as (or more than)
 242 floods, whereas in years with large magnitude events the
 243 floods moved much more sediment than did fish. Nonethe-
 244 less, the greater frequency of the small events means that
 245 overall fish can move a large proportion of the net sediment
 246 transported (as shown above).

247 [14] Two examples of bed surface surveys (Forfar 250 in
 248 1996 and Forfar 1050 in 1997) illustrate typical patterns of
 249 response surveyed in these mountain streams. Channel
 250 morphology prior to the 1996 nival flood shows a typical
 251 riffle-pool morphology (Figure 2a). The median net scour
 252 and fill values for both fish and flood events are approxi-
 253 mately 10 cm (Figures 2b, 2c, and 2d). Few areas in these
 254 reaches experience more than 30 cm of net erosion or net

255 deposition. The nival flood of May 1996 produced a typical
 256 uncorrugated sub-reach scale morphology of pools, riffles
 257 and bars (Figure 2b). Approximately half of the study area
 258 underwent net sedimentation; 40% was scoured and no net
 259 change was recorded in the remainder. The 1996 summer
 260 flood was small, and its effects were similar to those of the
 261 nival flood: riffles were scoured and there was minor filling
 262 in the pools (Figure 2c). Similar results were obtained for
 263 the 1996 floods in Forfar 1050 (Figures 2e–2g).

264 [15] In contrast to the minor morphological effect of high
 265 flows, the spawning activity of sockeye salmon in August
 266 produced major changes in channel morphology (Figure 2d).
 267 Several cycles of redd excavation created a small-scale
 268 topography of mounds and hollows which persisted into
 269 early spring. Overall there was a net excavation of those
 270 areas most suitable for fish spawning (riffles and bars), and

271 deep pools were filled with sediment excavated from bars.
 272 As stream flow increased due to spring snowmelt and
 273 summer floods, sediment deposited in pools by bioturbation
 274 was remobilized downstream, replenishing the surface of
 275 bars and riffles downstream, providing new areas for
 276 salmon spawning, and resulting in further net transport.
 277 These patterns were typical of the study streams and net
 278 scour and fill distributions measured across all study reaches
 279 show comparable ranges for both fish and floods.

280 [16] The hummocky surface created by fish and the
 281 relatively smooth surface created by the nival and summer
 282 floods reveal two distinct signatures: one for flood events
 283 and another associated with fish spawning (Figures 2h–2l).
 284 Moreover, areas that are scoured by floods are refilled by
 285 fish activity and visa-versa (i.e., in general, the bed mor-
 286 phology resulting from fish excavation is spatially antipha-
 287 sic to the morphology associated with nival and summer
 288 flood events). This pattern recurs annually, and is affected
 289 by both flood magnitude and the number of returning
 290 spawners. Due to the lack of winter floods in these streams,
 291 the post-spawning bed configuration lasted from August to
 292 May. Hence, salmon are a primary determinant of sub-
 293 reach-scale habitat form and dictate the overall bed mor-
 294 phology of the streams for most of the year.

295 [17] Cores from the study reaches were used to evaluate
 296 the degree of surface coarsening due to both floods and
 297 spawning activity. The surface layer of river beds in humid
 298 regions typically has a coarser surface ‘armour’ layer with a
 299 diminished sand component [e.g., *Dietrich et al.*, 1989;
 300 *Hassan et al.*, 2006]. The armouring ratio (median surface/
 301 median subsurface grain size) is usually >2 for gravel-bed
 302 channels in humid regions [*Hassan et al.*, 2006]. In contrast,
 303 armouring ratios for the study channels ranged from about 1
 304 up to 1.4, presumably due to the frequent digging by fish
 305 disrupting both the vertical sorting and the development of
 306 stable bed-surface structures [*Hassan et al.*, 2006].

307 4. Discussion and Conclusions

308 [18] Using various complementary methods our analyses
 309 show that spawning salmon are a first-order, although
 310 highly variable, control on sediment transport in the study
 311 streams. Each method has its own limitations (e.g., potential
 312 for filling of bed load traps), but the close correspondence
 313 of the bed load estimates from trap and tracer data gives us
 314 confidence in our results. Moreover, the general agreement
 315 in the range of scour and fill distributions for both fish and
 316 flow-induced transport events provides further support for
 317 the interpretation that salmon spawning is a first-order
 318 control on bed load transport.

