

DIFFERENTIAL REPRODUCTIVE SUCCESS AND HERITABILITY OF ALTERNATIVE REPRODUCTIVE TACTICS IN WILD ATLANTIC SALMON (*SALMO SALAR* L.)

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Abstract.—A critical step in understanding the evolution and maintenance of alternative reproductive tactics is to obtain accurate comparisons of their fitness and to determine factors influencing individual status. In this study, we first used individual multilocus genotypic information to compare reproductive success between two alternative reproductive tactics of anadromous Atlantic salmon (*Salmo salar* L.) in their natural environments. We also documented the effects of the quality of the rearing environment and of paternal reproductive tactics on heritability of juvenile growth, which is an important component of individual status. Results showed that large dominant salmon (multisea winter) had higher reproductive success than smaller satellite individuals (grilse). Also, there was a status difference associated with both habitat and male tactic. Overall, offspring produced in streams were bigger than those produced in the main river stretch. Grilse also produced bigger offspring than those fathered by multisea winter males. Heritability of juvenile growth was significant but varied according to quality of habitat: higher heritability estimates were observed in higher quality habitats (streams) than in lower quality habitats (main river stretch). Heritability estimates for juvenile growth varied as well, depending on male tactic, with progeny fathered by multisea winter males having higher values than those fathered by grilse. Together, these results indicate that a combination of additive genetic effects, parental life history and habitat quality will ultimately shape juvenile growth rate, which is the main determinant of status and of subsequent choice of life-history tactics.

Key words.—Alternative strategy, environmental effects, fitness, juvenile growth, Salmonidae.

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A major objective in evolutionary biology is to understand processes by which polymorphisms associated with alternative reproductive phenotypes are maintained within species. Theoretical frameworks, based on game theory (Maynard Smith 1982), have been elaborated to study alternative reproductive phenotypes in relation to their costs and benefits to evolutionary fitness (reviewed in Gross 1996). The first and rarest means by which phenotypic diversity within a sex may arise is through a genetic polymorphism for two strategies (Ryan et al. 1992; Lank et al. 1995). Two additional theoretical frameworks to explain the coexistence of alternative reproductive morphs in a same population involve the “mixed” and the “conditional” strategy (Maynard Smith 1982; Gross 1996). Both of these strategies propose the existence of genetically monomorphic alternative tactics within a strategy. A strategy refers to the underlying genetic basis of alternative life histories, whereas a tactic is the phenotype that results from the strategy (Gross 1996). Therefore, the mixed strategy proposes that frequency-dependent selection could result in equal fitness between alternative phenotypes, but little empirical evidence exists to support this model (Gross 1996; but see Sato 1998).

The majority of known alternative reproductive phenotypes are thus interpreted as alternative tactics within a conditional strategy (Crespi 1988; Radwan 1995; reviewed in Gross 1996; see also Brockmann 2001). This theory proposes that individuals are required to make a “decision” regarding the tactic they will adopt based on their relative status (competitive ability) in the population that depends upon their individual condition (Gross 1996). This results in unequal average lifetime fitness of alternative reproductive tactics within the population, but it is hypothesized that the chosen tactic will provide the individual with the highest fitness possible between alternatives, given its relative status at a given

time. Furthermore, theoretical studies have shown that two alternative tactics with unequal fitness could be maintained in equilibrium, given a heritable component of the status (Hazel et al. 1990; Gross and Repka 1998a), and that such an equilibrium might be stable (Hazel and Smock 1993; Gross and Repka 1998b).

In many species, individual status is related to juvenile growth or size attained at a given age (Bohlin et al. 1990; Wiegmann et al. 1997; Hofmann et al. 1999; Moczek and Emlen 1999; Garant et al. 2002). For natural populations, it is generally believed that local environmental conditions and environmental heterogeneity are the major determinants of juvenile growth and hence of status (Hutchings and Myers 1994). For example, in smallmouth bass (*Micropterus dolomieu*), it has been shown that environmental changes could alter the proportion of males that would adopt a given reproductive tactic through its influence on size attained at a given age (Wiegmann et al. 1997).

