

Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo salar*

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Summary. Mature male parr successfully fertilized eggs of anadromous female Atlantic salmon, *Salmo salar*, in competition with anadromous males under simulated natural conditions. Mating situations were created in which mature male parr and anadromous males competing for the opportunity to spawn with an anadromous female differed in allelic forms of the same enzyme. Females deposited eggs into a sequence of 3 or 4 eggs nests. The mean proportion of eggs in a redd fertilized by parr increased with increasing numbers of parr present at a redd, reaching 23% at male parr: anadromous male ratios of 20:1. Single male parr fertilized, on average, 5% of the eggs in a redd. The proportion of eggs in an egg nest fertilized by parr also depended upon the order of egg nest construction, such that parr mating success was highest at the initial nest constructed and lowest at the final nest. Parr have relatively high fertilization success for their size when compared with the smaller maturation phenotype of other salmonids.

Key words: Frequency-dependent selection – Parr maturation – *Salmo salar* – Mating strategies – Canada

Male Atlantic salmon, *Salmo salar*, commonly mature as one of two life history forms. Male parr mature in fresh water and can be a year or more younger and considerably smaller (25–50 g vs. 1.5–10.0 kg) than anadromous males which mature following a feeding migration to sea (Jones 1959; Myers 1984). It is not uncommon for more than 80% of the males in a population to mature as parr (Myers et al. 1986).

Prior to spawning, a dominant anadromous male defends access to an anadromous female during courtship while mature male parr establish a linear dominance hierarchy immediately downstream of the courting pair with the largest parr nearest the female (Jones 1959; Myers and Hutchings 1987). The ratio of mature male parr to anadromous males exceeds 20:1 at the spawning site in some populations (Hutchings 1986). Mature male parr dart in close to anadromous pairs and shed sperm at the time of egg extrusion. Jones (1959) suggested that the relatively small size of male parr may allow them to position themselves

closer to the female's vent and fertilize more eggs than the anadromous male.

There are major demographic and economic consequences associated with parr maturation in male Atlantic salmon. The increased mortality and delay in time of seaward migration of mature male parr, relative to immature male and female parr, is responsible for the loss of 60% of the male salmon production in some Newfoundland populations (Myers 1984). This represents a substantial loss to both the commercial and sport fisheries.

The evolution of male Atlantic salmon life histories cannot be evaluated without knowledge of the relative mating successes of male parr and anadromous males (Caswell et al. 1984; Myers 1986). Estimates of male mating success are also necessary to predict how salmon populations will respond evolutionarily to current management practises that are designed to increase the numbers of spawning multi-sea-year salmon. These practises will increase selection pressures for delayed maturation in females. The degree to which selection pressures for male age at maturation will be affected, however, is dependent upon the relative gametic contributions of male parr and anadromous males during spawning.

The objectives of this study were (1) to quantify the relative gametic contributions of mature male parr and anadromous male Atlantic salmon during spawning, and (2) to determine how the proportion of eggs in a redd fertilized by male parr varies with the number of parr at the redd (nest site).

Materials and methods

Fish collection

Anadromous Atlantic salmon were collected at the fishway on Great Rattling Brook, Newfoundland (48°59'N, 55°35'W), in late September, 1985, and immediately transported in a cooled, aerated 2700 litre tank with recirculating water to holding facilities at the Northwest Atlantic Fisheries Centre (NAFC), St. John's, Newfoundland. Mature male parr were collected over spawning substrate in mid October, 1985, from the inlet stream of Junction Pond, Northeast River (46°21'N, 53°40'W), using back-pack electroshocking equipment and an apron seine. Parr were transported to the NAFC facilities in cooled 900 l tanks shortly after capture. Anadromous salmon and mature male parr were held in separate, continuous flow 2700 l tanks at ambi-

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ent water temperature (3–6° C) 1 week prior to the experiment.

