North American Journal of Fisheries Management

Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/ujfm20

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To link to this article: http://dx.doi.org/10.1080/02755947.2012.741556

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Multicompartment Gravel Bed Flume to Evaluate Swim-Up Success of Salmonid Larvae

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Abstract
Swim-up success, the proportion of fry emerging from a gravel redd, is difficult to quantify in the field, and currently available laboratory systems are limited. We used custom-built gravel bed flumes to assess the swim-up success of Rainbow Trout Oncorhynchus mykiss, Brook Trout Salvelinus fontinalis, and Cutthroat Trout Oncorhynchus clarkii. Flumes were built with compartments to separate individual egg batches, eggs were buried under gravel, and oxygenated water was supplied to simulate upwelling through the gravel. Temperature, dissolved oxygen, pH, and flow were constant between compartments and flumes operating in parallel. Swim-up success was scored both by the emergence of fry relative to the number of eggs placed in the flume (59–85% depending on species) and the hatching success (proportion of eggs that hatch and resorb their yolk sac) of a sample from the same clutch reared in a vertical incubator (62–84% depending on species). The gravel bed flumes could be used to estimate the swim-up success of salmonid egg clutches from hatchery stocks or fish from the wild or under experimental regimes of relevance to fishery or environmental assessment, including changes in pH, siltation, temperature, toxicants, or events simulating floods or droughts.

Reproductive endpoints are used to compare the performance of individuals, genetic strains, or populations and to evaluate the impacts of environmental stressors (Barlaup et al. 1994; Brännäs 1995), swim-up success is a key reproductive endpoint and a potential bottleneck for recruitment of populations (Coleman and Fausch 2007). It is difficult to capture newly emerged fry in the field and relate these to the number of eggs laid, and systems used in the laboratory to estimate swim-up success are limited by the small number of clutches they can accommodate and the flow characteristics. We describe here a custom-built, multicompartment gravel bed flume that was used to estimate swim-up success of up to 18 egg clutches simultaneously and simulate conditions optimal for developing salmonid larvae.

In the wild, salmonids locate suitable spawning sites based on species-specific habitat characteristics, including adequate stream flow, groundwater upwelling, and substrate (Crisp and Carling 1989; Snucins et al. 1992; Curry et al. 1995; Malcolm et al. 2003). Fertilized eggs are deposited into a gravel depression created by the spawning pair and covered by flushed up gravel (Barlaup et al. 1994; Blanchfield et al. 2003). Eggs hatch into larvae (alevins) which remain underground until most or all of their yolk has been absorbed, and the “buttoned-up” fry swim up to the surface through the interstitial spaces of the gravel. This phenomenon, referred to as “swim-up”, is an important test of larval fitness (Brännäs 1989). Many factors can impede swim-up of fry, including fine sediments clogging interstitial spaces, larval deformities, and edema (Kondolf 2000; Sternecker and Geist 2010). Moreover, prior to emergence many eggs and alevins...
die from lack of oxygen, fungus, predation, or disease (Snucins et al. 1992; Rubin 1995; Dumas and Marty 2006).

Swim-up is challenging to study in the field because fry are difficult to capture, swim-up can occur over an extended period, and the number of eggs buried by spawning fish is not known (Rubin 1995; Groves et al. 2008). Researchers have simulated redds in the laboratory, where a known number of eggs is placed in an artificial redd and all fry that emerge are captured. One of the first designs was a gravel-filled box, with water entering from the top and trickling down through the gravel (Dill 1970). Eggs or alevins were inserted under the gravel using a pipe. Godin (1980) modified this design by switching the inflow and outflow pipes to create upwelling, and Fraser et al. (1994) placed this “redd box” in a flume with an outflow at the back of the flume and space behind the box to retain swim-up. Other designs covered the gravel with plastic, leaving larvae to swim up through the pipes (Godin 1980; Brännäs 1989; Mirza et al. 2001; Sundström et al. 2005). Palm et al. (2009) buried eggs under gravel at the bottom of an aquarium and used a propeller at the front of the tank to increase water velocity.

