Effects of silt and very fine sand dynamics in Atlantic salmon (*Salmo salar*) redds on embryo hatching success[1]

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Abstract: We conducted a 2-year field experiment examining the survival to hatching of Atlantic salmon (*Salmo salar*) in relation to the seasonal and spatial variations of silt and very fine sand (SVFS; <0.125 mm) content within a large set of artificial redds at two spawning sites of the Sainte-Marguerite River, Quebec, Canada. Each artificial redd consisted of an infiltration cube (30 cm × 30 cm × 20 cm) buried in a morpho-sedimentological unit resembling a salmon redd. One hundred fertilized Atlantic salmon eggs were inserted in a number of infiltration cubes during redd construction. The results indicate no significant relation between survival to hatching in spring and values of the sand index or total percent fine sediment <2 mm in redds at that time. However, the proportion of SVFS in the redds explained 83% of the variation in embryo survival, with a threshold at approximately 0.2% SVFS, above which survival dropped sharply below 50%. Infiltration of these very fine fractions mostly occurred under ice cover, during the low-flow winter period. However, during the spring flood period, infiltration–flushing patterns varied spatially and reflected spatial differences in local intensity of bed-load transport and fine sediment availability.

Résumé : Une expérience de terrain de deux ans nous a permis d'examiner la survie jusqu'à l'éclosion de saumons atlantiques (*Salmo salar*) en fonction des variations saisonnières et spatiales des quantités de limon et de sable très fin (SVFS, <0,125 mm) dans un important réseau de nids artificiels à deux sites de reproduction de la rivière Sainte-Marguerite, Québec, Canada. Chaque nid artificiel consiste en un cube d'infiltration (30 cm × 30 cm × 20 cm) enfoui dans une unité morpho-sédimentologique ressemblant à un nid de saumon. Nous avons introduit cent oeufs fécondés de saumon atlantique dans plusieurs des cubes d'infiltration durant la construction des nids. Nos résultats indiquent qu'il n'y a pas de relation significative entre la survie jusqu'à l'éclosion au printemps et les valeurs de l'indice de sable, ni avec le pourcentage total de sédiments fins <2 mm dans les nids à ce moment. Cependant, la proportion de limon et de SVFS dans les nids explique 83 % de la variation de la survie des embryons, avec un seuil d'environ 0,2 % de SVFS au-dessus duquel la survie tombe rapidement sous 50 %. L'infiltration de ces fractions très fines se fait surtout sous la glace durant la période d'étiage d'hiver. Cependant, durant la période de crue printanière, les patrons d'infiltration et de curage varient d'un endroit à l'autre en fonction des différences spatiales de l'intensité de la charge de fond transportée et de la disponibilité des sédiments fins.

[Traduit par la Rédaction]

Introduction

Numerous laboratory and field studies have shown that the presence of excessive amounts of fine sediment in salmonid spawning gravels is detrimental to the survival of incubating embryos (see reviews of Chapman 1988; Reiser 1999; and Armstrong et al. 2003). However, the nature and severity of this impact depends on the precise size distribution of the infiltrated fine fraction (Acornley and Sear 1999). While coarse sand may form a seal at the surface of the redds, which decreases the emergence success of fry (Beschta and Jackson 1979; Crisp 1993), finer sand infiltrates deeper in the redds where it negatively affects embryo survival by reducing substrate permeability and the intragravel flow necessary for the oxygenation of the eggs (Turnpenny and Williams 1980; Peterson and Metcalfe 1981; Reiser and White 1988).

Although it is well documented that silt (<0.0063 mm) reduces substrate permeability much more than sand (Vukovic and Soro 1987; Rehg et al. 2005), the potential effect of the

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silt fraction on embryo survival has only recently been considered. Lapointe et al. (2004) have shown in laboratory incubations of Atlantic salmon (*Salmo salar*) embryos that a unit weight of silt is on average three times as detrimental to embryo survival than a similar weight of sand and that survival could be seriously reduced at silt levels as low as 1.5%. In a field experiment examining the relationship between survival of Atlantic salmon embryos contained in incubation baskets and the characteristics of fine sediment infiltrated within the baskets during incubation, Julien and Bergeron (2006) showed that survival to pre-eyed and eyed stages of development were most strongly affected by silt, although this size fraction always represented less than 0.8% of the grain size distributions inside the incubation baskets.

However, despite the growing interest concerning the potential negative effect of silt on the quality of spawning gravels (Acornley and Sear 1999; Armstrong et al. 2003), field data documenting the sensitivity of salmonid embryos to this very fine size fraction are still scarce, and very little is known about the spatial and temporal dynamics of silt in redds of gravel bed salmon rivers. Payne and Lapointe (1997) proposed that the lateral position of redds with respect to the high- and low-flow velocity zones found across a riffle has an effect on the probability of sand accumulation in redds. However, because the source zones and transport behaviour of silt may differ qualitatively from those of sand, it is unclear whether such spatial patterns apply to silt infiltration over spawning zones. There is also a lack of information concerning the temporal variations of silt within redds, despite the fact that it has been recognised that the precise timing of fines infiltration may be important in determining reproductive success (Kondolf 2000). For example, Reiser and White (1988) suggested that there could be higher mortality associated with fine sediment accumulation occurring in early embryonic development stages compared with the stages after the circulatory process becomes functional.

Finally, the dynamics of fine sediment infiltration in ice-covered streams is poorly documented. In most Atlantic salmon rivers, a large portion of the embryo incubation period coincides with winter low-flow conditions and the presence of an ice cover. Although occasional warm winter spells can lead to ice breakup, jamming, and local scour, the most common effect of an intact ice cover is to reduce flow velocity through an increase of resistance to flow, thereby decreasing sediment transport capacity over both riffles and pools (Beltaos et al. 1993; Prowse 1994). Thus, the ice cover period should be most suitable for the infiltration of fine sediment into spawning gravels. However, this specific phenomenon has never been studied.