Additional effects may be potentially important in determining juvenile growth and status. Nonadditive parental effects such as maternal (reviews in Mousseau and Fox 1998) and paternal (see Hunt and Simmons 2000; Pakkasmaa et al. 2001) effects have been proposed as major factors controlling offspring characteristics (reviewed in Qvarnström and Price 2001). Also, the heritable additive genetic component and its interaction with factors that act on offspring characteristics is clearly an important part of offspring growth and status that should be evaluated (Roff 1996). However, there are still relatively few estimates of heritability of phenotypic traits in the wild, largely due to logistical constraints (but see Sivero and Zamudio 2001), and consequently, most estimates available are derived from controlled experiments (e.g. Mousseau and Roff 1987). Heritability estimates in nature come mainly from bird studies using cross-fostering exper-

iments for species in which parental identity can be assigned with a certain degree of confidence by field observation (Dhondt 1982; Merilä 1997; Merilä and Fry 1998). Such techniques, however, are almost impossible to use in species with high juvenile mortality and dispersal (Ritland 2000). Furthermore, heritability estimates have been shown to vary with the quality of rearing habitat, and are hypothesized to be greater in high- than in low-quality habitat (Qvarnström 1999). This underlines the importance of measuring heritability under natural conditions.

Several studies have revealed that fitness pay-offs associated with alternative tactics could be unequal (Brockmann et al. 1994; Foote et al. 1997; Coltman et al. 1999). None of them, however, have fulfilled the complete set of criteria to demonstrate a conditional strategy convincingly (but see Hunt and Simmons 2001). Namely, fitness estimates in these studies have been equated to reproductive success quantified under controlled conditions or indirectly by means of behavioral observations (Clutton-Brock 1988), which could be inappropriate in situations in which extra-pair fertilizations occur (Gibbs et al. 1990). Recent advances in the use of individual multilocus genotypic information have made it possible to accurately reconstruct pedigree and thus parental relationships in natural conditions. This has allowed precise measurements of reproductive success without manipulations in the wild (e.g., Weatherhead and Boag 1997; Zamudio and Sinervo 2000; Garant et al. 2001). DNA genotyping, in combination with new statistical approaches, has also improved the accuracy and availability of data for quantitative genetic analysis and thus permitted estimates of heritability in the field. Specifically, this has been performed using restricted maximum likelihood (REML) and animal model procedures and applied to population data for birds (Merilä et al. 2001) and mammals (Réale et al. 1999; Kruuk et al. 2000; Milner et al. 2000). Despite its obvious particular interest for the study of poikilotherms with high juvenile mortality and dispersal capability, the use of individual multilocus genotyping to infer reproductive success has been limited thus far (Avisé 2001), and no study has assessed the genetic basis of fitness-related traits in fishes.

Atlantic salmon (*Salmo salar* L.) exhibit among the greatest within-population variability in size and age at maturity of all vertebrates (reviewed in Fleming 1998). In this species, males generally exhibit three alternative reproductive tactics associated with marked size differences. First, there is the small precocious male phenotype that consists of salmon who reach maturity in fresh water as early as their second summer of life and that attempt to sneak fertilization. There is also the larger anadromous male phenotype consisting of fish who require a minimum of three to four years, including an oceanic phase, to mature and who compete among themselves for the opportunity to guard females (Belding 1934; Jones and Ball 1954; reviewed in Fleming 1998). There are two distinct phenotypes within anadromous males that are also associated with two distinct reproductive tactics. First, there is the multisea winter tactic (MSW), which consists of salmon that have stayed two or more years at sea before returning to freshwater to reproduce. Fish adopting this tactic attain large sizes and are typically dominant individuals on spawning grounds. The second anadromous tactic involves fish,

known as grilse, who remain only one year at sea before returning to fresh water to spawn. These males are much smaller than MSW fish and accordingly, they are known to behave like subordinate males on the spawning grounds (see Fleming 1998).

Reproductive success in natural populations of Atlantic salmon has been recently assessed (Garant et al. 2001; Taggart et al. 2001). However, no estimates of reproductive success are yet available to specifically compare the alternative anadromous tactics found in this species. Furthermore, evidence that age and size at sexual maturity are both under genetic and environmental control in this species comes from experimental and controlled experiments (Naevdal et al. 1976; Thorpe et al. 1983; Glebe and Saunders 1986; Berglund 1992). Although there is mounting evidence that high growth rate of juvenile stages is one of the most important factors contributing to the development of precocious maturity in Atlantic salmon (Lundqvist 1980; Myers et al. 1986; Hutchings and Jones 1998; Whalen and Parrish 1999; Garant et al. 2002), very little is known about the influence of juvenile characteristics on the choice of the two anadromous tactics (MSW vs. grilse). Furthermore, as there are no heritability estimates of juvenile growth in the wild, it is unclear to what degree genetic and environmental components determine these life-history tactics in Atlantic salmon. At the habitat level, the amount of organic drift is more abundant in small streams than in bigger rivers (Naiman et al. 1987; Erkinaro and Niemelä 1995), and invertebrates on which juveniles feed mainly in early life stages are bigger in streams (Keeley and Grant 2001). This influence of habitat might be so important that it could trigger individuals with typically lower growth rates to develop tactics different from that under restricted conditions, thus increasing the proportion of individuals beyond the threshold value for early sexual maturation (see Hutchings and Myers 1994).