Spawning facilities

Two types of simulated streams were used in the experiments. Both were recirculating systems with water replacement rates varying from 10 to 18 l/min. Mean water depth was 28 cm (range 25–30 cm) and mean current velocity was 12–15 cm/s. Water temperature ranged from 3 to 6° C. These conditions were well within the range of natural spawning conditions for Newfoundland salmon populations (Pratt 1968). The first type of simulated stream, a stream tank, was 9.1 m long and 3.0 m wide, consisting of a wooden and glass flume with recirculated water. A channel 1.2 m wide and another 0.6 m wide were joined by a 1.5 m wide pool section (see Gibson (1981) for a detailed description), providing 14.3 m² of substrate (geometric mean size 3–6 cm) available for spawning. The second type, a modified 2700 l holding tank, had water circulating around a cylindrical fibreglass container (77.5 cm diameter) over 1.8 m² of substrate (a 1:1 mixture of 1.9 and 3.8 cm washed stone).

Five modified holding tanks and one stream tank were used in the experiment. Two modified holding tanks contained one anadromous male, one anadromous female, and one mature male parr. The three remaining tanks held an anadromous pair with 5, 10, or 15 parr. The stream tank held 20 parr with an anadromous male and female. Fish were in the tanks 3–4 weeks prior to spawning. Observations were made once every 1–3 days for evidence of spawning activities, i.e. egg nest construction. Fish remained in the simulated streams 2 months after spawning had occurred. Eggs were collected from the substrate once they had reached the eyed stage of development in March, 1986.

Electrophoretic analyses

Atlantic salmon populations in Newfoundland are known to be polymorphic at the malate dehydrogenase (MDH)-B loci *Mdh-3* and *Mdh-4* (Clayton 1984; E. Verspoor, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld. A1C 5X1, unpublished work). Both loci have the same common electrophoretic alleles – *Mdh-3,4(100)*, *Mdh-3,4(120)* and rarely *Mdh-3,4(140)* (Clayton 1984). Electrophoretic variability at the MDH locus has been extensively studied by Cross and Ward (1980). The genetic model of duplicated *Mdh-B* loci sharing alleles has been confirmed by Johnson (1984). Individuals used in the present study expressed the alleles *Mdh-3,4(100)* and *Mdh-3,4(120)*. Allozyme phenotypes of *Mdh-3,4* can be determined from muscle tissue biopsies. Both paternal and maternal alleles are expressed at the eyed stage of development (Jones 1976). Genetic typing of embryos facilitated collection of offspring for analysis and minimized time (and egg mortality) between fertilization and electrophoretic analysis.

Muscle tissue was removed from 12 anadromous males and females and 105 mature male parr. Fish were anaesthetized with CO₂ (Hutchings 1986), measured (fork length to the nearest 1 mm), and individually marked with an alcian blue dye injected onto the fin membranes for identification following determination of MDH genotypes. Samples of muscle tissue (approx. 25 mm³) were removed with forceps through an incision made in the epaxial musculature immediately anterior to the origin of the dorsal fin. Muscle

samples were placed in marked plastic vials and immediately frozen at –20° C. Following recovery, fish were placed in a bath of terramycin for 2–3 h to prevent infection (Piper et al. 1982). This antibiotic proved to be very effective as none of the fish developed infections. Using observations of behavioural interactions between parr and anadromous salmon in the stream tank, we were unable to discern any deleterious effects resulting from the removal of muscle tissue. Once the allozyme phenotypes of each fish had been identified, male parr and anadromous males possessing different MDH genotypes were placed in simulated streams with an anadromous female and allowed to spawn. Samples of 82 to 105 “eyed” eggs were randomly chosen from each egg nest (3 or 4 nests per mating situation) and electrophoretically examined. Whole embryos were removed from the eggs for the analyses. Muscle tissue was sampled from all spawning salmon to verify identification of MDH genotypes.

Muscle and embryo samples were stored at –20° C until required. Samples were prepared for electrophoreses by placing the tissue into a 2 cm well in a ceramic block containing 12 such depressions, adding 1–2 drops of distilled water and grinding manually with a glass rod. The homogenate was then absorbed directly on to 3 × 6 mm squares of filter paper.

