Interactive effects of substrate sand and silt contents, redd-scale hydraulic gradients, and interstitial velocities on egg-to-emergence survival of Atlantic salmon (*Salmo salar*)[1]

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Abstract: We conducted laboratory incubation experiments with Atlantic salmon (*Salmo salar*) eggs to test a number of hypotheses concerning the relative sensitivity of the incubating eggs to variations in silt (diameter < 0.063 mm) in interaction with sand (0.63 mm < diameter < 2 mm) fractions in the incubating gravels, as well as to different strengths of local hydraulic gradients pushing flow across the egg pocket. Our results show that variations of only a few percent of silt content can strongly degrade survival to emergence. Higher silt loadings (>0.5%) are detrimental to survival for all substrate mixtures, except those that are very sparse in sands (<5%). For sand contents over 10%, an increment of 1% silt has over three times the effect on survival as a 1% increment in sand. Increasing hydraulic gradients had a positive effect on median survival, but the effect depended both on the details of the fines composition and on the gradient level. Our results suggest that silt loadings over 1.5% in redds cannot easily be mitigated by stronger gradients. Our data conclusively show that there is no single threshold interstitial flow velocity that insures survival to emergence. Even when maintaining a constant interstitial velocity, survival tended to reduce in higher fines-content substrate.

Résumé : Nous avons effectué en laboratoire une étude d'incubation d'œufs de saumon atlantique (*Salmo salar*) afin de tester la sensibilité relative des œufs aux variations du pourcentage de limon (le diamètre < 0,063 mm) et de sable (0,63 mm < le diamètre < 2 mm) dans le substrat d'incubation, ainsi qu'aux variations du gradient hydraulique. Nos résultats indiquent que des variations très faibles du contenu en limon réduisent fortement la survie à l'émergence. Des contenus en limon élevés (>0,5 %) réduisent la survie pour tout les substrats étudiés, sauf ceux ayant de très faibles contenus en sable (<5 %). Lorsque le contenu en sable est supérieur à 10 %, une augmentation de 1 % des limons a un effet sur la survie plus de trois fois supérieur à une augmentation comparable de sable. L'augmentation du gradient hydraulique augmente la survie médiane mais l'ampleur de l'effet dépend de la composition exacte en sédiments fins et du gradient hydraulique. Nos résultats suggèrent que des teneurs en limons supérieurs à 1,5 % sont difficilement compensables par un gradient hydraulique élevé. Les données montrent aussi l'inexistence d'un seuil unique de vitesse d'écoulement interstitiel permettant d'assurer la survie des œufs; même à vitesse intersticielle constante, la survie des œufs tend à diminuer avec une augmentation du contenu en fines.

Introduction

Assessing the quality of spawning habitat is of great importance for the management of salmonid populations in rivers. Current research suggests that spawning habitat quality cannot easily be summarized by a single metric; it is affected by multiple environmental controls operating at different physical and temporal scales. Redd site selection must not only ensure sufficient interstitial water flow locally around the egg pocket over the whole incubation period, its location within the river pattern must also minimize the vulnerability of egg pockets during seasonal extremes to freezing, scouring, and sediment entombment (Sowden and Power 1985; Prowse 2001; Lapointe et al. 2000). Nonetheless, for the purposes of habitat management, fines content within gravel–cobble substrate remains a primary predictor of

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spawning habitat quality. This study aims to quantify the effects on reproductive success of interactions between sand and silt contents combined with the effects of variations in strength of local hydraulic gradients pushing flow across the egg pocket (here silts refer to particle sizes under 0.063 mm).

The detrimental effects of excessive fine sediment on substrate permeability, intergranular flow velocities, and resultant survival of salmonid embryos and (or) sac fry have been documented in numerous laboratory studies (Peterson and Metcalfe 1981; Tappel and Bjornn 1983; Young et al. 1991). Unfortunately these studies refer to a range of very broad measures of fines content, such as total fraction under 2 or 8 mm, and most fail to explicitly account for the large differences in inherent permeability among finer alluvial fractions. Yet, the detrimental effects for reproductive success of a unit mass of alluvial silt (diameter (*D*) under 0.063 mm) may be much greater than that of an equivalent mass of sand. Because the permeability (or hydraulic conductivity) of uniform granular material varies with the square of particle diameter (Vukovic and Soro 1992), relative permeability varies, for example, 30-fold between pure 1-mm coarse sand and 0.15-mm fine sand and 30-fold again between fine sand and 0.03-mm silts. While Peterson and Metcalfe (1981) acknowledged, through their "sand index" (see Methods), the greater effect on reproductive success of fine sand (*D* between 0.06 and 0.5 mm) compared with coarse sands (*D* between 0.5 and 2 mm), no extant study has determined threshold values of silt content for egg survival. Although absolute silt content in gravel alluvium is usually very low, it is spatially variable and can locally reach a few percent in some salmon rivers draining friable, fine-textured parent rock (Wilson 2003).

