

Modelling the probability of salmonid egg pocket scour due to floods¹

Michel Lapointe, Brett Eaton, Steve Driscoll, and Christian Latulippe

Abstract: Flood disturbance plays a key but complex role in structuring lotic ecosystems. Empirical models proposed here allow salmonid resource managers to quantify the probability of egg pocket scour during floods and to predict how the expected losses vary with flood strength and reach characteristics. The models are based on comparisons between published salmonid egg pocket depth criteria and statistics on the intensity and spatial distribution of scour and fill produced by three flood events of widely different magnitudes in three separate reaches of a gravel-cobble Atlantic salmon (*Salmo salar*) river in the Saguenay region, Quebec. A simple substrate mobility index, based on reach-scale geomorphic characteristics and flood hydraulics, was shown to provide useful predictions (R^2 up to 74%) of the fraction of the area of potential spawning zones undergoing flood scour greater than 30 cm. Any Atlantic salmon egg pockets present in these deeply scoured areas would be destroyed. The models also predict the distribution of fill (net rise in bed) potentially causing fry entombment at redds. The flood disturbance data suggest that average probability of scour of an Atlantic salmon egg pocket in the study reaches ranges from under 5% for frequent-recurrence spring floods to approximately 20% for an extreme, multicentenary-recurrence flood.

Résumé : Les perturbations causées par les crues jouent un rôle clé mais complexe dans la structuration des écosystèmes lotiques. Les modèles empiriques proposés ici permettent aux gestionnaires des ressources de salmonidés de quantifier la probabilité d'affouillement des poches d'œufs pendant les crues et de prédire comment les pertes prévues vont varier en fonction de la force de la crue et des caractéristiques du tronçon. Les modèles se fondent sur des comparaisons entre des critères publiés sur la profondeur des poches d'œufs de salmonidés et sur des statistiques concernant l'intensité et la distribution spatiale de l'affouillement et du colmatage produits par trois épisodes de crue d'ampleur très différente, survenus dans trois tronçons séparés d'un cours d'eau à saumon à fond de gravier et de cailloux de la région du Saguenay, au Québec. Un indice simple de la mobilité du substrat, fondé sur des caractéristiques géomorphologiques à l'échelle du tronçon et sur l'hydraulique de la crue, a fourni des prévisions utiles (R^2 jusqu'à 74%) de la fraction de la superficie des frayères potentielles qui subissait un affouillement sur plus de 30 cm. Toutes les poches d'œufs de saumon atlantique présentes dans ces zones profondément affouillées seraient détruites. Les modèles prédisent aussi la distribution du colmatage (hausse nette du lit), qui risque de causer l'étouffement des alevins prisonniers des nids. Les données sur les perturbations causées par les crues permettent de penser que la probabilité moyenne d'affouillement d'une poche d'œufs de saumon dans les tronçons d'étude va de moins de 5% pour les crues printanières fréquentes à environ 20% pour une crue extrême à récurrence pluricentenaire.

[Traduit par la Rédaction]

Introduction

The physical and spatial complexity of stream microhabitat poses real challenges to the study of running-water ecosystems. However, the paradoxical role of flood disturbance in structuring running-water communities arguably poses even greater challenges to understanding lotic ecosystems. The problem of defining optimum physical disturbance regimes for various lotic communities, raised by several authors (e.g., Resh et al. 1988; Allen 1995; Sparks and Spink 1998), applies in particular to stream salmonid communities.

On the one hand, substrate entrainment by flood flows is necessary to maintain the long-term productivity of gravel stream habitat for salmonids. Indeed, the curtailment of regular high-flow events and associated gravel transport (e.g., following reservoir construction) can lead to excess sand encroachment into substrate, resulting in degradation of spawning habitat (e.g., Kondolf and Wilcock 1996; Wilcock et al. 1996; Milhous 1998) and in the displacement of the lithophilous benthic insect populations, a major food source during juvenile salmonid growth (Waters 1995). Conversely, intense and frequent disturbances to gravel substrate may limit salmonid production by destroying fish eggs during incubation (Seegrist and Gard 1972; Holtby and Healy 1986; Lisle 1989), by temporarily decimating benthic insect populations (Elwood and Waters 1969; Milner et al. 1981) or by directly inhibiting foraging by juvenile salmonids.

In particular, flood scour of salmonid eggs in spawning beds can directly affect cohort and population dynamics. Numerous studies have indicated the importance of spawning bed grain size distribution in controlling intergravel flow, egg maturation, and fry emergence (Scrivener and Brownlee

Received June 25, 1999. Accepted January 19, 2000.
J15217

M. Lapointe,² B. Eaton, S. Driscoll, and C. Latulippe.
Department of Geography, McGill University,
805 Sherbrooke St. West, Montreal, QC H3A 2K6, Canada.

¹A contribution to the scientific program of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique).

²Author to whom all correspondence should be addressed.
e-mail: lapointe@geog.mcgill.ca

1989; Kondolf and Wolman 1993). However, the impact on salmonid reproductive success of flood disturbances to spawning beds has been poorly studied. Payne and Lapointe (1997) showed that, in an unstable gravel–cobble river, high rates of erosion of sand-rich cutbanks during floods did not necessarily lead to enhanced sand encroachment into the spawning substrate in the reach. Their study did not, however, address the possible effects of intense spawning bed disturbance during floods on embryos incubating in such unstable channels.

A variety of flood-related geomorphic processes can directly hinder salmonid incubation and emergence from redds. Sediment fill (i.e., accreting sediment producing a net rise in bed level) over egg pockets during floods may be harmful to fry emergence, particularly if the accreting sediments have a high content of fine sediments. Conversely, substrate mobilization (i.e., scour) down to egg pocket depths can entrain and destroy embryos (DeVries 1997). Allen (1951) and Elwood and Waters (1969) highlighted the transient effects on salmonid communities of the destruction of incubating eggs by strong flood flows. Montgomery et al. (1999) hypothesized that interreach geomorphic contrasts in flood scour patterns constrain salmonid distributions through the requirement that egg burial depth must exceed typical scour depths in spawning beds. In particular, egg loss due to flood scour has also been thought to affect the relative distribution of spring- versus fall-spawning species, depending on the seasonal timing of high flows (Kondolf et al. 1991; Pearsons et al. 1992). Finally, the simple infiltration of fine sediments into egg pockets in fresh redds during high-flow events can also smother incubating embryos (Gibbons and Salo 1973). Lisle and Lewis (1992) presented a model predicting embryo losses due to this latter process. Their model is particularly useful in regions such as northern California where repeated, moderate-winter high flows, capable of mobilizing sands on the river bed, can occur during the period of incubation. The model did not, however, quantify the losses directly due to egg pocket scour during stronger floods, the focus of this paper. For Atlantic salmon (*Salmo salar*) populations in northeastern North America, which spawn mainly in fall and whose fry emerge in late spring, very low winter flows are typical of much of the egg incubation period. In such settings, disturbance to egg pockets during the dominant, gravel-mobilizing, late-winter or spring flood associated with snowmelt is a notable but poorly quantified cause of juvenile loss.

To begin understanding the complex role that floods play in structuring salmonid stream communities, ecologists need analytical methods developed by geomorphologists to model how severely physical disturbances affect stream habitats and organisms at various life stages using those habitats. This study proposes tools to quantify the flood damage to salmonid egg pockets. Based on observations on the Sainte-Marguerite River, Quebec, empirical models are presented that predict the intensity of scour and fill affecting spawning redds as a function of local stream characteristics and flood strength. An unusually broad range of flood intensities during the study period provided a unique opportunity to characterize a response curve for disturbance to spawning beds. Observed scour patterns were then compared with typical salmonid egg pocket depths (DeVries 1997) to estimate

probabilities of egg pocket losses due to various flood events.