Horizontal gel electrophoreses were carried out in starch gels (Connaught Laboratories, Toronto), measuring 200 × 100 × 6 mm, using the citrate-morpholine pH 6.0 buffer system described by Clayton and Tretiak (1972). Gels were run at 300 V for 3 h at room temperature. Following this, gels were horizontally sliced and stained for MDH (modified from the stain described by Harris and Hopkinson 1976).

The proportions of egg batches fertilized by male parr were calculated using the method of maximum likelihood for estimating gene frequencies at a 2-allele locus (Crow and Kimura 1970; Appendix 9). All male parr and females were homozygotes. Anadromous males were heterozygous for MDH in three of the matings.

Results

Spawning occurred in 4 of the 6 simulated streams. Anadromous females constructed redds and deposited eggs in the tanks containing 5, 10 and 20 parr and in one of the tanks containing a single parr (Table 1). Eggs were deposited at each redd into either 3 or 4 separate nests which were linearly positioned parallel to the direction of water flow (Table 2). The number of eggs per nest ranged from 82 to 394 (Table 2). Egg mortality from fertilization to time of collection (eyed stage of embryo development) ranged from 0.02 to 0.21. Some eggs were retained in the body cavities of all females. All male parr (including those that died – see below) were either spent or partially spent (testes width of 5–10 mm). Male parr that were partially spent were generally the largest parr at the redd. All anadromous males that had spawned were spent. The possibility that some of the sperm had been resorbed, however, cannot be discounted. One parr died in the tank containing 10 parr and all parr died in the tank containing 5 parr. These mortalities occurred after spawning and were caused by anadromous male aggression (Hutchings and Myers 1987).

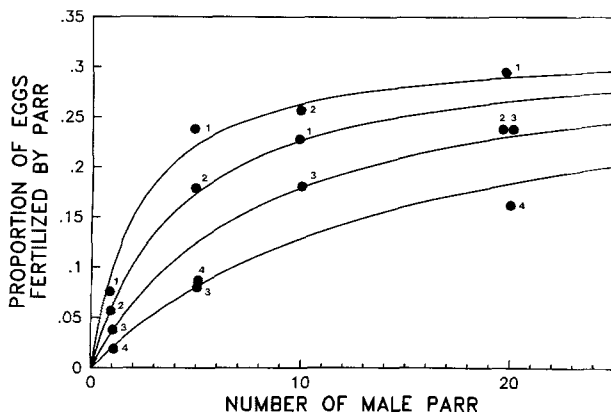
The proportion of eggs fertilized by male parr varied with the number of parr at each redd and with the order

Table 1. Sizes (fork length in cm) of Atlantic salmon in the simulated streams

Facility	Number of parr	Mean parr length \pm s.d.	Anadromous male	Anadromous female
Tank 1	1	16.3	51.3	54.0
Tank 2	5	15.4 \pm 1.3	54.6	47.0
Tank 3	10	17.2 \pm 1.8	52.0	51.8
Stream tank	20	15.0 \pm 1.5	52.7	49.1

Table 2. Redd characteristics in the simulated streams in which spawning occurred (lettering of egg nests indicates order of completion, e.g. the first egg nest completed in a redd = a)

Facility	Number of parr	Number of egg nests	Number of live eggs per nest	Egg mortality
Tank 1	1	4	a - 185 b - 147 c - 238 d - 151	0.14
Tank 2	5	4	a - 208 b - 167 c - 181 d - 140	0.21
Tank 3	10	3	a - 131 b - 82 c - 150	0.10
Stream tank	20	4	a - 394 b - 195 c - 290 d - 161	0.02

**Fig. 1.** Observed proportions (●) of eggs per egg nest fertilized by male Atlantic salmon parr, competing with a single anadromous male, as a function of the number of male parr present per mating. Numbers (1-4) refer to the order in which egg nests were constructed. Lines are fitted curves (see text)

of egg nest construction (the nest situated furthest downstream was assumed to have been the initial site of egg deposition at each redd (Jones 1959; Pratt 1968)). The mean proportion of eggs fertilized by male parr at each redd was an increasing function of parr number (Fig. 1). The mean proportion of eggs fertilized by an individual male parr decreased from 0.05 to 0.01 as the number of parr present increased from 1 to 20. The mating success of male parr generally decreased with order of nest construction, independent of parr density (Fig. 1), such that parr mating suc-

cess per egg nest was greatest at the first nest constructed and lowest at the last nest to have been constructed.