The general aims of this study were to document the seasonal and spatial variations of fine sediment among a large set of artificial Atlantic salmon redds in two sites of an ice-covered river and to quantify the impact of these variations on embryo survival. More specifically, the study intended to (*i*) assess the relative variability in time and space of artificial redd content in medium and coarse sand (0.125–2 mm) compared with very fine sediment fractions (<0.125 mm); (*ii*) determine the relative importance of these size fractions as predictors of salmon embryo survival to hatching; (*iii*) determine the nature of seasonal variations in infiltration of very fine fractions in salmon redds; and (*iv*) investigate to what extent potential silt infiltration is controlled by redd location within the channel.

Materials and methods

Study sites

The study was conducted on the Principale branch of the Sainte-Marguerite River (SMR) in the Saguenay region, Quebec. This gravel–cobble bed river, which supports Atlantic salmon and brook trout (*Salvelinus fontinalis*) populations, drains a Canadian Shield catchment of 1500 km^2 dominated by coniferous forests. A stable ice cover is generally present on the river from mid-November to the end of March. Peak discharge typically occurs between March and mid-May after ice breakup. The bank-full width of the channel is approximately 45 m near the river mouth, where bank-full discharge is approximately 110 m^3·s^{-1}.

Two distinct riffle sections used by Atlantic salmon for spawning were chosen as study sites. The Glass Pool site is located 41.2 km from the mouth and has been the most intensely used spawning riffle on the main branch of the SMR over the past decade. In contrast, the once important Bras des Murailles spawning site, located 49.7 km from the mouth, has been degraded over the 1970s and 1980s by increased sand content in local substrate tied to increasing sediment production from a large-scale, anthropogenic meander rectification upstream (Talbot and Lapointe 2002*a*, 2002*b*). At 21.8 mm, the median bed surface (pavement) particle size (D_{50}) at the Bras des Murailles site is finer than that at Glass Pool (28.7 mm). Mean subpavement sand content of Glass Pool riffle substrate is under 15%, while it exceeds 25% in certain zones within the Bras des Murailles site. The morphology and hydraulics of the Glass Pool site is that of a classic riffle bar set between two oppositely curved river bends with deep pools (Fig. 1*a*). In contrast, the Bras des Murailles site is much less sinuous and a large, abandoned oxbow lake reconnects with the SMR a few metres upstream of the study site (Fig. 1*b*).

Fine sediment infiltration and embryo survival measurements

The general approach was to obtain, for two consecutive incubation periods (2000–2001 and 2001–2002), concurrent field measurements of fine sediment content and Atlantic salmon embryo survival in artificial redds. We wanted to replicate, as closely as possible, the morphology and grain size composition of natural salmon redds, as well as the flow and sediment transport conditions experienced by embryos in natural redds during the incubation period.

Artificial redd construction

Using the method described in Levasseur et al. (2006), each artificial redd consisted of an infiltration cube containing a known amount of fertilized eggs and buried in a morpho-sedimentological unit resembling a salmon redd. The infiltration cube method is a modification of the infiltration bag sampling method described by Lisle and Eads (1991). An infiltration cube was made up of a rectangular (30 cm × 30 cm × 20 cm) steel frame with no walls, which

Fig. 1. Plan view of (*a*) Glass Pool and (*b*) Bras des Murailles study sites with positions of artificial redd patches in year one (white circles) and in year two (solid circles). Arrows indicate the direction of flow at each site.

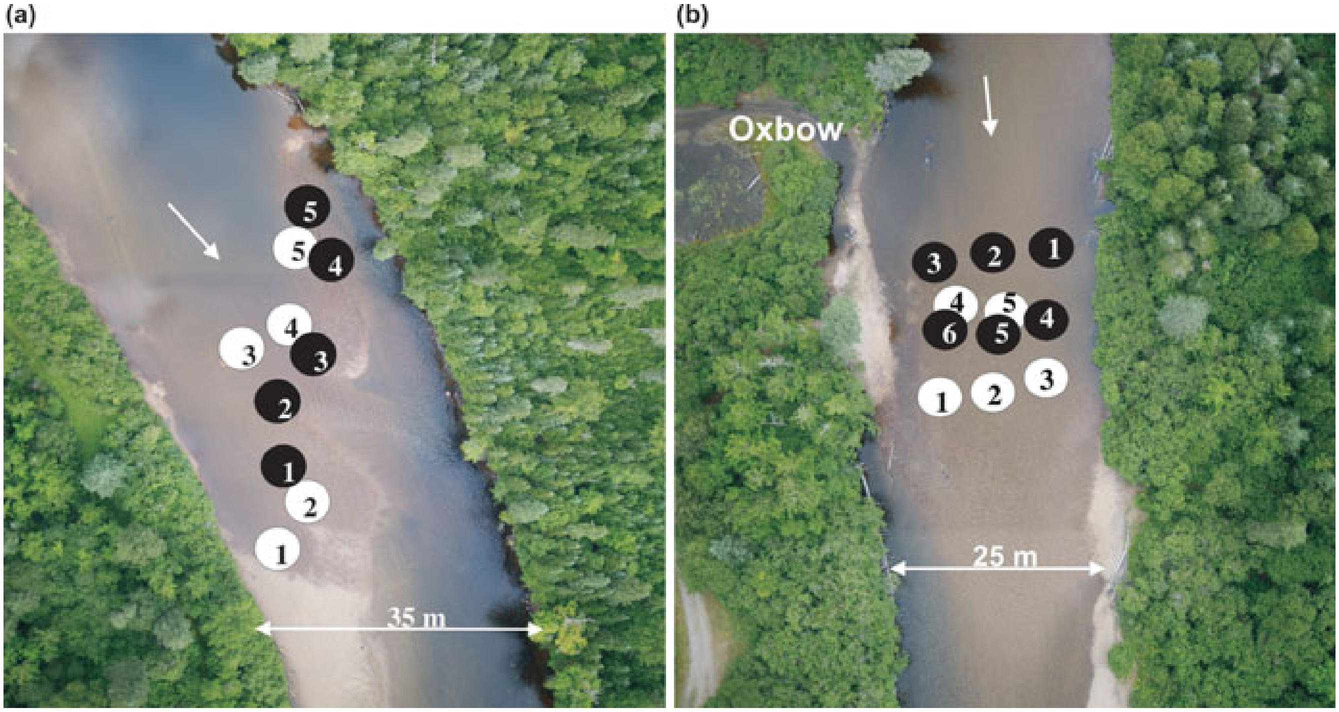
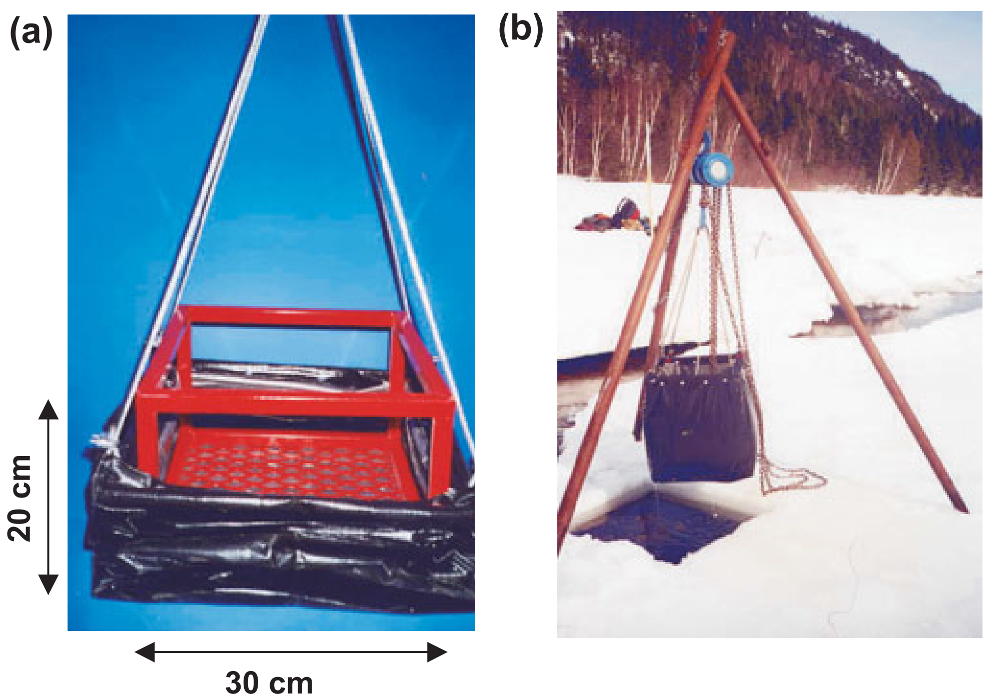


