Emergence of Atlantic Salmon Fry from Gravels of Varying Composition: A Laboratory Study

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by

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ABSTRACT

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Atlantic salmon eggs were incubated in various gravel and sand mixtures with various water flows and two directions of water current. Fine sand (0.06-0.5 mm) was more effective than coarse sand (0.5-2.2 mm) in reducing numbers of emergent fry. The number of fry emerging was related to the formula $S_f/8 + S_c/16$ where S_f = proportion of fine sand and S_c proportion of coarse sand in the gravel mixture. Emergence was not affected by reduction of water supply to the eggs. Strong upwelling water currents mitigated the effects of sand to some degree. Upwelling water currents also induced earlier fry emergence. There was a tendency for smaller fry to emerge later.

Key words: Atlantic salmon, gravel composition, fry emergence, coarse sand, fine sand

RÉSUMÉ

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On a fait incuber des oeufs de saumon de l'Atlantique dans divers mélanges de sable et de gravier tout en faisant varier le débit d'eau et en maintenant une circulation d'eau dans les deux sens. La réduction du nombre d'alevins sortant du mélange fut plus marquée avec le sable fin (0,06 à 0,5 mm) qu'avec le gros sable (0,5 à 2.2 mm). Le nombre de sorties a été associé à la formule $S_f/8 + S_g/16$ où S_f = la proportion de sable fin et S_g = la proportion de gros sable dans le mélange de gravier. La diminution du débit d'eau n'a pas eu d'effet sur la sortie des alevins. De puissants courants de remontée ont jusqu'à un certain point atténué les effets du sable et provoqué une sortie plus rapide des alevins. Les alevins plus petits avaient tendance à sortir du gravier plus tard.

INTRODUCTION

Atlantic salmon (Salmo salar L.) deposit their eggs in excavations in stream gravels. The eggs are then covered to a depth of about 30 cm.

Experiments with eggs artificially incubated in gravels have been performed from two points of view. On the one hand, evidence has accumulated, particularly for Pacific salmon species, that fry obtained from gravel incubation have superior stream survival qualities over fry obtained from more traditional hatchery methods (Bams and Crabtree 1976; Mead and Woodall 1968). On the other hand, several investigations, the present one included, have been concerned with the deleterious effects of fine sediments on the survival of salmon eggs and alevins during their residence within the medium (Hausle and Coble 1976; Hall and Lantz 1969; Wickett 1958; Shaw and Maga 1943; Hobbs 1937; Shapovalov 1937).

Fine sediments may decrease egg and alevin survival by reducing the permeability of the gravel to water percolation, thereby denying the required oxygen for proper development (Terhune 1958). The relationship between dissolved oxygen concentrations and minimal required water velocities has been investigated for steelhead trout and chinook salmon embryos (Silver et al. 1963). In addition, it has been suggested that fine sediments may also decrease emergence success by "trapping" fry within the gravel (Koski 1966, in Hall and Lantz 1969; Hausle and Coble 1976; Phillips et al. 1975), perhaps by impeding alevin movement. The relative impact of various sized sand fractions has not been studied previously.

In this laboratory study we examined the influence of the amounts and particle sizes of fine sediments on emergence success expressed as a percentage of total number of eggs buried, time of emergence, and size of emerged fry. Differences in the influence of two size fractions of sand on the above parameters were investigated. We have also examined, to a lesser degree, emergence under differing percolation rates through the gravel mixtures.

MATERIALS AND METHODS

APPARATUS

Two types of apparatus were used to incubate eggs in the gravel mixtures. That used most was a column of polyvinyl pipe (Fig. 1A) of 14.5 cm I.D. The column floor was a plastic disc screen perforated with 3-mm diameter holes (6-7/cm^2). The perimeter of this floor formed a dam around the outside of the pipe to prevent water from flowing out of the system between the inside of the column and the gravel it contained. Gravel filled the apparatus to a depth of 24.5 cm with the eggs buried at a depth of 16.5 cm. The top of the gravel was about 2 cm below the water surface as determined by the lower level of a screen in the side of the column.

Supply water flowed into the top of the column in excess of the percolation rate through the column, thus maintaining a constant head. The excess water flowed out through the side screen and down the outside of the column. Percolation water was collected in a funnel glued to the floor and the flow rate was controlled with a hose clamp at the elbow on the bottom of the funnel. A hole at the bottom of the elbow was kept stoppered except immediately after the addition of gravel to the column, when it was unstoppered briefly to permit exit of the small amount of fine sediments which passed through the perforated floor.

While most of the experiments were performed with the columns described above, a second type of

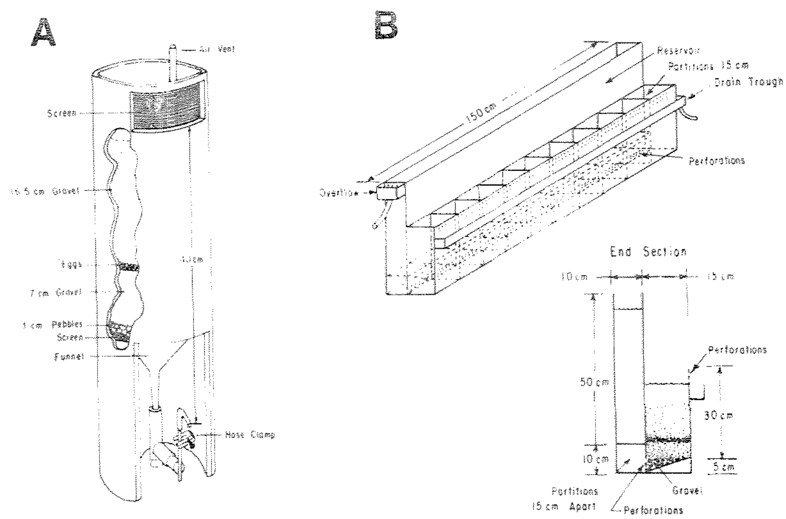

Fig. 1. A. Diagram of a column in which eggs were reared in various gravel mixtures. Water flowed into the top of the column and out the bottom where flow rate was controlled by a hose clamp.

B. Diagrams of the chambers. The taller compartment provided hydraulic head with water flowing from it into the gravel through the perforations. Water then flowed upward through the gravel and out the upper set of perforations into the drain trough.

apparatus (Fig. 1B) called "chambers" and constructed of black, 0.6-cm thick plexiglas was used in one series of experiments. Supply water flowed into a 150 x 10 x 60 cm high reservoir to form the water head. The water then flowed through perforations in the lowest 5 cm of the inside wall of the reservoir into 10 chambers (10 x 15 x 60 cm), each of which contained a gravel mixture to a depth of 25 cm. Water percolated upward through the gravel in the chambers (as opposed to downward in the columns described above), then out through perforations in the top of the outer chamber wall into a drain trough. Percolation rates could be increased by removing Silastic® plugs from perforations in the reservoir. Eggs were buried at a depth of 16.5 cm as for the columns. Much higher percolation rates were used in the chambers than in the columns. The numbers of columns and chambers used each year of the experiments are given in Table 1. The chambers with upward, much faster flow rates were used to see if the deleterious effects of sand could be offset by a strong upward water current.