319 [19] More specifically, our analyses of bed load transport
 320 data indicate that mass-spawning salmon: (1) cause direct
 321 sediment movement accounting for between a third and half
 322 the bed load moved; (2) increase bed surface roughness;
 323 (3) prevent development of well armoured surfaces; and
 324 (4) create a distinct hummocky channel morphology super-
 325 imposed on the longer-wavelength pool-riffle bed forms.
 326 Grain size and roughness effects of spawning activity have
 327 been commented upon previously [e.g., *Kondolf et al.*,
 328 1993; *Montgomery et al.*, 1996]. However, the impact on
 329 channel morphology and direct sediment transport quantify
 330 previously speculative influences of salmon on their habitat.

[20] In regard to the effect of mass-spawning fish on 331
 sediment mobility during subsequent flood event, the in- 332
 crease in bed form roughness from spawning is likely to 333
 reduce flow strength and hence decrease sediment mobility 334
 [*Montgomery et al.*, 1996]. However, the disruption of 335
 surface armouring caused by fish excavation is likely to 336
 increase sediment mobility by post-spawning flow events. 337
 Consequently, the net effect of these two opposing factors 338
 depends on the balance between them, something that we 339
 do not address here. 340

[21] The observation that mass spawning salmon can 341
 account for substantial bed load sediment transport — 342
 averaging between a third and half the annual flux in the 343
 streams studied — suggests strong, heretofore unquantified, 344
 links between the biology and channel morphology of 345
 gravel-bed streams. When considered together with recent 346
 recognition of the key role of bed load sediment transport 347
 on setting river longitudinal profiles [*Sklar and Dietrich*, 348
 1998] our findings further suggest fundamental linkages 349
 between the population dynamics of mass spawning salmon 350
 and evolution of their mountain streams. Regional physio- 351
 graphic change is thought to have spurred the evolution of 352
 the Pacific salmon [*Montgomery*, 2000], but our results 353
 suggest that conversely the rise of mass spawning salmon 354
 may have also influenced channel morphology and sedi- 355
 ment transport, and potentially thereby reach slopes and 356
 hence to some degree perhaps even the physiographic 357
 evolution of the region. Moreover, efforts to recover salmon 358
 stocks both in Europe and North America through hydro- 359
 geomorphic (habitat) restoration would be further compli- 360
 cated if, as suggested here, historic river morphology and 361
 dynamics were greatly influenced by larger numbers of 362
 mass-spawning fish. For therein lies a potential conundrum 363
 for restoration ecologists: what must one recover first, the 364
 fish or the stream? 365

[22] **Acknowledgments.** Eric Leinberger prepared the figures. The 366
 detailed, critical and provocative comments of two anonymous reviewers 367
 also proved useful in revising the manuscript. 368

References 369

- Butler, D. R. (1995), *Zoogeomorphology: Animals as Geomorphic Agents*, 370
 241 pp., Cambridge Univ. Press, New York. 371
 Chapman, D. W. (1988), Critical review of variables used to define effects 372
 of fines in redds of large salmonids, *Tran. Am. Fish. Soc.*, 117, 1–21. 373
 DeVries, P. (1997), Riverine salmonid egg burial depths: Review of pub- 374
 lished data and implications for scour studies, *Can. J. Fish. Aquat. Sci.*, 375
 54, 1685–1698. 376
 Dietrich, W. E., J. W. Kirchner, H. Ikeda, and F. Iseya (1989), Sediment 377
 supply and the development of the coarse surface layer in gravel-bed 378
 rivers, *Nature*, 340, 215–217. 379
 Gottesfeld, A. S., M. A. Hassan, J. F. Tunnicliffe, and R. W. Poirier (2004), 380
 Sediment dispersion in salmon spawning streams: The influence of floods 381
 and salmon redd construction, *J. Am. Water Resour. Assoc.*, 40, 1071– 382
 1086. 383
 Hassan, M. A., and M. Church (2001), Sensitivity of bedload transport in 384
 Harris Creek: Seasonal and spatial variation over a cobble-gravel bar, 385
Water Resour. Res., 37, 813–825. 386
 Hassan, M. A., R. Egozi, and G. Parker (2006), Effect of hydrograph 387
 characteristics on vertical sorting in gravel-bed rivers: Humid versus arid 388
 environments, *Water Resour. Res.*, 42, W09408, doi:10.1029/ 389
 2005WR004707. 390
 Kondolf, G. M., and M. G. Wolman (1993), The sizes of salmonid spawn- 391
 ing gravels, *Water Resour. Res.*, 29, 2275–2285. 392
 Kondolf, G. M., M. J. Sale, and M. G. Wolman (1993), Modification of 393
 fluvial gravel size by spawning salmonids, *Water Resour. Res.*, 29, 394
 2265–2274. 395
 Montgomery, D. R. (2000), Coevolution of the Pacific salmon and Pacific 396
 Rim topography, *Geology*, 28, 1107–1110. 397