To allow separation of individual clutches to compare swim-up success of egg batches from different females under the same conditions, Fudge et al. (2008) divided the box into compartments separated by mesh screens and created upwelling through pipes in the bottom. A pump was installed at one side of the box to increase water flow and an intake at the other end allowed recirculation of water. This design separated egg batches and provided upwelling, but it did not simulate natural stream flow, as the water was funnelled towards the outflows located at the back of the central compartment. Sternecker and Geist (2010) used four-compartment boxes arranged in series in a flume, with water delivered through the front of the flume, entering the boxes through mesh screen at the bottom and exiting through a screen at the back of the box.

The objective of the present study was to create artificial redds in a gravel bed flume that had separate compartments for multiple \((n = 18)\) egg batches to be tested simultaneously, with constant upwelling and flow through each compartment. The flume was designed to make the collection of swim-up larvae easy and accurate, to allow for flexibility in the size of the compartments, to increase ease of dismantling and storage, to provide potential for use in the field, and to be built with low cost materials. To test the performance of our artificial redd flume, we compared swim-up success in three species, Rainbow Trout \(Oncorhynchus mykiss\), Brook Trout \(Salvelinus fontinalis\), and Cutthroat Trout \(Oncorhynchus clarkii\).

**METHODS**

**Experimental approach.**—A known number of eggs from each clutch was deposited into compartments of two custom-built gravel flumes to estimate the proportion of larvae that emerged from the gravel (swim-up), and simultaneously a subsample of the eggs from each clutch was placed into a vertical incubator tray to estimate hatching success (proportion of eggs that hatch and resorb their yolk sac, i.e. “button-up”). Swim-up success then represents the proportion of the eggs that hatched and emerged above gravel, divided by the proportion of fry that hatched and resorbed their yolk sac in the vertical incubator.

**Flume design.**—Two replicate flumes were made from sheets of plexiglass bonded together with methylene chloride. The dimensions of the flumes were 200 cm (length) \(\times\) 40 cm (width) \(\times\) 30 cm (height), with 8-mm notches (4-mm deep) cut in the side panel every 10 cm along the length of the flumes, for insertion of removable dividers (Figure 1) to create 20 compartments. Dividers were made by bonding aluminum window screen between two plexiglass frames, 40 cm (length) \(\times\) 25 cm (height) \(\times\) 4.76 mm (width) and 3.175 mm (width), with a 5-cm border. The outflow hole (dia\(\text{meter} = 1.9 \text{ cm}\)) was drilled 44 mm from the top center of the back panel and a bulkhead was placed in the hole to streamline water flow out of the downstream end of the flume (Figure 1).

Treated dechlorinated (City of Lethbridge) water was delivered at 32 pounds per square inch gauge through a 2.54-cm-diameter hose connected to a PVC pipe (dia\(\text{meter} = 6.35 \text{ cm}\)) that ran the length of each flume. From this pipe, five PVC pipes (dia\(\text{meter} = 1.27 \text{ cm}\)) entered the flume at compartment 2, 6, 10, 14, and 18 and connected to forks with four capped prongs that ran along the bottom of the flume to supply water to sections A–E of the flume (Figure 1). Five evenly spaced perforations (dia\(\text{meter} = 0.16 \text{ cm}\)) were drilled into each prong running along the bottom of each compartment, ensuring each compartment had its own water flow upwelling through the gravel (see *Gravel bed simulation*, below), as shown in Figure 1. Ball valves were placed in between the pipe connected to the hose and the main pipe running the length of the flume and also on each pipe that ran into the flume from the main pipe. Ball valves were partially closed at the top of the flume, closest to the water source, and left open at the bottom of the flume to create uniform water pressure and flow throughout the entire flume, as pressure decreased along the main pipe due to distance from the water source. Flumes were flushed for several days with treated water to ensure any residue from the bonding agents as well as air pockets, which could cause interference in flow, were removed from the pipes. Each compartment was then filled with gravel, and flushed with processed water for a minimum of 24 h, before fertilized eggs were deposited at a specific depth under the gravel (see *Gravel bed simulation*).

