

A Genetic Evaluation of Mating System and Determinants of Individual Reproductive Success in Atlantic Salmon (*Salmo salar* L.)

D. Garant, J. J. Dodson, and L. Bernatchez

The primary objective of this study was to use highly polymorphic microsatellite loci to estimate individual reproductive success in Atlantic salmon based on the number of surviving juveniles (young of the year) at the population level under natural conditions. We inferred reproductive strategies adopted by both sexes by applying a maximum likelihood method to determine parent-offspring genotype relationships. A high degree of variance in individual reproductive success for both males and females was revealed. The high number of mates used by both sexes is not concordant with previous behavioral studies proposing that females are mainly monogamous in this species. We found little evidence supporting the prediction from previous reports of a positive relationship between individual size and realized reproductive success for either males or females. For both sexes, however, there was a significant correlation between the number of mates and the number of offspring. These results indicate that this species' mating system is more flexible than previously thought and suggest that factors such as potential genetic benefits or environmental uncertainty may also be driving the evolution and the plasticity of mating systems in Atlantic salmon.

Mating systems are defined by the reproductive strategies adopted by individuals of both sexes (Clutton-Brock 1989), and numerous behavioral studies have examined the various strategies leading to mating success. In many species, females are considered as the limiting resource to be courted and monopolized by males (Darwin 1871; Emlen and Oring 1977; Trivers 1972) and this has led to a focus on the tactics of males to access female reproductive resources. Typically monitored are the number of copulations (rate at which each male mates) or the number of social associations during which time a male may have exclusive access to a female (see Brandt 1989; Clutton-Brock 1988; Howard 1978).

However, the use of behavioral observations to quantify reproductive success has several limitations. First, behavioral observations may lead to incorrect assignments of offspring to particular individuals in cases where extrapair fertilizations occur (see Gibbs et al. 1990; Westneat 1987a,b). Furthermore, due to the logistical constraint of daily monitoring, behavioral studies often involve a small number of specimens and, as such, are inappropriate to evaluate variance in individual reproductive success. Finally, for species

that are difficult to observe, much behavioral monitoring has been done under controlled laboratory conditions (see Shapiro and Dewsbury 1986). Thus there is an evident trade-off between the availability of behavioral observations for animals that are difficult to observe in nature and the reliability of the behaviors observed under artificial conditions.

To more firmly establish the determinants of the reproductive strategy employed by individuals of both sexes, and also to measure fitness more properly, one needs to accurately measure the relationship between an individual's phenotype and its realized lifetime reproductive success (Howard 1979). Major improvements could be achieved by working at the population level in natural conditions and by tabulating the number of surviving offspring that an individual produces.

In the past decade, mating system analyses have benefited from molecular technologies to evaluate parameters such as genetic relatedness between individuals (Blouin et al. 1996; Queller and Goodnight 1989), the genetic correlates of complex social systems (Amos et al. 1993; Packer et al. 1991), and genetic parentage (Burke 1989; Morin et al. 1994; Pemberton et al. 1992; Westneat 1990). More recently, high-

From the Université Laval, Département de Biologie, Pavillon Vachon, Room 4042A, Ste-Foy, Quebec, Canada G1K 7P4. The authors are grateful to John C. Avise and two anonymous reviewers for their constructive comments. We acknowledge A. Boivin and D. Bussi eres from CIRSA for logistical and field assistance, P. Duchesne for development of analytical tools, and S. Martin, L. Papillon, and N. Tessier for laboratory assistance. The authors would like to thank the Association de la rivi ere Sainte-Marguerite Inc. who provided facilities for fish transportation. Funding for this project was provided to L.B. and J.J.D. and the members of CIRSA by the Natural Sciences and Engineering Research Council of Canada (Collaborative Special Projects), the Fondation de la Faune du Quebec, the Government of Quebec (Minist ere de l'Environnement et de la Faune), the government of Canada (economic development), and the financial partners of CIRSA Inc. (Corporation de soutien aux initiatives de recherche sur le saumon Atlantique). D.G. was financially supported by funding from the Fond pour la Formation de Chercheurs et l'Aide   la Recherche (FCAR), CIRSA, and GIROQ. Address correspondence to Louis Bernatchez at the address above or e-mail: louis.bernatchez@bio.ulaval.ca. This paper was delivered at a symposium entitled "DNA-Based Profiling of Mating Systems and Reproductive Behaviors in Poikilothermic Vertebrates" sponsored by the American Genetic Association at Yale University, New Haven, CT, USA, June 17-20, 2000.

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ly polymorphic genetic markers such as microsatellite loci have been used to measure individual reproductive success by directly comparing parental and offspring multilocus genotypes (see Marshall et al. 1998). In some taxa, these studies have revolutionized the understanding of mating strategies by revealing major discrepancies between the behavioral and genetic estimates of reproductive success (see Hughes 1998). For example, extrapair paternity was demonstrated in many avian species that were previously thought to be exclusively monogamous (Birkhead and Møller 1992). Likewise in mammals, a high proportion of offspring often have proved not to be sired by the observed social partner (Amos et al. 1993; Coltman et al. 1999; Worthington Wilmer et al. 2000). Whereas the evaluations of genetic mating systems in mammalian and avian taxa have received much attention, far less has been given to the analysis of reproductive strategies of poikilotherms, particularly fishes (but see DeWoody et al. 1998; Jones and Avise 1997; Rico et al. 1992). This is surprising given the fact that these organisms evolve in a multidimensional environment that favors the evolution of a great diversity of mating systems and reproductive strategies (Gross 1984).

