

Primary Research Paper

## Effect of fine sediment infiltration during the incubation period on Atlantic salmon (*Salmo salar*) embryo survival

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### Abstract

The existence of a negative relationship between fine sediment infiltration during the incubation period and salmonid embryo survival has often been discussed in the literature. However, few studies have specifically addressed this relationship in the field. We conducted a field experiment to examine the relationship between survival of Atlantic salmon (*Salmo salar*) embryos contained in incubation baskets and the patterns of fine sediment infiltration into the baskets during the incubation period. The results indicate that survival to pre-eyed (STPE), eyed (STE) and hatched (STH) stages of development were all negatively correlated with the percentage of fine sediment entering the baskets. STPE and STE were most strongly affected by silts and clays (<0.063 mm) although this size class represented only a small fraction of the grain size distribution inside the incubation baskets (0.03–0.41%). STH was most strongly correlated with the infiltration of medium sand (0.25–0.50 mm) material. On average, 66% of the implanted embryos survived to the pre-eyed stage of development compared to 63% for the eyed and 48% for the hatched stages of development.

### Introduction

Many studies have suggested that a high concentration of fine sediment in the spawning gravel of salmonid fish may affect embryo survival through a reduction of the intragravel flow necessary for the oxygenation of the incubating eggs and a decrease of the emergence success of fry (for review see Chapman (1988), Reiser (1999) and Armstrong et al. (2003)). However, because the construction of the redd by the female fish causes the winnowing of a substantial proportion of fines from the substrate (Everest et al., 1987; Young et al., 1989; Kondolf et al., 1993), it has been suggested that almost regardless of the original fine sediment content of the gravel, the cleaning action of the spawning female is sufficient to create

an initial incubating environment that allows a proper influx of oxygen to the embryos (Burner, 1951; Cordone & Kelley, 1961). Thus, the negative effect of fine sediment on embryos may depend more on the amount of fine sediment infiltrating the redds in the period between spawning and fry emergence than on the grain size characteristics of the spawning gravel before or immediately after reproduction (Lisle & Lewis, 1992; Acornley & Sear, 1999). Field verification of the negative relationship between embryo survival and the amount of fine sediment infiltration in a redd during incubation remains scarce (Parkinson et al., 1999).

Previous studies have shown the importance of understanding the effect of different sizes of sediment at different stages of embryonic

development. For example, it has been demonstrated that finer sands are more detrimental to incubating eggs than coarser sands (Peterson & Metcalfe, 1981; Reiser & White, 1988) because they infiltrate deeper in the redds where they fill the gravel voids from bottom up, thereby reducing permeability, intragravel flow rate and oxygen supply to the eggs (Turnpenney & Williams, 1980). In contrast, coarser sands are more harmful to emerging fry because they may form a sand seal in the upper layer of the redd which restricts the upward movement of fry and reduce emergence success (Beschta & Jackson, 1979; Crisp, 1993). Although the effect of the silt fraction ( $<0.063$  mm) on embryo survival is now increasingly being considered as an important factor controlling the quality of spawning gravels (Acornley & Sear, 1999; Armstrong et al., 2003), little is known about the sensitivity of the embryos to this very fine size fraction.

The objectives of this work were (i) to test the hypothesis of a negative relationship between fine sediment infiltration and Atlantic salmon embryo survival, and (ii) to evaluate the effect of various size classes of fine sediment, including the silt

fraction, on survival at the pre-eyed, eyed and pre-emergent fry stages of embryonic development. We conducted 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 in the period between spawning and pre-emergence in the Sainte-Marguerite River, Québec, Canada.

