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Spawning history influence on fecundity, egg size, and egg survival of Atlantic salmon (*Salmo salar*) from the Miramichi River, New Brunswick, Canada

Jenny E. Reid[1] and Gérald Chaput[2]*

[1]*Miramichi Salmon Association, 485 Route 420, South Esk, New Brunswick, Canada E1V4L9*
[2]*Fisheries and Oceans Canada, PO 5030, Moncton, New Brunswick, Canada E1C 9B6*

**Corresponding author: tel: +1 506 851 2022; fax: +1 506 851 2620; e-mail: gerald.chaput@dfo-mpo.gc.ca.*

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There is an increasing abundance of repeat spawners in the Atlantic salmon (*Salmo salar*) population in the Miramichi River that, owing to their larger size, can be expected to contribute greater egg depositions and better offspring survival than primarily maiden spawning populations. Currently, there is little information on the reproductive contribution of repeat-spawning salmon. In this study, the fecundity, egg size, and egg survival for 235 maiden and repeat-spawning wild female Atlantic salmon were examined over a period of 3 years. Relative fecundity did not differ among the largest body size group of salmon, but consecutive repeat spawners had a higher fecundity than maiden 2SW salmon and alternate repeat spawners. Egg diameter also increased with body size, but consecutive repeat spawners had significantly smaller eggs, in absolute terms and relative to their body size, than maiden 2SW salmon and alternate repeat spawners. The egg survival rate of consecutive repeat spawners was significantly lower than that of 2SW maiden salmon and alternate repeat spawners. Consecutive repeat spawners are different in that egg diameter and egg survival did not follow the general positive association with female body size, probably because of the short time that they spend reconditioning in the ocean and consequently their available energy reserves.

Keywords: Atlantic salmon, egg size, egg survival, fecundity, repeat spawners.

Introduction

The Atlantic salmon (*Salmo salar*) is an iteroparous species with spawning populations consisting of first time (maiden) and repeat-spawning individuals. In Canada, maiden salmon can spend between 1 and 3 years at sea before first maturing and in some populations can spawn more than six times (Ducharme, 1969; Moore *et al.*, 1995; Atkinson and Moore, 1999; Klemetsen *et al.*, 2003; O'Connell *et al.*, 2006). The percentage of repeat spawning salmon in the Miramichi River (Canada) has increased from <5% before the early 1980s to up to 25% since the mid-1980s (Chaput and Jones, 2006). Similarly, in the River Teno (Finland), the number of repeat-spawning salmon has increased over the past 30 years (Niemelä *et al.*, 2006). These increases in absolute terms have been attributed to reductions in exploitation (Moore *et al.*, 1995), although changes in the environment such as warmer sea temperatures have also been associated with increased abundance of repeat spawners (Niemelä *et al.*, 2006).

In eastern Canada, Atlantic salmon are managed based on attaining river-specific minimum levels of egg deposition, known as the conservation level, which are assumed to result in adequate juvenile production or maximum yield of adult salmon (Chaput *et al.*, 1998). In the majority of assessments, all eggs, regardless of maternal age or size, are considered equal.

It is well established that the number of eggs produced by female Atlantic salmon generally increases with fish size (Thorpe *et al.*, 1984; Randall, 1989; Fleming, 1996; Heinimaa and Heinimaa, 2004; Moffett *et al.*, 2006). Additionally, egg size is under maternal effect in many fish species, with larger females and older females generally producing larger eggs, and with an increased probability of survival of offspring from larger eggs (Thorpe *et al.*, 1984; Fleming, 1996; Johnston and Leggett, 2002). Consequently, the increased abundance of repeat spawners, which are longer and generally heavier than salmon at their corresponding maiden spawning age (Moore *et al.*, 1995), would be expected to increase relative egg depositions and recruitment per fish compared with populations dominated by maiden spawners.

There are two types of repeat-spawner maturation strategies: alternate spawning, in which salmon spend one or more years at sea reconditioning before returning to spawn, and consecutive spawning, in which salmon spend a few months reconditioning and spawn in consecutive years (Moore *et al*., 1995; Klemetsen *et al*., 2003; Niemelä *et al*., 2006). Variation in egg characteristics between the different types of repeat spawners and maiden spawning salmon has not been studied. The purpose of this study is to determine how spawning histories as well as maternal features, including age and size at maturity of female Atlantic salmon, influence fecundity, egg size, and survival to pre-hatching in a hatchery environment.