Materials and methods

Study sites and flood events

The Sainte-Marguerite River drains a catchment of 2135 km² into the Saguenay Fjord, Quebec, Canada (Fig. 1). The river supports an Atlantic salmon sport fishery, which plays a prominent role in the local economy. Research was carried out along the upper section of the main branch of the Sainte-Marguerite River, an area draining a 285-km² subbasin. In several locations along this section of valley (Fig. 2), meanders were rectified over 35 years ago to facilitate highway construction. This reach displays a general downstream decrease in channel gradient and concomitant substrate sizes, a common pattern along gravel rivers. Atlantic salmon have been observed to spawn on riffles with gravel to cobble substrate at various points along the upper 8 km of the reach shown in Fig. 2.

Three flood events, covering a particularly wide range of magnitudes, occurred during the 1995–1997 study period. The May 1996 and May 1997 events, both generated by spring snowmelt, were moderate (recurrence period 8–10 years) and small (2–3 years) in magnitude, respectively. In contrast, the July 1996 event was a flood event of very large magnitude, the largest on record in the study basin, with a recurrence period measured in centuries. This high-intensity flooding occurred when an extreme frontal precipitation system stalled for 48 h over the entire Saguenay region (Lapointe et al. 1998). Although this July flood did not coincide with a period of salmonid egg incubation, it provided a unique opportunity to assess the level of physical disturbance to spawning habitat corresponding to a very large flood.

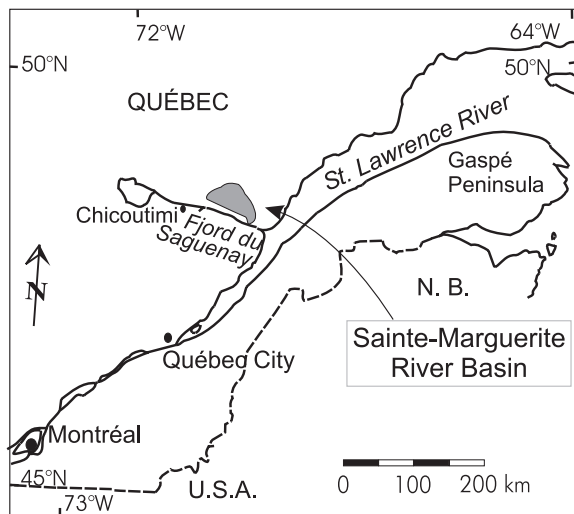
For each event, detailed patterns of flood disturbance to the spawning zones were studied in three reaches (Fig. 2). There are no significant tributaries in this section of valley, and the three study reaches share a common discharge regime. These study reaches were selected to represent a range of sedimentological, morphological, and channel slope characteristics (Table 1) typical of the spawning habitat in this section of valley. Within these three reaches, a total of seven separate riffle spawning zones were monitored in detail for flood disturbance. Two potential spawning zones were directly flanked by artificially stabilized banks.

Delimitation of potential spawning zones

Potential spawning zones were carefully identified before each flood event to focus on scour and fill patterns that could affect incubating embryos. The limits of these zones were defined based on generally accepted sedimentological, morphological, and hydraulic criteria for Atlantic salmon spawning habitat (Beland et al. 1982; Gibson 1993). Due to year-to-year variations in spawning pressure, the seven spawning zones monitored in this study were not used by spawners every year. Zone locations are consistent, however, with historical redd location patterns in this reach. Potential spawning zones were operationally defined here as the segments of the low-flow (summer-stage) channel extending one bankfull width upstream of each riffle crest (the latter defined as the local peak in bed elevation between pools) (Fig. 3). In the study reaches, mean flow depths at the lateral edges of these zones would generally be 15–25 cm in October, the usual spawning season. The upstream limit of each zone corresponds to sectors where depths increase rapidly upstream towards the preceding pool. Analysis showed that the statistics on bed disturbance probabilities presented below are not very sensitive to the precise lateral and upstream limits used to delimit potential spawning zones.

During high flows, stronger velocities tend to be concentrated towards the outside of a bend, due to the effects of channel sinuosity (Chang 1992), producing lateral gradients in flood shear

Fig. 1. Location map of the Sainte-Marguerite River study basin.



stresses and substrate size distributions at riffle cross sections (Payne and Lapointe 1997). To account for this spatial variation in geomorphic conditions, spawning zones were laterally broken down into three subzones (Fig. 3). The thalweg subzone was defined as a 3-m-wide swath centred on the thalweg within each spawning zone. High-velocity subzones (on the cutbank side with respect to the previous bend) and low-velocity subzones (on the point bar side of the previous bend) were identified on each side of the thalweg subzone.

Observations of scour and fill in potential spawning zones

A key parameter for modelling egg scour is the depth of egg pocket emplacement at redds. In a review of data on egg burial depths for various salmonids, DeVries (1997) proposed scour depth criteria corresponding to the typical levels of the top and the bottom of egg pockets. At Atlantic salmon redds, scour to a depth of 15 cm below the original bed level begins to affect the top of egg pockets, while 30 cm of scour would generally reach the base of egg pockets, causing total egg loss (DeVries 1997). For most other salmonid species, thresholds for the start of egg scour varied from 10 to 15 cm (top of egg pockets below the original bed level), while egg pocket bottom depths varied from 20 to 50 cm. Unfortunately, no study is available yielding precise criteria on thickness of fresh flood fill (i.e., net rise of bed level) over egg pockets leading to inhibition of fry emergence and entombment.

Initially, scour chains were emplaced at riffle sites during the 1995–1996 period. However, floods during the study period were powerful enough to produce easily surveyed net scour or fill with clear implications for egg pocket integrity. Scour chains were not employed after 1996. Between each flood, repeated high-resolution topographic surveys of the bed in the three study reaches were carried out under low-flow conditions. Topographic soundings were collected approximately every 3–4 m (i.e., 500–600 survey points in a 400 × 25 m wetted zone) using 5-mm-precision total station surveys. Analysis of replicate surveys showed that this technique yields digital elevation models with a mean vertical uncertainty of approximately 5 cm (due mainly to interpolation errors between sounding points). All surveys were precisely referenced to permanent benchmarks on the floodplain, allowing for an accurate assessment of net topographic changes caused by intervening flood events. Maps of the topographic changes (net scour and net fill) associated with each flood event were derived by subtracting the preevent topographic model from the postevent model. To the extent that observed net lowering (or raising) of the bed at spawning sites can destroy (or entomb) eggs, these net change maps yield

conservative or minimal estimates of embryo loss probabilities. The potential of additional egg losses due to deep scour followed by fill during a single event is addressed in the Discussion.

Predictors of substrate scour and fill depths

Bed scour depths have been empirically correlated with peak flood discharges and associated bed load transport rates in a number of studies (Carling 1987; Ziemer et al. 1991). However, scour depth (and egg pocket integrity) during floods cannot be accurately predicted solely from peak discharge values. The substrate scouring potential of a discharge level in a particular stream reach depends on a number of local geomorphic variables, such as channel cross-sectional geometry and slope, as well as sediment calibre (size) on spawning beds. Erman et al. (1988) argued, for example, that variations in the height of banks along Sagehen Creek (due to differential snow buildup in winter) produced, at the same flood discharges, downstream variations in the bed shear forces, bed scour, and salmonid egg loss. Fluvial geomorphologists model substrate transport intensity using measures such as bed mobility ratios or “Shield’s stresses” (Chang 1992; Montgomery et al. 1996). These parameters express the ratio of the hydraulic mobilizing forces of the flood at its peak (shear stresses, τ_o) to the mechanical forces resisting substrate entrainment (critical entrainment stresses, τ_c), which depend on substrate grain sizes.