The objective of this study was to use individual multilocus genotyping to compare reproductive success between the two alternative reproductive tactics associated with distinct phenotypes in anadromous male Atlantic salmon. We thus tested the null hypothesis that there is no difference in reproductive success between the MSW and the grilse anadromous tactic. Second, we documented the effects of both the quality of the rearing environment and of the paternal reproductive tactic on juvenile growth and its heritability. We tested the null hypothesis that growth and its heritability value will be the same in both high- and low-quality habitats and for both paternal reproductive phenotypes.

MATERIALS AND METHODS

Sample Collection and Characteristics

This study was conducted on the Sainte-Marguerite river (48°20'N, 70°00'W), Québec, Canada, which sustains a natural population of Atlantic salmon. Anadromous salmon migrate into this river in the middle of summer (July and August) and spawn during the fall (October and November). Salmon fry (young of the year) emerge from the spawning gravel in late June the following year and move to nursery grounds adjacent to spawning grounds. In July 1995, we caught 76 adult fish, specifically 41 males (31 grilse and 10

TABLE 1. Results of a factorial analysis of variance for potentially significant fixed effect on juvenile length in 0+ offspring (527 individuals). Values in bold indicate significant effects on offspring size.

Effect	Sum of squares	df	Mean squares	F	P
Habitat	181.5	1	181.5	9.27	0.002
Female length (FL)	105.8	5	21.2	1.08	0.370
Male mating tactic (MMT)	72.1	1	72.1	3.68	0.056
Habitat × FL	93.9	5	18.8	0.96	0.442
Habitat × MMT	3.7	1	3.7	0.19	0.664
FL × MMT	120.2	5	24.0	1.23	0.294
Habitat × FL × MMT	69.6	5	13.9	0.71	0.616
Error	9846.2	503	19.6		

MSW) and 35 females (MSW), at a fish ladder located on the northeast branch of the Sainte-Marguerite River. These fish were measured, sexed, and their adipose fins clipped and collected. They were then transported upstream to a river stretch previously uninhabited by salmon that shared ecological characteristics similar to the populated stretch of river regarding depth, flow, and refuge. They subsequently spawned in fall of the same year. This stretch of river is 19 km long and is isolated by two impassable waterfalls. As a result, we eliminated the potential contribution of precocious parr to fertilization and we increased our capacity to establish parentage because we knew all of the potentially reproductive fish. From 1996 to 1998, during the first week of September, we electrofished throughout all accessible nursery areas of the river stretch to sample as many offspring as possible from each of the 0+ (1996), 1+ (1997) and 2+ (1998) age classes. A total of 1029 offspring were sampled over the three years. For each offspring, sampling location was noted as either stream (small tributaries, offering rich food sources for juvenile salmon) or river (main reach, offering poorer food resources relative to stream habitat). Length (mm) was also measured for each fish and was used as an indicator of growth for the remainder of the analysis. Whole progeny and adult adipose fins were preserved in 95% ethanol until genetic analysis. In all analyses in which the effect of habitat was measured, we used 0+ offspring (579 fish) only. The 1+ (297 fish) and 2+ (153 fish) fish might show high dispersal throughout river habitats over time (McCormick et al. 1998) and thus the actual capture locations of 1+ and 2+ fish are probably not representative of past spawning and rearing habitat. Although we cannot categorically state that 0+ fish captured in streams were necessarily spawned there, they are the juvenile stage with the lowest dispersal (Crisp 1995; Webb et al. 2001) and thus represent the most likely individuals for which a habitat effect could be detected.

Genetic Analyses and Parentage Assignment

Total DNA extraction was performed from approximately 30 mg of tissue, according to Bernatchez et al. (1992). Microsatellite polymorphism was analyzed as detailed in Garant et al. (2001). We used 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). Parentage assignment was conducted using a maximum-likelihood procedure as detailed in Bernatchez and

Duchesne (2000) and Garant et al. (2001) using the software PAPA V1.0 (Duchesne et al. 2002). Briefly, 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.