**Vertical incubator.**—A 16 tray MariSource vertical incubator was used in this study to compare hatching success ([number of buttoned-up fry/number of eggs deposited in incubator trays] \(\times\) 100) in the incubator and emergence of swim-up fry in the flumes ([number of fry emerged from gravel/number of eggs deposited in flume redd compartment] \(\times\) 100). The incubator was also used to compare lag time between development of larvae in the incubator and appearance of fish larvae above the gravel in the flumes.
**FIGURE 1.** Flume schematic presented in sections (A–E) to demonstrate chronological time in the experiment: A–empty flume with PVC pipes, B–compartments separated by screens with 5 cm of gravel (for Rainbow Trout) added to the compartments, C–eyed eggs added in oval-shaped “redd”, D–compartments have gravel topped up to 20 cm, and E–emerged fry appear above the gravel in each compartment. (Two replicates flumes were used in each experiment; only one flume is shown in the schematic).

**Water parameters.**—Water quality parameters were recorded in three areas of each flume; the first section (top), midway (middle), and just before outflow (bottom). Subtle adjustments to flow rate (3.5–4.0 L/min) or ball valve positions were executed in order to maintain equal flow conditions in all compartments of the flumes. Dissolved oxygen and temperature were measured using a YSI-85 probe, and pH was measured using a CEL850 Sension I portable pH meter with Platinum Series electrode. The optimal conditions required for swim-up were 8–10°C, water flow of 3.5–4 L/min in the flume and 18–20 L/min in the vertical incubator, pH of 8, and 8–10 mg O₂/L. See Table 1 for water quality data.

**Gravel bed simulation.**—Trout spawning redds were simulated in the experimental flumes to create standardized, optimal conditions for the fry to swim up through the gravel. Two sizes of washed round rock (28 mm and 14 mm) purchased from a local landscaping center were mixed 1:1. These sizes were chosen since similar sizes have been reported for salmonid redds in the literature (Crisp and Carling 1989; Kondolf 2000). The gravel was rinsed with water to remove any fines, disinfected with a 1% Ovadine solution (Syndel Laboratories), and thoroughly rinsed with processed water. Gravel was added to the flumes to a depth of 5 cm for Rainbow Trout (see Figure 1) and 10 cm for Brook Trout and Cutthroat Trout. Eggs were gently deposited (see Placement of eggs and collection of emerged fry, below) onto the gravel, followed by adding 15 cm of gravel for Rainbow Trout, and 10 cm of gravel for Brook and Cutthroat Trout for a total gravel depth of 20 cm (Figure 1). Thus Rainbow Trout eggs were placed deeper in the gravel than the Brook and Cutthroat Trout eggs. The mature Rainbow Trout were much...
TABLE 1. Water quality in the gravel bed flume and in the vertical incubator. Temperature, O₂, and pH are given as mean ± SE. No significant differences were detected between different sections in the flumes tested at the same time (Student’s t-test, P < 0.05).

<table>
<thead>
<tr>
<th>Species</th>
<th>System</th>
<th>Flow rate (L/min)</th>
<th>Area measured</th>
<th>Temperature (°C)</th>
<th>O₂ (mg/L)</th>
<th>pH</th>
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</thead>
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<tr>
<td>Rainbow</td>
<td>Flume 1</td>
<td>3.7</td>
<td>Top</td>
<td>8.51 ± 0.34</td>
<td>9.53 ± 0.36</td>
<td>8.02 ± 0.09</td>
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<td></td>
<td></td>
<td></td>
<td>Middle</td>
<td>7.93 ± 0.21</td>
<td>9.72 ± 0.20</td>
<td>8.06 ± 0.08</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Bottom</td>
<td>7.68 ± 0.13</td>
<td>10.00 ± 0.27</td>
<td>8.11 ± 0.06</td>
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<tr>
<td></td>
<td>Flume 2</td>
<td>3.7</td>
<td>Top</td>
<td>8.06 ± 0.32</td>
<td>9.19 ± 0.30</td>
<td>8.19 ± 0.09</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Middle</td>
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<td>9.76 ± 0.17</td>
<td>8.24 ± 0.08</td>
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<td></td>
<td></td>
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<td>Bottom</td>
<td>7.47 ± 0.15</td>
<td>9.81 ± 0.11</td>
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<td>Incubator</td>
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<td>Bottom</td>
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<td>11.06 ± 0.08</td>
<td>8.24 ± 0.04</td>
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<td>Brook</td>
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<td>Top</td>
<td>9.43 ± 0.02</td>
<td>10.82 ± 0.15</td>
<td>8.34 ± 0.05</td>
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<td>Bottom</td>
<td>9.22 ± 0.03</td>
<td>10.75 ± 0.15</td>
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<tr>
<td></td>
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<td>9.59 ± 0.04</td>
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<td></td>
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<td></td>
<td></td>
<td>Bottom</td>
<td>9.22 ± 0.02</td>
<td>10.58 ± 0.18</td>
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<tr>
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<td>Bottom</td>
<td>10.10 ± 0.01</td>
<td>8.53 ± 0.14</td>
<td>8.35 ± 0.02</td>
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<td>7.85 ± 0.50</td>
<td>8.21 ± 0.05</td>
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<td>8.19 ± 0.08</td>
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<td>Bottom</td>
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<tr>
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<td>9.93 ± 0.08</td>
<td>8.66 ± 0.35</td>
<td>8.21 ± 0.09</td>
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<tr>
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<td></td>
<td></td>
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<td>8.72 ± 0.35</td>
<td>8.17 ± 0.08</td>
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<tr>
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<td></td>
<td></td>
<td>Bottom</td>
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<td>8.71 ± 0.34</td>
<td>8.22 ± 0.06</td>
</tr>
<tr>
<td></td>
<td>Incubator</td>
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<td>Bottom</td>
<td>10.53 ± 0.32</td>
<td>8.96 ± 0.10</td>
<td>8.30 ± 0.10</td>
</tr>
</tbody>
</table>