In Atlantic salmon (*Salmo salar* L.), age and size at maturity are highly variable for both sexes, and those parameters are believed to be the principal determinants of a salmon's reproductive strategy (Fleming 1996). This implies that various reproductive strategies linked to distinct phenotypes occur at the individual level, and that they can result in differential reproductive success. In anadromous males, access to mating opportunities appears to be the primary reproductive constraint. Consequently it is generally accepted that body size of individuals has evolved as the major determinant of dominance among anadromous males (Jarvi 1990; Mjølnerød et al. 1998). The relation between body size and reproductive success in anadromous males, however, tends to be nonlinear (Fleming et al. 1997). For females, a larger body size may have been favored in evolution because of its strong correlation with individual fecundity (Jonsson et al. 1996). Larger body size is also associated with the production of larger eggs, which often produce larger juveniles (Kazakov 1981a) with higher survival rates (Wankowski and Thorpe 1979). A single female mating with one dominant male seems to be the most common strategy, even when multiple-male spawning has been docu-

mented (see Fleming et al. 1997; Webb and Hawkins 1989).

Whereas the reproductive behavior of Atlantic salmon has been investigated extensively (Belding 1934; Fleming 1996, 1998; Jones and Ball 1954), no genetic evaluation of this species' mating system has been performed. Furthermore, no direct quantification of salmon reproductive success has been performed at the population level in nature, nor have studies that sample older life-history stages of progeny been specifically designed to evaluate the contribution of a spawner to the next generation. Most previous efforts to define reproductive success and estimate the Atlantic salmon mating system are based on behavioral monitoring only (see Baglinière et al. 1990; Beall and Marty 1983; Fleming et al. 1996, 1997; Webb and Hawkins 1989). The few studies that used molecular tools to quantify reproductive success in nature have been mainly restricted to a limited number of spawners that generated insufficient numbers of matings to support definitive statements about the determination of reproductive success (see Martinez et al. 2000; Moran and Garcia-Vasquez 1998). Conversely, experiments performed under controlled conditions (O'Reilly et al. 1998) or designed to evaluate parentage of farmed individuals (Norris et al. 2000) may not have been representative of natural spawning situations.

In this study we used highly polymorphic microsatellite loci to estimate individual reproductive success in Atlantic salmon based on the number of surviving juveniles (young of the year) at the population level under natural conditions. We also established the variance in individual reproductive success and inferred the possible reproductive strategies adopted by both sexes. More specifically we tested the standard prediction of a positive relationship between individual size and realized reproductive success.

Materials and Methods

Study Site and Salmon Reproductive Behaviour

The study site was the Ste-Marguerite River (48°20'N, 70°00'W), Quebec, Canada. Anadromous salmon migrate into this river in July and August to spawn during October and November. Females build their nests within a redd (area of disturbed gravel; Crisp and Carling 1989; White 1942) where they deposit their eggs over a period of 5–6 days. Once nesting is complet-

ed, the eggs are buried and females leave the spawning grounds (Fleming 1998). Males do not participate in nest construction, but rather compete for access to ovipositing females (Fleming 1996, 1998). Salmon fry (young of the year) emerge at the end of spring or at the beginning of summer and subsequently move to nursery areas adjacent to the spawning grounds.

Sample Collection and Characteristics

At the end of July 1995, 41 adult male and 35 adult female salmon were caught at the fish ladder located on the northeast branch of the Ste-Marguerite River. These were measured, sexed, and their adipose fins clipped and collected. Due to the conservation context in which this study was conducted, and to reduce the probability of imposing serious stress to fish given the high water temperature at the time of the transfer, the manipulation of spawners was kept to a minimum. Thus only a single measurement of length per fish was done (at a 50 mm precision level). Therefore we estimated a measurement error defined as 50 mm/median fish length. All spawners were then relocated in an upstream part of the same river branch. This river stretch, not previously occupied by Atlantic salmon, is 19 km long and is isolated by two impassable waterfalls located at km 30 and 49. We chose a stretch of river previously devoid of Atlantic salmon so as to sample uniquely the offspring of introduced spawners. From August 27 to September 6, 1996, electrofishing was conducted throughout accessible spawning and nursery areas to sample as many progeny as possible. A total of 650 fry were sampled over a 4-day period. Whole fry and adult adipose fins were preserved for genetic analysis in 95% ethanol.

The total weight of each spawner was estimated from linear regression models relating length to weight. Based on salmon caught in the Ste-Marguerite River from 1982 to 1996, we estimated the following relationships: $\text{weight} = -6.596 + 0.01529[\text{length}]$ for females ($r^2 = 0.91$), $\text{weight} = -6.562 + 0.01523[\text{length}]$ for males > 550 mm ($r^2 = 0.91$), and $\text{weight} = -0.5 + 0.004[\text{length}]$ for males < 550 mm ($r^2 = 0.91$). Potential fecundity of females (defined as the number of eggs produced as a function of size) was estimated according to an equation developed by Fleming (1996) for fish in the Restigouche River, New Brunswick, Canada: $\text{fecundity} = 0.31(\text{length})^{2.3423}$ ($r^2 = 0.89$).