From physical principles, sediment size composition and permeability affect intergranular flow rates (which control transport of oxygen and removal of metabolic wastes). A number of studies have thus cited, as thresholds for reproductive success, minimum intergranular flow velocities rather than maximal fines contents (Wickett 1954; Cooper 1965). Based on Darcy's law

$$(1) \qquad V = -K(\Delta H/\Delta X)$$

the bulk flow velocity (*V*, also called specific discharge) through the spawning gravel is a function, on the one hand, of the substrate hydraulic conductivity (*K*) controlled by grain size distribution and packing and, on the other hand, by the strength of the gradients ($\Delta H/\Delta X$) in hydraulic heads (*H*) driving interstitial flow through the riffle substrate over a distance ΔX. In theory, a sufficiently strong hydraulic gradient can thus compensate for a low permeability substrate and yield any level of interstitial velocity required to transport oxygen and wastes. Moreover, shallow sub-bed hydraulic gradients vary spatially over rivers, partly controlled by channel and bedform morphology (Cooper 1965; Geist and Dauble 1998; Geist 2000). There is indirect evidence that spawners may select for local gradient conditions in addition to substrate composition. Bigger, more complex spawning bars, often associated with stronger hyporheic gradients, in some cases with suboptimal substrate, appear to be preferred spawning sites for certain salmonids (Geist and Dauble 1998; Baxter and Hauer 2000; Coulombe-Pontbriand and Lapointe 2004).

However, even if strong gradients produce adequate interstitial flow rates, embryo emergence from the substrate may be hindered if substrate fines content is too high, leading to smaller pore spaces and stronger compaction. Thus, it is unclear whether reproductive success depends solely on interstitial flow velocity, irrespective of substrate fines content and the extent to which fish selection of spawning beds under stronger interstitial gradients can compensate for high substrate fines content. To test these questions, we conducted laboratory incubation experiments to clarify the relative sensitivity of reproductive success (defined here as egg to emergence survival) to varying proportions of sands and silts under different hydraulic gradients and resultant flow velocities across the egg pocket.

Three hypothesis were tested: (*i*) over a range of sand contents, variations in silt contents have a clear effect on reproductive success, and reproductive success is significantly more sensitive to silts than to similar amounts of sands; (*ii*) for any given substrate mixture, survival increases with the strength of the local hydraulic gradient driving flow across the egg pocket; and (*iii*) while interstitial flow velocity integrates the effects of substrate size and local hydraulic gradients, it cannot on its own completely predict reproductive success; at any given interstitial velocity, survival to emergence still varies with the amount of fines present in the incubating substrate.

Methods

A series of laboratory experiments were conducted between November 2002 and March 2003 in the Laboratoire régional des sciences aquatiques (LARSA) at Laval University, Québec (Canada). In these experiments, Atlantic salmon (*Salmo salar*) eggs were incubated in cylinders containing varying sediment size mixtures and subjected to different hydraulic gradients. Sixteen sediment mixtures were created using an orthogonal design, made up of four percentages of sand and four percentages of silt, each of which were subjected to three different hydraulic gradients ($\Delta H/\Delta X$= 0.009, 0.006, 0.012). (Here, a gradient of 0.012 or 1.2% represents a drop of 1.2 cm of hydraulic head over a 1-m downflow path).

Experimental sediment mixtures consisted of a common control mixture of gravels to which was added varying combinations of sands and silts. The coarse control gravel did not include sediment smaller than 2 mm and its grain size distribution (10% under 4 mm, 25% under 10 mm, 50% under 26 mm, and 90% under 55 mm) was selected to be broadly representative of a typical Atlantic salmon redd in Quebec streams. The proportion of sand in a mixture was quantified with the sand index (SI) developed by Peterson and Metcalfe (1981)

$$(2) \qquad \mathrm{SI} = (S_c/16 + S_f/8)$$

where S_c and S_f are, respectively, the percentages of coarse sand (0.5–2 mm) and fine to medium sand (0.06–0.5 mm). Owing to space and time limitations, we could not test independently varying combinations of these two sand fractions; in all mixtures, the ratio of coarse sand to fine sand was held constant at 3.3, again a typical value for riffle alluvium in Quebec salmon rivers.