### Study area

The study was conducted on the Sainte-Marguerite River ( $48^{\circ} 27' N$ ,  $69^{\circ} 95' W$ ), a north shore tributary of the Saguenay River, Québec, Canada (Fig. 1). This cobble-bed river, which supports Atlantic salmon (*Salmo salar* L.) and brook trout (*Salvelinus fontinalis*) populations, drains a catchment of  $2151 \text{ km}^2$  and has a mean annual discharge of approximately  $60 \text{ m}^3 \text{ s}^{-1}$ . The catchment is dominated by coniferous forests. The river is divided into two main branches: the Principale Branch and the Nord-Est Branch, with each flowing around 100 km. The two branches are

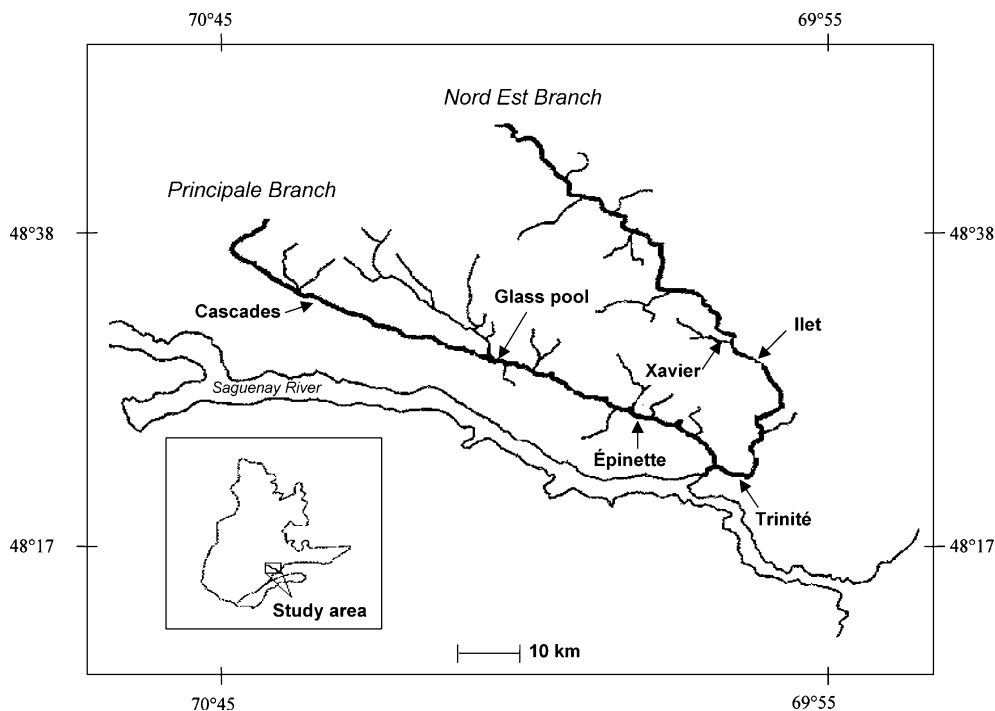


Figure 1. Location of the study sites within the Sainte-Marguerite River system.

Table 1. Characteristics of selected spawning sites on the Sainte-Marguerite River (Québec)

|                   | Sites      | Channel width (m) | Bed material size |          |          | Number of natural redds |
|-------------------|------------|-------------------|-------------------|----------|----------|-------------------------|
|                   |            |                   | D16 (mm)          | D50 (mm) | D84 (mm) |                         |
| Principale branch | Cascades   | 7                 | 3.1               | 29.2     | 63.8     | 6                       |
|                   | Glass pool | 42                | 3.2               | 36.7     | 78.2     | >15                     |
|                   | Épinette   | 53                | 1.2               | 33.9     | 116.9    | >15                     |
| Nord-Est branch   | Xavier     | 8                 | 7.2               | 64.0     | 133.3    | 1                       |
|                   | Ilet       | 27                | *                 | *        | *        | >10                     |
|                   | Trinité    | 58                | 9.2               | 50.4     | 87.8     | >15                     |

D16, D50 and D84, respectively correspond to the 16th, 50th and 84th percentiles of the bed material grain size distribution.

\*Data not available due to high flow conditions.

approximately 40 m wide at bankfull discharge at their confluence. Peak discharge value typically occurs between March and mid-May after the ice break-up. A stable ice cover is generally present from mid-November to the end of March.