larger than the other two species and had larger eggs, and the depth to which we decided to bury the eggs was based on the work of Crisp and Carling (1989) and Steen and Quinn (1999), who showed that larger-sized females dug deeper redds.

Adult female fish.—Adult females were selected from the existing broodstock at Allison Creek Brood Trout Station (Coleman, Alberta) and held at the hatchery for the duration of the experiment. Five-year-old Rainbow Trout (n = 9, mean ± SE fork length 65.17 ± 1.25 cm, mean ± SE body weight 3890 ± 33 g), 3-year-old Brook Trout (n = 9, mean ± SE fork length 39.33 ± 0.76 cm, mean ± SE body weight 937 ± 83 g), and 3-year-old Cutthroat Trout (n = 9, mean ± SE fork length 35.23 ± 0.87 cm, mean ± SE body weight 497 ± 33 g) were used in the experiments. Adult Rainbow Trout were held from August 2009 to December 2009 until they were spawned and eggs were collected. Brook Trout were held from July 2010 to November 2010 until spawned, while Cutthroat Trout were held from December 2010 to April 2011. All adult females were fed EWOS Salmonid Brood Feed trout chow throughout the entire period. Experimental protocols were approved by the Animal Welfare Committee (University of Lethbridge) in accordance with Canadian Council on Animal Care guidelines.

Placement of eggs and collection of emerged fry.—As the predicted spawning season neared, fish were anaesthetized and examined for signs of maturation (a soft underside). Females identified as ready for spawning were injected with Ovaprim (Syndel Laboratories) at 0.5 mL/kg body weight to induce ovulation. A week later fish were euthanized with tricaine methane-sulfonate (MS-222; 0.1 g/L) and gently squeezed to extrude eggs into labeled, individual spawning pails. Milt pooled from multiple males was used to fertilize the eggs; saline solution (0.6% NaCl) was added to improve sperm motility and aid mixing. Eggs were rinsed after 2 min and placed into a pail of water for 2 h to water harden. When the eggs were firm to the touch, a subsample from each clutch was placed single file on a V-shaped trough that was 30 cm × 2 cm and counted. The number of eggs per liter and average size of eggs was determined for each adult female using the von Bayer egg chart (von Bayer 1950). Total volume of eggs produced per female was determined using glass beakers before eggs were placed in an incubator tray. Trays with the eggs were placed into a tub with Ovadine (1%) for 5 min and then set in the vertical incubator. Iodophor treatment is a standard fish hatchery practice to reduce the bacterial load on the eggs. Eggs were incubated at the Allison Creek Brood Trout Station until the eyed stage (eye pigment spots were visible), and then a subsample from each female was transported to the Aquatic Research Facility at the University of Lethbridge for the flume swim-up experiment. Eggs were transported by ground (150 km) in plastic mesh tubes, wrapped in wet foam, in a cooler with ice.
Upon arrival, the tubes were soaked in a 1% Ovadine solution for 5 min then rinsed with processed water. Eggs from individual females were placed in a beaker to measure the total volume and ensure that a known number of eyed eggs from individual females were deposited into labeled compartments of the two experimental gravel bed flumes. Approximately 1000 eggs/compartment redd were placed for Rainbow Trout (December 2009) and Brook Trout (November 2010), and 450 eggs/compartment redd were placed for Cutthroat Trout (April 2011) due to lower numbers of eggs spawned per female. Eggs were gently poured in an oval-shape formation onto the gravel bed in each compartment (Figure 1) to simulate a redd. Gravel was then gently added by hand until the eggs were fully covered, and the remaining gravel was slowly poured on to reach a total gravel depth of 20 cm. Eggs were not added to compartment 1 or compartment 20, where gravel lies between a flow-through divider and a solid pane (Figure 1). The remaining eggs at the Allison Creek Trout Brood station were kept in the vertical incubator until alevin had absorbed their yolk sac. The fish were then euthanized with MS-222 and stored in Davidson’s solution (50% formalin, 10% acetic acid, 10% glycerol, 30% ethanol). Fish that appeared above the gravel were collected every day using a small net and a large pipette. Fish were euthanized with MS-222, counted, and stored in jars of Davidson’s solution. Fry collected from each compartment were stored in one jar. Data were analyzed using JMP software from SAS, and ANOVAs with a Student’s t-test done post hoc were used on the data.