The spatial distribution of peak shear stresses during a flood, locally over the various zones of the spawning riffle, is extremely difficult to measure or reconstruct. However, the average shear stress over a whole reach can be estimated from hydraulic principles (Chang 1992) using simple measures of the flood flow geometry, particularly the flow hydraulic radius (approximately mean flow depth) and energy slope (approximately water surface slope). Precise peak water surface levels for all three flood events were reconstructed using observations from maximum stage recorders installed at the upstream and downstream limits of each study reach. Flood flow geometry (cross-sectional depths, etc.) was derived by comparing the channel topographic model (excluding floodplain zones) with the elevation of the flood water surface. The average shear stress on the bed at flood peak ($\bar{\tau}_o$) is given by

$$(1) \quad \bar{\tau}_o = \rho g R S$$

where ρ is water density and g is acceleration due to gravity. The flood hydraulic radius (R) in each reach was averaged over several cross sections. The energy slope (S) was assumed equal to the water surface slope to a good approximation, since peak flow cross sections (and thus mean velocities) were very similar at the entrance and exit sections of each reach.

The nominal critical shear stress (τ_c) required to entrain the surface layer of substrate at riffles was estimated from riffle surface median diameter (D_{50}) using Shield’s law (Dingman 1984):

$$(2) \quad \tau_c / (\rho_S - \rho) g D_{50} = 0.06$$

which corresponds to the rough equivalence τ_c (pascals) = D_{50} (millimetres) for particles with the density of quartz ($\rho_S = 2.65$ times the density of water). The average riffle zone median grain size (D_{50}) in each reach was estimated from standard Wolman, or grid-by-number, samples (Church et al. 1987) measured on the high-velocity side of each riffle or at the adjacent point bar head (Fig. 3). Where riffle substrate could not be sampled accurately underwater, samples were taken at the head of the adjacent point bar, as close as possible to water’s edge and to the submerged riffle (a common practice in fluvial geomorphology). Such bar head samples taken at low stages generally reflect the coarsest mobile alluvium within a pool–riffle reach and have a median size comparable with that found on the adjacent high-velocity side of the submerged riffle. Finally, the reach-average mobility ratio was defined as

Fig. 2. Map and long profile of study reaches A, B, and C located in the upper section of the main branch of the Sainte-Marguerite River approximately 50 km from the mouth of the river in the Saguenay Fjord.

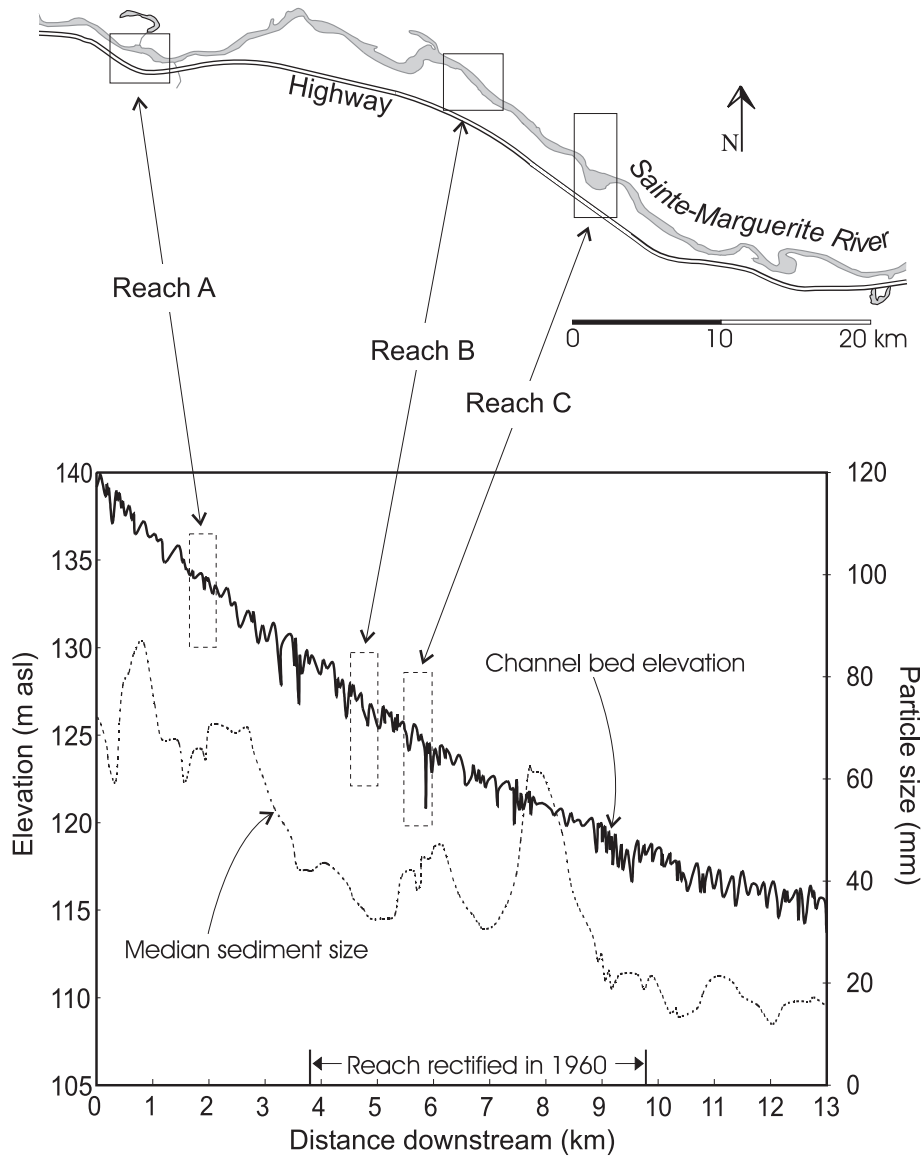


Table 1. Main geomorphological characteristics of the study reaches.

Study reach	Total length (m)	Bankfull width (m)	Bankfull water surface slope	Average D_{50} on bar heads (mm)
A	385	44	0.0033	42.5
B	335	38	0.0028	29
C	392	58	0.0026	45.5

Note: D_{50} refers to the median diameter of surface pavement particles.

(3) Mobility ratio = $\bar{\tau}_o / \bar{\tau}_c$

where $\bar{\tau}_o$ is the estimate of reach-average shear stresses and $\bar{\tau}_c$ applies to the reach-average riffle zone substrate (i.e., applying eq. 2 to the average D_{50} for all riffle zones in the reach).

For ease of estimation and application to other systems, the simple form of mobility index used here is based on reach-average

shear stresses (rather than difficult to estimate local stresses) and riffle zone mean substrate size (rather than the much harder to estimate reach-average substrate size). Because of variations in bed pavement structure, there is some uncertainty in the literature concerning the precise value of Shield's constant (0.06 in eq. 2 is the conventional value) that best describes the onset of sediment motion (Dingman 1984). The value selected under any given conditions will affect the computed τ_c and predicted local bed transport rates. However, given the uncertainty in the precise distribution of local shear stresses, and given the variation in substrate size among individual riffles in a reach, the computed reach-average mobility ratio (eq. 3) is not intended, nor is it designed, to produce meaningful estimates of local gravel transport rates. The mobility ratio is used here only as an empirical predictor, useful for explaining observed variations in levels of spawning bed disturbances across a range of reach characteristics and flood levels.

Results

The main hydraulic variables reconstructed for each flood

Fig. 3. Definition diagram illustrating the distinction between high- and low-velocity sides of the thalweg at riffles and potential spawning zones. See text for further explanation.