Methods

From 2006 to 2008, 235 female and 221 male wild Atlantic salmon were collected for broodstock from ten tributary stocks within the Miramichi River (Canada; 47°N 65°W). Salmon were collected between 25 August and 9 October in each year and held at the Miramichi Salmon Conservation Centre, South Esk, New Brunswick, in 2.4-m diameter tanks until they were ready to spawn. Fish were checked every 3 d from 10 October on to determine if they were ripe for stripping. Spawning occurred between 10 October and 8 November in all years.

Females were anaesthetized using $\sim$50 mg l^{-1} of MS222®. Before spawning, the females' fork length and total weight were measured, and a scale sample was taken. Approximately ten scales were taken from the standard sampling position (Shearer, 1992), for the determination of river age, sea age at maiden spawning, and spawning history. Spawning histories were recorded as follows: the adult sea age at first maturity (number), followed by the subsequent spawning histories (letter). For example, a fish with spawning history recorded as 1A is a fish with an adult age at maiden spawning of 1 sea year and a second spawning as an alternate (C for consecutive). Total adult age refers to the number of years from the onset of smolt migration, with 1 June as the standard date. For example, the adult age of a 1A fish is 3 years, with 1 year for the age at maiden spawning, 1 year for the time spent in river on the first spawning event in year 2, and 1 year spent at sea reconditioning before returning to spawn for a second time in year 3. Similarly, a fish with spawning history of 2CC has an adult age of 4 with 2 years at sea before its maiden spawning, 1 year in river on the first spawning event, but returning for a second spawning after a few months in year 3 and returning for a third spawning after a few months in year 4.

Mating of spawners was stock-specific. Salmon male choice for the crosses was determined by availability. Of the males for which age could be determined (64% of all males), 76% were one-sea-winter (1SW) maiden fish and the remainder were 2SW fish and repeat spawners. Eggs were stripped from each female into two dry metal mixing bowls, and the eggs in each lot were fertilized with milt from a different male specific to that stock (2 × 2 crosses). The eggs were rinsed with water and placed in 15 × 25 cm egg pans to harden in ambient river water. Eggs were distributed evenly among pans, with the larger females with more eggs requiring from two to four pans. Over the 3 years, eggs were distributed and incubated in 476 pans. After 4 h, the eggs were disinfected with Ovadine® for 10 min. Egg pans were laid on 2.5-cm diameter rebar spacers in 5.9 × 0.6 m troughs in the egg-incubation building and supplied with ambient river water from Stewart Brook, the source of water for the hatchery. The eggs were incubated undisturbed in brook water until $\sim$250 degree days. Subsequently, any dead eggs were counted in each pan and removed weekly. Egg survival was defined as the percentage of extruded eggs that survived up to the time when eggs were transferred to emergence boxes. Water temperatures during the experiment ranged from 0.2 to 10°C.

Estimates of egg numbers were obtained by the volumetric method during February. The eggs from an individual pan were transferred to a fine-mesh aquarium dipnet, lightly shaken about five times to remove excess water, then transferred to a graduated cylinder containing 400 ml of water and the volume of water displaced recorded. The conversion from the volume of eggs to the number of eggs was made by determination of the volume displacement of a known quantity of eggs, between 50 and 100 eggs depending on the sample, for each egg pan. Actual egg counts were obtained from 24 pans and regressed against the number of eggs estimated by the volumetric method. The egg samples for the total counts ranged from 467 to 5027 eggs per pan and were from female salmon ranging from 50.9 to 105 cm fork length and with various spawning histories. There was a strong linear association ($r^2 = 0.99$; $n = 24$) between egg number by volume and egg number by actual count, but there was a slight underestimate of the number of eggs by the volumetric method. The following correction equation was applied to all volumetric estimates: $Eggs_{\mathrm{count}} = 1.055 \times Eggs_{\mathrm{volumetric}} + 51$.

The diameter of the eggs was estimated by placing ten eggs on a ruler modified as a V-trough. This was done three times for each egg pan. The variation in the estimated diameter of the eggs was small. More than 60% of the replicate samples had a coefficient of variation (*CV*) of <1%, more than 95% of samples had a *CV* of <2%, and the maximum *CV* was 5.2%. The mean egg diameter from the replicates was used in subsequent analyses.

Eggs were treated as required with a 1:600 formalin solution for 15 min to treat pathogens. Just before hatching, the eggs were placed in incubation boxes for further development. All surviving fry were stocked in the Miramichi River as part of the Miramichi Salmon Association's juvenile stocking programme.