Reproductive Success Estimates

Reproductive tactic (grilse or MSW fish) and mean reproductive success (number of offspring assigned) were established for each male. The largest reproductive male was removed from the analysis as it was presumably a repeat spawner and thus could not be compared with other fish that were in their first reproductive event (see also Garant et al. 2001). All remaining MSW fish had spent two winters at sea before reproduction (also called 2SW). We then calculated Pearson correlation coefficients (from Statistica 5.5; StatSoft 1999) between the proportions of offspring assigned for each male in each year to establish whether reproductive success estimates were stable over the three-year sampling period. Next, we estimated the number of offspring assigned for each male within each tactic for each offspring age class and overall. An analysis of variance (ANOVA) was then performed to estimate potential significant differences in numbers of offspring assigned between tactics within each age class and for the three age classes combined.

Factors Influencing Offspring Growth (0+ Offspring)

We first conducted a factorial ANOVA (from Statistica 5.5, General linear model module; StatSoft 1999) to evaluate which fixed factor or interactions between these factors significantly effected growth in 0+ offspring. Habitat of capture, paternal reproductive phenotype (grilse or MSW), and female size (length) were included in the analyses. There were significant impacts on offspring size for both habitat and male life history but not for female size (Table 1). Therefore, habitat and male life history phenotype were the only fixed effects taken into consideration for the subsequent analyses (if not explicitly stated). We then determined the degree of significant differentiation for offspring growth between both habitat types and for both male reproductive phenotypes overall and within each habitat using one-way ANOVAs.

Variance Components and Heritability

Variance components and heritability values for length (in both habitat types, for both male reproductive phenotypes and globally) were estimated using a derivative-free restricted maximum likelihood procedure implemented in DFREML 3.0 (Meyer 1998). This method fits a linear mixed model to estimate variance and covariance components for continuous traits (Meyer 1998). It uses information on relationships within a pedigree and constrains heritability to between 0 and 1. It also partitions phenotypic variance of a quantitative character into its additive genetic and other fixed and random

TABLE 2. Number of individuals (n), mean, variance, range of reproductive success, and mean offspring size (mm) at each age for both male alternative reproductive tactics. MSW, multisea winter tactic; grilse, one-sea winter tactic. Significant comparisons indicated in bold characters.

Reproductive tactic (n)	Reproductive success			Mean size of offspring		
	Mean	Variance	Range	0+ ($n = 527$)	1+ ($n = 269$)	2+ ($n = 140$)
MSW (9)	37.0	716.0	4–77	53.2 ± 4.5	90.3 ± 7.7	121.2 ± 9.1
Grilse (31)	19.4	269.2	0–44	54.8 ± 4.7	92.1 ± 8.0	124.2 ± 10.3
Overall	23.3	409.6		54.2 ± 4.7	91.5 ± 7.9	123.1 ± 10.0
<i>P</i> -value (analysis of variance)	0.019	0.099		<0.001	0.065	0.088

components such as maternal effect or common environment (Meyer 1989). Restricted maximum likelihood procedures give estimates with little bias and have clear advantages over the least-squares method in cases of unbalanced design (Knott et al. 1995). We therefore used information obtained from parentage assignments and from offspring length measurements to build an animal model for each offspring age class as:

$$y = Xb + Za + e, \quad (1)$$

where y is a vector of phenotypic values (length), b and a are the vectors of fixed and random additive effects, e is the vector of residual values, and X and Z are the corresponding design matrices which relate the effects to y . For each offspring age class, the fixed effects included in the model were habitat (streams or river) and male reproductive phenotype (MSW or grilse). We also included maternal identity as a random effect to prevent the maternal environment from being confounded with the genetic effect (Falconer 1989). Total phenotypic variance (V_P) was therefore partitioned into additive genetic variance (V_A), maternal (V_M) and environmental variance (V_E). The narrow-sense heritability was consequently estimated as: $h^2 = V_A/V_P$ and the maternal effect was quantified as $m^2 = V_M/V_P$. Standard errors for variance components and heritabilities were computed by DFREML. We also estimated heritability for each habitat and each male phenotype separately for the 0+ offspring age class. In this case, the fixed part of the model included only the remaining fixed effect: either habitat or male tactic.