At the end of October 1997, immediately after the spawning period of the Atlantic salmon, the Principale and Nord-Est branches of the Sainte-Marguerite River were surveyed in order to locate six spawning sites actively used by salmon (Fig. 1). The sites were selected to be representative of a range of channel widths (from 7 to 58 m) and bed material sizes (D50 from 29.2 to 64.0 mm) used by salmon in the Sainte-Marguerite River system (Table 1). At each site, the area used by salmon for spawning was delimited from the location of natural redds. Three volumetric samples of the sub-pavement bed material were extracted from each

spawning zone and analysed using conventional bulk sampling techniques (Church et al., 1987). Sampling was performed using a flow isolation chamber constructed according to the design of Payne & Lapointe (1997).

#### Materials and methods

Depending on the size of the studied spawning sites, from 6 to 10 incubation baskets, each containing 60 fertilised Atlantic salmon (*Salmo salar*) green eggs, were buried in the substrate immediately after the natural spawning period and retrieved during the estimated hatching period (Fig. 2). At a given site, the baskets were distributed evenly across the active spawning zone. The baskets had a cylindrical form (16×13 cm) and

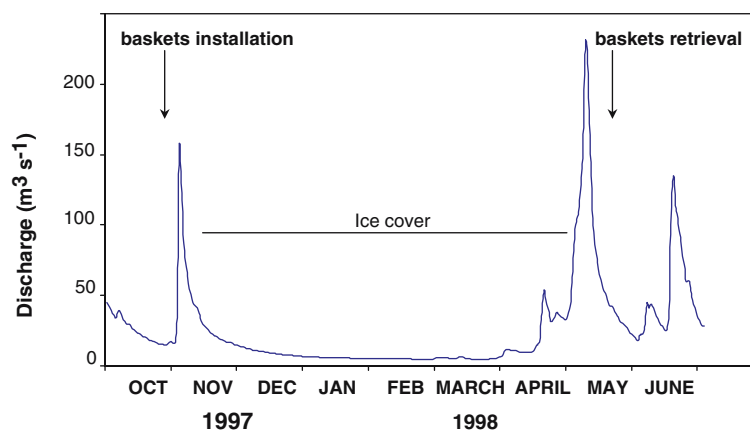


Figure 2. Discharge variations during the study period as measured at stream gauge No. 62802 of Ministère de l'Environnement du Québec located on the downstream portion of the Nord-Est branch of the Sainte-Marguerite River near its confluence with the Principale branch.

were made of ABS (Acrylonitrile butadiene styrene) plastic tubing and 1 mm Nitex netting (Fig. 3). A floatable, 1 m-long, fluorescent green silicone tubing was glued to each basket in order to facilitate their localisation and recovery. Each was filled with sieved gravel ranging from 0.4 to 8 cm in diameter in order to eliminate initial fine sediment content. For each basket, this gravel was taken from the area immediately surrounding the location where the basket was to be buried. Eggs and milt were collected from Atlantic salmon adults native of the Sainte-Marguerite River. The eggs were fertilised and water-hardened at the Tadoussac hatchery located approximately 25 km from the river, and then transported to the field in cooled water filled jars. The eggs were kept at the same temperature as the stream water to avoid thermal shocking during basket installation. In order to evaluate egg fertility and viability ratios, 500 green eggs were kept as a control sample at the hatchery. While inserting the eggs in a basket, care was taken to distribute them evenly to prevent eventual fungal contamination from adjacent dead eggs. For the same reason, the number of eggs per basket was limited to 60, thereby reducing the probability of contact between the eggs of a basket. Once filled, the basket was closed with a

plastic cap, thereby ensuring that neither eggs nor fry could enter or leave. Installation of the baskets containing the eggs was completed within 36-h from fertilisation in order to avoid mortality that might occur when manipulating the eggs after they entered the tender stage.