EGGS AND FRY

The eggs used were of Miramichi River stock in 1974-75, of Magaguadavic River stock for the next 3 yr, and of Waweig River stock in 1979-80. All eggs were stripped, fertilized, water hardened, then placed in the columns or chambers within 12 h after fertilization. The eggs were buried in the gravel mixtures as follows. First, a layer of fine to medium gravel (2.3-22.0 mm particle size) was added to the apparatus to a depth of 1 cm to prevent loss of sand through the floor perforations and to provide a shield against possible downward movement of alevins (Dill and Northcote 1970). A layer of the appropriate gravel mixture was added to a depth of 7 cm. The eggs (50 per column or chamber) were then distributed over the gravel and covered to a depth of 16.5 cm with the gravel mixture. All such additions were made with the apparatus filled with water to reduce the possibilities of crushing eggs while adding the gravel and of trapping air. In each year five to six groups of 100 eggs were incubated in plexiglas incubating boxes to determine the percentage of non-viable eggs. In 1976-77, 40% of the eggs were not viable, so this percentage was used to correct for the numbers of emergent fry from the columns. In all other years the numbers of non-viable eggs amounted to less than 10% and no corrections were applied.

The gravel surfaces of the columns and chambers were checked occasionally for emerged fry while measuring temperatures and percolation rates until emergence was considered imminent. Thereafter, they were checked once or (usually) twice daily. Fry were removed by suction, anaesthetized, and measured (fork length).

GRAVEL AND SAND MIXTURES

The gravel mixtures used in the experiments consisted of a basic ratio of coarse gravel (particle size 22.0-62.0 mm) to medium-fine gravel (2.3- 22.0 mm) of about 5:3 (1.67 - range of 1.0-4.2) (Table 1). The mean ratio approximates that found in natural Atlantic salmon spawning areas (Peterson 1978). "Control" mixtures contained only the two gravel fractions, while up to 35.6% "coarse sand" (0.5-2.3 mm) by weight and 10.9% "fine sand" (0.06-0.5 mm) were added to the test mixtures in varying combinations (Fig. 2). One week after emergence had terminated, the contents of each chamber and column were wet sieved into the four fractions. After inspection of the sieved fractions for eggs and alevins, each gravel fraction was dried and weighed, and the percent composition of the various fractions determined. The percentages given in this report are final percentages obtained after sieving the columns.

The gravel from 17 columns and 8 chambers was removed in four quarters (from top to bottom) for sieving. Sand tended to settle to the bottom during the experiment (Table 2). Settling was more pronounced in the columns than in the chambers, perhaps due to some countering effect of the greater upwelling water velocities in the latter apparatus. Two columns were frozen prior to quartering and sieving the contents to see if stratification occurred during removal of the gravel. Stratification had occurred to a similar extent in those two columns. The degree of stratification appeared to be independent of the total amount of sand present (Table 2). For purposes of relating numbers of emergent fry to amounts of sand in the gravel, the average percentages of coarse and fine sands for the entire column were used. The eggs were placed near the bottom of the third quarter which contained about as much sand as the average for the columns. Most dead eggs and alevins were also recovered near this depth.

Media porosity (which we define as the percentage of the total column or chamber volume not

Table 1. Numbers of columns and chambers and coarse gravel (22-62 mm) to medium gravel (2.3-22 mm) ratios for the five years when experiments were performed. One column in 1975-76 and one in 1979-80 are omitted from the analyses due to failure of water supply.

Year	No. of columns	No. of chambers	Mean coarse/medium gravel ratio for for all columns or chambers	Range of ratios for individual columns or chambers
1974-75	14	0	1.77	1.21-2.40
1975-76	26	0	2.49	1.04-4.27
1976-77	12	0	1.85	1.55-2.21
1977-78	12	10	1.70	1.40-2.03
1979-80	14	0	1.43	1.31-1.65

Table 2. Stratification of sand in columns and chambers. Figures are mean percentages of the total amount of sand for 17 columns and 8 chambers.

	Coarse sand Top 1/4	Coarse sand 2nd 1/4	Coarse sand 3rd 1/4	Coarse sand bottom 1/4	Fine sand Top 1/4	Fine sand 2nd 1/4	Fine sand 3rd 1/4	Fine sand bottom 1/4
Columns	13.1	19.4	23.9	43.6	15.8	21.6	24.7	38.9
(ranges)	(0-21.7)	(14.0-33.3)	(18.7-31.3)	(30.0-58.0)	(0-28.0)	(10.2-30.0)	(13.0-36.1)	(21.2-50.8)
Chambers	19.4	22.4	19.0	39.1	19.8	27.2	20.8	35.7
	(8.4-25.3)	(9.6-30.2)	(7.4-21.3)	(31.2-66.7)	(0-66.7)	(0-66.7)	(0-23.0)	(28.0-56.8)

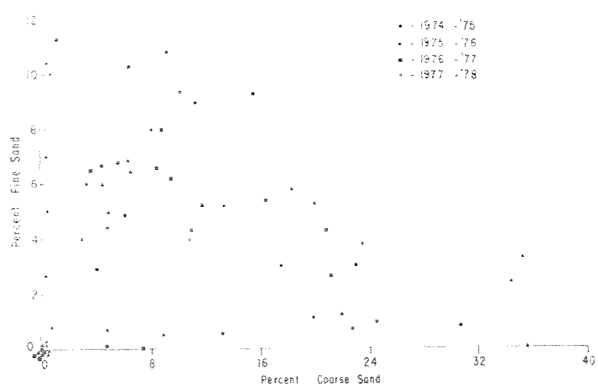

Fig. 2. The combinations of coarse and fine sand (as percentages of total gravel weight) used in the columns for the years indicated.