Genetic Analysis

Microsatellite selection. To determine a priori the number and characteristics of loci suitable for parentage analysis, we used a “parentage model” (Bernatchez and Duchesne 2000) that infers the probability of assigning offspring to parental couples as a function of population size, number of loci, and allelic diversity. This model predicts that when allelic diversity is high, the number of loci required to achieve high assignment success is low, even if the number of spawners in the population is large. With 76 spawners and approximately 15 alleles at each of 5 loci, this model predicted a correct parentage assignment for as many as 90% of offspring. We also considered single- and multilocus exclusion probabilities (Estoup et al. 1998; Sancristobal and Chevalet 1997; Smouse and Chakraborty 1986). Based on both the “parentage model” and the probability of exclusion, we chose to employ five loci previously developed for *S. salar* (*SSOSL85*, Slettan et al. 1995; *Ssa171*, *Ssa197*, *Ssa202*, O’Reilly et al. 1996) and *S. trutta* (*MST-3*, Presa and Guyonard 1996).

Microsatellite polymorphism analysis. Total DNA extraction was performed from approximately 30 mg of tissue according to Bernatchez et al. (1992). Microsatellite polymorphism was analyzed as in Garant et al. (2000). Briefly, we performed polymerase chain reaction (PCR) amplification with one of the primers of each locus 5'-labeled with different fluorescent dyes. *MST-3* was amplified alone, and multiplexed PCR was used for *Ssa197* and *SSOSL85*, and for *Ssa171* and *Ssa202*. All reactions were performed with the following profile: an initial denaturing step of 4 min at 95°C, followed by 35 cycles of 30 s at 94°C, 30 s at 56°C, and 30 s at 72°C.

Statistical Analysis

Informative content and possible bias. Genetic diversity in the adult population was quantified by the number of alleles per locus and observed and expected (from Hardy–Weinberg) heterozygosities. Conformity to Hardy–Weinberg equilibrium [exact test of Guo and Thompson (1992)] was conducted to detect the possible presence of null alleles, a common feature of microsatellite markers that could bias the assignment procedures (Pemberton et al. 1995). We also tested for possible linkage disequilibrium among loci, as we used a maximum likelihood method for parentage analysis (see next section) which assumes that all loci segregate independently.

These tests were calculated using the GENPOP software, version 3.1 (Raymond and Rousset 1995). Finally, we calculated Queller and Goodnight’s (1989) r_{xy} statistic, an unbiased estimate of true relatedness between all possible pairs of adult individuals. Values were used to test the basic assumption that spawners were representative of the whole population in which individuals are no more related to each other than by chance alone. A high value of mean relatedness would also reduce confidence in parentage assignment (Marshall et al. 1998).

Parentage assignment. We used a maximum likelihood-based method as detailed in Sancristobal and Chevalet (1997) to infer parentage for all offspring sampled. This method identifies the most probable parental pair for a given offspring starting with no prior information on the mating events. This is achieved by computing the probability of occurrence of a given offspring genotype among the potential offspring of each possible parental pair in the population. Once the probability of occurrence of its multilocus genotype is obtained, the offspring is assigned to the parental pair showing the highest probability of producing it. A detailed but simple description of the mathematical method is provided in Appendix 2 of Bernatchez and Duchesne (2000).

The probability of erroneous scoring of allelic size (such as allele designation, stutter-related scoring, or upper allele dropout errors) in an individual genotype must be considered when conducting maximum-likelihood parentage analysis (Sancristobal and Chevalet 1997). Therefore a nonzero error rate should be taken into account when assigning the most likely parental pair to a given progeny. For all analyses, we used an error rate (*epsi*) of 0.02, which corresponds to that reported in a controlled study on *S. salar* using several of the same markers (see O’Reilly et al. 1998). Previous methods that included the error rate in computing the likelihood calculation have considered either that individual alleles were randomly replaced by nonidentical alleles (Sancristobal and Chevalet 1997), or that incorrectly typed alleles are replaced by the most frequent alleles in the population (Marshall et al. 1998). We propose that a more realistic modeling of error should assume that rates of substitution between alleles depend on their differences in size, with alleles having highly different repeat numbers less prone to be confounded than alleles differing by only a single repeat. To

take this into account, we used a “decreasing rate of error” ($= 1/d^2$) that distributes the error rate over the neighboring alleles. Consequently, by using an appropriate decreasing rate of error where $d = 12$, we were able to confine typing error only to alleles adjacent in size (equivalent to one mutation step). All calculations were performed using the algebraic computer system Maple V (release 5.1, Waterloo Inc. 1999).

To test for the efficiency of the assignment method, we used all adult male and female genotypes to generate a random group of 10,000 simulated offspring and then performed assignment simulations (with *epsi* = 0.02 and $d = 12$). By doing so we were able to estimate the maximum potential success of the loci used in the study in reassigning a simulated offspring to its original parental pair. Each time a progeny was assigned to its correct pair of parents, this was counted as a reassignment success. We conducted these simulations by adding loci from the most to the least informative based on their probabilities of exclusion.

We then performed maximum-likelihood assignments using multilocus genotypes from putative parents and all offspring caught. We computed the likelihood of each offspring genotype for each pair of parental genotypes. By doing so we were able to obtain the number of offspring assigned to each parental pair and hence to each individual. By establishing all successful pairs of spawners (each pair to which an offspring had been assigned), we also obtained an estimate of the number of mates for each adult salmon.

Correlation analysis. We used the results obtained from these parentage assignment procedures to perform Pearson’s correlation analysis using the Statistica version 5.1 software (Statsoft 1997). The following were examined for possible significance ($P < .05$): body weight versus number of offspring, body weight versus number of mates, and number of mates versus number of offspring. For females, we also tested if there was a significant correlation between estimated fecundity and number of assigned offspring, because fecundity is proposed to be strongly correlated with reproductive success in fishes.