Fig. 2. (*a*) An infiltration cube with the folded bag attached to its base. (*b*) Extraction of an infiltration cube during winter.



had a folded plastic bag attached to its base (Fig. 2*a*). Four wires were affixed to the corners of the bag and projected above the bed surface after installation for later removal. These wires were used to raise the sides of the watertight bag and winch it up along with the substrate contained by the cube using a tripod installed on the river bed or ice surface (Fig. 2*b*). The infiltration cube provided a quick, easy, and robust method to pull relatively large samples (~65 kg), yielding more precise grain size statistics, out of underwater substrate even during tough winter field conditions. The cube design also precluded bias in infiltration rates by both allowing lateral sediment transport within substrate (absence of walls on the cube) and preventing loss of fine particles during retrieval from underwater. Each infiltration cube was buried in the substrate using a procedure aimed at reproducing a natural salmon redd. First, a depression about 30 cm deep and 75 cm wide was dug in the substrate by manually excavating the particles underwater and pushing them downstream of the current. The infiltration cube was then installed in the depression and buried by mobilizing particles from the bed just upstream in a manner similar to a spawning female salmon. This enabled fine sediments to be swept downstream by the flow, thereby constructing a redd composed of coarser lag gravels with fewer fines and larger pore sizes than outside the redd. Upon completion, each artificial redd therefore had the typical grain size and form characteristics of a natural salmon redd with an upstream pit and a downstream tailspill. Each artificial redd was paired with a circular bed-load trap (diameter 15 cm; depth 20 cm) buried flush with the bed surface. Each trap, initially installed empty with a cover, was activated by removing its cover, thereby enabling bed-load sampling for a predetermined period of time.

Spatial and temporal sampling design

Because current field techniques do not allow accurate determination of fine sediment content within redds in a way that is nondestructive of redd structure and function, it is currently not possible to directly determine the temporal variation of fine sediment content of a single redd through repeated observations of that redd. For this reason, we devised an approach that assesses temporal variation in redd fine sediment content at the local scale by monitoring a set of replicate artificial redds laid out within a relatively small (~4 m diameter), homogenous area of spawning habitat, called a patch. Within each patch, a group of five to six artificial redds were installed, in similar water depth, flow velocity, and bed substrate conditions, immediately following the spawning period of Atlantic salmon (late October in SMR). Infiltration cubes and bed-load traps within each patch were then extracted sequentially for grain size analysis at five periods during the incubation period. At the time of installation in October, one infiltration cube per patch was removed immediately following installation to quantify the initial proportion of fines in the artificial redds of each patch at time zero. At the same time, the sediment trap associated with the next infiltration cube to be extracted was activated. Then, an infiltration cube and its associated bed-load trap were removed from each patch at each of the four other sampling periods: in December during low-flow winter conditions, just prior to ice formation; in January following the formation of a solid ice cover; in late March prior to ice breakup; and in late May or June after the spring flood. We used the difference in fines content between successively extracted cubes within the same patch as our best estimate of the temporal change in fines content over the period at this patch.

To capture the spatial variation of fine sediment infiltration or flushing at each site, five to six of these patches were laid out to range both laterally across and along each spawning area (Figs. 1*a*, 1*b*). All patches were carefully delimited so that they were small enough to be homogenous in terms of water depth, flow velocity, and substrate size. The sampling design thus included two sites over 2 years, with five to six patches per site each containing five to six cubes (N = 116 cubes over 2 years). Note that newly installed cubes (in October) did not have uniform sedimentology across patches or sites. They rather collectively represented a large sample of fresh spawning redds incorporating natural variations due to variable spawning conditions along the river.