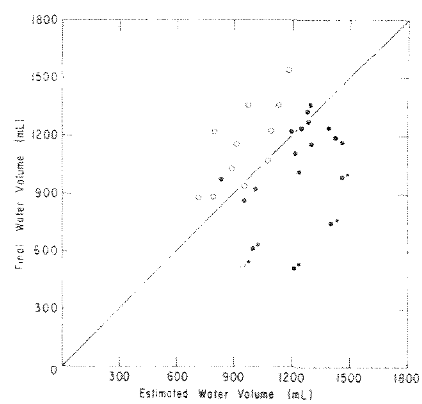

Fig. 3. Estimates of water volumes contained within columns of various gravels. The "drained" water volume was measured by draining the column after emergence was complete. The "displaced" water volume was obtained by pouring the dried gravel mixture from the column into a known volume of water to estimate gravel volume. This figure was then subtracted from total column volume. For further discussion see text. Closed circles, 1975-76 experiments; open circles, 1977-78 experiments. Asterisks indicate columns in which air entrapment may have occurred.

occupied by solids) was obtained for all columns and chambers upon completion of the tests by measuring the volume of water drained from the top of the gravel and sand mixture, subtracting the volume of funnel and elbow and adding the water content of the wet medium ("drained" water volume, Fig. 3). Porosity was also estimated for 30 columns by pouring the dried medium mixture into a known volume of water. The increase in volume equals the volume of the gravel mixture. Subtracting this volume from the column volume yielded an estimate of the pore space ("estimated" water volume of Fig. 3). The values obtained by the two methods were similar in most cases, but with considerable scatter about the line of equality. This scatter is partly due to error in determining the "top" of the gravel in the column, since the gravel surface was irregular. Also, some air became trapped in the columns due to increase in water temperature as it percolated through the gravel. Air accumulation would tend to decrease "drained" water volumes. The five points (asterisks in Fig. 3) lying well below the line may have contained the most air. As will be seen, the flow rates declined in those five columns. Reduction in flow may be associated with air entrapment or packing of sand, as these columns all had high sand contents. The porosity declined as the percentage of sand increased in the gravel mixtures (Fig. 4), and mixtures with little or no sand averaged more than 40% pore space. Part of the scatter in Fig. 4 is attributed to the fact that coarse and fine sand percentages were added, and

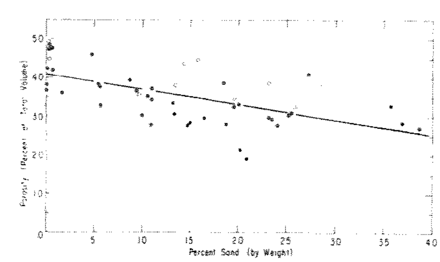

Fig. 4. The porosity (volume of pore space) contained in the gravel mixtures as a function of sand contents. The line of best fit is defined by the equation: porosity = 40.9 - 0.39% sand (r = -0.6, t = 5.14, df = 47). Open circles are data derived from chambers, closed circles from columns.

coarse sand would be more porous than fine sand. Physical characteristics such as angularity and packing arrangement, particularly of the larger sediments, would likely contribute greatly to the variability in porosity.

WATER SUPPLY

The freshwater supply for the Biological Station comes from the town of St. Andrews water mains (Chamcook Lake source) and is dechlorinated before entering the Station lines. The experimental water supply was run from the mains through a Cuno® filter containing an AquaPure® 110 filter cartridge (5 μ pore size cartridge, changed as required) into a 3-m high standpipe of 10-cm diameter polyvinyl pipe where it was vigorously aerated. From the standpipe the water was run to a second, 2-chambered plexiglas header tank where it was first heated, if required, then further aerated before being run into the experimental apparatus.

Water flow rates through the columns and chambers were measured daily. Mean rates in excess of 50 mL/min were maintained for most columns (Fig. 5).

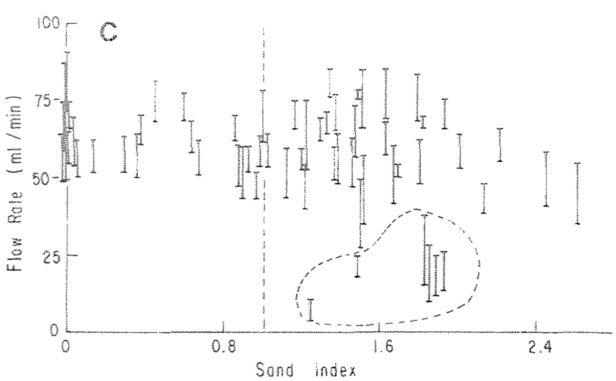

Fig. 5. Percolation rates through the gravel columns (1974-75 to 1977-78 inclusive) expressed as a function of sand index (described in text). Percolation rates for most columns were maintained between 50 and 75 mL/min. Dotted line encloses columns for which the flow decreased during the experiment.

The standard deviations for the percolation rates were quite high, ranging from 10-25 mL/min. Much of this variability occurred in the first few days after filling the columns when sand was settling. In six columns (enclosed by the dotted line in Fig. 5), the rates could not be maintained at the desired level, and declined during the experiment. Five of these columns were those in which air accumulation may have occurred as discussed above. Due to these decreases in flow rates in some of the columns, and the considerable variability in flow rates, 14 columns were operated in 1979-80 at lower flow rates to see if emergence was affected (Table 3). The mean flow rates through these latter columns varied from 12.0-15.2 mL/min with standard deviations of 3.6-9.3. In one column (10, Table 3), the rate could not be raised above 8 mL/min over the last 2 mo. Since there was no indication of air entrapment, slowing of flow was probably due to packing of sand in the column. In one column of 1975-76 flow rate failed over night and this column was discarded as well as the one with lowered flow rate in 1979-80.

Mean flow rates through the chambers (Table 4) were greater than those through the columns (Fig. 5). In chamber 7, with a mean flow rate of 620 mL/min, the flow was sufficient to make the sand "boil" at the surface.

Intragravel water velocity is critical to egg survival and the minimal velocities required depend upon egg diameter, egg-packing densities, temperature, and dissolved oxygen concentration. Egg-packing densities were low in these experiments as the eggs were scattered in essentially a single layer at one depth in the gravel, although clumping occurred to some degree. Temperatures were variable and were highest early in the incubation period, when oxygen requirements of the eggs would be minimal, and near emergence when the fry can actively pump water over the gills. Temperatures during greatest oxygen demand by eggs were 4-5°C. Alderdice et al. (1958) estimated that, for an incubation temperature of 8°C, the minimal velocity required to keep a single layer of eggs alive in air-saturated water was 0.08 cm/min. Bams and Crabtree (1976) advocated velocities of 2.5-3.5 cm/min for eight layers of Pacific salmon eggs in their gravel incubators. Mean interstitial water velocity may be calculated for our experiments by the equation:

$$v \text{ (cm/min)} = \frac{\text{flow rate (mL/min)}}{a \times \frac{P}{100}}$$

where: a = the cross-sectional area of the column,
$\frac{P}{100}$ = the porosity expressed as a fraction.