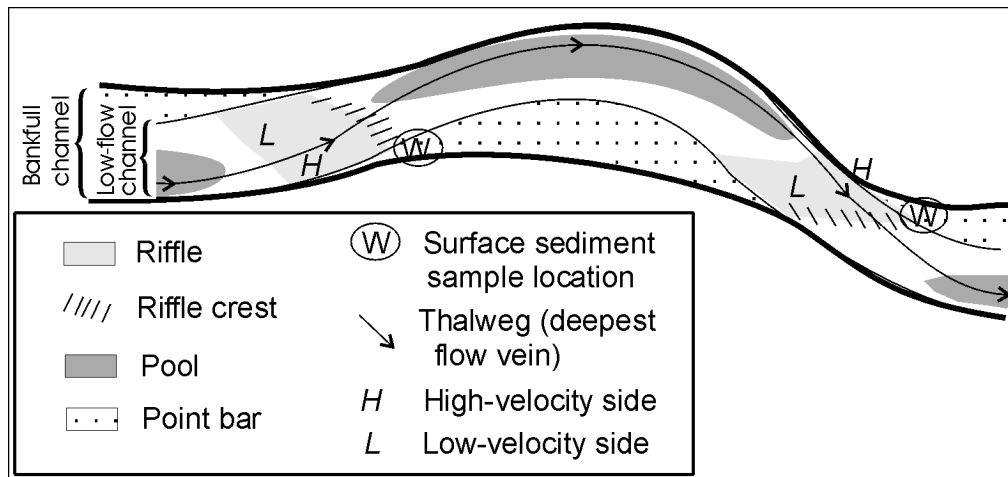


Table 2. Hydraulic and sediment transport characteristics of the study floods in each reach.

Flood event	Reach	Peak discharge ($\text{m}^3 \cdot \text{s}^{-1}$)	R (m)	$\bar{\omega}$ ($\text{W} \cdot \text{m}^{-2}$)	$\bar{\tau}_o$ (Pa)	$\bar{\tau}_c$ (Pa)	Mobility ratio
May 16, 1996	B	140	1.5	104	41	29.0	1.4
	C		1.5	61	38	45.5	0.8
July 20, 1996	B	250	2.0	178	54	29.0	1.9
	C		2.1	105	53	45.5	1.2
May 25, 1997	A	90	1.2	71	39	42.5	0.9
	B		1.4	54	38	29.0	1.3
	C		1.3	37	33	45.5	0.7

Note: $\bar{\omega}$ is the reach-average unit flow power (Dingman 1984). Other symbols are as described in Materials and methods.

in the three study reaches are presented for a total seven reach–flood combinations (Table 2). Reach A measurements were made only for the May 1997 flood. Mobility ratios vary by a factor of 2.7, from a minimum of 0.7 (May 1997 flood in reach C) to a maximum of 1.9 (July 1996 flood in reach B). Potential spawning zones and corresponding high-velocity, thalweg, and low-velocity subzones were delimited for each reach and flood event (e.g., Fig. 4). Reach A includes three distinct riffle zones, while reaches B and C each include two.

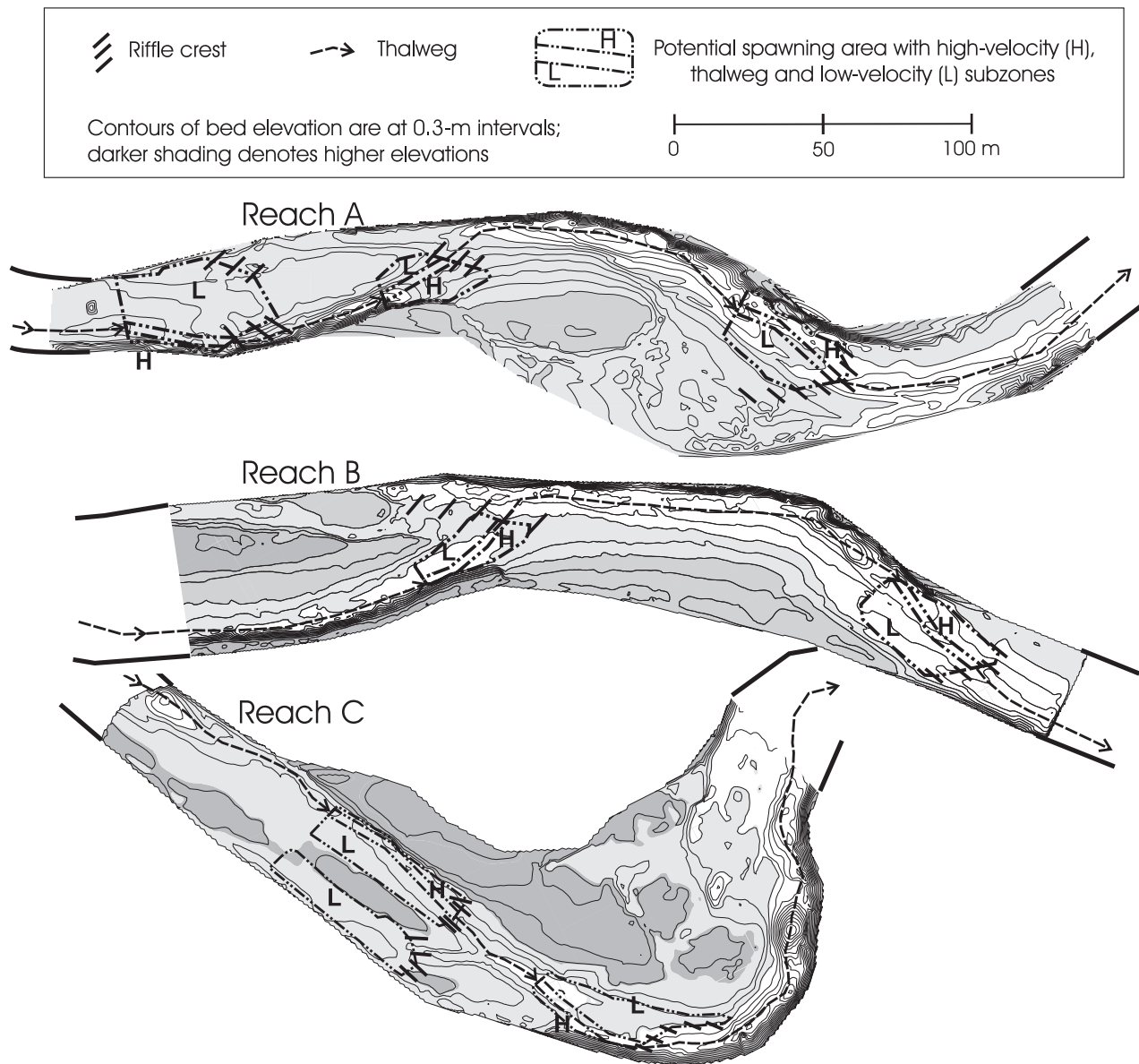
Important scour and fill disturbances were triggered in the study reaches and the corresponding spawning zones by each of the three study flood events (Fig. 5). Over large areas, vertical changes exceeded 0.4 m in amplitude. In the downstream half of reach B, the extreme July 1996 flood produced over 0.8 m of scour near the eroding left bank, extending to the head of the following point bar. Over 0.8 m of fill accompanied the advance of the right bank point bar in that zone.

The statistics on the distribution of scour and fill in the spawning zones and subzones are summarized for the three reaches and flood events (Table 3). During the extreme flood of July 1996, 43% of the entire potential spawning area of reach B underwent over 20 cm of net scour, with 78% of the high-velocity subzones similarly affected. Net fill greater than 20 cm, for the same event, affected 19% of the total spawning area in reach B and 36% of the low-velocity subzones. The 20- and 30-cm scour thresholds were chosen

conservatively, in light of the published egg scour criteria for Atlantic salmon (15 cm depth to top and 30 cm to bottom of egg pockets; DeVries 1997). These two thresholds thus correspond to different intensities of damage to existing egg pockets. Scour exceeding 20 cm would most likely lead to some egg loss at any Atlantic salmon redd site, while essentially complete egg loss would be expected where scour exceeds 30 cm. A symmetrical tabulation to that for scour was also done for fill using the same 20- and 30-cm thresholds (Table 3). However, until studies establish clear criteria for thickness of freshly accreted sediments (i.e., net fill) causing entombment, these results are merely descriptive and cannot be firmly tied to fry mortality. The probable implications of net accretion of more than 30 cm over redd sites will be considered further in the Discussion.