Results

Characteristics of Adult Fish

Both females and males exhibited a large range in body size (females 550–900 mm, mean 769 mm; males 450–1050 mm, mean

Table 1. Number of alleles (*A*), expected heterozygosity (*H_e*), individual probability of exclusion (*E_i*), and global probability of exclusion (*E_g*) for each loci in the adult population

Loci	<i>A</i>	<i>H_e</i>	<i>E_i</i>	<i>E_g</i>
<i>Ssa171</i>	22	0.92	0.831	0.831
<i>Ssa197</i>	14	0.84	0.762	0.960
<i>SSOSL85</i>	13	0.89	0.732	0.992
<i>Ssa202</i>	13	0.87	0.677	0.987
<i>MST-3</i>	8	0.75	0.517	0.998
Average	14	0.85	0.704	0.998

620 mm). Measurement error was estimated to be 6.7% (median fish length 750 mm). Estimated weight from the linear regression models ranged from 1.8 to 7.2 kg (mean 5.2 kg) for females and from 1.3 to 9.4 kg (mean 3.0 kg) for males. Potential fecundity for females was estimated to range from 3697 to 11,716 eggs per individual (mean 8271 eggs per individual).

Informative Content of Microsatellite Loci

As has been previously shown (McConnell et al. 1997; Tessier et al. 1997), the five microsatellite loci used were highly polymorphic (Table 1). Consequently the individual and combined exclusion probabilities were also quite high (Table 1). None of the loci showed a significant departure from Hardy-Weinberg equilibrium, and this observation, coupled with the absence of observed null homozygotes in adults, was indicative that null alleles were not common in our sample. Similarly, no significant genotypic disequilibria were detected in any pair of loci (results not shown). Finally, relatedness analysis of wild-caught spawning adults indicated that these fish did not share more alleles (and hence were not more related) than expected by chance: the mean global r_{xy} value was 0.0005 (minimum -0.4423, maximum 0.7162) (Figure 1).

Parentage Analysis

The method and basic parameters ($\epsilon = 0.02$ and $d = 12$) used in this study were highly efficient for parentage assignment, as demonstrated by the results of the reassignment simulations (Figure 2). Indeed, 9223 of 10,000 artificial offspring (92.2%) were assigned to their correct parental pairs based on the combined information from five loci. This result is in agreement with the predictions made a priori by the parentage model of Bernatchez and Duchesne (2000). We then performed the maximum-likelihood assignment procedure with the multilocus genotype of offspring and spawners. We unambiguously

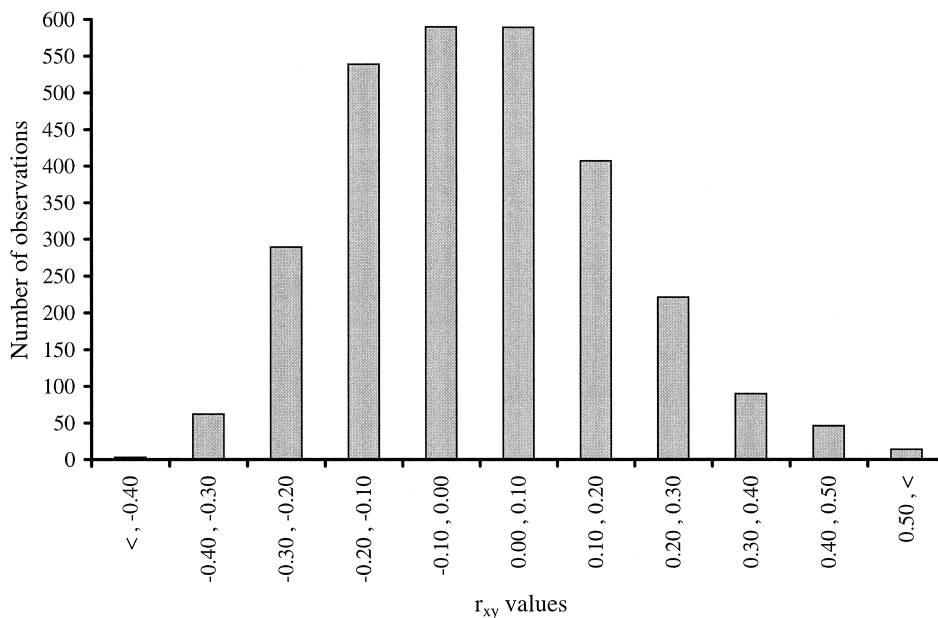


Figure 1. Distribution of relatedness values (r_{xy}) for all possible pair of spawners.

assigned 593 of the 650 offspring (91.2%) to a single pair of spawners. Twenty-six fry (4.0%) were traced to two possible couples and two fry (0.3%) were attributed to three possible pairs out of the 1435 potential crosses. Twenty-nine fry (4.5%) could not be assigned to any parental pair.

Reproductive Success and Number of Mates

Individual reproductive success was compiled as the total number of offspring assigned to each adult in the above analysis.

For females, this number ranged from 0 (three females) to a maximum of 50, with a mean number of offspring per female of 16.9 (variance = 151.0). For males, the number ranged from 1 to 48 offspring, with a mean of 14.5 offspring per male (variance = 124.8). Thus there was a high variance in reproductive success for both sexes: the ratios between the variance and the mean number of assigned offspring was 8.9 for females and 8.6 for males.