Obviously, for a constant flow rate and constant cross-sectional area, mean velocity varied inversely with the porosity. For columns with percolation rates of 50-80 mL/min, the calculated intragravel velocities varied from greater than 2 cm/min at low porosities (high sand content) to slightly less than 1 cm/min in columns without sand (Fig. 6). The velocities in gravel mixtures where the flow rates could not be maintained (with asterisks in Fig. 6) averaged about 0.7 cm/min. The velocities in the chambers ranged from 2-10 cm/min. Since the flow rates varied widely among the chambers, there was no obvious relationship to porosity. Porosities were measured for 11 of the 14 columns with percolation rates of about 15 mL/min. These had velocities ranging from 0.45 cm/min for gravels with a lot of sand to 0.2 cm/min for columns with no sand. All calculated velocities are higher than the minimum suggested by Alderdice et al.; although some are low enough perhaps to influence the ultimate size of the emergent fry (Silver et al. 1963). These are mean velocities, and the true interstital velocity at any given site where an egg is developing could vary considerably from this mean value.

Dissolved oxygen concentrations in the effluent water from the gravel columns were measured with a Beckman Model 160 gas analyzer. Measurements were made only occasionally in 1974-75 on columns with flow rates maintained at 50-80 mL/min, but more frequently on columns with flow rates of about 15 mL/min (Table 5). No values less than 85% of air saturation were obtained, although greater local decreases in the columns may have occurred. The effluent showed some supersaturation at the lower temperatures, usually less than 5% but sometimes to

Table 3. Percolation rates through gravel columns in 1979-80 (mL/min). Sand contents (coarse/fine) in parentheses. Distributions of rates appeared nearly normal.

Column no.	1 (0.5/4.5)	2 (4.8/3.9)	3 (0.6/5.0)	4 (4.5/0.1)	5 (8.7/4.4)	6 (0.5/0)	7 (5.4/5.1)	8 (0.3/0)	9 (5.3/9.6)	10 (9.6/9.3)	11 (15.9/0.4)	12 (18.1/0.6)	13 (6.0/9.1)	14 (9.2/9.1)
Mean rate	13.9	14.7	14.7	15.4	14.8	14.4	14.6	15.2	14.7	12.0	14.8	14.9	14.7	14.4
S.D.	7.3	4.8	4.9	9.3	8.0	3.6	4.4	4.6	6.4	4.1	3.4	9.1	6.8	4.6

Table 4. Percolation rates (mL/min) through the chambers. Sand contents (coarse/fine) in parentheses. Distributions of flow rates were nearly symmetrical in distribution.

Chamber no.	1 (0.6/12.8)	2 (0.2/0.05)	3 (9.2/5.1)	4 (8.5/7.3)	5 (10.4/9.2)	6 (23.8/2.0)	7 (22.8/5.5)	8 (8.3/1.3)	9 (20.8/2.3)	10 (0.3/0.05)
Mean rate	437	195	444	146	104	171	620	296	125	320
S.D.	70	108	99	88	33	188	211	125	50	155

Table 5. Dissolved oxygen levels (% saturation) in effluent from gravel columns operated in 1979-80 (mean flow rates ca. 15 mL/min).

Date	Temp. (°C)	Affluent supply	Column no. 1	2	3	4	5	6	7	8	9	10	11	12	13	14
19.XI.79	7	-	89	94	96	98	97	100	98	93	97	91	92	92	88	91
13.XII.79	5.5	-	98	97	97	97	97	97	96	100	99	99	97	99	96	96
9.I.80	4.8	-	97	102	102	102	98	101	101	102	98	100	100	97	99	99
23.I.80	4.5	-	111	102	104	112	106	111	107	94	102	102	100	101	101	102
8.II.80	4.5	-	98	110	107	113	99	107	109	111	105	98	103	100	102	102
19.III.80	7.5	101	82	96	93	98	92	93	97	88	86	93	89	92	92	92

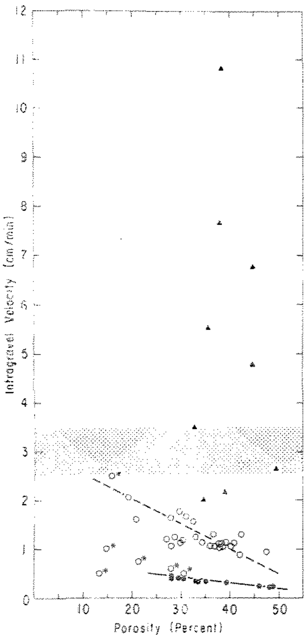

Fig. 6. The relationship between intragravel water velocity and gravel porosity. ▲ - chambers; ● - columns, 1979-80, ○ - columns, other years. Hatched area indicates velocities recommended by Bams and Crabtree (1976).

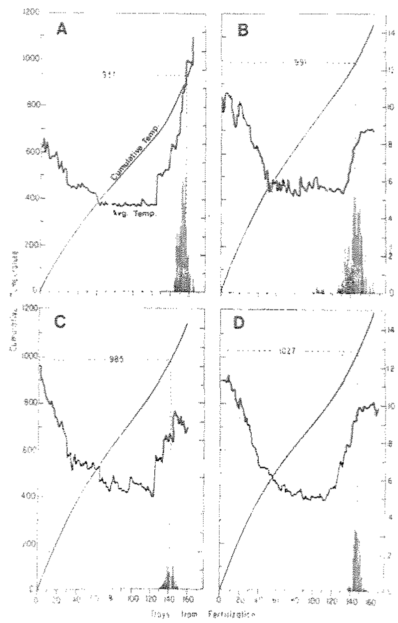

Fig. 7. Daily average temperatures, cumulative temperatures (degree-days) and emergence patterns from the gravel columns in 1974-75 (A), 1975-76 (B), 1976-77 (C) and 1977-78 (D). Dotted vertical line indicates median emergence and, on the horizontal arm, the number of degree-days accumulated to median emergence. The emergence data are pooled for each year.

greater than 10%, which may have been due in part to heating as the water passed through the column. Because of the higher flow rates in the chambers, dissolved oxygen concentrations in the effluent of these were not measured.

Water temperatures of the supply flowing into and out of each column and chamber were monitored daily with a battery-operated thermistor box and probe. The water warmed an average of 0.3°C (range 0.1-1.1) in the columns, less in the chambers, as it percolated through the gravel. This temperature increase was minimized in the columns by the spillage of excess water down the outside walls (ca. 100 mL/min/column). Affluent and effluent temperatures were averaged to estimate the mean incubation temperature. The incubation temperatures followed those of the ambient freshwater supply for most of the incubation period, but for about the last month of the incubation period they were raised gradually from the winter low of 4-5°C to 8-14°C by the end of the emergence period (Fig. 7, 8). Variations in daily incubation temperatures among the columns or chambers for any given year were never greater than 1°C and were usually less than 0.5°C. The chambers averaged 0.5-1.0°C cooler than the columns of the same year.