The SI values tested in this experiment (0.5, 1.0, 1.5, 2.0) were selected to be representative of the range of values encountered in natural salmon streams. According to Peterson and Metcalfe (1981), embryo survival is generally excellent when SI is <1.0, whereas it is very poor when SI is >1.5. These authors, however, gave no details on the range of applicability of this threshold in terms of silt levels or gradient conditions. For each SI value, four different percentages of silt representative of the range of values (0.2%, 1.2%, 2.2%, 3.2%) generally found in Quebec salmon streams were tested. To assemble each mixture, we weighed and thoroughly mixed its three components (control gravel, sands, and silts) while dry, in the order of finer fractions to coarser fractions. Resultant mixtures were then carefully inserted in layers in a polymer cylinder (diameter 15 cm × height 50 cm).

The porosity (p) of each mixture was determined in the laboratory from

$$p = V_e / V_t \quad (3)$$

where V_e is the volume of water needed to saturate the total volume (V_t) of the cylinder containing the dry sediment mixture. Three replicate groups of 16 cylinders, each group covering the range of study mixtures, were then installed in separate basins to undergo different gradient conditions. Each basin was divided into an outer and a central section. The cylinders were installed in the outer section, each cylinder being connected to the central section by a 2-cm diameter pipe located immediately above the bottom of the cylinder (Fig. 1). A hydraulic gradient was created inside the cylinders by maintaining different water levels in the outer and central sections of the basin. All flow paths between these two sections, other than from the top of each cylinder to its outlet pipe, were carefully sealed. All cylinders inside each of the three basins were thus subjected to exactly the same hydraulic gradient.

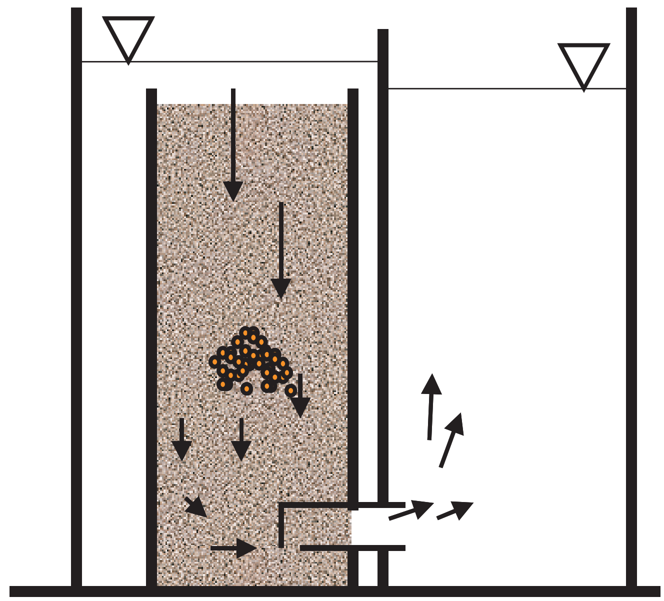
The mean velocity in pore spaces, also called mean intersticial velocity, (V') for each sediment mixture and gradient was measured from

$$V' = V / p = Q/(Ap) \quad (4)$$

where Q is the water discharge coming out of a cylinder, V is the bulk velocity or specific discharge used in Darcy's law (eq. 1), p is the porosity of the sediment mixture, and A is the surface area of the cylinder. Water discharge in a cylinder was determined by attaching a plastic bag to the end of the pipe located in the central section of the basin and averaging replicate measurements of the total volume of water flowing into the bag over a given period of time. The median hydraulic gradient used in these experiments (0.006) produced a flow velocity in the interstices of 0.015 $cm \cdot s^{-1}$ in a cylinder containing only the clean control mixture. This value is typical of flow velocities measured in salmonid redds from which fine sediments were winnowed by the digging action of the female fish.

The Atlantic salmon eggs used in the experiment were provided by the Société Cascapédia and came from adults of the Cascapédia River (Québec, Canada). Within 24 h of fertilization, all eggs were water-hardened, transported to the laboratory in water-filled mason jars maintained at a temperature of 4 °C, acclimated to water basin temperature (8.8 °C) by increasing water temperature at a rate of 1 $°C \cdot h^{-1}$, and placed in the experimental incubating substrates. A control batch of fertilized eggs was kept aside in an incubator to determine the percentage of nonviable eggs. The percentage of nonviable eggs was under 10% and no correction was applied to survival to emergence data. For each cylinder, a 15-cm-thick layer of sediment was first put at the bottom of the cylinder. Then, 100 eggs were distributed over the gravel surface and covered by another 15-cm-thick layer of sediment. This manipulation was done while the cylinders were filled with water to reduce damage to the eggs.