RESULTS

Parentage Assignment and Reproductive Success

Informative content of microsatellite loci are presented in Garant et al. (2001). Assignment procedures performed with PAPA V1.0 (methods detailed in Garant et al. 2001) yielded an overall 91% assignment success by using a two percent scoring error rate and five microsatellite loci. Specifically, a total of 936 offspring were assigned to a single parental pair (0+ = 527 offspring, 1+ = 269, 2+ = 140). Reproductive success (in terms of total number of observed juvenile progeny) was significantly higher for MSW than for grilse (ratio grilse/MSW = 0.52; Table 2). This significant difference was also present when each year of sampling was analyzed separately in ANOVA ($F = 4.76$, $P = 0.035$ for 0+; $F = 4.40$, $P = 0.043$ for 1+; $F = 4.79$, $P = 0.035$ for 2+). Pairwise estimates of relative reproductive success between years was highly correlated with $r = 0.75$ between 0+ and 1+, $r =$

0.60 between 0+ and 2+, and $r = 0.61$ for 1+ and 2+ ($P < 0.001$ in all comparisons). These results indicated that the proportions of offspring from different pairings were consistent over years, and that bias due to sampling error was limited and/or that differential selection for survival was relatively stable over time with respect to the different families.

Influence of Habitat and Male Tactic on Offspring Growth

Both the habitat and the parental phenotype significantly affected growth in 0+ offspring. Specifically, 0+ fish in streams were bigger ($n = 242$, mean length ± standard deviation = 55.8 mm ± 4.2 mm) than 0+ fish in the main river ($n = 285$, 52.9 mm ± 4.7 mm). This difference was highly significant when all 0+ offspring were considered ($F_{1,525} = 51.92$, $P < 0.001$), but also when comparing grilse offspring caught either in streams or in the river ($F_{1,339} = 38.17$, $P < 0.001$) and for MSW offspring ($F_{1,184} = 11.28$, $P < 0.001$) in the two habitats. This supports the view that streams represent high-quality habitat relative to the main stem of the river. Overall, difference in size was also significantly different between the two parental phenotypes with the offspring of grilse being bigger than those of MSW males ($F_{1,525} = 14.64$, $P < 0.001$) (Table 2). This difference was unlikely due to a single-male effect as all P -values remained significant (at $P < 0.05$) when removing each male one at a time and repeating the ANOVA (results not shown). The difference in size attributable to parental phenotype was also important within each habitat, with grilse offspring being significantly bigger than MSW offspring in streams ($F_{1,240} = 9.72$, $P = 0.002$) and marginally nonsignificantly bigger in the main river ($F_{1,283} = 3.54$, $P = 0.061$; Fig. 1). Finally, difference in size between offspring of the two parental phenotypes remained marginally significant at 1+ ($F_{1,267} = 3.45$, $P = 0.065$) and 2+ ($F_{1,138} = 2.96$, $P = 0.088$; Table 2). When combining P -values using the Fisher method (Sokal and Rohlf 1995, p.795) we found a significant overall P -value for 0+, 1+, and 2+ together ($P < 0.001$), as well as for 1+ and 2+ together ($P = 0.035$).

Variance Components and Heritability Estimates

Variance components attributable to additive, environmental, and maternal effects and the derived heritability estimates are summarized in Table 3. Heritability estimates were moderate to high and all significantly different from zero in 0+ offspring but not in 1+ and 2+ offspring. Within 0+ offspring, rearing habitat influenced heritability of growth, as estimates were higher in streams (high-quality