RESULTS

There were no significant differences in dissolved oxygen, temperature, or pH between different sections (top, middle, bottom) of individual flumes (Table 1) or between flumes tested at the same time within the incubation period (December 2009–March 2010 for Rainbow Trout eggs, November 2010–March 2011 for Brook Trout eggs, and April 2011–June 2011 for Cutthroat Trout eggs). Water quality and flow remained constant even when all flume compartments were filled with eggs.

A significant difference in emergence success ([number of swim-up fry/number of eggs buried] × 100) was detected between species (Figure 2; Student’s t-test: $t = 2.07$, df = 24, $P < 0.05$). While Rainbow Trout and Cutthroat Trout had mean ± SE emergence success of 58.1 ± 9.7% and 52.9 ± 5.6%, respectively, the emergence success of Brook Trout was significantly higher at 85.2 ± 6.4%. The success of hatching and survival to the fry stage (buttoned-up or yolkless fry) in the vertical incubator was similar; the mean ± SE was 58.1 ± 9.7% for Rainbow Trout, 61.9 ± 4.8% for Cutthroat Trout, and 82.7 ± 6.9% for Brook Trout and not significantly different from emergence success for any of the species. The swim-up success, calculated as emergence success/hatching success, was ∼100% (85.2/82.7) for Brook Trout, 85% (52.9/61.9) for Cutthroat Trout, and 94% (58.1/61.5) for Rainbow Trout. These estimates were not significantly different from each other or from 100%.

FIGURE 2. Emergence success ([number of emerged fry/number of eggs placed in gravel redd compartment] × 100; mean ± SE) and hatching success ([number of buttoned-up fry/number of eggs placed in vertical incubator] × 100; mean ± SE) scored for individual females from each species (Rainbow Trout $n = 7$, Brook Trout $n = 9$, Cutthroat Trout $n = 9$). Different letters indicate a significant difference; small letters for hatching success, capital letters for emergence (Student’s t-test, $P < 0.05$).
Mean egg diameter was 5.31 mm, 4.45 mm, and 4.32 mm for Rainbow Trout, Brook Trout, and Cutthroat Trout, respectively; however, no correlation was observed for emergence success based on egg size (Figure 3).

The timing of emergence, which closely corresponded to the appearance of buttoned-up fry in the vertical incubator, is illustrated by S-shaped curves (Figure 4) with different slopes and ranges and appears species-specific, with differences in the
The simultaneous use of the vertical incubator to evaluate hatching success with a sample of eggs from each female provided a unique approach to estimate the true swim-up success, by dividing emergence success in the flume by hatching success in the vertical incubator. Since the estimates for emergence success and hatching success were not significantly different for any of the species (Figure 2), the estimates of swim-up success were not significantly different from 100%. In order to achieve more precise estimates, more clutches would be required. The average SD among clutches for both emergence and hatching success for the three species was 30%. Thus if two flumes were used at full capacity \( (n = 36) \), then SE estimates of 5% \( (\approx 30/\sqrt{36}) \) could be expected for both measures and SE of \( \approx 7\% \) would be expected for swim-up success. If greater precision was required, more flumes could be operated in parallel.