Grain size analysis

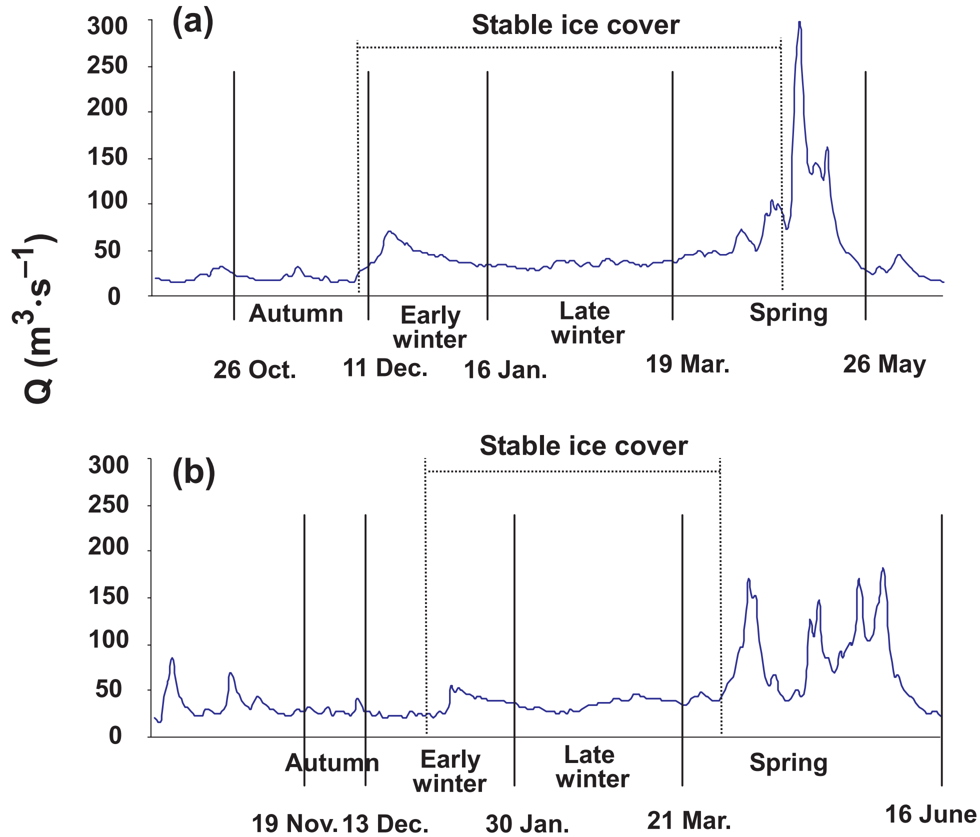
The coarser part of the sample recovered from each infiltration cube (particle sizes >16 mm) was wet-sieved and weighed in the field, and a well-mixed subsample of the <16 mm fraction was taken in the laboratory for a standard dry sieve analysis at 1 phi intervals (phi = $-\log_2 D$). This study focused on the fine sediment content of each cube (as a weight percentage of the entire sample) for four grain size fractions: medium–coarse sand (MCS, 0.250–2 mm), fine sand (FS, 0.125–0.250 mm), very fine sand (VFS, 0.063–0.125 mm), and silts (SILTS, <0.063 mm).

Embryo survival

Embryo survival was studied by inserting, at artificial redd construction, 100 fertilized Atlantic salmon eggs in some of the infiltration cubes of each patch. In 2000–2001, one of the five cubes installed contained eggs, while in 2001–2002, two of the six cubes installed contained eggs. The eggs and milt were obtained from the Tadoussac hatchery. The eggs were of the same genetic stock as the Atlantic salmon adults native to the SMR. The eggs were fertilized and water-hardened at the hatchery (located ~25 km away from the river) and then transported to the field in cool, water-filled jars. The eggs were kept at the same temperature as the stream water to avoid thermal shock during artificial redd construction and infiltration cube installation. Within an artificial redd, the eggs were positioned ~20–25 cm below the surface, which is the typical range of burial depths for Atlantic salmon eggs (DeVries 1997). All artificial redds were completed and eggs buried in the substrate within 24 h of fertilization.

The infiltration cubes containing embryos were extracted from the bed when it was determined that the embryos had hatched but prior to emergence to prevent the possible loss of emerging fry. For each year, the hatching period was estimated from hourly temperature data records obtained from temperature data loggers buried within the substrate of each site. At the beginning of May of each year, water temperature data were retrieved from the loggers and used to estimate the progression in the development and hatching dates of the embryos from the degree-day curve for Atlantic salmon published by Ministère Agriculture, Pêcheries et Alimentation Québec (MAPAQ 1996). For both years, it was estimated that by the third week of May, a large proportion of the surviving eggs should have hatched while most of the dead eggs would have not had the time to decompose, thereby allowing the evaluation of mortality. Immediately following extraction, these cubes were carefully inspected using rinsing water to recover and count the number of dead and live embryos. Survival to hatching in an artificial redd was determined by calculating the ratio of recovered hatched fry (dead or alive) to the total number of recovered embryos (fry + dead eggs), as opposed to the number initially buried. While we acknowledge the possibility of overestimating sur-

Fig. 3. Sampling periods and discharge (Q) variations during the study periods of (a) year one (2000–2001) and (b) year two (2001–2002) as measured at the stream gauge number 62803 of the Ministère de l'Environnement du Québec located on the downstream portion of the Nord-Est branch of the Sainte-Marguerite River near its confluence with the Principale branch.



vival as noted by Pauwels and Haines (1994), we prefer this method when the cause of egg disappearance is unknown. Once all embryos and fry from a cube were recovered and counted, the substrate was analyzed for fine sediment content using the procedure described above.

Results

Infiltration cube sampling periods and recovery success

The infiltration cube sampling periods varied slightly between years because of environmental factors. In year one, because of early ice formation, the infiltration cubes that we planned to retrieve prior to ice cover formation were instead recovered just after a stable ice cover had formed (Fig. 3a). In year two, persistent high water levels in the spring prevented the timely recovery of the infiltration cubes containing the hatched embryos (Fig. 3b). These cubes were thus recovered 16 June in year two compared with 26 May in year one.