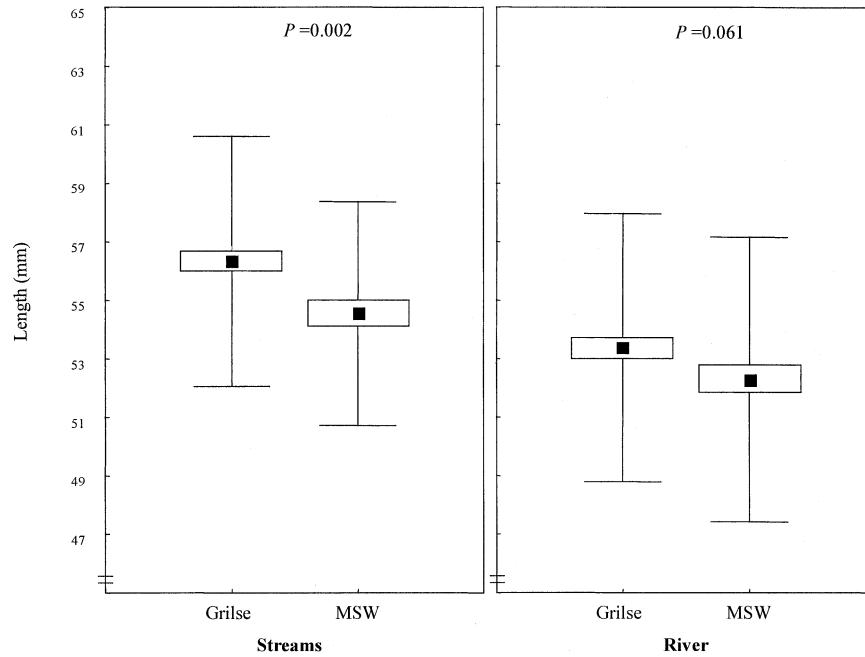


FIG. 1. Box plots (mean/standard error/standard deviation) illustrating comparisons of length of offspring assigned to males of each tactic within each habitat for 0+ offspring. Differences are significant within streams and marginally significant in the river. Also, differences are significant between habitat for grilse (one-sea winter; $P < 0.001$) and MSW (multisea winter; $P < 0.001$) offspring.

habitat) than in the river (low-quality habitat). There was also a difference between heritability estimates of growth obtained for the two parental phenotypes, with MSW having a higher heritability estimate for growth than grilse. Lower heritability estimates for grilse and in river habitat were both a consequence of additive variance (V_A) being lower and environmental variance (V_E) being higher (Table 3). Finally, the maternal component of variance (V_M) was very low and the maternal effect (m^2) was not significantly different from zero at any age (Table 3).

DISCUSSION

This study provides the first estimates of reproductive success of alternative reproductive tactics in anadromous At-

lantic salmon. We have demonstrated that differential juvenile growth is achieved by the offspring of the two alternative reproductive phenotypes in two habitat types differing in the availability of food resources. We have also provided the first heritability estimates of growth in fish under natural conditions. Altogether, these results revealed that different parental phenotypes found in anadromous salmon have unequal reproductive success and that offspring of each parental phenotype exhibit different body sizes influenced by both environmental and additive genetical components.

Reproductive Success

We first rejected the null hypothesis of equal reproductive success by directly estimating the proportion of offspring

TABLE 3. Variance components and heritability estimates (with standard error in parenthesis) for juvenile length in streams, river, grilse (one-sea winter), MSW (multisea winter), and overall in 0+ offspring, and for 1+ and 2+ offspring. n , number of offspring; V_A , additive variance; V_M , maternal variance; V_E , environmental variance; V_P , phenotypic variance; m^2 , maternal heritability; h^2 , heritability.

	n	V_A	V_M	V_E	V_P	m^2	h^2
Streams	242	6.78 (3.16)		10.87 (2.34)	17.65 (1.88)		0.38* (0.15)
River	285	5.97 (2.82)		16.27 (2.48)	22.24 (2.00)		0.27* (0.12)
Grilse	341	5.43 (2.29)		14.37 (1.95)	19.81 (1.65)		0.28* (0.11)
MSW	186	12.44 (5.62)		9.22 (3.58)	21.66 (3.03)		0.57** (0.20)
Total 0+	527	6.02 (2.77)	0.02 (1.08)	14.04 (1.85)	20.08 (1.41)	0.001 (0.054)	0.30* (0.13)
Total 1+	269	1.83 (7.31)	2.54 (2.98)	44.07 (6.24)	48.44 (4.33)	0.052 (0.061)	0.04 (0.15)
Total 2+	140	2.44 (22.85)	7.03 (8.94)	73.99 (17.22)	83.46 (10.66)	0.084 (0.107)	0.03 (0.27)

* $P < 0.05$, ** $P < 0.01$.

fathered by males of both tactics. The MSW fish had higher reproductive success than grilse, which was congruent with our previous estimations based on the analysis of 0+ fish only (see Garant et al. 2001). Because the probability of spawning more than once in a lifetime has been estimated to be less than 5% in the studied river (Centre Interuniversitaire de Recherche sur le Saumon Atlantique, unpubl. data), we consider that this phenomenon is negligible and that one may use reproductive success as a surrogate of fitness. Establishing lifetime fitness from coupling reproductive success with the probability of reproducing from different individuals might be an oversimplification (see Wolf and Wade 2001). Yet, the relative reproductive success estimates between the two tactics (37:19.4 or 1.0:0.52) indicate that a MSW tactic has twice the fitness value of the grilse tactic. Thus, the persistence of the grilse tactic demands a higher probability of return, on average, so as not to be eliminated. This is consistent with the observation that grilse undertake less extensive marine migrations than do MSW fish (Anderson 1985).