We also determined the number of mates for each adult based on the identity of in-

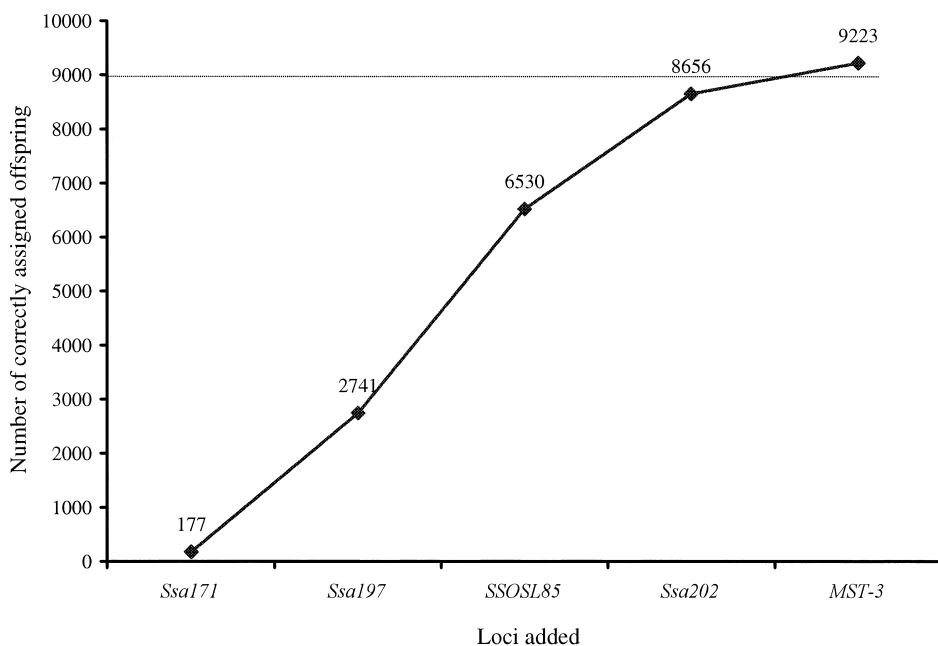


Figure 2. Results of the reassignment simulation procedure (10,000 artificial offspring), adding loci from most to least informative.

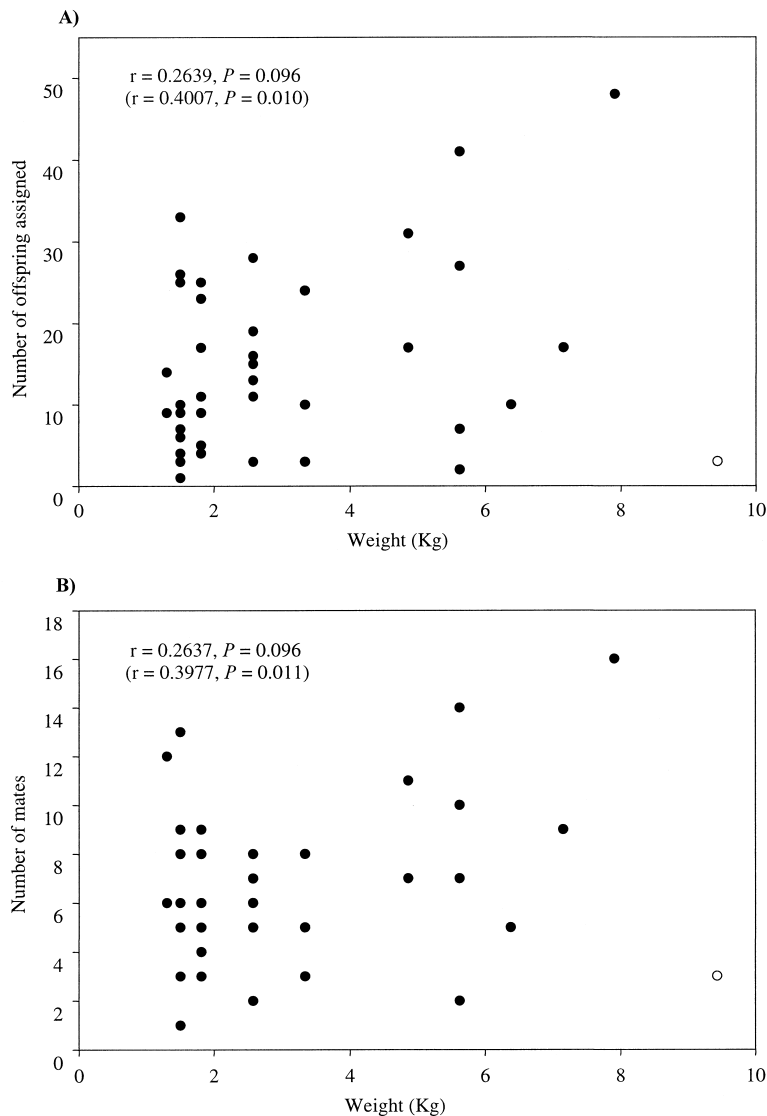


Figure 3. Results of Pearson's correlation analysis for males: (A) weight versus reproductive success, (B) weight versus number of mates. Values in parentheses indicate the correlation results after excluding the one repeat spawner (open circle) from the dataset.

individuals forming the successful parental pairs. The mean number of mates for females was 7.5, and one female had 18 mating partners. Males spawned on average with 6.4 females (range 1–16).