Each incubation basket was installed using a procedure that aimed to mimic the construction and structure of 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 and pushing them downstream. The basket was then installed horizontally at the bottom of the depression with the long axis oriented perpendicularly to the flow. The centre of the basket was positioned approximately 20–25 cm below the surface, which is within the range of typical burial depths of Atlantic salmon eggs (DeVries, 1997). Finally, the basket was completely buried in the substrate by lifting upstream particles over it in a manner that enabled fine particles to be swept downstream by the flow, so mimicking the winnowing action of the female salmon. Once installed, incubation baskets and cross sections were positioned with an electronic total station in order to facilitate their localisation during winter and their recov-



*Figure 3.* Photograph of one of the incubation basket used in this study. The basket has a cylindrical form (16×13 cm) and is made of 1 mm Nitex netting and ABS (Acrylonitrile butadiene styrene) plastic tubing.

ery in the following spring. In January 1998, each site was surveyed in order to assess dewatering or freezing of the incubation baskets during winter low flows.

The incubation baskets were retrieved from the substrate between May 16th and 21st 1998, during the hatching period. The hatching period was estimated from hourly temperature data records obtained from a temperature data logger buried within the substrate of the Glass Pool study site, and by extrapolating the degree-day hatching threshold published by MAPAQ (1996). The 12th of May was the estimated date at which 50% of the eggs would have hatched. It was considered that on May 16th, 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 at different pre-emergent life stages. Baskets were extracted from the substrate by gently removing bed particles until the top portion of the basket was reached. The basket was then delicately pulled from the substrate and, while still underwater, immediately put in a plastic bag in order to minimise the loss of fine sediment which had infiltrated the basket. During basket extraction from the substrate, the Nitex netting was inspected to detect any potential clogging of the mesh or formation of a sand seal around the basket.

In the laboratory, each basket was carefully examined in order to determine the number of eggs and fry falling into each of the following categories according to the terminology of Legendre & Bergeron (1987): dead pre-eyed egg (DPEE), living pre-eyed egg (LPEE), dead eyed egg (DEE), living eyed egg (LEE), dead sac fry (DSF), living sac fry (LSF) and absent or partly decomposed egg (X). Absent or partly decomposed eggs were assumed to have died during the pre-eyeing incubation period. Since the degree-day hatching threshold at 10 °C (510 deg-day) is twice that of the eyeing stage (245 deg-day) (MAPAQ 1996), we considered that living non-eyed eggs retrieved at this date would have not survived to the pre-eyeing incubation period. For each basket, three different survival ratios were calculated using the following equations:

Survival-to-pre-eyed stage of development (STPE):

$$\text{STPE} = 100X(\text{DEE} + \text{LEE} + \text{DSF} + \text{LSF})/60$$

Survival-to-eyed stage of development (STE):

$$\text{STE} = 100X(\text{LEE} + \text{DSF} + \text{LSF})/60$$

Survival-to-hatched stage of development (STH):

$$\text{STH} = 100X(\text{LSF} + (\text{LEE})X\text{Egg\_Alev})/60$$

where Egg\_Alev is the estimated ratio of live eyed eggs (LEE) which would eventually have successfully hatched and survived (LSF). The use of this equation supposes that all LEE retrieved at this period would have reached the hatched stage either dead or alive. Egg\_Alev was calculated from the following equation developed for each basket:

$$\text{Egg\_Alev} = \text{LSF}/(\text{LSF} + \text{DSF})$$

The sediments contained in each artificial basket were oven-dried and weighted to obtain the total dry-weight of sediments. The grain size fraction <1 mm, corresponding to particles that infiltrated through the netting of the baskets, was then sieved into smaller grain size classes corresponding to coarse sand (0.5–1 mm), medium sand (0.25–0.5 mm), fine sand (0.125–0.25 mm), very fine sand (0.063–0.125 mm) and silts and clays (<0.063 mm). For each basket, the percent weight of a given size fraction was then calculated as a proportion of the total dry-weight of sediments measured in the basket. The effect of fine sediment infiltration on embryo survival was analysed by performing a correlation analysis between the different infiltrated sediment size classes and the survival ratios measured for each basket ( $n = 43$ ).

