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INFLUENCE OF INDIVIDUAL BODY SIZE AND VARIABLE THRESHOLDS ON THE INCIDENCE OF A SNEAKER MALE REPRODUCTIVE TACTIC IN ATLANTIC SALMON

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Abstract.—In the conditional strategy model, divergence in reproductive phenotypes depends on whether the individual's condition is above or below a genetically determined threshold. The relative contribution of the genetic and environmental components that lead to the expression of a reproductive tactic by an individual is not well understood. In the present field study, we determined when condition diverged between males that develop the mature parr phenotype and those that do not in Atlantic salmon (*Salmo salar*). We also investigated the uniformity of the threshold value in the population. We sampled mature parr and immature males at age one, of the same population at six different sites for four consecutive years. Our study provides an example of the interaction of genotype and environment on the expression of a reproductive tactic. Size was significantly greater for future mature parr than for future immature males as early as 20 days after hatching (emergence), suggesting that there may be a parental effect component in the tactic adopted, since no exogenous feeding takes place before this time. Size advantage at emergence was maintained through the next spring at age one to different degrees depending on the year, thus suggesting the presence of an environmental component of tactic expression. Our results support the contention that within the conditional strategy, the environment faced by a male and his condition at the moment of reproduction consistently predicts neither the environment faced by his offspring nor the fitness they will obtain by expressing the same tactic as their father. Furthermore, higher mean size at a site did not always translate into a higher proportion of mature parr, therefore supporting the hypothesis that thresholds vary across habitats within the same population.

Key words.—Development, genotype-by-environment interaction, life history, otolith, phenotypic plasticity, *Salmo salar*, threshold trait.

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Males often exhibit two considerably divergent phenotypes: reproductive-resources-controlling males (bourgeois) and sneak-mating opportunistic males (parasitic; Gross 1996; Taborsky 2001; Moczek et al. 2002). Such alternative phenotypes have different morphological, behavioral, and reproductive characteristics. The evolution and proximate causes and consequences of these extreme divergences in phenotype have been studied in several theoretical frameworks, for example: the alternative strategy, in which variation in phenotype is determined directly by a genetic polymorphism for the trait (Ryan et al. 1992; Lank et al. 1995); and the conditional strategy, in which the expression of phenotype depends on exceeding a threshold condition (Roff 1996) such as observed in insects (Mozcek and Emlen 1999), marine invertebrates (Brockmann 2002), and different species of fishes (reviewed in Gross 1996; Taborsky 2001). In this case, gains in fitness of a phenotype are condition-specific (Roff 1996). In a given habitat, a male may gain a higher fitness by expressing the sneaker phenotype rather than the fighter phenotype even though it has a lower average fitness and could be suboptimal for individuals with other condition values (Gross 1996). This assumption has been supported by direct estimates of fitness functions in relation to condition for each phenotype, although very few studies have been performed (Hunt and Simmons 2001).

The expression of a tactic is the result of the interaction of this condition and of the threshold value of the condition. The condition of an individual is defined as a continuous trait that is under polygenic control and is also influenced by the environment (Hazel et al. 1990; Falconer and Mackay 1996). All individuals with a condition higher than the threshold value will express one phenotype whereas all others will express the alternative phenotype. Appreciation of the impact of each element is crucial to our understanding of the evolution of a conditional strategy. Hazel et al. (1990) proposed that the threshold has a fixed value for a given genotype, and that one or more genotypes may be present in a population. It is clear that threshold values may vary among environments when the fitness value of a tactic for a given condition varies among populations and environments (Hutchings and Myers 1994; Gross 1996). A habitat-dependent threshold value is an advantageous adaptation since it adjusts the expressed phenotype of the male of a given condition with the probability of maximizing fitness in that particular environment. In this case, the variation in threshold value is assumed to be the result of differential selective pressures of the environment and not simply the result of random factors such as drift (Moczek et al. 2002). The evolution of different threshold values among populations or environments has been suggested for diverse dichotomous tactics including pupal color polymorphism in butterflies (Hazel and West 1982), mating tactics in horned beetles (Moczek et al. 2002), and trophic polyphenism in toads (Frankino and Pfennig 2001). However, no study has focused on the possible variability of the threshold within a single population occupying a highly heterogeneous environment. Moczek and Emlen (1999) presented evidence for a uniform threshold value in a population on an ecological time-scale. Cases in which one population uses several heterogeneous habitats have not yet been studied.

The Atlantic salmon (*Salmo salar*) is an iteroparous anadromous species that exhibits alternative reproductive tactics

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that have drawn biologists' interest for more than a century (reviewed in Orton et al. 1938; Fleming 1996). The life cycle and mating system of this promiscuous species have been well described (see Fleming 1998) and the trade-offs associated with alternative male phenotypes (fighter-bourgeois/sneaker-parasitic) have been partly established. After a freshwater juvenile stage of one to four years and a sea migration phase lasting one to three years, large anadromous males return to their river of origin and fight to monopolize females on spawning grounds (Fleming 1996). A portion of the males become sexually mature before migrating to sea, at a younger age and at a size five to 10 times smaller than their anadromous counterparts (Jones and Orton 1940). Because of this size difference, they sneak into the nests of anadromous females to fertilize eggs instead of fighting to gain access to females (Hutchings and Myers 1988). Mature parr, as they are called, reproduce at a younger age and have a greater probability of surviving before reproduction, but their fertilization success and number of partners are smaller than for the dominant anadromous males (Thomaz et al. 1997; Garant et al. 2002), and winter survival following maturation is believed to be lower (Myers 1984; but see Whalen and Parrish 1999).