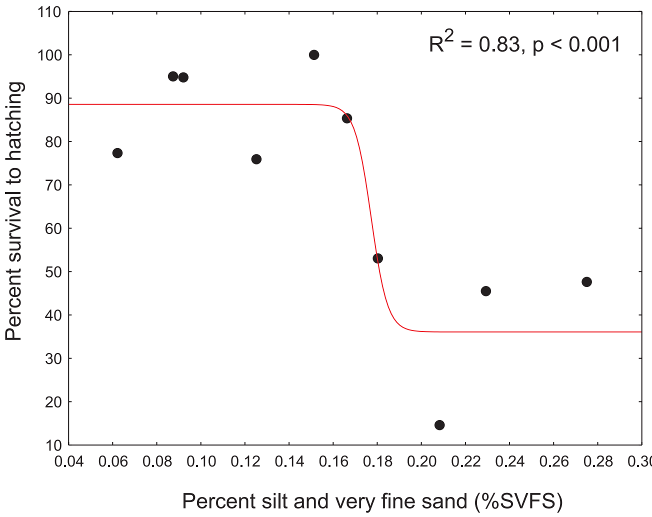
Of the 116 infiltration cubes that were installed in both years combined, only four were not recovered, representing an overall recovery success of 97%. In year one of the study (2000–2001), three cubes could not be recovered as planned because they were frozen in the riverbed. In year two (2001–2002), one cube was washed away from the bed during the spring flood. The recovery success of the bed-load traps was also very good. None of the 40 traps were lost in year one, while 4 of the 55 traps of year two were lost, all of them being scoured away from the Glass Pool site during the spring flood. However, many bed-load traps completely filled with sediments during both spring floods, despite the fact that larger traps were used for year two. Therefore, bed-load transport rates could not be reliably estimated, and it was decided to use the size of the largest particle found in each trap as an index of local flow competence.

The embryo recovery success was good in year one (64.8%) but poor in year two (38.7%). It is likely that the protracted spring flood of year two incited some of the pre-emerging fry to leave the redds to avoid being crushed by pavement mobilization or that they were simply scoured away. Because of the poor embryo recovery success of year two, only data from year one were considered in the remaining embryo survival analysis. However, data from both years were used in the analysis of the fine sediment content dynamics of the artificial redds.

Effect of fine sediment on survival to hatching

Large variations in percent survival to hatching were observed across the artificial redds (mean 69.0%, range 14.8%–100%). However, these variations failed to correlate significantly ($p > 0.05$) with simple extant metrics of overall fine contents, such as the Peterson and Metcalfe's (1981) sand index (SI) and the total percent fine sediment <2 mm, despite the existence of large variations in sand content (percentage <2 mm) across all redds sampled (mean 13.2%, range 0.4%–27%). We therefore pursued the analysis by

Fig. 4. Relation between the percentage of silt and very fine sand in redds (%SVFS) and the percent survival to hatching of Atlantic salmon (*Salmo salar*) embryos. % survival = 36.09 + 54.49/{1 + exp[(%SVFS − 0.17728)/0.0037]}.



subdividing the overall fine sediment <2 mm into four fractions: percent MCS, percent FS, percent VFS, and percent SILTS. While MCS did not correlate significantly ($p > 0.05$) with survival, FS, VFS, and SILTS all showed significant ($p < 0.05$) negative correlations with percent survival to hatching, with respective R^2 values of 0.3, 0.6, and 0.5. However, because the two finest fractions (VFS and SILTS) were strongly intercorrelated in our data set ($R^2 = 0.9$, $p < 0.0001$), their independent effects on survival could not be separated by a multiple regression analysis. This compelled us to examine the dependency of embryo survival on the percentage of VFS and SILTS combined, a fraction (<0.125 mm) we called silt and very fine sand (SVFS). There was a strong significant relation ($R^2 = 0.83$, $p < 0.001$) between these two variables (Fig. 4). This relationship, which appears to have a negative logistic form, showed a threshold at 0.2% of SVFS over which survival drops sharply below 50%. Multiple regression analysis demonstrated that once SVFS was included in the model, FS did not add significantly ($p < 0.05$) to the prediction of embryo survival to hatching.

To determine the impact of fine sediment content in redds at various sampling moments on embryo survival to hatching, we regressed hatching success data at incubation cubes of a patch against fines content from cubes that had been extracted at previous sampling moments in the same patch (i.e., autumn, early and late winter). This analysis yielded no major relationships between embryo survival and variations of any of the fine fractions over these earlier periods on the same patch.

Fine sediment dynamics

Statistics describing the relative variability of the different fine sediment fractions within the entire artificial redd data set (across all sites, seasons, and years) show a considerable range of fines content (Table 1). Although the absolute variability is greater for the coarser fractions than for the finer ones (e.g., standard deviation (SD) = 5.2 for MCS and 0.13 for SILTS), the finest fractions are relatively more variable (e.g., coefficient of variation (CV) = 40 for MCS and 85 for SILTS). This suggests that the processes driving the dynamics of the coarser and finer fractions in redds differ, and to the extent that the finer fractions are here shown to be biologically significant, the factors controlling this variability in space and time need to be understood.

Table 1. Statistics of the relative variability (standard deviation (SD) and coefficient of variation (CV)) in the different fine sediment fractions within the entire data set (all cubes, all sites, all periods, and all years).

	Sediment fraction (%)				
Statistic	<2 mm	MCS	FS	VFS	SILTS
SD	5.3	5.2	0.08	0.32	0.13
Mean	13.2	12.3	0.11	0.70	0.16
CV	40	42	77	46	85
Minimum	0.4	0.4	0.02	0.12	0.04
Maximum	27	26	0.5	1.6	0.72

Note: MCS, medium–coarse sand (0.250–2 mm); FS, fine sand (0.125–0.250 mm); VFS, very fine sand (0.063–0.125 mm); SILTS, silts (<0.063 mm).