Statistics

Condition was expressed as Fulton's *K*, where $K = weight\ (\mathrm{kg}) / fork\ length\ (\mathrm{cm})^3 \times 10^6$ (Koops *et al*., 2004). The associations between length, weight, fecundity, egg diameter, and egg survival by spawning history were analysed with a general linear model, with length and weight as covariates depending on the model tested. In all analyses, the model error was assumed to be multiplicative, and model fits were performed on natural log-transformed values of the continuous variables. The analyses of interest were those with a change in intercept among spawning history groups and with a common slope. All analyses were performed using the GLM procedure, and *post hoc* multiple comparisons were made and confidence intervals determined using Bonferroni correction (SAS, 2009).

Results

Age was determined from the scales of 228 of the 235 female salmon (Table 1), comprising 38 1SW maiden salmon (1M), 123 2SW maiden salmon (2M), 54 female salmon with one previous

Table 1. Characteristics of female Atlantic salmon spawned between 2006 and 2008, by spawning history and river age in the Miramichi River.

Spawning history	Previous spawnings	Adult age (years)	Number per river age (years)				Number per year of sampling			Total
			2	3	4+	Unknown	2006	2007	2008	
1M	0	1	19	15	–	4	17	15	6	38
1A	1	3	3	8	–	5	10	4	2	16
1AA	2	5	–	–	–	1	–	–	1	1
1AAA	3	7	–	–	–	1	–	1	–	1
1ACC	3	5	–	1	–	–	–	1	–	1
2M	0	2	47	59	1	16	54	39	30	123
2A	1	4	15	7	–	4	4	14	8	26
2AC	2	5	2	1	–	1	3	1		4
2C	1	3	5	7	–	–	2	9	1	12
2CA	2	5	1	1	–	–	–	–	2	2
2CC	2	4	1	–	–	1	1	1	–	2
2CCC	3	5	1	–	–	–	1	–	–	1
2CCCC	4	6	–	1	–	–	–	1	–	1
Unknown	–	–	–	–	–	7	1	3	3	7
Total			94	100	1	40	93	89	53	235

Spawning history describes the chronology of ages at each spawning event: 1 and 2 are adult age at maiden (M) spawning, A is each alternate spawning, and C is each consecutive spawning.

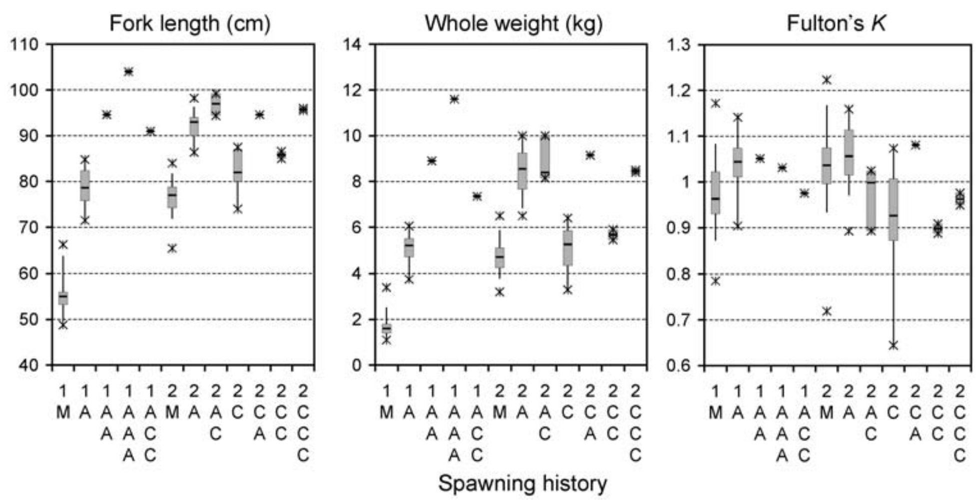

Figure 1. Summary of fork length (cm), whole weight (kg), and Fulton's *K* of Atlantic salmon by spawning history. Spawning histories are interpreted as in Table 1. Box plots are interpreted as follows: the horizontal line is the median, the shaded rectangle is the interquartile range, the vertical line the 5th to the 95th percentile range, and asterisks are minimum and maximum values.

spawning (1A, 2C, 2A), 9 female salmon with two previous spawnings (1AA, 2CC, 2CA, 2AC), 3 female salmon with three previous spawnings (1AAA, 1AAC, 2CCC), and 1 female salmon with four previous spawnings (2CCCC). Spawning histories were diverse and included fish that were sequentially alternate spawners (1AA and 1AAA), sequentially consecutive spawners (e.g. 2CC, 2CCC), and both consecutive and alternate spawners (e.g. 1AAC, 2AC, 2CA; Table 1). The total adult age (post river age) varied from 1 to 7 years. Interpreted river ages were mostly 2 and 3 years (Table 1).