Fig. 1. Diagram showing one of the cylinders used to incubate Atlantic salmon (*Salmo salar*) eggs. Side view (elevation). Large, open triangles denote water levels in the different sections of the basin.



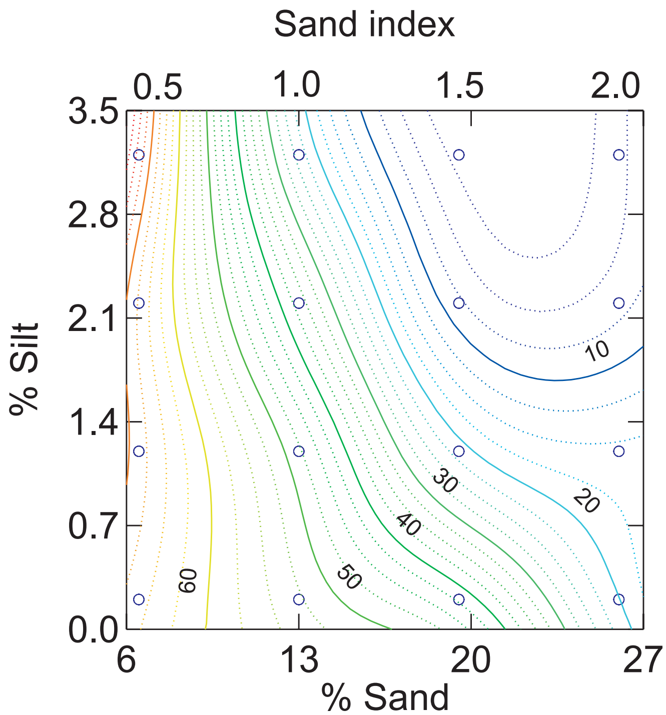
Unchlorinated water flowing through the cylinders was maintained at a temperature of 8.8 °C throughout the incubation period, which started on 7 November 2002. Starting 10 days prior to the expected date of the beginning of emergence at the end of January, each cylinder was inspected daily for emerged fry. On each occasion, emerged fry were counted and removed. Survival to emergence was measured as the total number of fry collected from each cylinder over the incubation period.

Results

Interactive effects of silt and sand contents on survival

Curves of mean survival rates averaged over the three study gradients are presented as a function of % Silt and % Sand (or equivalent SI values; Fig. 2). Isolines representing percent survival were interpolated using a distance-weighted least squares procedure. The overall trends of the contours reveal an interaction between the effects of silt and sand contents on survival. While scarcity of data points limits our ability to resolve thresholds with great precision, large silt contents have negligible effect on mean survival at SI values under approximately 0.75 (percent sand under 10%). In contrast, the effects of rising silt content is quite marked at sand

Fig. 2. Percent survival (numbers on lines) to emergence of fry averaged over the three study gradients as a function of % Sand (or Sand Index, top) and % Silt. Circles locate data points.



indices greater than 1.25 (percent sand over 16%). Similarly, with increasing silt contents, a given value of SI is associated with progressively lower survival rates.

A simple regression model based solely on substrate texture (eq. 5) and neglecting gradient values, with highly significant ($p < 0.0003$) SI and sand–silt interaction terms, predicted 50% (adj R^2) of the variations in experimental survival data. The sand–silt interaction term adds 6% to the variance explained by SI as single predictor.

$$(5) \quad \%\,\text{Survival} = 83 - 29(\text{SI}) - 6(\text{SI} \times \%\,\text{Silt}), \quad R^2 = 50\%,\ p = 0.00001$$

or equivalently

$$\%\,\text{Survival} = 83 - 2.3(\%\,\text{Sand}) - 6(\%\,\text{Sand} \times \%\,\text{Silt})$$