- 398 Montgomery, D. R. (2003), *King of Fish: The Thousand-Year Run of Salmon*, 290 pp., Westview, Boulder, Colo. 425
- 399
400 Montgomery, D. R., J. M. Buffington, P. Peterson, D. Scheutt-Hames, and 426
401 T. P. Quinn (1996), Streambed scour, egg burial depths and the influence 427
402 of salmonid spawning on bed surface mobility and embryo survival, *Can.* 428
403 *J. Fish. Aquat. Sci.*, 53, 1061–1070. 429
- 404 Rennie, C. D., and R. G. Millar (2000), Spatial variability of stream bed 430
405 scour and fill: A comparison of scour depth in chum salmon (*Oncorhynchus keta*) 431
406 redds and adjacent bed, *Can. J. Fish. Aquat. Sci.*, 57, 928– 432
407 938.
- 408 Scrivener, J. C., and J. S. Macdonald (1998), Interrelationships of 434
409 streambed gravel, bedload transport, beaver activity and spawning sock- 435
410 eye salmon in Stuart-Takla tributaries, British Columbia, and possible 436
411 impacts from forest harvesting, in *Land Management Practices Affecting* 437
412 *Aquatic Ecosystems*, edited by M. K. Brewin and D. M. A. Monita, pp. 438
413 267–282, Can. For. Serv., Calgary, Alberta. 439
- 414 Selby, M. J. (1993), *Hillslope Materials and Processes*, 451 pp., Cambridge 440
415 Univ. Press, Oxford, U. K.
- 416 Sklar, L., and W. E. Dietrich (1998), River longitudinal profiles and bed- 441
417 rock incision models: Stream power and the influence of sediment supply, 442
418 in *Rivers Over Rock: Fluvial Processes in Bedrock Channels*, *Geophys.* 443
419 *Monogr. Ser.*, vol. 107, edited by K. J. Tinkler and E. E. Wohlleds, 444
420 pp. 237–260, AGU, Washington, D. C.
- 421 Statzner, B., E. Fievet, J.-Y. Chamagne, and R. Morel (2000), Crayfish as 445
422 geomorphic agents and ecosystem engineers: Biological behaviour af- 446
423 fects sand and gravel erosion in experimental streams, *Limnol. Ocea-* 447
424 *nogr.*, 45, 1030–1040. 448
- Trimble, S. (1994), Erosional effects of cattle on stream banks in Tennessee, 425
U.S.A., *Earth Surf. Processes Landforms*, 19, 451–464. 426
- Yoo, K., R. Amundson, A. M. Heimsath, and W. E. Dietrich (2005), Pro- 427
cess-based model linking pocket gopher (*Thomomys bottae*) activity to 428
sediment transport and soil thickness, *Geology*, 33, 917–920. 429
- Zimmermann, A., M. Coulombe-Pontbrian, and M. Lapointe (2005), Biases 430
of submerged bulk and freeze-core samples, *Earth Surf. Processes Land-* 431
forms, 30, 1405–1417. 432
- G. K. C. Clarke, Department of Earth and Ocean Sciences, University of 434
British Columbia, Vancouver, BC, Canada V6T 1Z4. 435
- A. S. Gottesfeld, Skeena Fisheries Commission, P.O. Box 229, Hazelton, 436
BC, Canada V0J 1Y0. 437
- M. A. Hassan, H. Jones-Cox, R. Poirier, and G. Wynn, Department of 438
Geography, University of British Columbia, Vancouver, BC, Canada V6T 439
1Z2. (mhassan@geog.ubc.ca) 440
- H. Herunter and E. MacIsaac, Fisheries and Oceans Canada, Co- 441
operative Resource Management Institute c/o REM, Simon Fraser 442
University, Burnaby, BC, Canada V5A 1S6. 443
- S. J. Macdonald, Department of Fisheries and Oceans, Centre for 444
Aquaculture and Ecological Research, West Vancouver, BC, Canada V7V 445
1N6. 446
- D. R. Montgomery, Earth and Space Sciences, University of Washington, 447
Johnson Hall 070, Box 351310, 4000 15th Avenue NE, Seattle, WA 448
98195–1310, USA. 449
- J. F. Tunncliffe, National Institute of Water and Atmospheric Research 450
(NIWA), P.O. Box 8602, Christchurch, New Zealand. 451