Size, in terms of fork length and whole weight, was adult-age-specific, with 1M salmon being the smallest (length and weight) and multiple repeat spawners the largest (Figure 1). There were three broad weight groups among the female salmon (Figure 1); the lightest group consisted of 1M salmon which were generally under 2 kg (<60 cm fork length); fish in the middle group weighed between 4 and 6 kg (75–85 cm) and consisted of 2M, 1A, and 2C salmon; and the heaviest group contained the multiple repeat spawning salmon ranging in weight from 7 kg to just under 12 kg (85–105 cm).

Length was a significant explanatory variable of weight over all sea-age groups and within size groups (Table 2). Within the middle size group, the 2C spawners were lighter by ~0.5 kg at a common length than both the 2M and the 1A repeat spawners (Table 2). In the large size group, the 2A spawners were heavier by ~0.6 kg than the group of multiple repeat spawners with more than two spawnings (Table 2). Consecutive repeat spawners generally had lower condition factors than maiden and alternate repeat spawners (Figure 1).

Because of deficiencies in egg extrusion and fertilization success (17 females were excluded), usable observations were obtained

Table 2. Weight-to-length associations for females by spawning histories.

Group	ln(α)	β	Explained variance (%)	n	Predicted weight (kg) at length (cm)
All females	−11.924	3.099	97.5	213	
1M	−12.920	3.344	88.3	37	
Middle size group by fork length ($p < 0.001$) and spawning history ($p < 0.001$)					At length 80 cm
1A	−10.304	2.731	70.3 ($p < 0.001$)	14	5.27 (5.05–5.49)[a]
2M	−10.309			115	5.24 (5.14–5.35)[a]
2C	−10.418			11	4.70 (4.48–4.93)[b]
Large size group by fork length ($p < 0.001$) and spawning history ($p < 0.001$)					At length 90 cm
2A	−13.630	3.480	85.1	25	7.61 (7.40–7.82)[a]
Prev 2+	−13.716			11	6.98 (6.68–7.29)[b]

Values of p for explanatory variables in the covariance models represent the statistical significance of the variable with all other explanatory variables in the model (Type III in SAS PROC GLM). Bonferroni-adjusted confidence intervals and pairwise tests are also shown. Groups that share a common letter are not statistically different at $p = 0.05$.

Table 3. Fecundity (eggs extruded per fish) by spawning history of females.

Explanatory variable	α	β	Explained variance (%)	n	Predicted eggs
All spawning history types					
Fork length (cm)	0.051	2.700	84.7	217	
Whole weight (kg)	1 663	0.871	87.1	215	
Spawning history only					
1M	2 539	–	73.8 ($p < 0.001$)	37	2 539 (2 342–2 754)[a]
2M	6 320	–		116	6 320 (6 037–6 616)[b]
Repeat-A	9 064	–		43	9 064 (8 407–9 772)[c]
Repeat-C	8 443	–		19	8 443 (7 540–9 454)[c]
1SW maiden only					
Fork length	0.006	3.244	47.7 ($p < 0.001$)	37	2 539 (2 375–2 715)
Whole weight	1 556	1.028	60.7 ($p < 0.001$)	37	2 539 (2 397–2 691)
Fork length ($p < 0.001$) and spawning history ($p = 0.75$)					At L_F 90 cm
2M	0.058	2.671	60.2 ($p < 0.001$)	116	9 698 (8 938–10 523)[a]
Repeat-A	0.058			42	9 692 (9 146–10 271)[a]
Repeat-C	0.056			19	9 352 (8 580–10 193)[a]
Whole weight ($p < 0.001$) and spawning history ($p = 0.27$)					At weight 6 kg
2M	1 629	0.882	64.9 ($p < 0.001$)	114	7 910 (7 552–8 285)[a]
Repeat-A	1 603			42	7 786 (7 348–8 250)[a]
Repeat-C	1 731			19	8 406 (7 540–9 454)[a]

The explanatory models for fecundity were: *fecundity* (egg number) $= \alpha_j \times Spawntype_j \times Size^{\beta} e^{\epsilon}$, with size either fork length (cm) or whole weight (kg). The table is interpreted as described in Table 2.

from 217 females for the estimation of fecundity, from 217 females for the characterization of egg diameter, and from 200 females for the estimation of survival.