An empirical description of the data is needed for modelling Atlantic salmon life histories and for testing the hypothesis that order of egg nest construction affected the proportion of egg batches fertilized by mature male parr. The data suggested that this proportion should increase asymptotically to some maximum proportion as the number of parr increase. The data were fit to a model whose systematic component was

$$p(N, i) = \frac{\beta_1 N}{N + \beta_3 \beta_2^i}$$

where N = number of parr at each redd;

p = proportion of eggs fertilized by male parr;

i = order of egg nest completion, ($i = 1, 2, 3$ or 4);

$\beta_1, \beta_2, \beta_3$ are model parameters.

The asymptote is β_1 and the slope at the origin for the i_{th} egg nest is $\beta_1/\beta_3 \beta_2^{i-1}$. The parameters of the model were fit by maximum likelihood, assuming a binomial sampling error, with the sample size for each observation given in Table 2. A Fortran subroutine (ZXMIN) from the International Mathematics and Statistics Library (IMSL 1985) was used to estimate the maximum likelihood solutions. Estimates of the standard errors of and the correlations among the parameter estimates were computed from the inverse of the observed information matrix (Cox and Hinkley 1974). The maximum likelihood estimates for the parameters were

$$\hat{\beta}_1 = 0.32 \pm 0.14 \text{ (SE)}$$

$$\hat{\beta}_2 = 3.10 \pm 1.07 \text{ and}$$

$$\hat{\beta}_3 = 2.17 \pm 0.95.$$

The largest correlation between parameter estimates was between $\hat{\beta}_1$ and $\hat{\beta}_2$ ($r = 0.88$). The hypothesis that the proportion of eggs fertilized by male parr decreases as the number of egg nests increases was tested by a likelihood ratio test. That is, the model was re-fit with β_3 constrained to be zero, and the resulting maximum log-likelihood was compared with that from the 3 parameter model. There is strong evidence that the proportion of eggs fertilized by male parr decreases as the number of egg nests per redd increases ($P < 0.005$). Alternative 3 parameter models were also fit to the data, e.g. having the asymptote be a function of i ; however, these models gave a lower maximum log-likelihood. The model shows that the mean proportion of eggs fertilized by male parr at each redd was an increasing function of parr number before approaching an asymptote at male parr: anadromous male ratios exceeding 20:1 (Fig. 1).

Discussion

Mating success of male parr

While it has long been known that the sperm of male parr is capable of fertilizing eggs (Shaw 1836), and that eggs so fertilized can produce viable offspring (Jones and King 1950; Thorpe and Morgan 1980), the present study is the first to confirm that male parr fertilize eggs when allowed to spawn with an anadromous female in competition with an anadromous male.

The mating success of male parr depends upon the number of parr present and the number of egg nests dug at the redd site. Male parr do not fertilize more eggs than

anadromous males during spawning. The proportion of eggs in a redd fertilized by all male parr increases with increasing parr number before reaching a proportion of about 0.25 (when four egg nests are constructed) at male parr: anadromous male ratios of 20:1 (Fig. 1). However, fertilization rates when 1 to 5 parr are present at a spawning are required before the functional form of the curves in Fig. 1 can be fully described. Detailed observations determining the actual number of parr that participate at each spawning would also be useful. Individual mating success of male parr decreases, on average, as the number of parr present increases. The proportion of eggs in an egg nest fertilized by parr depends upon the order of egg nest construction. Anadromous females deposited eggs in either 3 or 4 nests per redd in the present study. Jones (1959) reported that as many as 8 egg nests may be constructed by large females (5.6 kg fish depositing up to 6000 eggs).