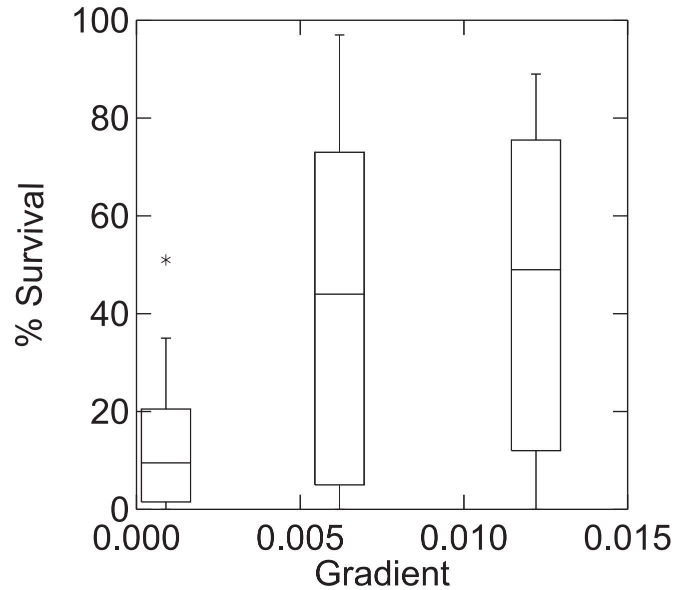
Over much of the mixture space corresponding to moderate to high sand contents (i.e., for SI between 0.8 and 1.6 or percent sand in the range of 10%–22%), the isolines of % Survival remain more broadly parallel (Fig. 2) For this range, a simplified linear model (eq. 6) in sand and silt (without interaction term) captures 52% of the variation in mean survival across the study gradients

$$(6) \quad \%\,\text{Survival} = 103 - 10(\%\,\text{Silt}) - 3(\%\,\text{Sand}), \quad p < 0.00001$$

Effects of changing hydraulic gradient on egg-to-emergence survival

Increasing hydraulic gradients had a positive but somewhat nonlinear effect on median survival over all sediment mixtures tested (Fig. 3). The increase in survival associated with a given increment in gradient depends both on the details of the fines composition as well as on the level of gradient (as illustrated in Figs. 4*a*, 4*b*). The interpolated contours (Fig. 4*a*) reveal that increasing gradients (from low to mid-range, yielding a 40% median increase in survival overall; cf. Fig. 3) broadly increase survival rates across the spectrum of composition, except at the very highest sand content tested. The most pronounced effect of ramping hydraulic gradients from low to mid-range first occurs in clean (low sand, low silt) mixtures, where the increment in survival exceeds 50%.

Fig. 3. Box plots of survival to emergence of fry as a function of imposed hydraulic gradient. The middle line represents the median survival, the box splits the remaining halves again, the whiskers are 1.5 times the interquartile range, and the asterisk is less than three times the interquartile range.



Increasing hydraulic gradient by a further, comparable increment (from the mid-range (0.005) to the highest value tested (0.012)) only enhanced median overall survival by a few percentage points (cf. Fig. 3). However, this had a strong beneficial effect (Fig. 4*b*) for the subset of mixtures with high sand but lower silt contents, where survival increased by 20%–50%. We summarize the contrast in overall survival response to increasing gradients between silt-rich (Fig. 5*a*) and silt-poor mixtures (Fig. 5*b*), with arbitrary separation at 1.5% silt. While median survival increases continuously with gradient across all silt-poor mixtures, the median survival response of silt-rich samples is muted as gradients are increased between low and mid-range and are nonexistent between mid-range and high gradients.

Adding hydraulic gradient terms to the sediment composition predictors in eq. 5 increases by 27 percentage points the variance explained in the survival data (i.e., from 50% (eq. 5) to 77% (eq. 7)). This regression model incorporates only three highly significant ($p < 0.00001$) predictors: gradient, % Sand, and an interaction term between gradient and fines content (% Sand × % Silt).

$$(7) \quad \%\,\text{Survival} = 51 - 2(\%\,\text{Sand}) + 5070\,(\text{Gradient}) - 69(\text{Gradient} \times \%\,\text{Silt} \times \%\,\text{Sand}), \quad R^2 = 77\%,\ p < 0.00001$$

Fig. 4. Percent change of survival (numbers on lines) to emergence resulting from an increase of gradient (*a*) from low- to mid-level gradients and (*b*) from mid- to high-level gradients.