Fork length or total weight explained a large proportion (>85%) of the variation in fecundity (total eggs) of female salmon over all spawning history types (Table 3, Figure 2). Fecundity differed significantly among spawning history groups, in large part because of the differences in size (length or weight) among these (Table 3, Figure 2). The average absolute fecundity of 1M salmon was less than half that of 2M salmon, and the average fecundity of alternate repeat spawners was 50% higher than 2M salmon and the highest of all spawning history groups, with just over 9000 eggs per female. When adjusted for a common size, there was no significant difference in the average fecundity of 2M and repeat spawners although, by weight, consecutive repeat spawners had the highest average and the broadest range of total eggs (Table 3). The 1M salmon had an average relative fecundity of just under 1600 eggs kg^{-1}, whereas the 2M salmon and repeat spawners had average relative fecundities of 1300–1400 eggs kg^{-1}.

Egg diameter was positively associated with length and weight of female salmon, explaining 46 and 52% of the variation in egg diameter over all spawning history groups, respectively (Table 4, Figure 3). In part because of this association with size, egg diameters were significantly different by spawning history type, with 1M salmon having the smallest eggs and alternate repeat spawners the largest (Table 4, Figure 3). The 2M and consecutive repeat spawners had eggs of similar size. Egg diameter of 1M fish averaged 5.6 mm and was positively associated with length and weight of the fish, but these covariates only explained 11–12% of the observed variation in egg diameter (Table 4). Within the 2M and repeat spawning group, length and weight were also significant explanatory variables of egg diameter, explaining 21 and 25% of the variance, respectively (Table 4). When corrected for length, the egg diameters of the consecutive repeat spawners (95% confidence interval range 6.0–6.2 mm) were significantly smaller than those of the 2M fish (6.2–6.4 mm), and the eggs of alternate repeat spawners were significantly larger than the other groups (6.4–6.6 mm; Table 4). When corrected to a common weight, the predicted egg diameter of 2M maiden salmon did not differ from the alternate repeat spawners, but the prediction is not realistic, because the common 6 kg weight is outside the range of observed weights of 2M salmon in this study (Figure 1).

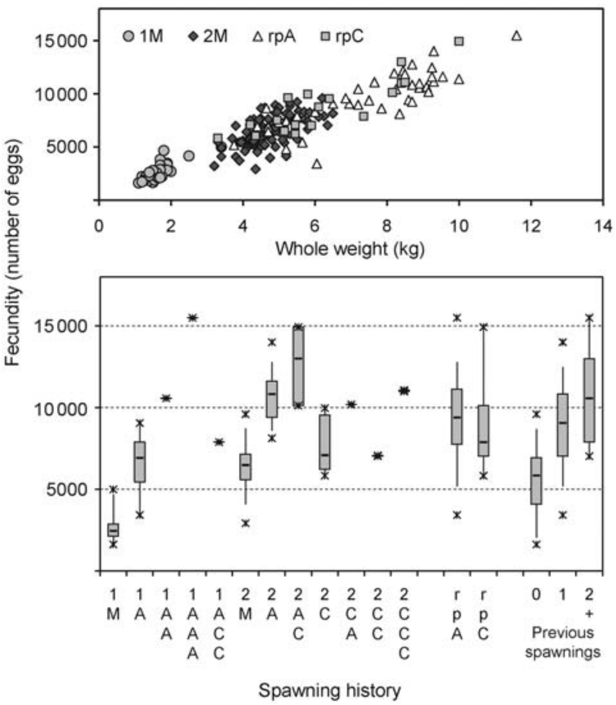

Figure 2. Summaries of fecundity by size (weight; upper panel) and spawning-history type (lower panel). In the lower panel, the life-history types are interpreted as in Table 1; and additionally, rpA denotes all repeats that are alternate spawners on their most recent return (1A, 1AA, 1AAA, 2A, 2CA) and rpC all repeats that are consecutive on their most recent return (1ACC, 2AC, 2C, 2CC, 2CCC, 2CCCC) and the number of previous spawnings. Box plots are interpreted as in Figure 1.

After excluding egg batches with poor initial fertilization because of male or female deficiencies, egg survival to placement in emergence boxes was very high, ranging from a low of 67% for a 2M female to a maximum of 99.4%; 95% of the measured survival rates exceeded 81%, and half of the measured survival rates were >95% (Figure 4). Female size (length or weight) and egg diameter did not account for any variation in the observed survival rates (Figure 4). Spawning history was a statistically significant explanatory variable, but it accounted for just 8% of the measured variation in survival; the survival rate of consecutive repeat spawners was significantly lower than for 2M salmon and alternate repeat spawners (Table 5).