Variable Juvenile Growth Rate and Influence on Subsequent Status

We have shown that there was variable juvenile growth associated with habitat quality and with male reproductive tactic. Specifically, 0+ fish in streams were bigger than 0+ fish in the main river, but this difference was also present when comparing grilse offspring in streams and the river, as well as for MSW offspring in the two habitats. Larger offspring size found in streams relative to the main river is congruent with previous findings (Erkinaro and Niemelä 1995). Furthermore, the influence of habitat was such that MSW stream-born offspring were bigger than grilse river-born offspring. Such variation in growth on a small geographical scale raises the possibility that different habitats may confer context-dependent advantages. Context-dependent advantage in growth related to social status has been shown in *Haplochromis burtoni*, an African cichlid fish, in which more individuals gain access to a reproductive opportunity under fluctuating environmental conditions (Hofmann et al. 1999). In our case, the habitat could potentially overwhelm the influence of the genetic component in determining the size that individuals may attain at a given age, therefore modifying the proportion of males expressing a tactic in a given habitat. Assuming that increased juvenile growth is reducing age at maturity in this species (reviewed in Hutchings and Jones 1998), then this salmon population should be characterized by a high proportion of individuals maturing at an earlier age. For example, individuals in the studied river stretch were much larger at 1+ and 2+ than juveniles of other parts of the river system caught in the same years; which are, however, part of the same genetical population (see Garant et al. 2000). Specifically, 1+ fish (mean size = 91.5 mm) were almost as large as 2+ fish found elsewhere in the river (mean size = 93.3 mm; N. Aubin-Horth and J. J. Dodson, unpubl. data). Such a size difference is partly due to the absence of older juvenile salmon cohorts with whom the offspring would have to compete. Thus, we could predict that many individuals would exceed the size

threshold permitting the first sexual maturation as precocious males in freshwater (Hutchings and Myers 1994). However, these individuals had no opportunity to reproduce at this stage because there were no females available due to the experimental transfer to a habitat previously unoccupied by salmon. Consequently, these young male salmon may have suffered very little mortality compared to what is generally observed in other populations (Myers 1984; Hutchings and Jones 1998) and one would thus predict a high proportion of individuals returning as grilse. Two observations support this hypothesis. First, we observed 100% of precocious maturation among 1+ and 2+ males (data not shown) caught in the studied stretch of river. Secondly, the number of grilse in 1999 (first potential year of return after one year at sea for the juveniles of our system) on the northeast branch of the Sainte-Marguerite River was the highest of all years from 1996 to 2001 (grilse in 1999 = 139, mean number of grilse in other years = 44; Société de la faune et des parcs du Québec, unpubl. data).

However, in contrast to what was previously proposed to explain the relationship between growth rate and age at maturity in salmon (see Hutchings and Myers 1994), juvenile growth rate was not random with respect to genotype as there was a clear influence of male tactic. Undoubtedly, grilse offspring were bigger than MSW offspring in both habitats. This constant difference in offspring size between reproductive tactics indicates that there was an environmental and a genetical effect on growth but no genotype-by-environment effect (Falconer 1989; Nager et al. 2000). In addition, 30% of the variation in size was explained by the additive genetic component of variation. Furthermore, the tactic effect (represented by the average of V_E in the two habitats, 13.8%; see Table 3) undoubtedly reflects a genetic basis which adds to this additive effect and thus it could be argued that overall, more than 43% of the variance in juvenile growth is explained by a male-related genetic effect. Also, even if the heritability values were no longer significant at 1+ and 2+, the growth differences between individuals fathered by both tactics remained significant. Consequently, the grilse progeny will be bigger on average, which should provide them a higher status relative to MSW offspring.