Given the interreach variability in slope, channel geometry, and substrate size, the estimated reach-scale mobility ratios, integrating information on these three types of factors, can be used as empirical predictors of the intensity of scour and fill disturbance for various flood events and reaches (Fig. 6). Regressions are given for the percentages of reach-aggregate spawning areas having undergone more than 20 and 30 cm of scour and fill plotted against mean event mobility ratio in each reach ($N = 7$, corresponding to each reach–event combination listed in Table 2). The plots display clearly that the higher the mobility ratio achieved by the peak flow, the more spatially extensive are the spawning areas deeply disturbed by either scour or fill (all regression

Fig. 4. Bed topography prior to the first study flood in the three study reaches. Potential spawning zones and corresponding hydraulic subzones for that period are shown.



slopes are significantly greater than zero at the $p = 0.05$ level). In the study reaches, the nominal mobility ratio explains between 31 and 58% of the variations in the relative extent of disturbed areas within the potential spawning habitat (i.e., combining all subzones).

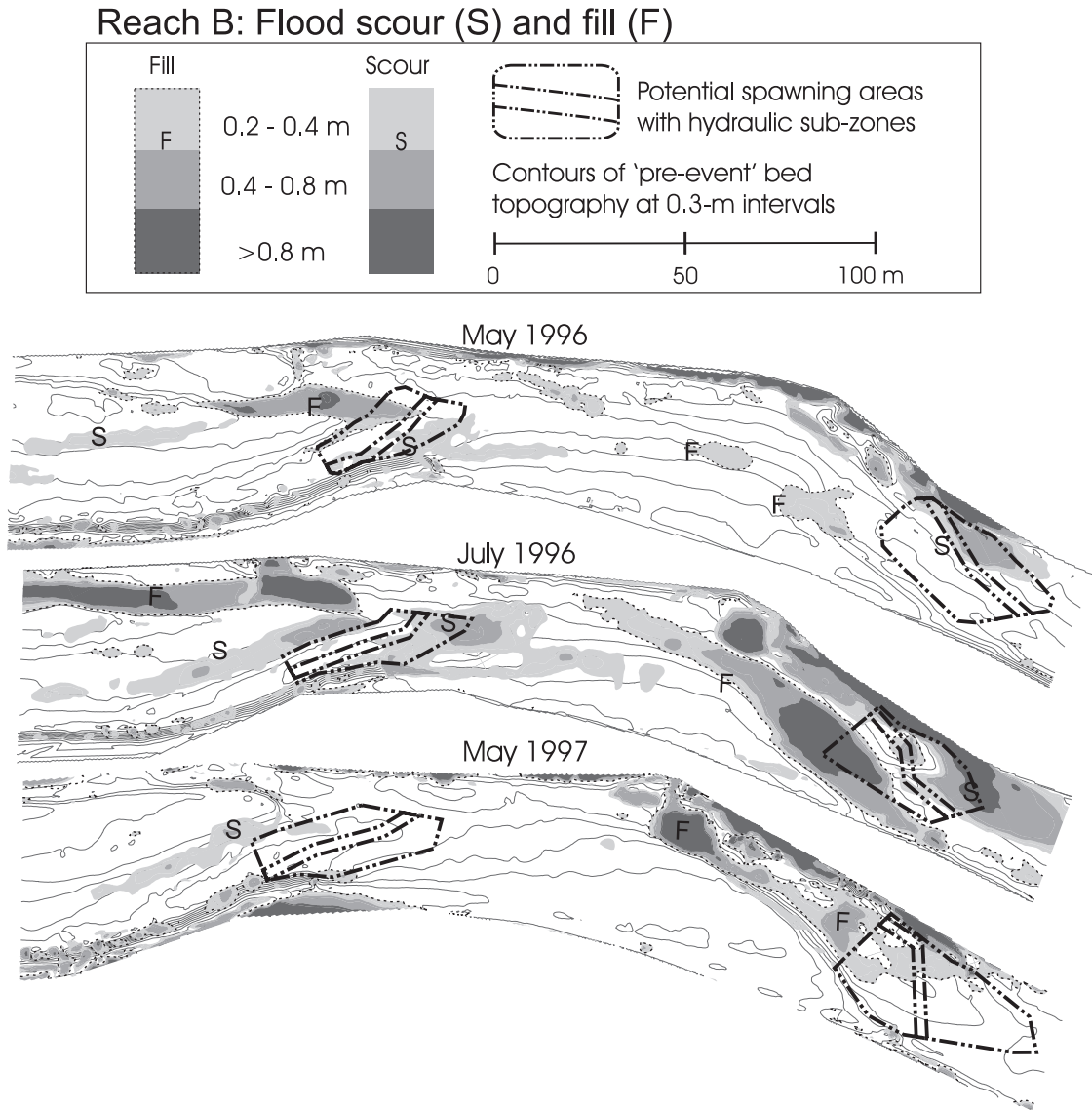
Analysis of the disturbance patterns for each hydraulic subzone separately (Fig. 7) discloses spatial differences among subzones (i.e., high velocity, thalweg, and low velocity) in the susceptibility to scour or fill, particularly for stronger flood events. The relationships for scour exceeding 20- and 30-cm thresholds (Fig. 7) reveal that the percentage of spawning areas undergoing significant scour increases with event mobility ratio in the high-velocity and thalweg subzones (although less rapidly in the latter). In the low-velocity subzones, however, the percent scoured areas (approximately 10%) is essentially invariant with flood mobility

ratio (Fig. 7c). The patterns for the spatial distribution of net fill (Fig. 7) are qualitatively the opposite of those just described for scour. The proportions of areas within the low-velocity subzones undergoing significant fill increase with mobility ratio (Fig. 7c), while in the thalweg and high-velocity zones, they are variable and relatively unresponsive to flood strength. The mobility ratio explains around 75% of the variation in areal extent of scour within high-velocity subzones (Fig. 7a) and 75–79% of the areal extent of fill within low-velocity subzones (Fig. 7c).

Discussion

The residual scatter observed about the regression models is to be expected, given the simplified nature of the reach-average mobility ratio as a predictor of riffle surface distur-

Fig. 5. Maps of net changes to the channel bed (scour or fill) in reach B caused by each of the three flood events. Note that because of the ongoing bed change, the limits of the potential spawning zones were redefined prior to each flood using the criteria described in the text (see Materials and methods).



bance. This scatter mostly reflects the considerable variability of local geomorphic conditions over riffles of various shapes within a natural reach. The overall trends are relatively clear, however, linking mobility ratio to average percentage of spawning area undergoing significant scour or fill.

It is important to recall that the mobility ratio calculated here does not represent a ratio of shear stress at one riffle to the threshold for the entrainment of the bed material at the same location. Instead, a much more easily estimated ratio was employed, relating reach-average shear stress to the nominal stress level necessary to mobilize the average material located on riffles (or point bar heads) within the reach. Therefore, scour that was observed in riffle zones at mobility ratios as low as 0.7–0.8 in our data set reflected that, during floods, shear stresses systematically greater than reach-averaged values tend to affect high-velocity sides of riffles and nearby point bar heads (Yen 1970).

Andrews (1984), Ferguson and Ashworth (1991), and

Milhous (1998) use reach-averaged mobility indices (or related Shield's stress ratios), conceptually similar to the one used here, to compare average sediment mobilization conditions among river reaches. Such reach-scale mobility ratios, although crude, provide a simple method of scaling flow strength by bed material calibre for interreach and interevent comparison. Development of more precise riffle-specific mobilization ratios based on two- or three-dimensional numerical resolutions of local stress distributions may eventually improve predictions of spawning bed evolution, but at a substantial cost in analytical complexity.