Female size, expressed as either length or weight, did not differ significantly ($p > 0.05$) between river age 2 and river age 3 fish within sea-age groups. The only reproductive characteristic which differed by river age was the egg diameter of 2M salmon and 1A salmon; the egg diameter of river age 3 fish was on average 2 and 3 mm larger than that for river age 2 fish for 2M ($p < 0.001$; $r^2 = 0.15$; $n = 103$) and 1A ($p = 0.02$; $r^2 = 0.47$; $n = 10$) spawners, respectively. Egg survival from river age 3 2M females was generally higher (by ~2%) than the survival of eggs from 2M river age 2 females, although only 4% of the variation ($p = 0.06$) in survival was accounted for by river age.

Discussion

The Atlantic salmon population in the Miramichi River is abundant and has a broad age structure that provides an opportunity to examine the relationships between maternal characteristics and reproductive traits for different spawning histories of female salmon. The findings in this study are consistent with most of the existing literature regarding the effects of maternal characteristics on reproductive products. Absolute fecundity increases with

Table 4. Egg diameter (mm) associations with spawning history and fork length or whole weight of female Atlantic salmon.

Explanatory variables	α	β	Explained variance (%)	n	Predicted egg diameter (mm)
All females					
Fork length (cm)	1.88	0.274	46.1 ($p < 0.001$)	217	
Whole weight (kg)	5.38	0.092	51.5 ($p < 0.001$)	214	
By spawning history type					
1M	5.58		54.4 ($p < 0.001$)	37	5.58 (5.49–5.66)[a]
2M	6.24			118	6.24 (6.19–6.29)[b]
Repeat-A	6.51			44	6.51 (6.43–6.60)[c]
Repeat-C	6.06			19	6.06 (5.94–6.19)[b]
1SW maiden group only					
Fork length	1.63	0.307	11.2 ($p = 0.043$)	37	5.58 (5.48–5.67)
Whole weight	5.34	0.091	12.4 ($p = 0.032$)	37	5.58 (5.48–5.67)
2M and repeat spawners					
Fork length ($p = 0.002$) and spawning history ($p < 0.001$)					At L_F 90 cm
2M	4.03	0.101	21.1 ($p < 0.001$)	118	6.34 (6.22–6.46)[a]
Repeat-A	4.14			43	6.52 (6.44–6.61)[b]
Repeat-C	3.87			19	6.09 (5.97–6.21)[c]
Whole weight ($p = 0.002$) and spawning history ($p < 0.001$)					At weight 6 kg
2M	5.75	0.053	24.8 ($p < 0.001$)	115	6.32 (6.25–6.40)[a]
Repeat-A	5.87			43	6.45 (6.36–6.54)[a]
Repeat-C	5.51			19	6.06 (5.95–6.18)[b]

The explanatory models for egg diameter were: egg diameter (mm) = $\alpha_j \times \text{Spawntype}_j \times \text{Size}^{\beta}\, e^{\varepsilon}$, with size either fork length (cm) or whole weight (kg). The table is interpreted as described in Table 2.

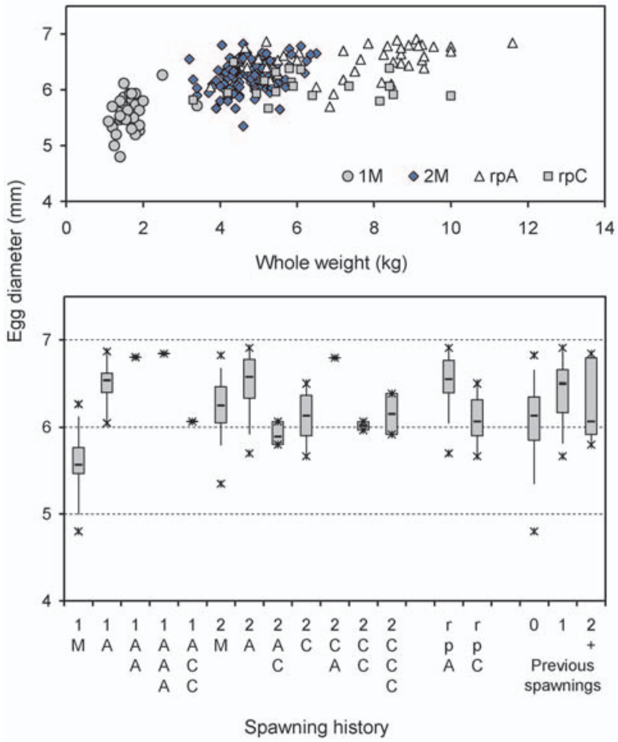

Figure 3. Summaries of average egg diameter per female salmon by weight (upper panel) and spawning history type (lower panel). In the lower panel, spawning history types are interpreted as described in Figure 2, and box plots as in Figure 1.