An important aspect of the flume was the depth of gravel in the artificial redds. To simulate natural conditions where larger females dig deeper redds (Crisp and Curling 1989), and since Rainbow Trout females in this study were larger than Brook Trout and Cutthroat Trout females, eggs from Rainbow Trout were placed under 15 cm of gravel while eggs from the other two species were placed under 10 cm of gravel. Since for all three species the hatching success and the emergence success were similar, the depth of egg burial of 10–15 cm appeared to have had little or no influence on either emergence or swim-up success. The effect of gravel depth on emergence success can be further investigated using the experimental system described here. To accommodate species that bury their eggs deeper than 15 cm, a deeper flume would be required to provide sufficient space for the gravel and for water flowing over the gravel.

Emergence of all three species from the gravel followed an S-shaped curve, with species-specific patterns of timing of appearance of the first larvae, numbers collected, and duration of the emergence period. These patterns closely mimicked the differences in developmental time between the three species observed in the vertical incubator, including the earlier emergence of Cutthroat Trout larvae (Sadler et al. 1986; Wagner et al. 2006), providing additional validation for the use of the gravel bed flume. It was noted that some of the early emerging Rainbow Trout and Brook Trout fry collected above the gravel still had partial yolk sacs. In our experiment there was no food given to entice the fry to the surface, so it is not clear why some fry appeared above the gravel at such an early stage. The environmental cues used by fry in the timing of the emergence could be investigated in the experimental gravel bed flume described here.

Our results indicate that the experimental gravel bed flumes can be used in the laboratory for a quantitative assessment of the swim-up success in salmonids. Uniform water quality \( (pH, \text{temperature, dissolved oxygen}) \) was achieved throughout each flume and it was possible to replicate these conditions in two different flumes running at the same time. A major improvement of our design, compared with the most recently developed systems (Fudge et al. 2008; Palm et al. 2009) is the delivery of water using five supply pipes branching into a total of 20 perforated prongs, lying below the gravel and supplying upwelling water to individual compartments. The upwelling system delivered water at a fast enough rate \( (3.5–4.0 \text{ L/min}) \) to maintain constant oxygen concentrations and temperature in different sections of the flume, despite an overall flow from the upstream (top section E) to downstream section (bottom section A). The flumes have not been tested for consistency of delivery of toxicants or other stressors; additional validation studies would be required. The flumes were affordable \( (\approx \$1000/\text{flume}) \) and easy to build. At the completion of the experiment, the flumes, pipes, and screens were rinsed with 1% Ovadine solution and dechlorinated water, all the PVC pipes were disconnected, the screens were removed, and the flumes were stacked for storage. The flumes could be used in the field with field-collected eggs; however, minor structural modifications would be required.

The design can be improved in future experiments by including a sturdy supporting base to hold the flumes at a waist height,
rather than having them on the floor as in the current study, to improve ergonomics while collecting swim-up. Stainless steel screens, rather than aluminum mesh, would also improve the durability of the divider mesh screens. Use of flexible plastic tubing (i.e., Tygon), instead of PVC, for the forks leading into the flumes would eliminate the need for a large number of 90° elbow connections. Positioning of the perforated bottom pipes could be also modified to avoid having to cut a corner out of some of the dividers (Figure 1) where foam had to be inserted to block movement of the fry between compartments. The experimental gravel bed flume described in this study offers exciting possibilities for future experiments to investigate the effects of temperature, oxygen saturation, gravel depth, siltation, toxicants, and flow rates on the swim-up success of larvae and to determine species-specific requirements. The experimental system described here would be a valuable tool for assessment of swim-up success of hatchery brood stocks or wild stocks and for predicting the impact of environmental stressors on the reproductive success of salmonids and other fish species that bury their eggs in gravel.

ACKNOWLEDGMENTS

We thank H. Bird, J. Fears, and K. Neilson for their tireless collection of swim-up, the Allison Creek Brook Trout Station staff for their expertise on spawning fish and egg incubation, and Sarah Bogart for the technical drawing of the flume. This project was funded by the Alberta Conservation Association and Metals in the Human Environment (MITHE)-NSERC Strategic Network.

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