Seasonal patterns in SVFS content

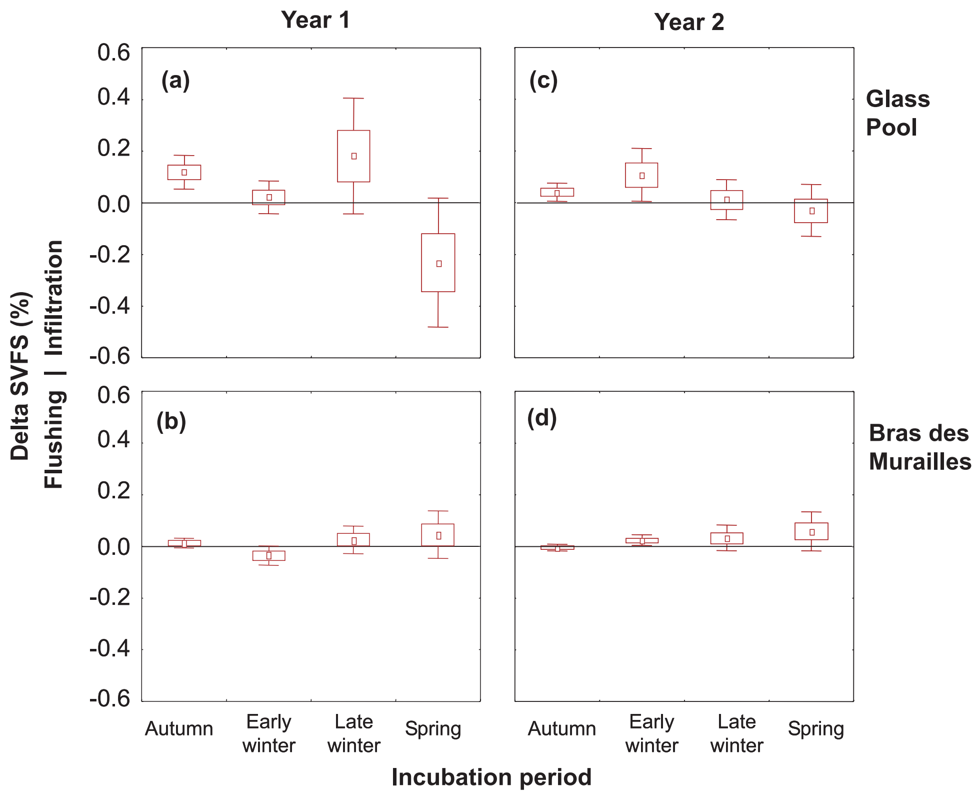
The seasonal evolution of SVFS, the fraction that best explained embryo survival data, showed relatively coherent temporal patterns of infiltration and flushing in the artificial redds (Fig. 5). For both sites and years, there was a systematic tendency for SVFS content in redds to increase during the autumn, early winter, and late winter periods. However, during the spring period, flushing of SVFS dominated in most patches of the Glass Pool site in both years (Figs. 5*a*, 5*c*), whereas infiltration dominated both years in most patches of the Bras des Murailles site (Figs. 5*b*, 5*d*). Although the measured increase or decrease in SVFS content for each period were small, they were well above detection level, since a 0.1% variation in SVFS content represents a change of 60 g in that fraction over a typical 60 kg infiltration cube sample.

Overall, the SVFS content in redds at the Glass Pool site was more variable than that at the Bras des Murailles site, both seasonally as expressed by large variations of the mean between sampling periods and spatially as indicated by larger SD values for any given period (Fig. 5). In some occasions, for example at the Bras des Murailles site during the late winter period (Figs. 5*b*, 5*d*), both infiltration and flushing of SVFS occurred at different redds patches within the same sampling period, possibly reflecting spatial variations in hydraulic and sedimentary conditions dependent on lateral patch location on the site.

Seasonal pattern in bed-load transport competence

An analysis of the seasonal pattern in bed-load transport competence, as measured by the size of the largest particle (D_{max}) found in each bed-load trap, revealed an overall trend of low-intensity bed-load transport during the autumn, early winter, and late winter sampling periods, at both sites and for both sampling years (Fig. 6). During these periods, D_{max}

Fig. 5. Temporal variations of infiltration (positive) and flushing (negative) of silt and very fine sand (SVFS) during the incubation period for both sites and sampling years. Each boxplot shows the mean, standard error, and standard deviation of the difference of SVFS content between two sampling periods for all homogenous patches of a study site.



values were generally much smaller than the D_{50} values of the patches of each site, thereby indicating phase one bed-load transport events. However, in year two, larger flow events caused by strong fall storms (Fig. 3*b*) mobilized particles coarser than the D_{50} at some patches of both sites (Figs. 6*c*, 6*d*). For both sites and years, the spring period was characterized by extreme hydraulic events (Figs. 6*a*, 6*b*) for which D_{max} was greater than D_{50}, indicating phase two bed-load transport events characterized by bed pavement mobilization.

Relation between SVFS and bed-load competence

A comparison of the seasonal patterns of SVFS content in redds (Fig. 5) and of bed-load transport competence (Fig. 6) indicates that periods with low transport competence (autumn, early winter, and late winter) tended to correspond to periods of SVFS infiltration at most redd patches. At the Bras des Murailles site, slight flushing of SVFS was measured during the early winter period of year one and during the autumn period of year two. However, both periods were characterized by bed-load transport events with some D_{max} values exceeding the D_{50} of the bed surface pavement. For both sites and years, the spring period was characterized by very competent flow events (Fig. 3), but the effect on SVFS content in redds differed markedly between sites. While these events were associated with SVFS flushing at the Glass Pool site (Figs. 5*a*, 5*c*), they were related to SVFS infiltration at the Bras des Murailles site (Figs. 5*b*, 5*d*). These results suggest the potential importance of the geomorphic characteristics of the sites and redd location on the relation between bed-load competence and SVFS content in redds.