RESULTS AND DISCUSSION

TEMPORAL DISTRIBUTION OF FRY EMERGENCE AND SIZE OF FRY AT EMERGENCE

Emergence distributions of salmon fry from the columns (Fig. 7, Fig. 8B) and the chambers (Fig. 8A) were apparently nearly symmetrical with no systematic skewness from year to year. These are combined values for all columns or chambers in a given year, so it might be argued that such combination might obscure any pattern inherent in the emergence from individual containers. Inspection of emergence

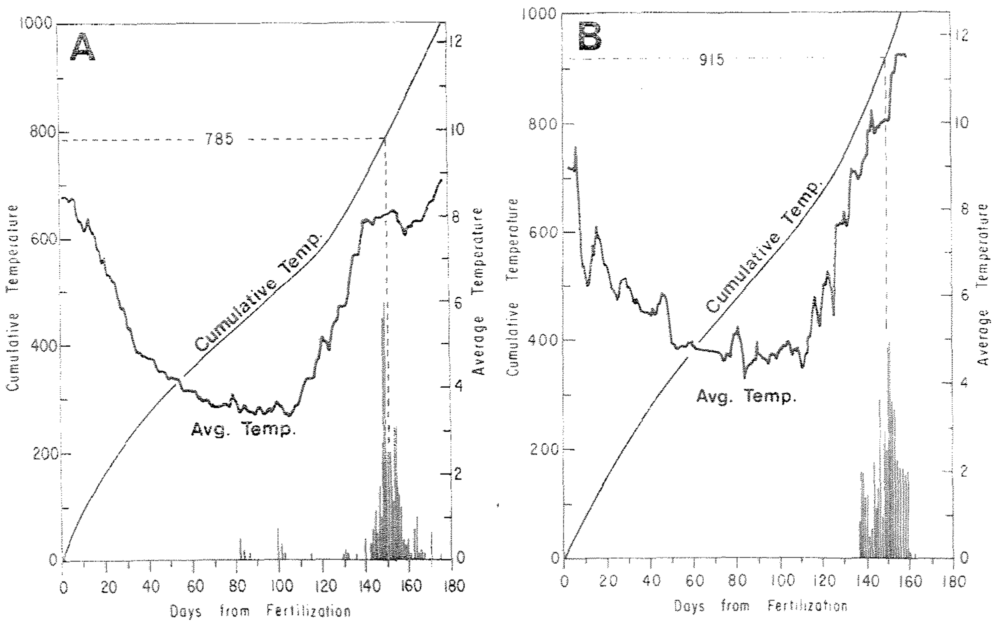

Fig. 8. Daily temperatures, cumulative temperatures and emergence patterns from the chambers in 1977-78 (A) and the columns of 1979-80 (B). Details as in Fig. 2.

patterns from individual containers, however, revealed no consistent deviations from symmetry which could be attributed to the nature of the gravel mixture. The accumulated degree-days to median emergence from the columns were 900-1000 (Fig. 7, 8). The higher values (991, 985, 1027) for 1975-76, 1976-77 and 1977-78 may be associated with the fact that the water supply was not heated as much as in 1974-75 and 1979-80 (937 and 915 degree-days). In the last mentioned, temperatures were higher during the early incubation phases (11-12°C vs 8-9°C), and were increased more rapidly during emergence (12-14°C vs 9-10°C by the end of emergence). The number of degree-days to specific stages of development is not a constant but varies with the incubation temperature regime (Peterson et al. 1977).

The number of degree-days to median emergence in the chambers was much lower (785) than in the columns. Temperatures in the chambers were consistently 1°C lower than in the columns run the same year, yet the times to median emergence were almost identical (150 d). Possibly the stronger upwelling currents in the chambers resulted in faster fry movement upward to the gravel surface.

Hausle and Coble (1976) found that peak emergence was delayed up to 20 d by increasing amounts of sand in the gravel mixtures. This was not the case in our experiments. For 11 columns with sand indices (this term will be defined later) greater than 1.2, and showing (reduced) emergence, the median emergence times averaged only 1 d less than the average of the median emergence time for all columns of the same year.

In two columns and one chamber, fry with large amounts of yolk (less than half the yolk resorbed) emerged "prematurely" (Table 6). In all three instances the gravels contained much sand - mostly coarse sand. The chamber from which 18 premature fry emerged had very high upwelling water velocities (ca. 600 mL/min) so that the sand "boiled" at the surface. This strong upward flow may have facilitated the movement of, or by itself moved, these relatively undeveloped alevins to the gravel surface. McCart (1967) found that up to 60% of sockeye fry (O. nerka) from the upper Babine River, particularly downstream migrants, migrated to Babine Lake in the yolk-sac stage. Early emergence of yolk-sac fry was associated with temperature increases. Mead and Woodall (1968) also obtained premature fry from their artificial incubation pens in Weaver Creek. Shelton (1955), Bams (1969), and Phillips et al. (1975) also observed the emergence of premature chinook (O. tshawytscha) and coho (O. kisutch) fry in their studies. Premature emergence (as defined in the first sentence of the paragraph) occurred only in three of our containers, all of which had high percentages of sand. It is considered probable that the premature emergence in these experiments is in response to an adverse intragravel environment. Premature emergence may be abetted by strong upwelling currents. Whether or not premature emergence occurs naturally for Atlantic salmon, as is apparently the case for sockeye fry, is unknown. Peterson (1978) obtained "premature" Atlantic salmon fry in emergence traps from artificial redds. These emergences may have been due to disturbance during trap installation.

The mean lengths of fry at emergence varied among the various years when experiments were performed (Table 7). These differences are probably not related to differences in gravel incubation procedures in different years, as similar differences were noted for the same lots of eggs reared under other circumstances (Peterson et al. 1977). They are more likely related to variations in egg sizes among the different years. There were no significant differences between the sizes of fry

Table 6. Numbers of "prematurely" emerging fry, their size, and associated sand indices.

Container	Coarse sand %	Fine sand %	Sand index	Mean alevin length and range (mm)	No. emerged
Chamber (1)	22.8	5.5	2.11	22.0 (20-23.5)	18
Column (2)	35.3	3.3	2.62	20.8 (15.1-21.5)	7
	34.5	2.4	2.46	21.0 -	2

Table 7. Mean lengths (mm) of emergent fry as related to sand index and emergence sequence. The quartile refers to the relative times of emergence with fry in the first quartile being the first 25% of the fry to emerge. N - number of columns:number of fry measured. The test of significance was a one-way ANOVA. Time to emergence is from fertilization. Emergence period is time from beginning to end of emergence averaged for all columns of each group. The analysis was applied only to groups where 12 or more fry emerged. One asterisk indicates $p < 0.05$, two indicate $p < 0.01$.