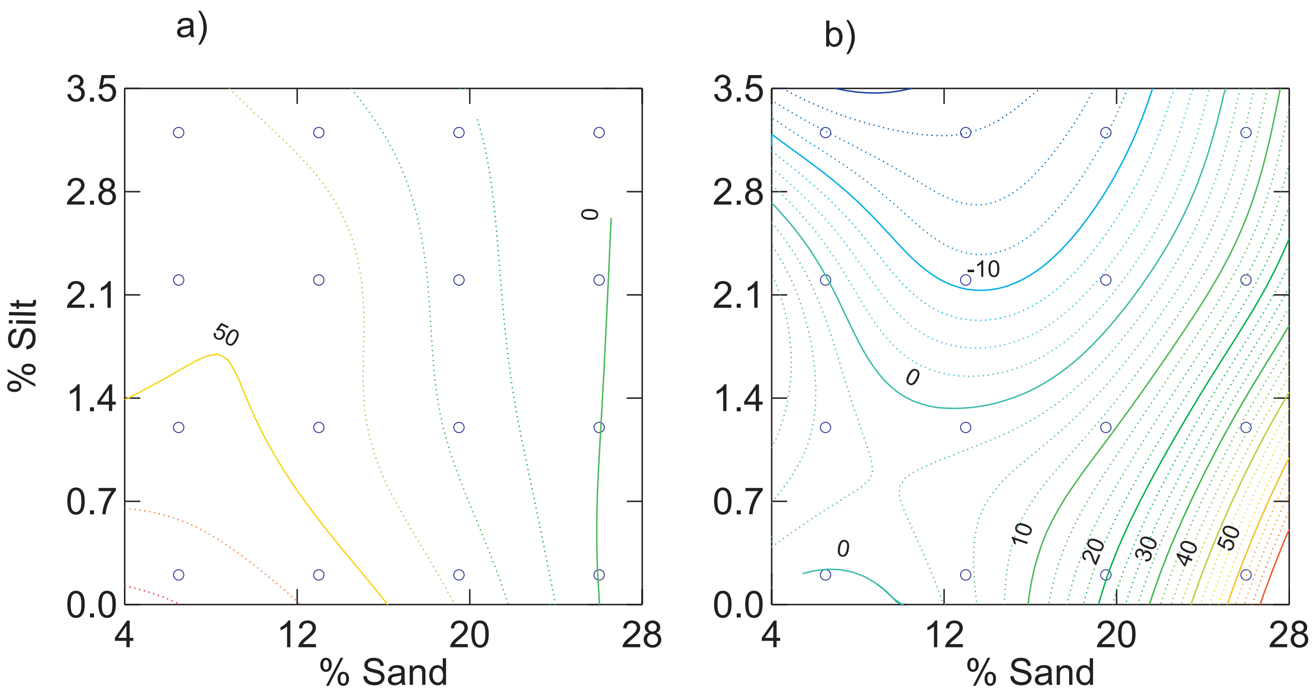
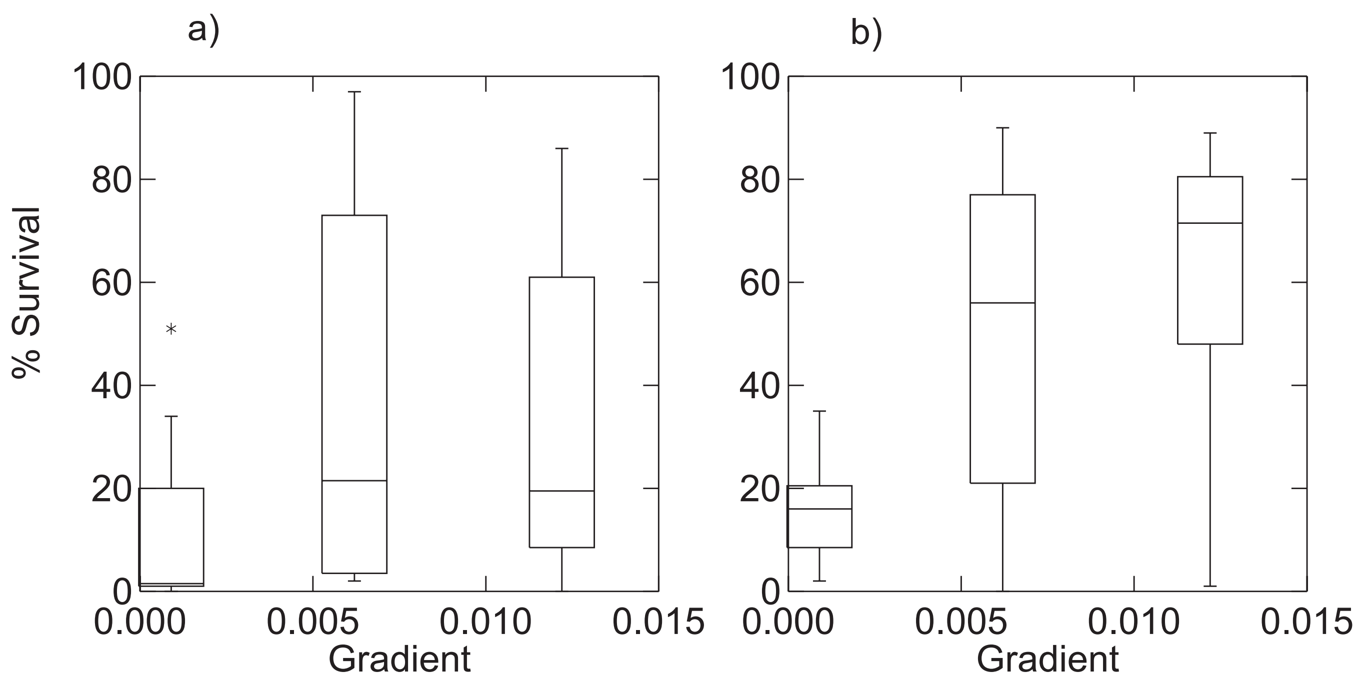