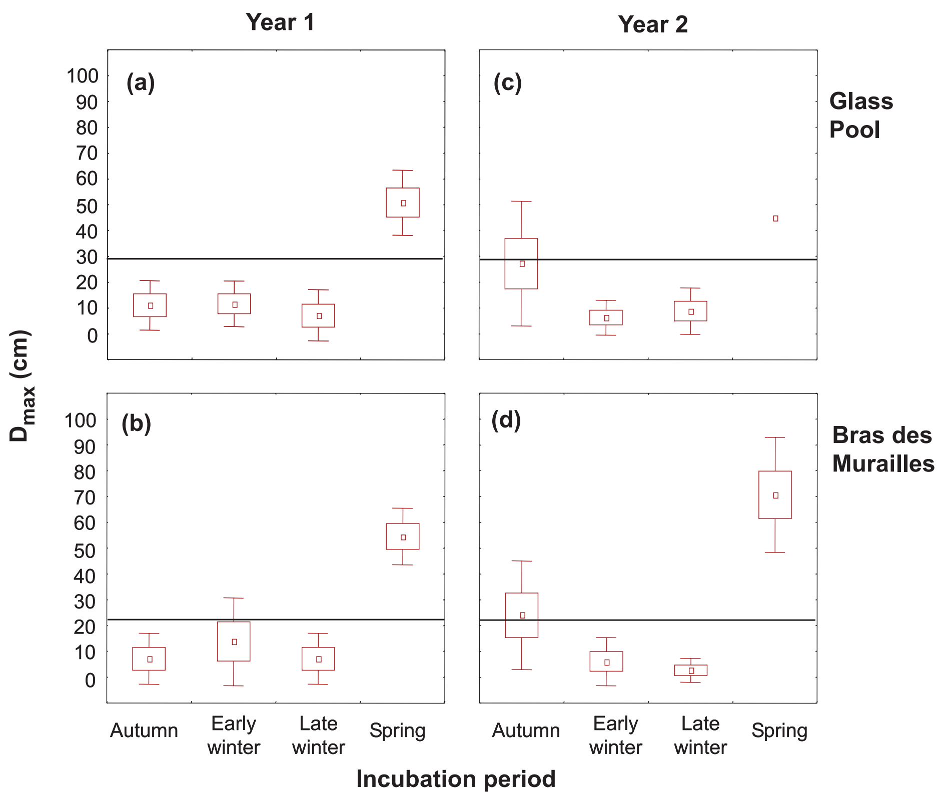
Spatial patterns

A comparison of the temporal patterns of SVFS content between patches of a site for a given year reveals coherent spatial trends between neighbouring patches showing similar geomorphic conditions (Fig. 7). These differences are not readily apparent during the autumn, early winter, and late winter periods because these periods are characterized by a general tendency for SFVS to increase gradually at most redd patches. However, during the spring period, clear groups of patches showing similar SVFS dynamics can be determined.

At the Glass Pool site in year one, patches 4 and 5 (Fig. 7*a*), located on the left side of the channel (Fig. 1*a*), show clear reductions of SVFS over the spring period. In year two, a similar reduction of SVFS occurs at patch 5 (Fig. 7*b*), also located on the left side of the channel (Fig. 1*a*). At the Glass Pool site, the left side of the channel corresponds to the outside of a bend where the flow is deeper and velocities are higher during large flow events.

The situation is more complex at the Bras des Murailles site, where fine sediment accumulates during flood recession at a lateral bar located at the exit of an oxbow along the right bank (Fig. 1*b*). Patch proximity to this fine sand and mud-rich bar seem to control patterns of fines infiltration or flushing in the spring at this site. Fines increased strongly over the spring period at patches 1, 4, and 5 in year one

Fig. 6. Temporal variations of bed-load competence during the studied periods. Each boxplot shows the mean, standard error, and standard deviation of the largest particle size (D_{max}) found in each bed-load trap opened at the beginning and extracted at the end of each sampling period for each site. The horizontal line corresponds to the value of the median bed surface particle size (D_{50}) at the site. This line is useful as an approximate grain size reference to distinguish phase 1 bed-load events (where only fine particles are moving) from phase 2 events (where the bed surface pavement is mobilized). Data points above the line represent more powerful sediment transport events allowing extensive bed substrate mobilization (D_{max} bed load > D_{50} bed), while the lower part is linked with low bed-load transport events not competent enough to allow pavement mobilization (D_{max} bed load < D_{50} bed).



(Fig. 7*c*) and at patches 2 and 6 in year two (Fig. 7*d*), which are all located near the oxbow exit and side bar. Fines decreased at patches 2 and 3 in year one and at patch 4 in year two, which are located in the deeper, more central part of the channel or closer to the left bank, away from this fine sediment accumulation area. These patterns demonstrate the importance of transverse redd location within the study site as a control on the temporal variations of fine sediment present in the substrate during the high-flow period.