Pearson's Correlation Analysis

For males, no significant correlation was found between body mass and either the number of offspring assigned (Figure 3A) or the number of mating partners (Figure 3B). There was nevertheless a tendency for some large males to gain a high reproductive success. Moreover, a second analysis showed that removing the largest male (a presumably repeat spawner with regard to his size) resulted in a significant correlation between male size and both reproductive success ($r = 0.4007$, $P = .010$) and the number of mates ($r = 0.3977$, $P =$

.011). However, a positive relationship between the number of mates with whom a male reproduced and his reproductive success was observed ($r = 0.8590$, $P < .001$).

For females, no significant correlation was found between body mass and either the number of assigned offspring (Figure 4A) or the number of mating partners (Figure 4B). Potential fecundity and number of offspring assigned also were not significantly correlated (Figure 4C). However, as observed for males, removing the nine largest females (>800 mm) (all females that were presumably repeat spawners which are known to exhibit lower fecundities than would be expected according to their size) revealed a significant correlation between both female size and reproductive success ($r = 0.5038$, $P = .009$), as

well as between fecundity and reproductive success ($r = 0.5041$, $P = .009$). On the other hand, the correlation between female size and the number of mates remained marginally nonsignificant ($r = 0.3708$, $P = .062$). As in the case of males, a positive relationship between the number of mates with whom a female reproduced and her reproductive success was observed ($r = 0.8106$, $P < .001$).

Discussion

The major objective of this study was to provide the first direct estimates of individual reproductive success in Atlantic salmon based on the number of surviving juveniles (fry) at the population level under natural conditions. We also established the degree of variance in individual reproductive success and inferred the possible reproductive strategies adopted by both sexes. More specifically, we tested the prediction of a positive relationship between individual size and realized reproductive success.

The approach was very efficient in establishing parent-offspring relationships. Using only five microsatellite loci, in combination with an "error-tolerant" maximum-likelihood method, we unambiguously assigned 91.2% of all offspring to a single possible parental pair. This achievement appears plausible given our a priori assignment expectations based on simulation procedures and on the predictions of the parentage model of Bernatchez and Duchesne (2000).

Interindividual Variance in Reproductive Success

A high variance in reproductive success applied to both sexes. Given the very small number of offspring sampled for some individuals, the mean number of mates is probably underestimated and our estimates of variance in reproductive success should be considered as conservative. Only a few such populational studies have evaluated the variance of individual reproductive success based on an exhaustive sample of sexually mature adults, so we cannot state whether such a high variance is typical for wild salmonids or other fishes. However, Gross and Kapuscinski (1997) also found a high variance in individual reproductive success for male smallmouth bass (*Micropterus dolomieu*): only 5.4% of all spawning males produced 54.7% of the offspring collected. Furthermore, in a study comparing wild and farmed Atlantic salmon for reproductive success in a seminatural environment, Flem-

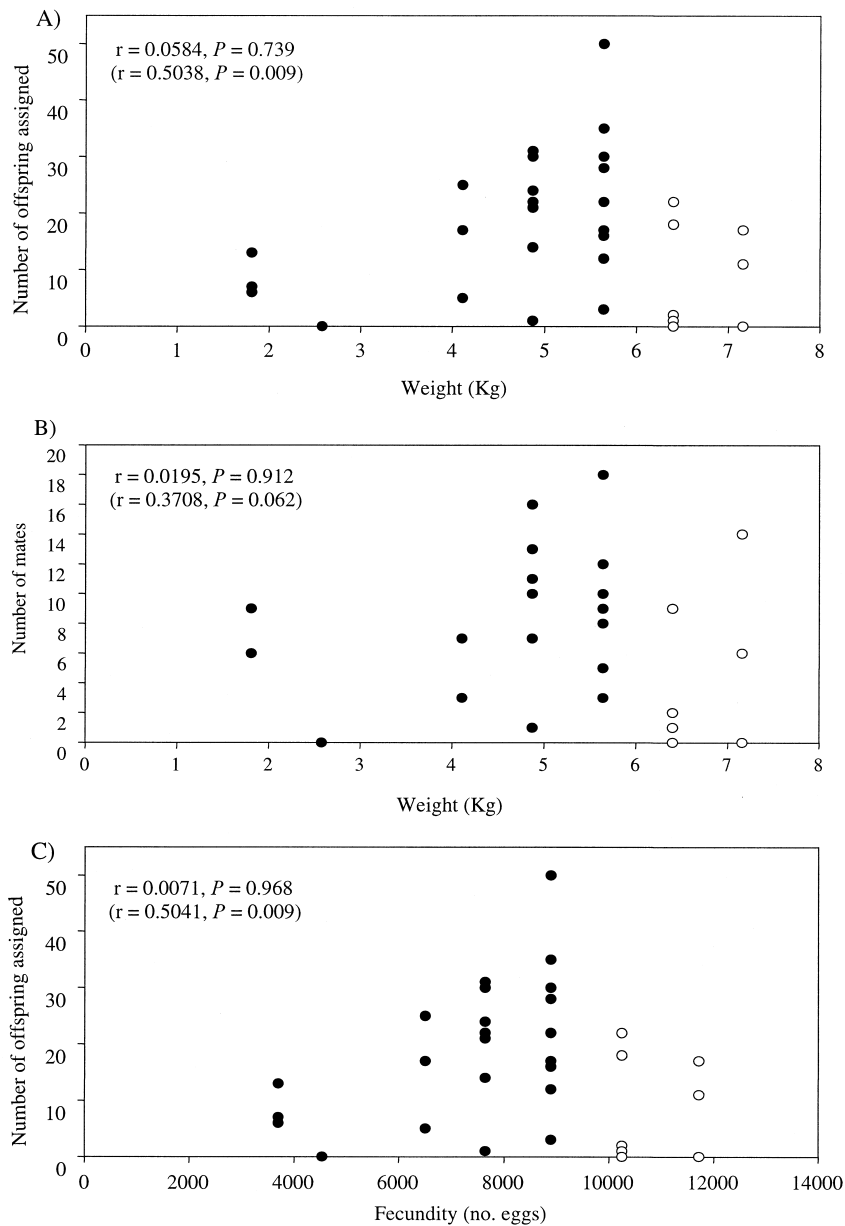


Figure 4. Results of Pearson's correlation analysis for females: (A) weight versus reproductive success, (B) weight versus number of mates, (C) fecundity versus reproductive success. Values in parentheses indicate the correlations after excluding the repeat spawners (open circles) from the dataset.