Interpreting scour and fill patterns in terms of egg loss probabilities

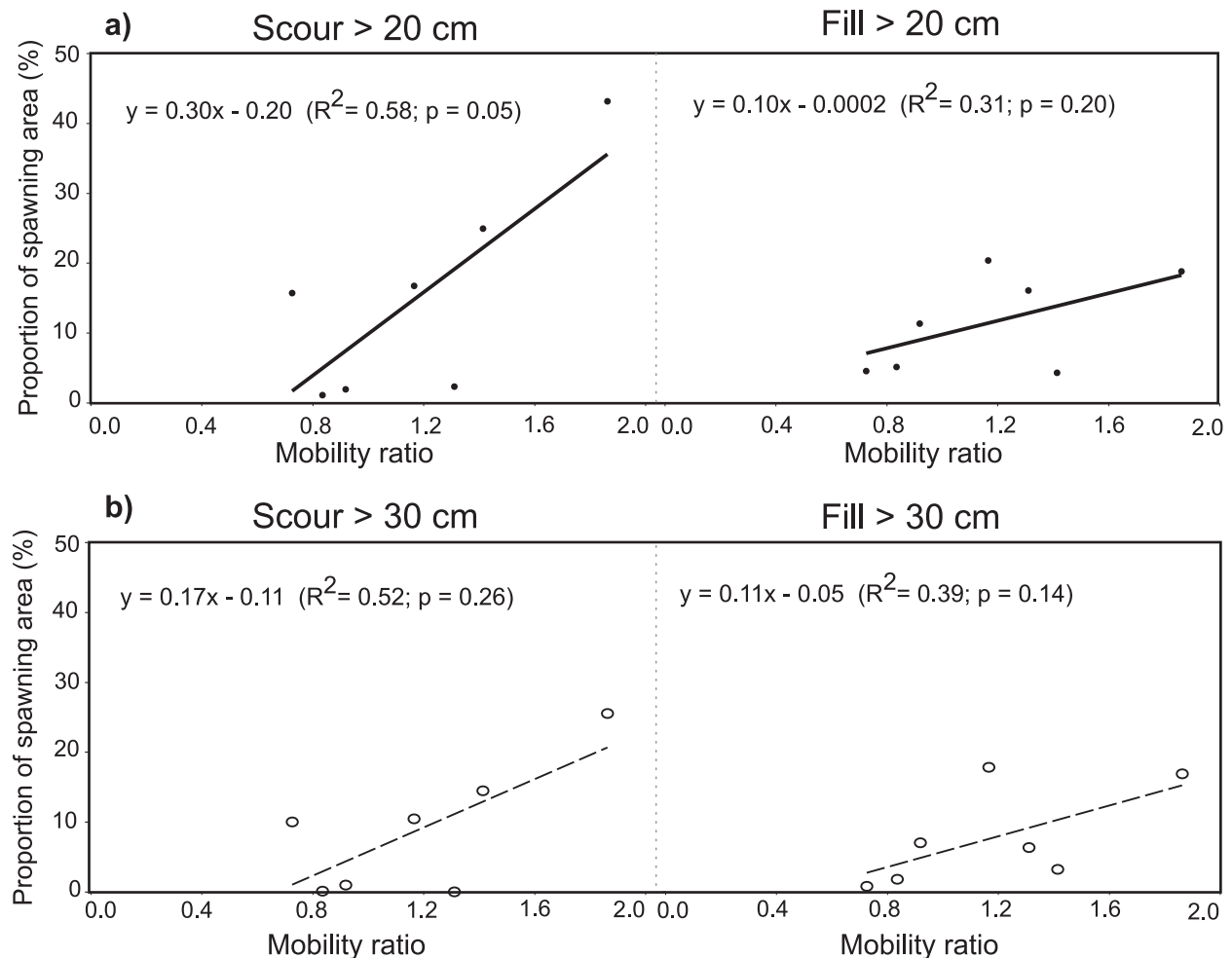
Observed scour patterns can further be interpreted in terms of probabilities of erosion of egg pockets for a flood of a given magnitude occurring during the egg incubation period. In light of the egg pocket scour criteria of DeVries

Table 3. Spawning zone disturbance statistics.

Reach	Event	Percentage of high-velocity subzone		Percentage of thalweg subzone		Percentage of low-velocity subzone		Percentage of total spawning area	
		S	F	S	F	S	F	S	F
A	May 1997	7 (5)	16 (14)	2 (0)	25 (12)	0 (0)	7 (4)	2 (1)	11 (7)
B	May 1996	57 (37)	0 (0)	32 (20)	0 (0)	6 (1)	8 (6)	25 (14)	4 (3)
	July 1996	78 (56)	6 (4)	37 (10)	10 (8)	12 (2)	36 (33)	43 (26)	19 (17)
C	May 1997	0 (0)	13 (5)	0 (0)	11 (6)	6 (0)	21 (8)	2 (0)	16 (6)
	May 1996	8 (1)	2 (0)	1 (0)	9 (5)	0 (0)	5 (2)	1 (0)	5 (2)
	July 1996	29 (26)	53 (48)	13 (8)	53 (47)	16 (9)	11 (9)	17 (10)	20 (18)
	May 1997	1 (0)	5 (3)	0 (0)	3 (1)	24 (15)	5 (0)	16 (10)	5 (1)

Note: Given are the percentages of the total area of spawning zones within each reach that underwent scour (S) or fill (F) exceeding significant thresholds during each flood event. Values are for scour or fill beyond the 20-cm threshold followed by values corresponding to the 30-cm threshold in parentheses.

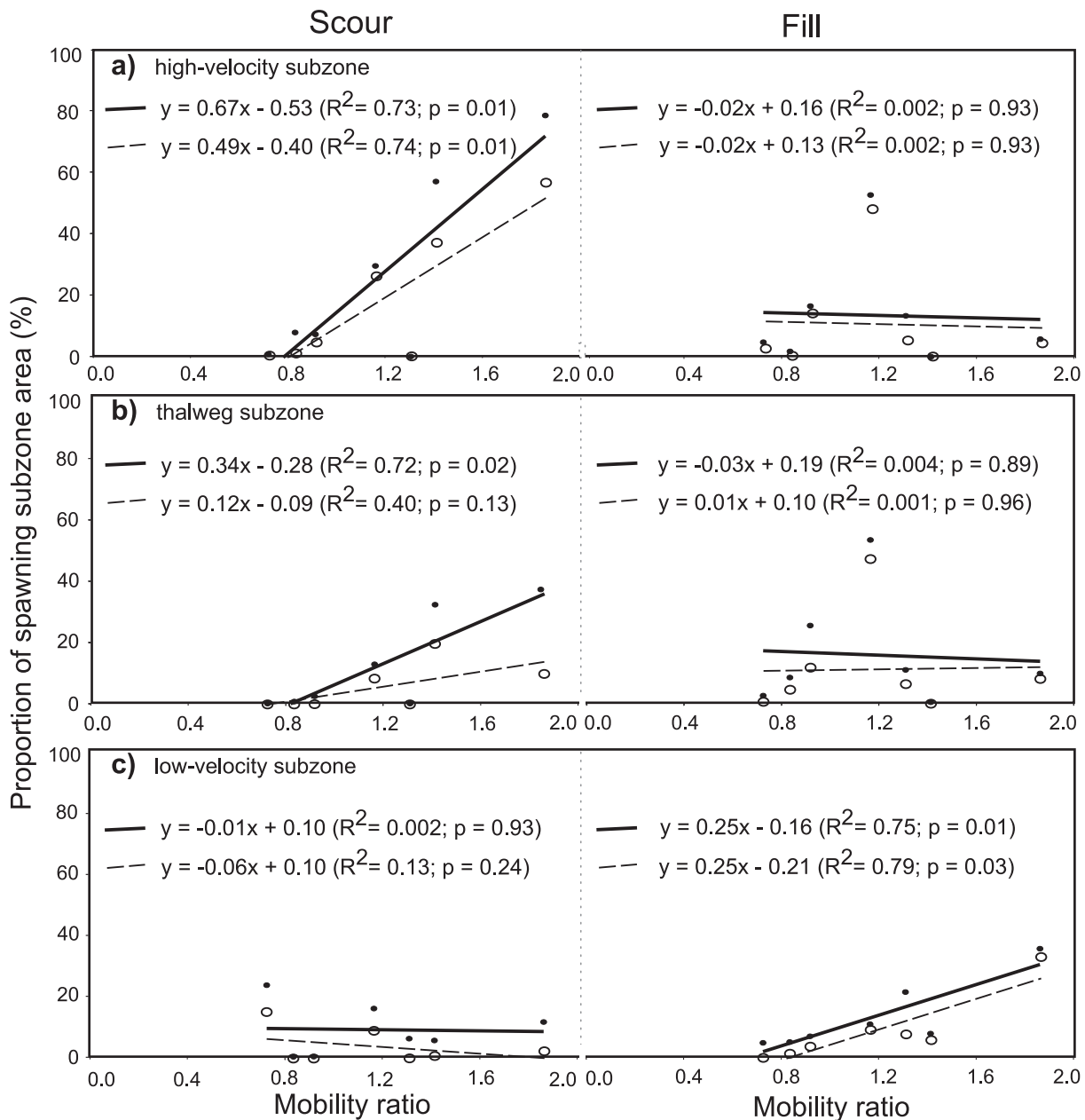
Fig. 6. Regressions of the proportion of the total spawning areas within each reach that was affected (a) by over 20 cm or (b) by over 30 cm of net scour or net fill against the mobility ratio achieved by the flood in the reach; *p* values for the slope terms are given.