## Results

### *Incubation baskets recovery and embryo survival*

Of the 53 incubation baskets installed in the fall, 43 were recovered in the following spring, representing an overall recovery success of 87% (Table 2). One basket was eroded away and lost at the Xavier study site, whereas six baskets were either partially or completely eroded at the Ilet study site. For the remaining four baskets of the Ilet study site, difficult field conditions due to high

Table 2. Mean percent dry weight of grain size fractions infiltrated in incubation baskets at each site

| Sites      | Ni | Nr | Silts and clays<br><0.063 mm | Very fine sand<br>0.063–0.125 mm | Fine sand<br>0.125–0.250 mm | Medium sand<br>0.250–0.5 mm | Coarse sand<br>0.5–1.0 mm | Total<br><1.0 mm |
|------------|----|----|------------------------------|----------------------------------|-----------------------------|-----------------------------|---------------------------|------------------|
| Cascades   | 8  | 8  | 0.03 (0.02)                  | 0.08 (0.05)                      | 0.34 (0.21)                 | 1.30 (0.63)                 | 1.58 (0.59)               | 3.33             |
| Glass pool | 9  | 9  | 0.06 (0.12)                  | 0.27 (0.59)                      | 1.18 (2.01)                 | 1.63 (1.38)                 | 1.42 (1.87)               | 4.56             |
| Épinette   | 10 | 10 | 0.05 (0.06)                  | 0.23 (0.23)                      | 2.06 (1.64)                 | 4.85 (3.70)                 | 3.13 (1.90)               | 10.32            |
| Xavier     | 6  | 5  | 0.04 (0.03)                  | 0.28 (0.21)                      | 1.61 (1.00)                 | 7.84 (3.97)                 | 19.47 (8.58)              | 29.24            |
| Ilet       | 10 | 4  | *                            | *                                | *                           | *                           | *                         | *                |
| Trinité    | 10 | 10 | 0.41 (0.20)                  | 1.22 (0.72)                      | 4.78 (2.84)                 | 9.12 (4.08)                 | 11.72 (7.17)              | 27.25            |
| All sites  | 53 | 46 | 0.13 (0.19)                  | 0.45 (0.63)                      | 2.14 (2.41)                 | 4.86 (4.35)                 | 6.46 (7.77)               | 14.04            |

\* Fine sediments lost due to very high spring flow conditions during baskets retrieval.

Ni – number of incubation baskets installed; Nr – number of incubation baskets retrieved.

Standard deviations in brackets.

spring flows caused fine sediment to be washed away from the baskets during their retrieval from the substrate. These baskets were thus analysed for egg and fry survival, but not for fine sediment content.

During basket extraction, no clogging of the mesh or formation of a sand seal around the baskets was observed. At retrieval, 55% of the planted eggs were hatched (13% dead and 42% live), while 12% were at the eyed stage (3% dead and 9% live) and 24% were at the pre-eyed stage (21% dead and 3% live). The remaining 9% were either lost or decomposed beyond recognition of their developmental stage. Table 3 presents the mean survival ratios STPE, STE and STH calculated for each site and for the total number of baskets retrieved. On average, 66% of the implanted embryos survived to the pre-eyed stage of development compared to the 63% and 48% that survived to the eyed and hatched stages of development, respectively. For all

three survival ratios, mean survival was lowest at sites Trinité (STPE 49%, STE 45%, STH 11%) and Xavier (STPE 55%, STE 53%, STH 30%) and highest at site Épinette (STPE 85%, STE 85%, STH 71%).

#### *Fine sediment infiltration and embryo survival*

There was a large variation among sites of the amount and grain size characteristics of the sediment that infiltrated the baskets during the incubation period (Table 2). The results of a Kruskal–Wallis test showed that the mean percent weight of particles infiltrated in the baskets differed significantly among sites ( $p < 0.05$ ). The largest values of fine sediment infiltration were measured at sites Xavier and Trinité where mean percent of sediment <1 mm were, respectively, 29.24 and 27.25% while the lowest values were measured at sites Glass pool (4.56%) and Cascades (3.33%). In terms of grain size characteristics of infiltrated sediments, site Trinité had much larger percentages of silts and fine sand than all other sites. Both Xavier and Trinité sites had larger percentages of medium and coarse sand infiltration than the other sites.