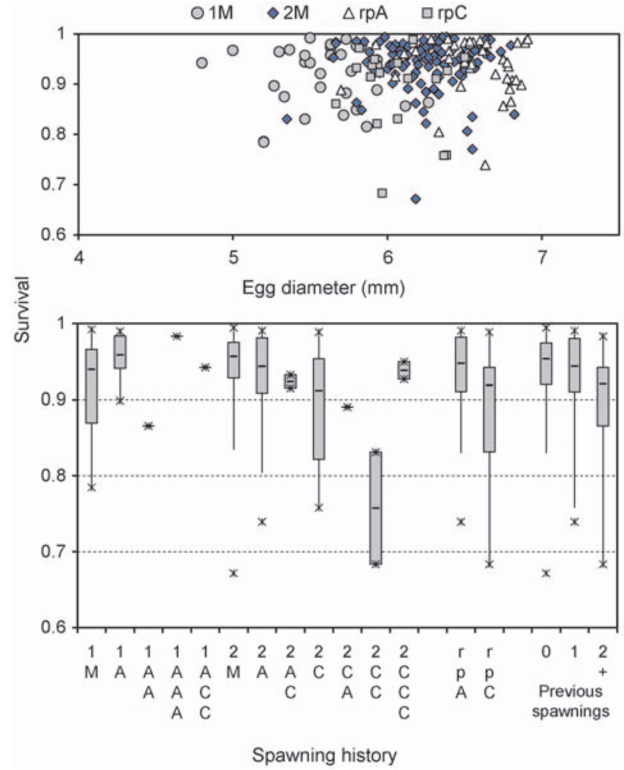

Figure 4. Survival to placement in hatching boxes by spawning history of females. Spawning history designations are as defined in the earlier figures.

body size, with slightly more of the explained variance in fecundity attributable to weight than to length (Koops *et al*., 2004). Similarly, fecundity increases with adult age at maturity, but age is confounded with body size because older fish are larger.

The findings in this study contrast to the general concept that egg size increases with female size and age (Johnston and Leggett, 2002). Differences in fecundity and egg size of Atlantic salmon for maiden, consecutive, and alternate repeat spawning strategies were noted. Although not statistically significant, relative fecundity at weight (mean and variance) was higher for the consecutive repeat spawners than for all other spawning history groups. Egg diameter also increased with body size, but consecutive repeat-spawning salmon had significantly smaller eggs at a standardized body size than maiden 2SW and alternate repeat spawners. Finally, the consecutive repeat spawners were of lower condition (weight per length) than the alternate repeat spawners and 2SW maiden fish.

The trade-off between smaller egg size but sustained high fecundity noted for consecutive repeat-spawning salmon may reflect energy limitation for gonad development. The majority of the energy acquisition of prespawning Atlantic salmon occurs at sea (Jonsson and Jonsson, 2003; O'Connell *et al*., 2006). In the Miramichi River, Atlantic salmon can spend between 6 and 10 months fasting in the river before returning to the ocean to recondition. In eastern Canada, consecutive repeat spawners typically return to the river after only a few months of reconditioning at sea (Hubley *et al*., 2008; Reddin *et al*., 2011), so may not have sufficient energy reserves to produce a large number of large-diameter eggs. Rather, fecundity is maintained but with smaller eggs with presumably less energy invested per egg.

The survival rate of eggs of consecutive repeat spawners was lower than that of 2SW maiden and alternate repeat spawners, but similar to that of 1SW maiden spawners. Although survival has been reported to be associated with egg size (Thorpe *et al*., 1984; Fleming, 1996; Johnston and Leggett, 2002), no association between egg diameter and survival was noted in this study, possibly because of the large variation in survival within and among the different spawning histories. Consecutive repeat spawners and 1SW maiden salmon produced smaller eggs and had spent less time in the ocean than 2SW maiden and alternate repeat spawners. This may result in differences in the energy content of eggs, as reported by Heinimaa and Heinimaa (2004). A future topic of research would be to consider assessing the chemical and energy content of eggs for different female spawning histories.

As a consequence of insufficient sample sizes, it was not possible to determine the effects of multiple repeat spawning (three or more spawnings) on fecundity, egg size, and egg survival. Based on the limited data in this study, spawning history (consecutive or alternate) appears to influence these traits more than the number of spawning events, possibly because alternate repeat spawners can fully recondition, whereas consecutive repeat spawners may only partially recondition.