(1997), the areal percentages of spawning zones with scour greater than the two thresholds can be interpreted as the probability of partial (scour >20 cm) or total destruction (scour >30 cm) of Atlantic salmon egg pockets, assuming that the pockets are uniformly distributed in the spawning zones of the reach. The trends for scour exceeding 30 cm imply that, during the weakest flood events recorded (mobility ratio = 0.7–0.8), egg pockets randomly distributed in the

spawning zones had approximately a 2–3% probability of being totally eroded. For an extreme flood (e.g., mobility ratio = 1.8) occurring while eggs are incubating, the probability of total egg pocket destruction rises to around 20%, although pockets situated in high-velocity subzones would have a better than even (i.e., >50%) chance of being eroded in such strong events. The effects on Atlantic salmon reproduction of flood fill deposits exceeding 20 or 30 cm over

Fig. 7. Regressions of the proportions of (a) high-velocity, (b) thalweg, and (c) low-velocity spawning area subzones that were affected by net scour or net fill over the 20- and 30-cm thresholds against the mobility ratio achieved by the flood in the reach. The solid circles and solid regression lines are for the 20-cm threshold, and the open circles and broken lines are for the 30-cm threshold; p values for the slope terms are given.



redds are less clear. Precise criteria based on thickness and sediment texture of flood accumulations will need to be developed and tested before our predictions of the extent of spawning zones with over 20 and 30 cm of fill can be interpreted explicitly in terms of probabilities of embryo mortality. However, the common occurrence of a high sand matrix content in flood fills over 30 cm thick, within low-velocity subzones in the study reaches, suggests a real potential for entombment of incubating embryos.

Potential egg scour in the absence of net bed lowering

In certain situations, egg scour might occur during floods in the absence of net bed lowering. During a single flood

event, scour greater than 20–30 cm over a given redd could potentially be followed immediately by comparable fill. As well, egg pocket scour could theoretically ensue simply from deep gravel mobilization over a redd site in association with very intense transport, the bed level remaining essentially constant throughout. In theory, both of these processes could lead to the scouring of egg pockets that would not be detected by our field surveys of net change.

Hydraulic principles and published scour chain surveys suggest, however, that alternating sequences of scour and fill during a single flood wave occur mostly at pool cross sections or at constricted cross sections that are narrower than the reach average and are less common at riffle sites. Fur-

thermore, the detailed analysis of all flood change maps in this study (e.g., Fig. 5) indicated that the nature of bed change (either net scour or net fill) at any point on the riffle was generally predictable from the lateral position of the point, the antecedent channel shape, and the volume of gravel produced upstream by an eroding bank. These patterns suggest that, at least in moderate-energy and -sinuosity streams such as the one in this study, flood-induced disturbance over individual egg pockets will consist predominantly of either scour or fill, depending on lateral position. In very high intensity transport systems (e.g., braided rivers) or during protracted flood events, the occurrence of alternating scour/fill at a given point on a riffle during a single flood may, however, be more common.

Diverse lines of evidence also suggest that the thickness of the layer of gravel in motion at any instant during high flow is less than the depth at which egg pockets of many salmonid species are buried. A range of gravel transport studies (Carling 1987; Wilcock et al. 1996) indicate that the mean thickness of the mobilized gravel layer is in the order of the diameter of the coarsest particles common in the surface substrate (approximated by the D_{84} or D_{90} diameters in the mix), with a maximum thickness of mobilized gravels at any given time that may approach twice the local D_{90} . Many large salmonids appear to excavate redds below this one- to two-particle-deep surface layer. After comparing scour chain and egg pocket depth data at chum salmon (*Onchorhynchus keta*) spawning sites in Washington and Alaska, Montgomery et al. (1996) concluded that the top of egg pockets systematically lay below the surface traction layer of flood-entrained gravel. At Atlantic salmon redds, median sub-armour particle diameter is often in the range of 1.5–3.0 cm, and the D_{90} at the redd surface rarely exceeds 7–8 cm (Peterson 1978; Kondolf and Wolman 1993). Thus, the maximum thickness of entrained bedload layers at high flow may in general be less than 15 cm, the typical depth corresponding to the top of egg pockets (DeVries 1997), implying that egg pocket scour is unlikely in the absence of bed lowering. This evidence suggests that our surveys of net change captured the dominant mode of egg pocket scour in the study reaches. We believe that the egg scour probability estimates presented above, although they may be conservative, are generally realistic for moderate-energy and -sinuosity streams comparable with the study system.

Redd location and spawner fitness: implications

The evidence presented, showing a systematic contrast in susceptibility to scour between high- and low-velocity sides of spawning zones, raises interesting questions concerning evolutionary pressures towards selection by salmonids of precise redd location at riffle sites. During the strongest floods, probabilities of significant scour are much greater in high-velocity subzones (over 50%), where flood shear stresses are particularly strong, compared with spawning sites on the low-velocity side of the riffles (probabilities under 10%). Our data thus indicate that there is a greater risk of loss of progeny if adults spawn on the high-velocity side of the thalweg, should a strong flood occur during the incubation period. Conversely, spawning on the low-velocity side may lead to higher probabilities of entombment due to fill during large floods. Moreover, gravel substrate on the low-

velocity side of riffles often has significantly higher sand content (Payne and Lapointe 1997) due to somewhat weaker flood shear stresses and a helical circulation pattern that accumulates a finer sediment mix on this side of the riffle, closer to the downstream end of the previous point bar. Thus, irrespective of the heightened risk of postflood entombment, sedimentary cues might induce females to avoid spawning in these low-velocity subzones. One can hypothesize that, at least for the kind of simple riffle geometries illustrated in Fig. 3, observed gradients in flood disturbance probabilities across spawning zones and their implications for fitness may entail a selection for spawning behaviour in the deeper thalweg subzone at riffle sites.

In conclusion, fisheries biologists are aware of the possible adverse effects of strong floods on incubating salmonid embryos. The challenge for resource managers, however, is to quantify, even approximately, the effect on subsequent fry emergence of a strong flood in a given spawning reach or to identify stream reaches that are, due to their geomorphic characteristics, more susceptible to geomorphic disturbance and salmonid egg scour. The models presented provide a simple tool for predicting the average degree of riffle substrate disturbance and potential egg loss associated with a flood event in a given reach. The validity of the empirical relationships fitted to the Sainte-Marguerite River should, however, be further tested in gravel bed rivers of very different size and sedimentology. In particular, these empirical models are unlikely to apply to very small boulder-rich streams, where flood shear stresses are largely dissipated on well-anchored boulder structures that shelter pocket-sized gravel-cobble spawning beds from the full force of the flood.