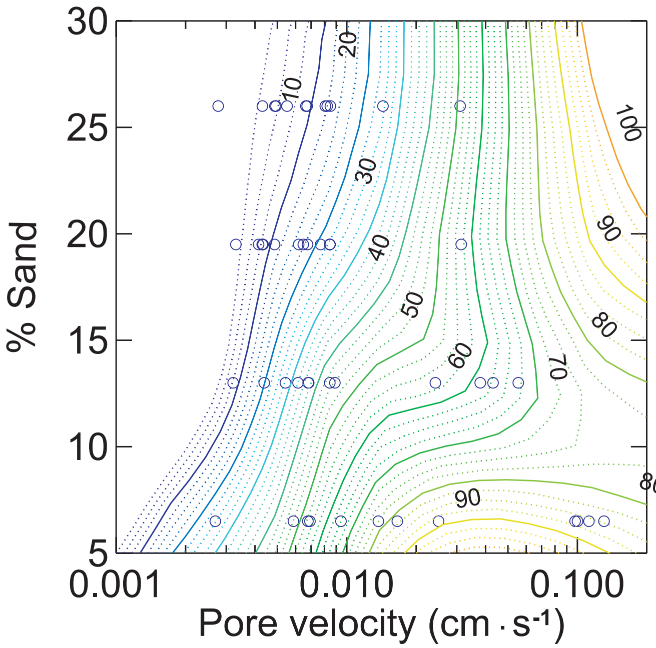
Fig. 5. Box plots showing effects of increasing the imposed hydraulic gradient on survival to emergence for (*a*) silt-rich (>1.5%) and (*b*) silt-poor (<1.5%) sediment mixtures. The middle line represents the median survival, the box splits the remaining halves again, the whiskers are 1.5 times the interquartile range, and the asterisk is less than three times the interquartile range.



Interstitial velocities and survival

As discussed in the context of Darcy's law (eq. 1), it may be expected that the combined effects of fines content and hydraulic gradient on survival can be integrated through the intensity of interstitial velocities, V' (eq. 4), flowing through the egg pocket. The associations among interstitial velocity, percent sand, and observed survival in our two experiments are illustrated (Fig. 6). Although survival increases with velocity for any sediment composition, at any given value of interstitial velocity lower survival rates occur with progressively higher sand contents (Fig. 6; note that isolines in the top right part of the panel are extrapolated beyond our data). Equation 8 predicts 70% of the variation in experimental survival rates based on velocity and fines content terms (% Sand and sand–silt interaction terms, three predictors that are each highly significant individually).

Fig. 6. Isolines of percent survival (numbers on lines) to emergence of fry as a function of interstitial pore velocity and sand content. Circles denote data points.



$$(8) \qquad \% \text{Survival} = 141 + 36\log(V') - 1.5(\%\text{Sand}) - 4.1(\%\text{Sand} \times \%\text{Silt}), \qquad R^2 = 70\%, p < 0.0001$$

While there is no correlation among sand, silt, and gradient in our experimental design, there is a modest negative correlation (–0.45) between the variables % Sand and observed interstitial velocity in the data (as also seen in Fig. 6). However, this correlation was too weak to cause multicollinearity problems in estimating equation 8; all tolerances were greater than 0.65 and all coefficient estimates had individual p values under 0.02. While velocities range over two orders of magnitude, observed substrate porosities (at 28% ± 3%) vary weakly across our mixtures. Thus, bulk velocities V were strongly correlated to interstitial velocities V' ($V \cong 0.28V'$) in our data set so that we cannot clarify if any of the two measures of intergranular velocity is superior to the other as a predictor of survival.