ing et al. (1997) used the number of live embryos to estimate standardized variation values (σ^2/mean^2). These ranged from 0.3 to 1.35 for wild individuals (comparable to our results of 0.59 and 0.53 for males and females, respectively). High variance in individual reproductive success has also recently been reported in the few studies performed at the population level in other vertebrates (e.g., Bouteiller and Perrin 2000; Weatherhead and Boag 1997).

Male determinants of reproductive success. In salmon, large body size has been proposed to be positively related to ejaculate volumes (Kasakov 1981b), access to higher quality females (Webb and Haw-

kins 1989), and number of surviving embryos (Mjølnerød et al. 1998). Indeed, male size explained between 23 and 45% of the total variance in reproductive success in previous behavioral studies (Fleming et al. 1996, 1997). In the current study, however, size seemed to be only a limited predictor of overall reproductive success, yielding only a mildly significant correlation ($r^2 = 16\%$) when the biggest male was removed. Even then, however, no strong evidence for a positive nonlinear relationship between body size and reproductive success was detected, a phenomenon that might have been an expected consequence of reproductive monopolization by

a few bigger males (Fleming et al. 1997). Instead, the relationship between body size and reproductive success tended to be linear and weak (Figure 3A). This is also in contrast to what has been found in Pacific salmon (*Oncorhynchus* sp.) where selection on male body size accounted for 42% of the opportunity for selection during breeding (Fleming and Gross 1994). However, considerable variation in status, among males of a given length, also exists within these species (Quinn and Foote 1994).

High interindividual variance in reproductive success and relatively poor correlation with size could also potentially result from the relatively high abundance of grilse (76% of males, $n = 31$) in the study population. Grilse spend only one winter at sea before returning to spawn, and in the Ste-Marguerite River, more than 90% of returning grilse are male. Grilse, more so than larger males, are known to wander more within rivers as they search for mating opportunities and try to avoid confrontation with larger males that have spent several winters at sea (Webb and Hawkins 1989). Consequently grilse may be less selective regarding mate choice and more prone to opportunistic multiple matings. Male grilse are known to act like secondary males (Fleming 1996), and as the proportion of embryos within nests fathered by secondary males has been documented to be highly variable (Thompson et al. 1998), this may account for the high variance in reproductive success in the current study. However, we found only a marginally significant difference ($P = .06$) in the variances of reproductive success between grilse and two sea-winter fish (Brown-Forsythe test for homogeneity of variance; Statsoft 1997).

In the current study we documented a positive relationship between the number of mates with whom a male reproduced and his reproductive success. Maximizing reproductive success by multiple mating is in general accordance with sexual selection theory which proposes that in species with no parental care, males should seek to mate with as many partners as possible (see Arnold and Duvall 1994). However, it is likely that the positive correlation between number of mates and reproductive success (in the case of both males and females; see the following section) may be an artifact related to the very small number of offspring sampled for some individuals. This relationship merits further investigation (using simulation procedures and the analysis of a greater

number of offspring) before concluding that the number of mating partners is the major determinant of both male and female reproductive success.

Females determinants of reproductive success. Large body size has also been proposed to increase the reproductive success of females. Larger females should have improved access to and defense of preferential breeding sites, and this in turn may enhance nest quality by allowing the construction of deeper nests less prone to destruction (Crisp and Carling 1989; White 1942). Indeed, large female size explained between 70 and 81% of the variance in reproductive success in other studies of the Atlantic salmon (Fleming et al. 1996, 1997). This has been described as well for other salmonids species such as coho salmon (*O. kisutch*), where female body size was the primary character under selection with 36% of the opportunity for selection during breeding (Fleming and Gross 1994). However, in our study, individual size was a weak predictor of female reproductive success. A similar outcome was also reported in coho salmon by Holtby and Healy (1986), who found for females, no significant reproductive advantage to being large.

Polyandry as the main reproductive strategy in females. In the current study we found a positive relationship between the number of mates (independent of body size) and realized reproductive success in females (but see remark above). Furthermore, polyandry was common far more so than inferred in previous studies of this species. Evidence for a polyandrous mating strategy in Atlantic salmon not only challenges the conventional view that females are monogamous in this species, but it also raises several questions about the selective benefits that may have driven the expression of this reproductive strategy given its possible energetic costs. Generally two classes of hypothesis have been proposed to explain why selection might favor the evolution of polyandry: the direct benefits (or the material benefits) view, and the genetics benefits concept (Reynolds 1996).

Direct (material) benefits. The most important material benefits that a female might get by mating with more than one male are additional parental care (Nakamura 1998) or adequate sperm supply for fertilization of all her eggs (Leviton and Petersen 1995). However, neither of these material benefits is likely to be the principal mechanism underlying polyandrous behavior in female Atlantic salmon, be-

cause postspawning parental care is lacking in this species (Fleming 1996) and a single male is potentially capable of fertilizing all of a female's eggs (Gjerde 1984).