This study also confirmed that growth rate advantage of grilse, which could explain their shorter residency at sea, was already present for their offspring in freshwater. This pattern was also proposed by Chadwick et al. (1986) who observed an inverse relationship between the smolt length and the percentage of MSW salmon observed in 34 Newfoundland rivers in Canada. Larger size of grilse offspring already present at the 0+ stage might also be the result of either an earlier emergence date resulting from an earlier fertilization event (Einum and Fleming 2000) or indicate that the growth rate difference was already present in an earlier life-history stage (see also Garant et al. 2002). Together, these results are concordant with prediction that earlier maturity is favored in part by larger juvenile size in this species (Ritter et al. 1986; Friedland and Haas 1996; reviewed in Hutchings and Jones 1998) and that it is a combination of parental state and environment that will ultimately determine juvenile growth rate, itself linked to status and subsequent tactic choice. An association of genetic and environmental conditions in determining age at maturation has previously been proposed by

Naevdal (1983), who conducted experiments under hatchery conditions in which typical grilse population produced a higher proportion of grilse but in which, overall, faster growing individuals became grilse in higher proportion.

Variation of Heritability as a Function of Habitat and Male Life History

For 0+ offspring, higher heritability estimates were obtained in tributary streams than in the main river. Such a pattern, whereby high quality habitat is associated with higher heritability, has been previously supported for many traits in birds (Larsson et al. 1997; Merilä 1997; Qvarnström 1999) and mammals (Réale et al. 1999). Three nonexclusive causes may account for such differences (Falconer 1989): (1) a lower additive variance (V_A) under poorer environmental conditions; (2) increased environmental variance (V_E) by such conditions; and (3) a variable genotype-by-environment interaction depending on habitat. In our study, lower heritability values in the river than in streams corresponded to both lower V_A and higher V_E components; a phenomenon that has also been observed in other studies (Simons and Roff 1994; Merilä 1997; Réale et al. 1999; but see Merilä and Fry 1998). Our results therefore support the contention that higher habitat quality removes the environmental effects on variation of juvenile growth rate. A higher additive genetic variance, resulting in a higher heritability of growth, is supportive of a potential higher rate of evolution for body size in high-quality habitat (see Merilä 1997). Furthermore, a change in genetic variance between environments may be the result of a low genetic correlation between traits expressed in these environments, potentially indicating that the trait is not influenced by the same genes in the two environments (Simons and Roff 1994).

Another difference was found when comparing heritabilities among male reproductive tactics. Even though we found significant heritability values for body size in both groups, values were substantially higher in MSW than in grilse. This was due to both higher values of additive genetic variance and lower environmental variance (Table 3). Accordingly, if the selection differential (S) is in the same range of magnitude on both genotypes, then the response on body size of MSW offspring should be stronger than in grilse (Falconer 1989). Evidence of higher heritability of body-size characters in MSW than in grilse has been supported by controlled selection experiments in salmon ranching (Jonasson 1993). In crosses involving grilse, Jonasson (1993) found a heritability of 0.11 for length at 190 days of age, which was smaller than the value obtained in crosses involving MSW fish ($h^2 = 0.38$). These differences between MSW and grilse could potentially be related to differential nongenetic paternal effect on egg size, which is present in salmon (see Pakkasmaa et al. 2001), namely through the process of egg swelling. This occurs at fertilization, which could influence the variation in growth we observed, and thus the heritability.

Maternal Effects

There was no effect of female size on the growth of offspring at 0+. This finding was quite surprising given the fact that maternal size is positively related to egg size, which in

turn should increase juvenile size (Kazakov 1981; Einum and Fleming 1999). However, absence of maternal effect on offspring size has also previously been reported in the chinook salmon (*Oncorhynchus tshawytscha*) by Heath et al. (1999), who showed that although maternal effect was important at the larval stage, this effect was null later on. Still, it could be argued that even if there was no indication of direct genetic maternal effect in our study, the choice of the spawning location by females had an effect on subsequent offspring growth as shown by the difference already present at 0+ age. This supports earlier proposals derived from empirical observations that argued that inherited environmental effect (apart from nuclear genes) could influence character evolution (reviewed in Rossiter 1996).

To conclude, although our results showed unequal reproductive success between salmon tactics, a clear demonstration of equality (or not) of lifetime fitness of alternative reproductive tactics would be very difficult to achieve under natural conditions. This is mainly because individuals originating from one tactic can potentially switch to the other tactic and also because heritability might be highly variable depending on different sets of environmental conditions. Also, the variation in heritability between habitats and tactics observed in this study shows that previous models aiming to explain the coexistence of alternative reproductive tactics in the context of the conditional strategy theory (Gross and Repka 1998a,b) based on a single heritability estimate for the entire population are likely inappropriate to capture the complexity of factors involved in the expression of alternative life-history tactics.

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