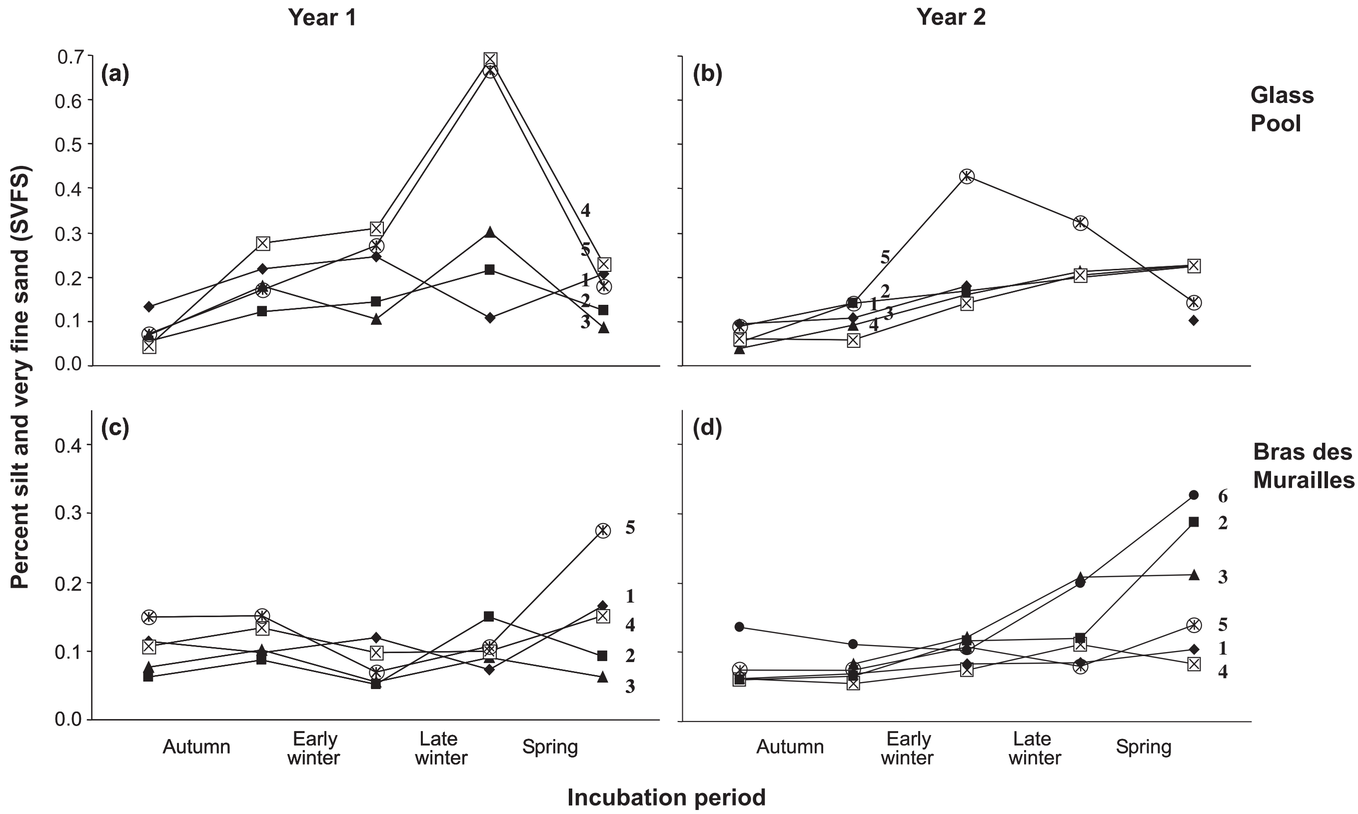
Discussion

Effects of SVFS content on embryo survival

Our results show the important effect on embryo survival of natural variations of even small amounts of SVFS content in Atlantic salmon redds. Although large variations of the traditional SI and sand content spawning substrate quality criterion were present in our data set of the SMR, no significant effect of these variables on survival to hatching was found. However, the proportion of SVFS in the redds explained 83% of the variation in embryo survival to hatching, with a threshold at approximately 0.2% SVFS, above which survival dropped sharply below 50%. This threshold value is broadly consistent with the 0.3%–0.4% silt content value below which survival of Atlantic salmon embryos dropped below 50% in a field experiment by Julien and Bergeron (2006), but it is much smaller than the 1.5% silt content level above which survival to emergence of Atlantic salmon embryos was found to be seriously reduced in a laboratory experiment by Lapointe et al. (2004). This difference is probably due to the difficulty of replicating, in the laboratory, the low values of subsurface hydraulic gradients responsible for driving the flow across the redds in the field. The laboratory study of Lapointe et al. (2004) indeed revealed that the impact of SILTS was stronger at lower hydraulic gradients.

The recent findings of Greig et al. (2005) may provide an explanation for our results by showing an important effect on embryo survival of very small amounts of SVFS. In their laboratory experiment on oxygen consumption by Atlantic salmon embryos approaching hatching, they found that clay-sized sediment created a thin, low permeable seal around the eggs, which restricted the availability of oxygen to the incubating embryos. They also found that clay-sized particles could physically block the micropore canals of the egg membrane, thereby restricting oxygen uptake. The results of Greig et al. (2005) provide a mechanism by which, in our study, very small amounts of SVFS particles may have reduced oxygen availability to the incubating eggs and reduced survival to hatching. In view of these recent findings,

Fig. 7. Temporal variations of silt and very fine sand (SVFS) content at each sampling period for both sites and sampling years. Each point of a line represents the SVFS content of an infiltration cube extracted from the same patch (1–6) at a distinct sampling moment throughout the incubation period. An increase corresponds to infiltration, while a decrease corresponds to flushing of SVFS. Note that scales are different between sites.



it is suggested that sediment fractions finer than those contained in the SI spawning substrate quality criteria need to be taken into account as a sedimentary control in the incubating environment.

Seasonal and spatial dynamics of SVFS

The infiltration cube method employed in this study prevented the loss of SVFS particles during retrieval of the substrate sample from underwater, which allowed the detection of small variations of this fine fraction. Although the proportion of SVFS rarely exceeded 1% of the redd, it was shown to vary seasonally and spatially and to play an important role in determining embryo survival to hatching.

We assumed that within-patch comparisons of cubes extracted at successive times mostly captured temporal variations due to the infiltration or flushing of fine sediment at that patch, with a small random noise effect due to minor spatial variations within the 4 m diameter patch. The validity of this last assumption was confirmed by the coherence of the temporal trends of fine sediment content between neighbouring patches of each study site.

At the two studied spawning sites, the overall pattern of variation of the biologically significant SVFS fraction was of a gradual accumulation at most patches during low flows, especially during the ice-covered winter period. This result supports the suggestion that reduced sediment transport capacity under winter ice cover favours the infiltration of fine sediment into spawning gravels. During the high-flow, pavement-mobilizing events that characterize the spring periods, local controls on the supply of SVFS, as well as flow patterns typical of asymmetric meander cross-sections, appeared to determine the flushing or infiltration of SVFS within the redds. At the Glass Pool site, we observed a pattern of flushing of fines in the redds located towards the outside of the bend and of infiltration in the redds located on the inner side of the bend, near the point bar. This result is consistent with the differential pattern of flushing and infiltration of sand previously observed by Payne and Lapointe (1997) on the high- and low-velocity zones of spawning riffles, respectively. At the Bras des Murailles site, an anomalous oxbow connection just upstream from the spawning site modified these simple spatial patterns by favouring, during flood recession, the accumulation of silt and fine sand on the lateral bar located at the exit of the oxbow. Despite the occurrence of pavement-mobilizing spring flows at this site, SVFS accumulated over that period in most redds located near the oxbow exit and lateral bar, whereas it decreased in redds located in the deeper, more central part of the channel, away from this fine sediment accumulation area. These results suggest that geomorphic controls on local supply and infiltration potential of SVFS may be important factors to be considered for spawning habitat management and conservation in Atlantic salmon rivers.

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