The reduction in parr mating success per egg nest as the number of nests per redd increases may reflect a physiological inability of parr testes to fully replenish the volume of sperm between spawnings. Data on yield of semen obtainable by several strippings of male parr are limited to those given by Alm (1943) and Kazakov (1981) who found no reduction in ejaculate volumes when sampled on 1–3 week intervals. However, limited data indicate that females deposit all of their eggs within either minutes or hours after their initial spawning (Jones 1959). Female chum salmon deposit their eggs within 36 h after starting construction of their first nest (Schroder 1981). Jones (1959) and Schroder's (1981) data are based on observations of spawning activity in the absence of female competition which could affect the duration of a female's spawning. Nevertheless, under conditions of high male parr:anadromous male: female ratios (e.g. 20:1:1), there may be little opportunity for male parr to spawn with more than one female. This would account for the presence of semen in parr following reproduction in populations having very high male parr:anadromous salmon ratios (Hutchings 1986).

Interspecific comparisons

The mating strategies of male salmonids, particularly Atlantic and Pacific salmon, *Oncorhynchus* spp., are such that subdominant males can be classified as satellites, hidlers or sneakers. Satellite males are similar in size to the dominant or alpha male, position themselves adjacent to or downstream of the courting pair, and acquire matings through fighting. Satellite males are found in both Atlantic and Pacific salmon (Ouellet 1977; Schroder 1982; Gross 1985). Hidlers are 50–75% smaller than the alpha male, position themselves in refuges along river banks, and rush toward the mating pair from these refuges to release sperm during oviposition. This behaviour has been reported for Pacific salmon "jacks" (notably coho salmon, *O. kisutch*; Gross 1985). Sneaker males are considerably smaller (relative size of sneaker to alpha male is generally 0.02–0.25) than the alpha male, position themselves on the stream substrate in a linear dominance hierarchy immediately downstream of the courting pair, and dart in close to the mating pair during oviposition to release sperm. This behaviour is characteristic of Atlantic salmon parr (Jones 1959; Myers and Hutchings 1987).

The relative mating successes of alternative male maturation phenotypes in salmonids have been examined for

the Miyabe char, *Salvelinus malma miyabei* (Maekawa and Onozato 1986). The spawning behaviour of small, stream resident male Miyabe char with large, lake resident females in competition with lake resident males closely approximates that of Atlantic salmon parr (Maekawa 1983). Electrophoretic analyses indicated that stream resident males fertilized an average of 16.9% (range 0–61.6%) of the eggs deposited when a single stream resident male was present (Maekawa and Onozato 1986). This percentage may be somewhat biased because it represents the fertilization success of only 3 stream resident and 2 lake resident males over 17 matings. The average mating success of stream resident males was reported to have decreased as the numbers of stream resident males present at a redd increased (Maekawa and Onozato 1986).

The gametic contributions of alpha and satellite male chum salmon, *O. keta*, have also been examined using electrophoretic techniques (Schroder 1981, 1982). However, the maturation of male chum salmon differs from that of Atlantic salmon and Miyabe char. All male chum salmon spawn following a 2–5 yr (usually 3–4 yr) residence at sea (Schroder 1981). Subsequently the difference in size between alpha and satellite male chum salmon is much less than it is for the two other salmonids. Single satellite males fertilized, on average, 24.6% (range 0–46%) of the eggs deposited by a female when spawning in competition with a large male. When two satellite males were present they collectively fertilized 47% of the eggs deposited into a single nest.