Year	1974-75		1975-76		1976-77		1977-78		1979-80	
Sand index	≤1.0	>1.0	≤1.0	>1.0	≤1.0	>1.0	≤1.0	>1.0	≤1.0	>1.0
N	6:267	5:177	13:471	3:88	3:70	1:13	3:136	3:97	6:264	4:151
					Means					
1st quartile	29.11	29.39	26.02	25.87	26.53	26.33	28.03	27.90	29.34	28.99
2nd quartile	29.17	29.27	25.96	25.71	26.65	27.00	28.02	28.04	29.42	29.24
3rd quartile	29.21	28.94	25.95	25.73	27.03	26.67	27.89	28.00	29.28	28.95
4th quartile	29.21	28.76	25.91	25.10	26.53	26.67	27.89	27.70	28.82	29.15
d.f.										
Treatment	3	3	3	3	3	3	3	3	3	3
Error	262	172	466	83	65	8	131	92	259	147
F value	0.186	4.817**	0.778	7.158**	0.831	0.160	0.954	2.320	8.696**	1.232
Median time to emergence	155	154	142	132	142	142	148	151	152	147
Mean emergence period (d)	13	11	25	23	14	9	14	14	16	17

emerging from gravel mixtures with sand indices >1.0 and from mixtures with sand indices ≤1.0. In several instances, however, the fry length was related to time of emergence. The mean lengths of fry emerging later in the emergence period were occasionally less than those emerging earlier. In three instances the lengths of emerged fry varied significantly according to the quartile of the emergence distribution (Table 7). In all instances the significant differences could be attributed to shorter fry emerging later. Although the fry were not weighed, smaller fry size late in the emergence period is believed not due to more yolk remaining in the later fry. Probably the smaller fry are less vigorous in working up through the gravel. Hausle and Coble (1976) reported similar results with brook trout fry emergence. They obtained largest fry in the middle of the emergence period and smallest ones at the end. They also found that weight of emergent fry was not correlated with sand content.

NUMBERS OF FRY EMERGING FROM COLUMNS AND CHAMBERS

The numbers of emergent fry obtained from all the columns (except for two columns which ran dry during the experiment) are illustrated in Fig. 9 as a function of the percentages of coarse and fine sand present in the gravel mixtures. The numbers seem to fall fairly consistently into three zones. The numbers of fry emerging from gravel mixtures containing less sand than bounded by the line connecting 8% fine sand and 16% coarse sand were usually greater than 40 (80%). The mean number of emergent fry per column was 42.8 (no. of columns = 31), and emergent fry were obtained from every column in this category, the minimum number being 13.

For gravel mixtures with sand content falling between the line described above and the line connecting 12% fine sand with 24% coarse sand, the number of emergent fry was very variable, and usually less in comparison with numbers emerging from gravels with less sand. The mean number of emergent fry was 18.2 (36.4%, n = 23). No fry were obtained from two of the columns in this category.

For gravel mixtures containing more sand than bounded by the line connecting 12% fine sand with 24% coarse sand, numbers of emerging fry were greatly reduced (mean no. of fry = 7.2, n = 22). No emergence was obtained from 14 of the columns, although over 40 emergent fry were obtained from 2 of the columns in this category.

Figure 9 suggests a threshold percentage of fine sand near 8%, above which fry emergence is reduced and a corresponding threshold for coarse sand near 16%. The effects of the two sand fractions appear additive in their effects on fry emergence because the threshold lines of Fig. 9 when drawn straight appear to fit the data. Based on these considerations, the percentage of emergent fry should be a function of the sand index (SI), defined as:

$$\frac{S_c}{16} + \frac{S_f}{8}$$

where: S_c is the coarse sand fraction,
S_f is the fine sand fraction.

Thus, an SI less than 1.0 is in the region below the lower line where no decrease in numbers of emergent fry occurred (Fig. 9). Values between 1.0 and 1.5 are the region of decreasing emergence bounded by

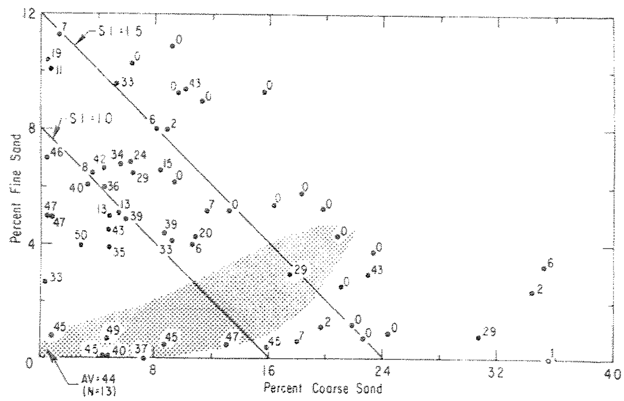

Fig. 9. Numbers of fry from various gravel mixtures in the columns (from 50 green eggs originally planted) containing different levels (in percent) of coarse and fine sand. The hatched area indicates combinations of coarse and fine sand measured from natural spawning gravels.

the two lines in Fig. 9, and values greater than 1.5 usually result in no emergence. For sand indices >1.0, the numbers of fry emerging from the chambers (Fig. 10) (with upwelling water flows and higher percolation rates) were generally greater than those emerging from columns of similar sand content. With the chambers, emergence was reduced above a sand index of about 1.5. However, for the columns with reduced percolation rate (ca. 15 mL/min), the numbers of emergent fry were similar to those obtained in columns with a higher flow rate.

Emergence was significantly correlated with sand content of the columns for all years (Table 8, Appendix 1) with correlation coefficients ranging from -0.72 to -0.93. The correlation coefficient for all years pooled is -0.79. Correlation

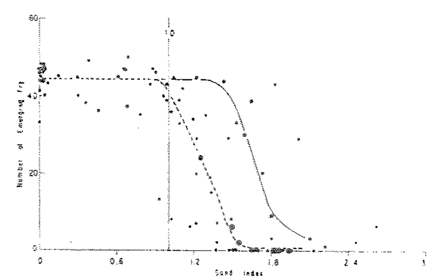

Fig. 10. Numbers of emergent fry from 50 planted eggs are plotted as a function of "sand index" of incubation substrate (see text for definition). Closed circles and dotted line, columns 1974-75 to 1977-78 inclusive; asterisks and solid line, chambers; triangles, columns 1979-80. Encircled points are for columns in which percolation rates could not be maintained at the desired level.

Table 8. Coefficients for correlations of sand, percolation rate, and numbers of emerging fry.