Table 4 presents the correlation matrix between the three embryo survival ratios and the five classes of infiltrated fine particles. All showed negative relationships, indicating that embryo survival decreases when the percentage of fine sediment infiltrated within the incubation baskets increases. However, some differences in the strength of these relations are observed depending on the grain size

Table 3. Mean percent (SD) survival to pre-eyed (STPE), eyed (STE), and hatched (STH) stages of development at each site

| Sites      | Pre-eyed<br>(STPE) | Eyed<br>(STE) | Hatched<br>(STH) |
|------------|--------------------|---------------|------------------|
| Cascades   | 72 (8)             | 68 (11)       | 63 (14)          |
| Glass pool | 66 (16)            | 64 (17)       | 59 (19)          |
| Épinette   | 85 (9)             | 85 (10)       | 71 (15)          |
| Xavier     | 55 (9)             | 53 (14)       | 30 (22)          |
| Ilet       | 68 (5)             | 60 (6)        | 49 (17)          |
| Trinité    | 49 (26)            | 45 (26)       | 11 (15)          |
| All sites  | 66 (21)            | 63 (22)       | 48 (29)          |

Table 4. Correlation matrix between the three embryo survival ratios and the percentage of each infiltrated grain size fractions (Pearson correlation,  $df=42$ )

| Infiltrated grain size fraction (mm) | Pre-eyed (STPE) ( $r$ ) | Eyed (STE) ( $r$ ) | Hatched (STH) ( $r$ ) |
|--------------------------------------|-------------------------|--------------------|-----------------------|
| Coarse sand: 0.5–1.0                 | –0.25 (0.1077)          | –0.24 (0.1229)     | –0.64 (0.0000)*       |
| Medium sand: 0.250–0.5               | –0.40 (0.0091)          | –0.37 (0.0161)     | –0.70 (0.0000)*       |
| Fine sand: 0.125–0.250               | –0.55 (0.0002)*         | –0.52 (0.0004)*    | –0.63 (0.0000)*       |
| Very fine sand: 0.063–0.125          | –0.65 (0.0000)*         | –0.64 (0.0000)*    | –0.66 (0.0000)*       |
| Silts and clays: <0.063              | –0.66 (0.0000)*         | –0.65 (0.0000)*    | –0.68 (0.0000)*       |

Significance level ( $p$ ) in brackets.

Marked correlations are significant at  $p < 0.05$  using the Bonferroni correction procedure: ( $\alpha = 0.05/\text{number of correlations} = 0.05/15 = 0.003$ ).

fraction considered. In the case of STPE and STE, correlations with coarse and medium sands are not significant once the Bonferroni correction is applied, while corrected correlations remain significant with fine sand, very fine sand and silts/clays. The results also indicate that the strength of the relationship increases as the size of infiltrated particles decreases, with the highest correlation being with particles finer than 0.063 mm for both STPE (Fig. 4a) and STE (Fig. 4b). In contrast to the results obtained for STPE and STE, STH is significantly correlated with all grain size fractions, with the strongest correlation being with medium sand (Fig. 4c).

## Discussion

### *Effect of fine sediment on embryo survival*

Our results indicated that survival to pre-eyed and eyed stages of development were most strongly affected by particles of the size of silts and clays (<0.063 mm), although these particles represented only a small fraction of the grain size distribution inside the incubation baskets (0.03–0.41%). Other recent laboratory and field studies have also found important effects of small amounts of silts and very fine sand on embryo survival (Lapointe et al., 2004; Levasseur et al., in press). This situation could be related to the tendency that we observed for silts and clays to adhere to the embryos and to form a thin coating of sediment. In a laboratory experiment on oxygen consumption by Atlantic salmon embryos approaching hatching, Greig et al. (2005) observed such thin coating around the eggs

created by clay-sized sediment and found that it restricted the availability of oxygen to the incubating embryos. They also observed that oxygen uptake was restricted by clay-sized particles which physically blocked the micro-pore canals of the egg membrane. Because these mechanisms require only small amounts of very fine sediment to restrict the oxygen consumption of the eggs, they may provide an explanation for our results showing an important effect on embryo survival of very small amounts of silts.