Genetic benefits. Alternatively in species with no or little direct material benefits, genetically based hypotheses are often proposed to explain the benefits of female multiple mating (reviewed in Jennions and Petrie 2000). These fall into two broad categories: (1) the acquisition of good genes and (2) an enhancement of genetic diversity within clutches. The first hypothesis states that when females encounter better males than their previous mates, they should remate so that their eggs are fertilized by the better male's sperm (Yasui 1997). The second hypothesis implies that increased offspring diversity resulting from multiple paternity enhances female fitness by reducing sibling competition or by serving as a hedge against environmental uncertainty. The two hypotheses depend on the combination of environmental predictability and on the ability of the female to assess which males possess fitter genes for her progeny (Yasui 1998). When environmental conditions are stable, good genes for the next generation should be more persistent and thus predictable. In these conditions, selection should favor females who are able to choose males that possess better genes (Reynolds and Gross 1992). Conversely, if environmental conditions are unstable, good genes for the next generation may not persist and a female might increase her chances of getting good genes by mating with a variety of males (Petrie and Kempenaers 1998). Instability is a hallmark of Atlantic salmon breeding habitat, with environmental variation driven largely by climatic factors acting upon river discharge. Spawning sites often may be displaced or destroyed, with genetically different individuals colonizing these new spawning grounds (see Garant et al. 2000).

Apart from facilitating survival under variable environmental regimes, a higher genetic diversity within a progeny array stemming from multiple mating by females might also serve to reduce the potential cost of inbreeding (Stockley et al. 1993), or it might be a way to reduce the deleterious effects of genetic incompatibility between two partners (Tregenza and Wedell 1998). This latter hypothesis was supported by a study of pseudoscorpions (*Cordylochernes scorpioides*) showing that females who mated with more than one male gave birth to 32% more offspring

than single-mated females (Newcomer et al. 1999).

Large size is not necessarily reflective of male quality, even if it provides an advantage in male-male competition and thus in access to females (Qvarnström and Forsgren 1998). Factors such as environmental state, individual behavior, and allelic composition at specific genes (such as the major histocompatibility complex; Jordan and Bruford 1998) should also be taken into account. Thus, in principle, a female may need to assess not only the quality of male genes, but also how well those genes might complement her own (Qvarnström and Forsgren 1998).

Hypothetical ecological benefits. In addition to material and genetic benefits potentially involved in driving the evolution of polyandry in Atlantic salmon, potential ecological benefits should also be considered. Environmental heterogeneity in time and space no doubt can affect the breeding system and efficiency in Atlantic salmon. Particularly during spawning times, changes in resource abundance, temperature, water flow, and predation can profoundly influence the demographics of salmon populations (and hence breeding systems) (Fleming 1998). It has been demonstrated that in unstable environmental conditions, strategies minimizing variances of fitness should be favored (Gillepsie 1977; Phillippi and Seger 1989). It has also been documented that female Atlantic salmon have the potential to adopt different egg-deposition strategies depending on temporal and spatial variation in offspring survival (Barlaup et al. 1994). Accordingly, in situations of environmental uncertainty (such as those created by low winter river discharge at northern latitudes), or in the case where optimal spawning territories are not available, females may adopt a multiple-redd strategy that probably reduces their fitness variance.

Low river discharge in the winter has previously been shown to cause high mortality of Atlantic salmon eggs (Gibson and Myers 1988). This is a likely also in the Ste-Marguerite River, where spawning substrate destruction can be both important and stochastic in time and space (Bergeon N, unpublished data). In such circumstances, selection might favor females that spread the risk of offspring mortality by dispersing their eggs in numerous smaller clutches rather than using a single nest site. This would correspond to a spatial analogy of bet-hedging whereby the best reproductive success is achieved by opti-

mizing the trade-off between the mean and the variance of fitness (Slatkin 1974).

Because we do not have the behavioral observations of courtship and spawning events, it is not possible to confirm that multiple matings occurred predominantly at different nest sites rather than at one location. However, in at least two respects our results indicate that individual females built several nests in different locations. First, fry exhibit low dispersal. Beland (1996) showed from extensive sampling throughout the year that 84% of juveniles were found within 1600 m of the original redd. Second, we observed a highly heterogeneous spatial distribution of families estimated from genotype compositions. For example, half sibs from the same mother were often collected 10 km apart, presumably because the breeding females themselves had moved between nest sites.

Of course mating systems may differ dramatically among Atlantic salmon populations, and this may account for the apparent disparity of our study population from those previously examined. Mating-system outcomes may vary locally depending on such factors as population-specific life-history strategies, fish density, or the variability of environmental conditions. Such interpopulation diversity in reproductive strategy has also been described previously in other fishes. For instance, Mousseau and Collins (1987) showed that the slimy sculpin (*Cottus cognatus*) was either polygynous in a population where potential nest abundance was low or monogamous in other populations where nests were more abundant relative to male density.

Overall this study provides an additional demonstration of the usefulness of a genetic approach to quantify variance in individual reproductive success and to investigate the possible determinants of individual fitness. Results indicate that discrepancies can exist between behavioral and genetic estimates of reproductive success and mating patterns in fishes. Polyandry appears to be a predominant reproductive strategy of female Atlantic salmon in at least some environmental or demographic circumstances. Clearly mating systems in this species may be far more flexible and variable than previously thought.

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