Acknowledgements

This project was funded through the senior author's Natural Sciences and Engineering Research Council of Canada grant and through the support of CIRSA (Centre Interuniversitaire de Recherche sur le Saumon Atlantique) and its main funding partners (Natural Sciences and Engineering Research Council of Canada special collaborative grant (1995–1998), Economic Development Canada, Ministère de l'Environnement et Faune du Québec, and Alcan).

References

- Allen, K.R. 1951. The Horokiwi stream: a study of a trout population. N.Z. Mar. Dep. Fish. Bull. No. 10.
- Allen, J.D. 1995. Stream ecology. Structure and function of running waters. Chapman and Hall, London, U.K.
- Andrews, E.D. 1984. Bed material entrainment and hydraulic geometry of gravel-bed rivers in Colorado. Geol. Soc. Am. Bull. 95: 371–378.
- Beland, K.F., Jordan, R.M., and Meister, A.L. 1982. Water depth and velocity preferences for spawning Atlantic salmon in Maine rivers. N. Am. J. Fish. Manage. 2: 11–13.
- Carling, P.A. 1987. Bed stability in gravel streams, with reference to stream regulation and ecology. In River channels: environment and process. Edited by K.S. Richards. Basil Blackwell, Oxford, U.K. pp. 321–347.
- Chang, H.H. 1992. Fluvial processes in river engineering. Krieger Publishing Co., Malabar, Fla.

- Church, M.A., McLean, D.G., and Wolcott, J.F. 1987. River bed gravel, sampling and analysis. In *Sediment transport in gravel bed rivers*. Edited by C.R. Thorne, J.C. Bathurst, and R.D. Hey. Wiley, Chichester, U.K. pp. 43–88.
- DeVries, P. 1997. Riverine salmonid egg burial depths: review of published data and implications for scour studies. *Can. J. Fish. Aquat. Sci.* **54**: 1685–1698.
- Dingman, S.L. 1984. *Fluvial hydrology*. W.H. Freeman and Company, New York.
- Elwood, J.W., and Waters, T.F. 1969. Effects of floods on food consumption and production rates of a stream brook trout population. *Trans. Am. Fish. Soc.* **98**: 253–262.
- Erman, D.C., Andrews, E.D., and Yoder-Williams, M. 1988. Effects of winter floods on fishes in the Sierra Nevada. *Can. J. Fish. Aquat. Sci.* **45**: 2195–2200.
- Ferguson, R.I., and Ashworth, P. 1991. Slope induced changes in channel character along a gravel bed stream: the Alt-Dubhaig, Scotland. *Earth Surf. Processes Landforms*, **16**: 65–82.
- Gibbons, D.R., and Salo, E.O. 1973. An annotated bibliography of the effects of logging on fish of the western United States and Canada. USDA For. Serv. Gen. Tech. Rep. PNW-10. Fisheries Research Institute, University of Washington, Seattle, Wash.
- Gibson, R.J. 1993. The Atlantic salmon in fresh water: spawning, rearing and production. *Rev. Fish Biol. Fish.* **3**: 39–73.
- Holtby, L.B., and Healy, M.C. 1986. Selection for adult size in female coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* **43**: 1946–1959.
- Kondolf, G.M., and Wilcock, P.R. 1996. The flushing flow problem: defining and evaluating objectives. *Water Resour. Res.* **32**: 2589–2599.
- Kondolf, G.M., and Wolman, M.G. 1993. The sizes of salmonid spawning gravels. *Water Resour. Res.* **29**: 2275–2285.
- Kondolf, G.M., Cada, G.F., Sale, M.J., and Felando, T. 1991. Distribution and stability of potential salmonid spawning gravels in steep boulder-bed streams of the Eastern Sierra Nevada. *Trans. Am. Fish. Soc.* **120**: 177–186.
- Lapointe, M.F., Secretan, Y., Driscoll, S.N., Bergeron, N., and Leclerc, M. 1998. Response of the Ha! Ha! River to the flood of July 1996 in the Saguenay Region of Quebec: large-scale avulsion in a glaciated valley. *Water Resour. Res.* **34**: 2383–2392.
- Lisle, T.E. 1989. Sediment transport and resulting deposition in spawning gravels, north coastal California. *Water Resour. Res.* **25**: 1303–1319.
- Lisle, T.E., and Lewis, J. 1992. Effects of sediment transport on survival of salmonid embryos in a natural stream: a simulation approach. *Can. J. Fish. Aquat. Sci.* **49**: 2337–2344.
- Milhous, R.T. 1998. Modelling of instream flow needs: the link between sediment and aquatic habitat. *Regul. Rivers Res. Manage.* **14**: 79–94.
- Milner, N.J., Scullion, J., Carling, P.A., and Crisp, T. 1981. The effects of discharge on sediment dynamics and consequent effects on invertebrates and salmonids in upland rivers. *Adv. Appl. Biol.* **6**: 152–220.
- Montgomery, D.R., Buffington, J.M., Peterson, N.P., Schuett-Hames, D., and Quinn, T.P. 1996. Stream-bed scour, egg burial depths, and the influence of salmonid spawning on bed surface mobility and embryo survival. *Can. J. Fish. Aquat. Sci.* **53**: 1061–1070.
- Montgomery, D.R., Beamer, E.M., Pess, G.R., and Quinn, T.P. 1999. Channel type and salmonid spawning distribution and abundance. *Can. J. Fish. Aquat. Sci.* **56**: 377–387.
- Payne, B.A., and Lapointe, M.F. 1997. Channel morphology and lateral stability: effects on distribution of spawning and rearing habitat for Atlantic salmon in a wandering cobble-bed river. *Can. J. Fish. Aquat. Sci.* **54**: 2627–2636.
- Pearsons, T.N., Li, H.W., and Lamberti, G.A. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. *Trans. Am. Fish. Soc.* **121**: 427–436.
- Peterson, R.H. 1978. Physical characteristics of Atlantic salmon spawning gravel in some New Brunswick streams. *Fish. Mar. Serv. Tech. Rep.* 785. Fisheries and Oceans Canada, St. Andrews, N.B.
- Resh, V.A., et al. 1988. The role of disturbance in stream ecology. *J. North Am. Benthol. Soc.* **7**: 433–455.
- Scrivener, J.C., and Brownlee, M.J. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. *Can. J. Fish. Aquat. Sci.* **46**: 681–696.
- Seegrist, D.W., and Gard, R. 1972. Effects of floods on trout in Sagehen Creek, California. *Trans. Am. Fish. Soc.* **101**: 478–482.
- Sparks, R.E., and Spink, A. 1998. Disturbance, succession and ecosystem processes in rivers and estuaries: effects of extreme hydrologic events. *Regul. Rivers Res. Manage.* **14**: 155–159.
- Waters, T.F. 1995. *Sediment in streams; sources, biological effects and control*. American Fisheries Society, Bethesda, Md.
- Wilcock, P.R., Kondolf, G.M., Graham Matthews, W.V., and Barta, A.F. 1996. Specification of sediment maintenance flows for a large gravel-bed river. *Water Resour. Res.* **32**: 2911–2921.
- Yen, C.-L. 1970. Bed topography effect on flow in a meander. *J. Hydraulics Division, ASCE*, **96**(HY1): 57–73.
- Ziemer, R.R., Lewis, J., Rice, R.M., and Lisle, T.E. 1991. Modelling the cumulative watershed effects of forest management strategies. *J. Environ. Qual.* **20**: 36–42.