It should be noted that the strength of the relationship between embryo survival and the finest particle size classes (silts and clays, very fine sand and fine sand) is largely due to the contribution of site Trinité. Because larger amounts of these finest size classes infiltrated the incubation baskets of this site, it extended the range of fine sedimentation conditions analysed in this study, which allowed the determination of the important, but long overlooked effect of small amounts of silts/clays and very fine sand on embryo survival. Although, the silts and clays percentages observed at site Trinité were markedly different than at all other sites analysed in this study, the values are not abnormally high and are well within the range generally found in Quebec salmon streams (Lapointe et al., 2004). Although survival to pre-eyed and eyed stages of development dropped below 50% at silt values larger than 0.3–0.4%, there was a large variability of survival at smaller silt values (<0.01%), indicating the effect of other variables on embryo survival. For example, Malcom et al. (2003) showed that spatial and temporal variations of groundwater–stream interactions due to fluctuating discharge affect hyporheic water quality by modifying its dissolved

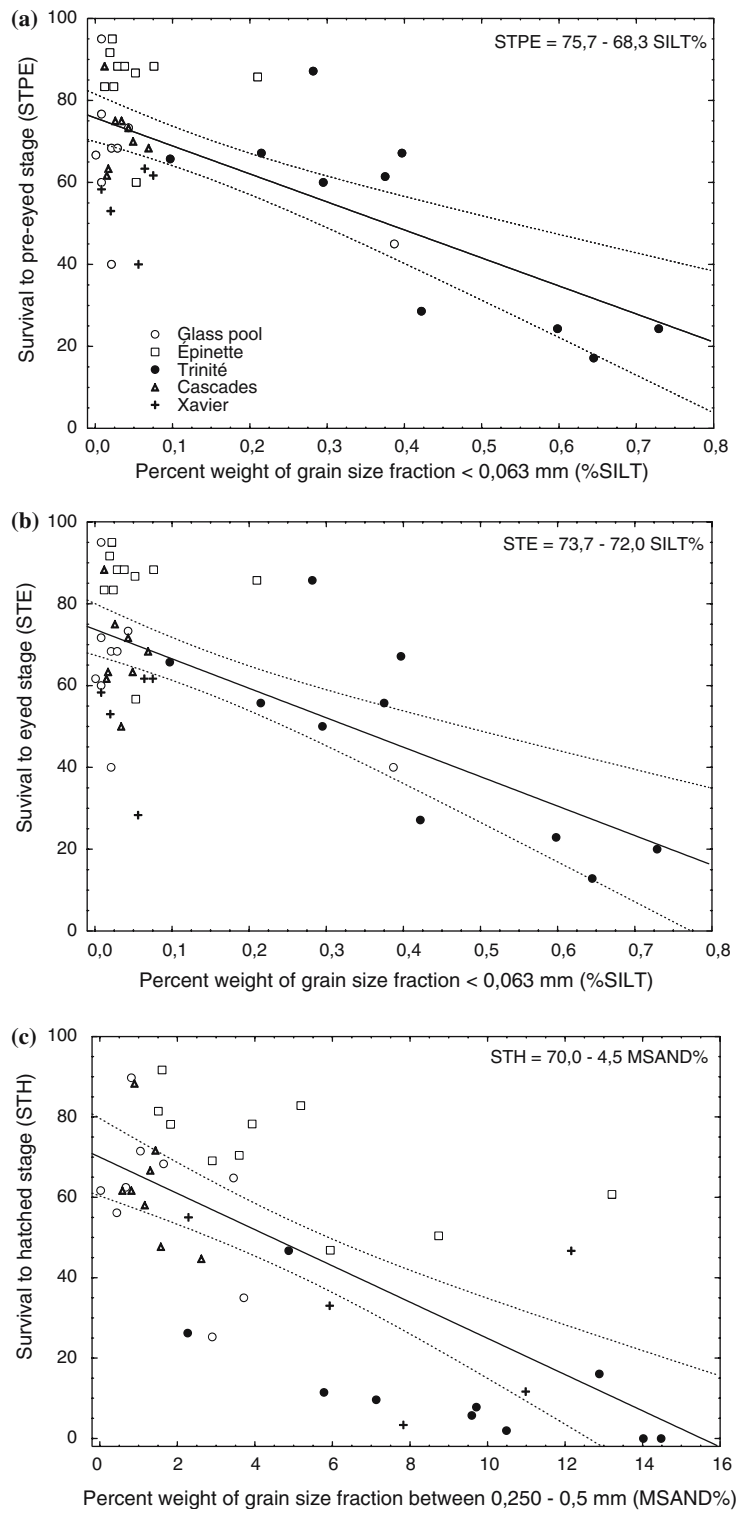


Figure 4. Effect of fine sediment infiltration on Atlantic salmon embryo survival to (a) pre-eyed, (b) eyed and (c) hatched stages of development.



oxygen (DO) content, which in turns, affect the survival and development of salmonid embryos.

Although larger sediments than considered in the current study have been reported to affect embryo survival, our study design would have not been able to detect such effect. However, the fact that the strongest correlations between fine sediment size and embryo survival were obtained for the finest particle size classes suggest that it would be unlikely that particles larger than 1 mm would have correlated more strongly with survival. It may also be argued that the 1 mm meshing of the incubation baskets created a sink favouring the infiltration of fine sediments at the level of the incubating eggs. However, natural salmon redds naturally have coarser grain size and larger pore spaces than surrounding gravels and are therefore themselves natural sinks for infiltration. In this sense, we suggest that the incubation baskets helped reproducing natural salmon egg pockets.

#### *Survival at various stages of embryo development*

While we observed that survival was low during the pre-eyed stage of development (STPE = 66%), Mackenzie & Moring (1988) found very good survival at that stage (STPE = 95%) from a study of Atlantic salmon eggs planted in Whitlock-Vibert boxes buried in a natural stream. According to the curve of embryonic development based on cumulative degree-days provided by the MAPAQ (1996), the pre-eyed stage should have ended, at our study sites, during the