Discussion

The relative effects of silt versus sands

Although a substantial portion of the silt and sand content is usually flushed out of fresh redd substrate by female digging activity (Kondolf et al. 1993; Montgomery et al. 1996), appreciable reinfiltration of fines around egg pockets can occur in fines-rich stream systems over the many months of the incubation period (Everest et al. 1987). Our results indicate that for the particular gravel mixture tested, high silt loadings are detrimental to survival for all substrate mixtures except those that are very low in sand content (<5%). For sand contents over 10%, an increment of 1% silt has over three times the effect on survival as a 1% increment in sand (eq. 6). Our data indicate that except for mixtures with low sand contents, variations of only a few percent of silt content in spawning substrate over the course of incubation can strongly degrade survival from egg to emergence. For example, at 15% sand (SI of 1.25) mean survival decreases from 60% to 20% as silt content increases over the range 0%–4%. Recall that only one control gravel mixture (fractions coarser than 2 mm) was tested; this was selected to be typical of salmon spawning substrate. Reported threshold values might vary somewhat for other gravel compositions, especially if the percentages of granules (2–4 mm) were very different than that tested (10%).

The interaction between sand and silt content evidenced in Fig. 2 and eq. 5 appears to reflect differences in resultant pore space organization under the effect of seepage forces caused by interstitial flow. At very low sand contents, even large masses of silt particles may be free to rearrange themselves slightly within the gravel framework, opening preferred routes for intergranular flow and maintaining substantial flow and emergence routes across the egg pocket. (In none of our experiments, however, did silt leach out of the cylinders into the receiving basin.) However, at higher sand contents, ubiquitous sand particles obstruct much of the intergravel space, allowing the silts to better bridge the remaining pore spaces. This interaction inhibits the establishment of connected macropores under greater seepage forces, reducing flow rates as well as hindering emergence more effectively.

Our data and regression model (eq. 5) also allows us to refine the interpretation of Peterson and Metcalfe's (1981) SI (eq. 2). For example, with less than 0.5% silt, an SI of 1.0 (Peterson and Metcalfe's nominal threshold separating good from mediocre substrate) yields an average survival of 70% over the range of four gradients tested. However, at 3% silt, survival is only 40% at SI = 1.0.

The interactive effects of hydraulic gradient and fines content on survival

Our results confirm that variations in local hydraulic gradients across redds, typically associated with variations in channel morphology (Cooper 1965; Baxter and Hauer 2000), could potentially be exploited by salmon to enhance reproductive success. However, they also highlight the complex, multifactorial nature of spawning habitat quality indices. While Peterson and Metcalfe (1981) state that SI values greater than 1.5 correspond to poor spawning substrate, at the highest gradient we tested (0.01), survival reached 60% in a mixture with SI of 2.0 and with low silt loading (<0.5%).

The data show that there is no single, threshold interstitial flow velocity that insures survival from egg to emergent fry; fines content also matters. For example, a 0.01 $cm \cdot s^{-1}$ interstitial velocity through a 6% sand mixture is associated with a 60% mean survival over the range of study gradients. However, when sand content is as high 26%, the same interstitial velocity is associated with only 20% mean survival. This is consistent with the view that fines, in addition to their effect on flow rate and hence potential metabolite transport rate, have mechanical effects on embryo development (such as membrane abrasion or hindrance to emergence).

Finally, the results indicate that the silt fraction plays a role in modulating how higher hydraulic gradients affect survival. As seen above, survival in high sand-loading mixtures can be enhanced at high gradients, as long as silt levels are relatively low. However, our results suggest that high silt, associated with moderate to high sand loadings in redds, cannot as easily be mitigated by stronger gradients, at least within the range tested. One possible implication of this is that in rivers with very high suspended silt transport regimes, particular riffle zones with unusually high subsurface hydraulic gradient conditions may not be as important to stock reproduction as they may be in sand-rich, low-silt systems.

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Correction after posting

After this article was posted, it came to our attention that the *y* axis of Fig. 5 (which read % Silt) in the Results section was mislabelled. This figure has now been corrected.

The paper was originally posted at 0600 on 10 February 2005. The correction was posted at 1000 on 17 February 2005.

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