Atlantic salmon parr fertilize significantly fewer eggs, when a single parr is present, than the smaller of the two male maturation phenotypes of Miyabe char and chum salmon. This can be attributed to the small size of Atlantic salmon parr relative to the size of anadromous males with whom they compete. The relative mean weight (g) of parr to anadromous male in the present study is $36/1650 = 0.02$. The relative weights of stream resident Miyabe char used in the study by Maekawa and Onozato (1986) (calculated from a weight-length relationship given by Armstrong and Morrow (1980)) averaged $18/156 = 0.12$. The relative mean weight of the smaller chum salmon used by Schroder (1981) was 0.75 (S.L. Schroder, Washington Department of Fisheries, Olympia, Washington 98504, unpublished work). Chebanov et al. (1983) reported that two satellite sockeye salmon, *O. nerka*, (relative mean weight = 0.73) fertilized 5% of the eggs spawned by a single female into 2 egg nests in the presence of a dominant male. Thus, the average proportion of eggs fertilized by the smaller male, or males, appears to be an increasing function of the relative weight of the small male to the large male (Fig. 2). (Note: Data on Miyabe char are the conservative estimates of fertilization rates taken from Maekawa and Onozato (1986; Table 3, column 11). A second mating reported by Chebanov et al. (1983) was not included because dominance of the 2 males alternated between spawnings.)

Mating success is also influenced by behaviour. Male Atlantic salmon parr fertilize more eggs, for their size, than do satellite male chum salmon (Fig. 2). This may be due to their relatively small size and their close proximity to the female afforded by their positions on the stream substrate from which they can generally avoid detection by the alpha male (but see Hutchings and Myers (1987)). Nonetheless, this tentative conclusion is based on limited data from species having different reproductive strategies.

The great variation in male parr maturation among pop-

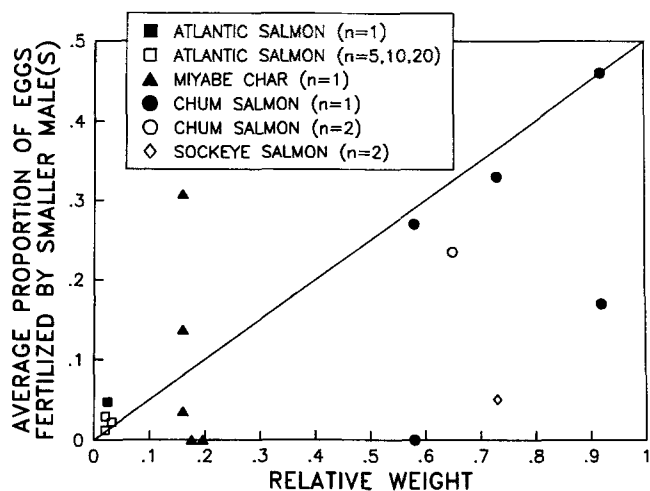


Fig. 2. Average proportion of eggs in a redd fertilized by the smaller male, or males, versus the relative weights of the small male(s) to the large male for Atlantic salmon, Miyabe char, chum salmon, and sockeye salmon (n = number of small males present per mating). The diagonal line is the expected fertilization by smaller males if fertilization is proportional to relative weight, and is provided for reference only

ulations of Atlantic salmon (Myers et al. 1986) suggests either that the evolutionary pressures on parr maturation vary among populations or that alternative evolutionarily stable strategies exist within populations (Gross 1985; Myers 1986). The relative gametic contributions of mature male parr and anadromous males determined herein can be used to test quantitative theories of the evolution of age at maturation in male Atlantic salmon (Caswell et al. 1984; Myers 1986). However, given that size is an important criterion in determining a parr's position in the spawning dominance hierarchy (Myers and Hutchings 1987), and that male mating success is apparently directly related to proximity to the female (Schroder 1981, 1982), there is still a need to determine the relative gametic contributions male parr of different ages and sizes make in the fertilization of eggs.

Acknowledgements. The assistance of R.H. Payne and E. Verspoor during the electrophoretic analyses is gratefully acknowledged. We thank C. Bourgeois, P. Griffen, K. Hillier, B. Mayer, J. Pratt, J. Yates, and the Marine Science Research Laboratory, Logy Bay, for assistance in fish collection and transportation. Unpublished data were kindly provided by S.L. Schroder. The technical assistance of J. Ryder was appreciated. J.A. Brown, W.E. Davidson, and two anonymous referees provided constructive criticisms on the manuscript. The work was supported by a Department of Supply and Services contract to JAH (UP-N-222) and sponsored by the Department of Fisheries and Oceans, St. John's. Newfoundland Institute For Cold Ocean Science Contribution No. 143.

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Received January 26, 1987