Year	Stock	No. of columns	Correlation coefficients: Sand vs. emergence	Sand vs. flow	Flow vs. emergence
1976-77	Waweig	12	-0.88	-0.31	0.06
1977-78	Waweig	14	-0.93	-0.44	0.54
1975-76	Waweig	25	-0.80	-0.46	0.55
1974-75	Miramichi	13	-0.77	-0.44	0.66
1979-80	Magaguadavic	12	-0.72	-0.37	0.61
Pooled		76	-0.79		

Multiple R (sand and flow vs. emergence) -0.80.

coefficients for sand content vs. flow rates were lower, ranging from -0.31 to -0.46 for various years. The pooled correlation coefficient for sand vs. flow was not performed as flow rates were manipulated to lower values in 1979-80 and pooled values would be meaningless. Correlation coefficients for flow vs. emergence ranged from 0.06 to 0.66 with a pooled coefficient of -0.06. The pooled value results from the fact that high emergence numbers were obtained for columns with low percolation rates in 1979-80. In pooling the data, we have assumed that emergence from eggs of various stocks responds similarly to changes in sand content and/or percolation rate. The multiple correlation coefficient for the effects of sand and percolation rate combined was -0.80, indicating that inclusion of percolation rate did not significantly improve the fit obtained with sand content alone (K = -0.79). Therefore, we conclude that sand content is the significant variable controlling numbers of emergent fry in these experiments.

A strong upwelling water flow through the gravel mixtures in the chambers did result in more emergent fry at the higher sand indices (Fig. 10). This increased emergence may be attributable to the effects of the strong upwelling water currents on the degree of packing of sand in the gravel. The upwelling may have kept it more loosely packed, thus preventing smothering of eggs or alevins, and perhaps permitting easier movement of alevins and fry within the gravel.

Hausle and Coble (1976) have summarized emergence data from a variety of sources. Emergence reduction usually begins at 15-30% sand composition and emergence approaches 0 at 60-70% sand. The variability in results can probably be explained, in part, by differences in the particle sizes used among the various experiments. Bjorn (1969) included all particles less than 6.35 mm in his "sand" fraction, while Hall and Lantz (1969) confined their studies to particles of 1-3 mm in diameter. Thus, both of these studies used coarser sediments which might be expected not to have an effect until the percent sand was relatively high. Hausle and Coble (1976) used a sand fraction of 2 mm or less, which probably corresponds more closely to the sum of the fine and coarse sand fractions in our experiments. Phillips et al. (1975) reported increased mortality of emerging fry from gravel mixtures with higher quantities of fine sand. Varying water velocities and vectors of water flow through the gravels could result in some differences among the various experiments.

Upon completion of emergence the gravel columns and chambers were searched for egg, alevin and fry remains (Table 9). Totals of egg and yolk-sac alevin fragments were combined as it was often not possible to distinguish between them due to decomposition. Eggs were frequently found intact (as in most of the tallies for sand indices <1.0) as the zona radiata apparently deterred decomposition so that fragments of yolk may well have been the remains of alevins, the embryos of which had decomposed. It is likely that most of the identifiable egg remains found in gravels with low sand content were of non-viable eggs since the percentages were not much larger than those observed in the hatching boxes on eggs from the same lot. The mortality prior to hatching was increased at SI's greater than 1.0 as 380 of the 596 dead eggs and alevins could positively be identified as eggs. For those columns with sand indices ≤1.0, over 90% of the planted eggs could be accounted for (Table 9). In gravel mixtures with sand indices >1.0, only 60-70% of the eggs planted could be accounted for mainly because of decomposition and difficulty in separating clusters of yolk fragments into individuals. Apparently, most of the mortality occurred before the end of yolk resorption, although dead fry and advanced alevins decompose rapidly and the numbers of these are undoubtedly also underestimated. The entrapped live fry would probably not have emerged as they were emaciated and had been unable to emerge for a week after the last of the other fry had emerged.

EXPERIMENTAL VS. NATURAL GRAVEL MIXTURES

Contents of coarse and fine sand in natural Atlantic salmon spawning gravels have been estimated (Peterson 1978). Similar values have been determined by McNeill and Ahnell (1964) and Campbell (1977) for the spawning gravels of other salmonids. Values obtained by Peterson (1978) are represented by the shaded area of Fig. 9. Nineteen of the 28 spawning sites sampled had sand indices <1.0 and only one had an index >1.5, so that some emergence would be expected to occur (on the basis of sand content) from 27 of the 28 sites. These percentages are mean values over 15 cm depth and the percentage of sand at the level of egg deposition might be more important. Levels of emergence obtained in our

Table 9. Summary of fate of eggs in gravel columns and chambers. Columns and chambers are classified into six categories based upon sand index. Data for 1976-77 columns where eggs had low fertility are excluded. N - no. of columns or chambers. Average per column or chamber in parentheses.

SI	Dead eggs + yolk-sac alevins	Dead fry	Entrapped live fry	Emergent fry	N	Fraction recovered
Columns						
0-0.1	78 (6.0)	1(0.1)	1(0.1)	544(41.8)	13	0.96
>0.1-0.5	38 (6.3)	0	0	239(39.8)	6	0.92
>0.5-1.0	35 (3.4)	10(0.9)	7(0.6)	495(45.0)	11	0.99
>1.0-1.5	>339(>15.4)	71(3.2)	4(0.2)	420(19.1)	22	0.76
>1.5-2.0	>147(>21)	31(4.4)	1(0.1)	80(11.4)	7	0.74
>2.0	>110(>22)	14(2.8)	0	38 (7.6)	5	0.65
Chambers						
0-0.1	1	1	0	90(45)	2	0.92
>0.1-0.5	-	-	-	-	-	-
>0.5-1.0	1	0	0	45	1	0.92
>1.0-1.5	1	0	0	89(44.5)	2	0.90
>1.5-2.0	>16 (4.0)	30(7.5)	2(0.5)	98(24.5)	4	0.73
>2.0	2	3	1	21	1	0.54

laboratory study at low sand indices are considerably higher than those reported from field studies (Wickett 1958; Peterson 1978) where usually less than 15% emergence occurs. Such field estimates may be severely underestimated due to trapping losses. Furthermore, the content of fine sediments is only one factor influencing sub-gravel water velocities in stream gravel beds, others being compaction of gravel, hydraulic head, and configuration and roughness of the stream bottom (Vaux 1962; Cooper 1965). In addition, factors such as predation, fungal infection, freezing, ice scouring, and shifting of gravel during freshets would contribute to mortality. G. LaCroix (pers. comm.) estimates 40-75% of egg mortality in two spawning areas of landlocked Atlantic salmon was due to ice scouring and gravel shifting.