Fast growth in freshwater is related to smaller egg diameter (Thorpe *et al*., 1984; Moffett *et al*., 2006). In this study, this association was found for 2SW maiden salmon. However, there was no such association either for 1SW maiden salmon, possibly because of the large variation in egg diameter and length of fish, or for repeat-spawning salmon, possibly because of the cumulative effects of age and multiple spawnings on the energy required for somatic and gonad growth and reconditioning.

Table 5. Survival to placement in incubation boxes by spawning history.

Explanatory variables	α	Explained variance (%)	n	Predicted survival (proportion)
1M	0.913	8.0 ($p < 0.001$)	32	0.913 (0.892–0.934)[a,b]
2M	0.940		110	0.940 (0.928–0.952)[b]
Repeat-A	0.936		40	0.936 (0.917–0.956)[b]
Repeat-C	0.883		18	0.883 (0.857–0.911)[a]
Previous spawning				
0 (1M, 2M)	0.934	2.7 ($p = 0.067$)	142	0.934 (0.923–0.944)[a]
1 (1A, 2A, 2C)	0.926		48	0.926 (0.909–0.944)[a]
2+ (others)	0.888		10	0.888 (0.851–0.926)[a]

The explanatory models for survival were: $survival = \alpha_j \times Spawntype_j \times e^{\epsilon}$. The table is interpreted as described in Table 2.

This study did not investigate differences in survival to hatch and emergence, or in the growth of juveniles derived from maiden and repeat-spawning salmon. It is widely accepted that large eggs produce large offspring with increased survival during the critical days after emergence (Thorpe *et al*., 1984; Fleming, 1996; Einum and Fleming, 2000; Johnston and Leggett, 2002).

Most studies of fecundity in Atlantic salmon have been conducted on younger adult ages and maiden spawners from populations with few repeat spawning salmon (Kazakov, 1981; Thorpe *et al*., 1984; Randall, 1989; O'Connell *et al*., 2008). There was little difference (<2%) in the fecundity estimates obtained by stripping fish in this study compared with those of Randall (1989), who counted eggs in ovaries of salmon collected from the Miramichi River between June and September. Consequently, atresia was not evident in Miramichi salmon, as reported by O'Connell *et al*. (2008) for other populations, possibly because the broodfish were exposed to less stress by being captured closer to spawning time.

The egg contribution by repeat-spawning salmon was estimated to represent ~25% of the total lifetime egg production by year class in the Miramichi River (Chaput and Jones, 2006). Increased abundance of repeat spawners can potentially buffer annual spawning runs when abundance of maiden salmon is low. The presence of repeat spawners also increases the number of year classes and increases effective population size (Saunders and Schom, 1985). More repeat-spawning females increase egg depositions per fish, particularly relative to populations that were primarily maiden spawners.

The proportion of consecutive repeat spawners within the runs of salmon on a second spawning migration has increased to >50% in recent years (Chaput and Benoît, 2012). From a total egg-deposition standpoint, consecutive repeat spawners produce a large number of eggs annually, whereas alternate spawners produce a large number of larger eggs in alternate years only. However, the egg quality of consecutive repeat spawners in terms of the survival of offspring is not known, and this topic merits further research.

The value of maiden spawning salmon should not be discounted. Repeat spawners are survivors of maiden spawners, so their abundance is equally dependent on the varying marine survival conditions encountered by post-smolts in the North Atlantic. These conditions have been less favourable in recent decades (Chaput, 2012). In addition, fisheries can impact the survival of maiden salmon. Management measures, such as those implemented on the Miramichi River, provide recreational fishery harvest opportunities on salmon <63 cm fork length (mostly 1SW maiden salmon), but require the mandatory release of salmon ≥63 cm fork length (predominantly 2SW maiden and repeat spawning salmon). These measures reduce the harvest of larger egg-bearing females, favouring the egg depositions by 2SW maiden and repeat-spawning female salmon. The resulting increased abundance of repeat-spawning salmon also has benefits for the recreational fishery experience (Atkinson and Moore, 1999).

The importance of repeat-spawning salmon increases during times of low marine survival because, partly because of size, more eggs per fish can be deposited in the river gravel. The survival of alternate repeat spawners returning for subsequent spawning is less than that of consecutive repeat spawners (Chaput and Benoît, 2012). Over time, this has resulted in an increasing number of consecutive repeat spawners in the repeat-salmon population in the Miramichi River (Chaput and Benoît, 2012). If this trend continues and sea survival does not decrease, there should be an increased number of eggs deposited annually by consecutive repeat spawners, but the egg quality (energy content and size) in terms of offspring survival is unknown. Therefore, the effect of spawning history on egg size and egg survival is an important characteristic in determining fecundity in populations of salmon with a large repeat-spawning component.

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