second week of February, thereby indicating that a large proportion of mortality occurred before mid-winter. It is possible that the high mortality observed at the pre-eyed stage of development was due to transport and handling mortality. Because we did not conduct a transport and handling control test, the effect of transporting the fertilised eggs from the hatchery to the sites and of handling them during basket installation cannot be assess directly. However, since pre-eyed survival was very good at some sites (e.g. 85% at site Épinette) and that there is no reason to believe that transportation and handling of the eggs at this site was better than at the other sites, we feel confident that these factors did not play an important role on mortality and that, even if they had played such a role, it should have affected all sites equally.

Mackenzie & Moring (1988) also found that survival remained high at the eyed stage (STE = 89%), a result which is in good agreement with the 93% STE value estimated by Jordan & Beland (1981) from the excavation of natural redds. These results showing low mortality at the eyed stage of development are consistent with the ones obtained in our study since we observed only a small 3% decrease of survival from the pre-eyed to the eyed stage of development (STE = 63%). Lower STE values were found by Pauwels & Haines (1994) from simulated redds in natural streams (range 19–61%) and by Harriman & Morrison (1982) from green salmon eggs planted in several scottish streams (average 43%). Finally, survival to the hatched stage of development varied from 11 to 71% among sites in our study (overall STH of 47%), which is in the range of the 7–88% values found in the literature for Atlantic salmon (Lacroix, 1985; Mackenzie & Moring, 1988; Pauwels & Haines, 1994). The observed variability of embryonic survival between studies may in part be due to differences in the experimental protocols. For example, Rubin (1995) suggested that redd excavation techniques may overestimate early embryonic survival since they neglect to include in their calculations the natural disappearance of eggs due to gravel movement, predation and decomposition.

In this paper, we provided field evidence that an important factor potentially limiting Atlantic salmon embryo survival in the Sainte-Marguerite River is the infiltration of fine sediment within the redds during incubation. The results from incubation baskets showed that survival to pre-eyed, eyed and hatched stages of development were all negatively correlated with the percentage of fine sediment infiltrated within the sediment matrix of the baskets. Survival to pre-eyed and eyed stages of development was most strongly correlated with the percentage of silts and clays (<0.063 mm), although these particles represented only a small fraction of the grain size distribution (0.03–0.41%) by weight.

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