The experiments described here indicate that, even in the presence of water supply sufficient for survival, fry emergence is reduced if the sand content in the gravel exceeds certain levels. The mechanism reducing survival and subsequent emergence is unknown. Several conjectures may help account for it, e.g. fine sediments settling around eggs and reducing the local flow of water around the egg surface to lower than critical levels. Dead eggs or alevins were frequently found in clumps encased with sand, particularly the fine sand. Similar effects may occur after hatching, since dermal gas exchange is probably important in alevins. In more advanced fry, excessive sand may infiltrate the oral and branchial cavities and interfere with respiratory flow. Sand may also block pathways for emerging fry prevent upward movement through the gravel.

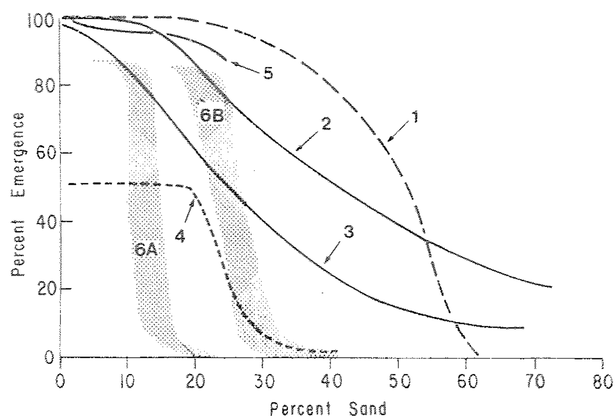

Fig. 11. Percent emergences of fry from gravel mixtures as a function of percentage of sand in the substrate are reported from several studies. Line 1: Bjorn (1969), steelhead, swim-up fry placed in gravel, fines <6.35 mm. Line 2: Phillips et al. (1975), steelhead, swim-up fry, fines 1-3 mm particle size. Line 3: As with line 2, but for coho salmon. Line 4: As for line 1, but with green eggs. Line 5: Hausle and Coble (1976), brook trout, alevins, fines <2 mm. 6A: This study, Atlantic salmon, green eggs, particles 0.06-0.50 mm, leading edge of shaded area for strong upwelling currents, trailing edge for slower downward percolation. 6B: As for 6A but for particle size 0.5-2.2 mm.

GENERAL DISCUSSION

Several studies on the influence of sand in incubation gravels on emergence suggest a sigmoidal relationship with a lower threshold level where sand starts to have noticeable effects (Fig. 11). This threshold varies, however, from 8-30% in the various studies. Several factors may influence the threshold and also the rate of decline once the threshold is exceeded. Sand particle size and direction of water flow were shown to be important in our study (Fig. 11, curves 6A, 6B). The coarse particle size used by Bjorn (1969) may have been responsible for the high percentage of emergence success obtained by him. The stage of development attained by the brood when the experiment is started appears to have an influence. Experiments utilizing green eggs (curves 4, 6A, 6B) had lower maxima percent of emergence, possibly reflecting non-viable eggs included in the experiment, and a sharper inflection once threshold sand concentrations were exceeded. This sharper inflection may reflect a specific effect of sand on the egg stages. Experiments utilizing advanced fry yielded higher emergence at higher sand concentrations. Finally, egg or fry size may influence emergence from a given gravel mixture. The emergence percentages obtained with steelhead fry (curve 2) were higher than those with coho fry (curve 3) for all sand levels. The smaller steelhead fry may be able to use smaller crevices to move upward through the gravel.

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Appendix 1

Various experimental parameters for the gravel columns for the 5 yr when experiments were conducted.

Year	Stock	Sand index	Mean flow rate (cc/min)	Emergence	% coarse sand	% fine sand
1974-75	Miramichi	0.00	60	44	0	0
		0.01	61	47	0.1	0
		0.30	63	40	4.7	0.1
		0.68	62	50	2.9	4.0
		0.88	61	47	13.1	0.5
		0.99	63	39	6.0	4.9
		1.12	59	42	4.4	6.7
		1.20	59	34	5.6	6.8
		1.47	63	29	17.5	3.0
		1.69	60	0	6.4	10.3
		1.70	54	0	16.4	5.4
		1.82	62	43	23.0	3.0
		2.02	64	29	30.8	0.8
		2.14	48	0	15.6	9.3
1975-76	Waweig	0.00	68	47	0	0
		0.00	64	41	0	0
		0.01	65	48	0	0.1
		0.04	69	40	0.3	0.2
		0.06	62	43	0.4	0.3
		0.15	62	45	0.8	0.8
		0.36	64	38	0.3	2.7
		0.38	70	49	4.7	0.7
		0.65	68	47	0.5	5.0
		0.86	70	43	4.8	4.5
		0.90	60	46	0.4	7.0
		0.93	59	13	4.9	5.0
		0.97	52	40	3.3	6.1
		1.03	64	36	4.5	6.0
		1.22	54	29	6.5	6.5
		1.25	11	24	6.3	6.9
		1.38	64	2	19.8	1.1
		1.50	25	6	8.0	8.0
		1.52	57	0	21.9	1.2
		1.86	28	0	18.3	5.8
		1.90	25	0	19.9	5.3
		1.94	26	0	9.2	10.9
		2.22	66	1	35.6	0.0
		2.46	58	2	34.5	2.4
		2.62	54	6	35.3	3.3
1976-77	Waweig	0.00	87	46	0	0
		0.00	72	33	0	0
		0.46	81	36	7.3	0
		1.03	78	8	3.6	6.5
		1.22	75	20	10.9	4.3
		1.34	85	15	8.4	6.6
		1.37	60	0	9.4	6.2
		1.38	77	7	11.7	5.2
		1.49	78	8	1.3	11.3
		1.55	49	2	8.8	8.0
		1.64	68	0	21.1	2.6
		1.84	38	0	20.8	4.3
1977-78	Waweig	0.01	90	45	0.1	0
		0.02	74	46	0.2	0.1
		0.61	73	45	8.8	0.5
		1.17	75	6	10.7	4.0
		1.30	69	35	0.7	10.1
		1.33	71	19	0.5	10.4
		1.48	73	0	13.3	5.2
		1.51	85	0	22.7	0.7
		1.64	85	0	24.5	0.9
		1.81	83	3	10.1	9.4
		1.83	70	0	11.3	9.0
		1.94	75	0	23.4	3.8

Appendix 1 (cont'd)

Year	Stock	Sand index	Mean flow rate (cc/min)	Emergence	% coarse sand	% fine sand
1979-80	Magaguadavic	0.02	15	48	0.3	0
		0.03	14	47	0.5	0
		0.29	15	45	4.5	0.1
		0.66	15	47	0.6	5.0
		0.79	15	35	4.8	3.9
		0.98	15	43	5.4	5.1
		1.04	15	45	15.9	0.4
		1.09	14	33	9.2	4.1
		1.09	15	39	8.7	4.4
		1.21	15	7	18.1	0.6
		1.53	15	33	5.3	9.6
		1.76	12	0	9.6	9.3