Many factors that determine whether an individual is the most fit in a given habitat will be reflected in body size in salmon. Characteristics such as metabolic efficiency, immune defense capacity, and territorial quality vary among individuals and among environmental conditions (e.g. temperature, parasite load, predator field), and this will be reflected in size. However, some traits are affected by size, such as individual fertilization success, which is variable and often correlates positively to size of the individuals (Hutchings and Myers 1988; Jordan and Youngson 1992; Thomaz et al. 1997; Jones and Hutchings 2001; Garant et al. 2002). Whether condition is affected or reflected by body size, size informs us of the overall quality of the individual and can be used as a measure of condition. Size has been observed to differ between future immature and mature males in the spring preceding maturation in the wild, which is six months before spawning (Prévost et al. 1992; Whalen and Parrish 1999). However, although these studies clearly implicate size as a variable influencing the expression of the phenotype, they do not provide information about the developmental trajectory of size divergence nor do they examine whether these differences are already apparent at birth or appear later during development.

Rivers within which Atlantic salmon grow are highly heterogeneous, resulting in patchy juvenile distribution patterns. Young salmon remain close to natal spawning grounds and are mainly sedentary in their first year of life (Armstrong et al. 1994). Individuals may therefore face distinct conditions as juveniles, even though they are from the same population, depending on the site where they were born. It has been shown that the incidence of mature parr among Atlantic salmon males can be variable within a population (Myers et al. 1986). This heterogeneity may reflect variation in mean size among habitats, but could also be linked to within-population variability of the threshold value. Therefore, the prediction that threshold values vary among sites should be tested.

This study aimed at testing the conditional strategy model in a natural system in which male Atlantic salmon exhibit a dichotomous reproductive pathway. We examined the interaction of genetic and environmental components that act on size and ultimately on the reproductive tactic expressed, by determining the moment of divergence of condition between future mature and immature males. We also tested the prediction that threshold is uniform in the population.

MATERIALS AND METHODS

Study Site, Sampling, and Analyses

Six sites documented as spawning/nursing areas in the Ste-Marguerite River (Québec, Canada; Garant et al. 2000) were studied (Fig. 1) for four consecutive years, from 1996 to 1999. These sites differ in distance from the mouth of the river, as well as in hydraulic characteristics (N. Aubin-Horth and J. J. Dodson, unpubl. ms.). For example, the three sites sampled on one branch correspond to three sections that exhibit important differences in slope (between 0.8 and 19.9 m/km). Such differences in the physical habitat affect biotic characteristics of the sites (Vannote et al. 1980; Beisel et al. 1998; Folt et al. 1998; Miyake and Nakano 2002). N. Aubin-Horth and J. J. Dodson (unpubl. ms.) observed that during the four years studied, ratios of early maturity in males aged one year (calculated as the number of mature parr over the total number of males of a similar age) varied between 0.09 and 0.75 depending on the site studied. Significant differences in the incidence of early maturity were found among these sites sampled in a given year for three of four years. The same individuals used to determine the incidence of early maturity were used in the present analyses, and therefore the sampling protocol is identical to that used by N. Aubin-Horth and J. J. Dodson (unpubl. ms.). Briefly, individuals were sampled by point electrofishing from 1996 to 1999 at the end of August when detecting sexual maturity by dissection is possible. A total of 40–80 fish was sacrificed in each sample and used to determine size, mass, sex, and maturity status. Age was estimated using otoliths (Campana and Jones 1992). In this study, we focused on individuals aged one year or older, because this is the first age at which maturation is possible at this latitude (no individuals less than one year old have been found to mature in this river; N. Aubin-Horth and J. J. Dodson, unpubl. ms.). The incidence of early maturity was determined for each site sampled for each of the four years. We assumed that juveniles caught at a given site were resident in the area since hatching because movement of juveniles during their freshwater life is limited and mature parr do not yet move toward spawning sites at the time of sampling (late August); thus we assume they are a representative sample of the subpopulation.

We estimated size at different life stages for individuals of both phenotypes, to reconstruct their lifetime growth history. Otoliths bear obvious marks at hatching, emergence from the nest, and at the beginning of spring preceding maturation the following autumn. Emergence occurs approximately 15–20 days after hatching at these latitudes (Meekan et al. 1998) and exogenous feeding starts only at this moment in life. Otolith and fish growth are proportional, thus allowing back-calculation of size at these three life stages using the biological intercept method (Campana 1990). Previous stud-

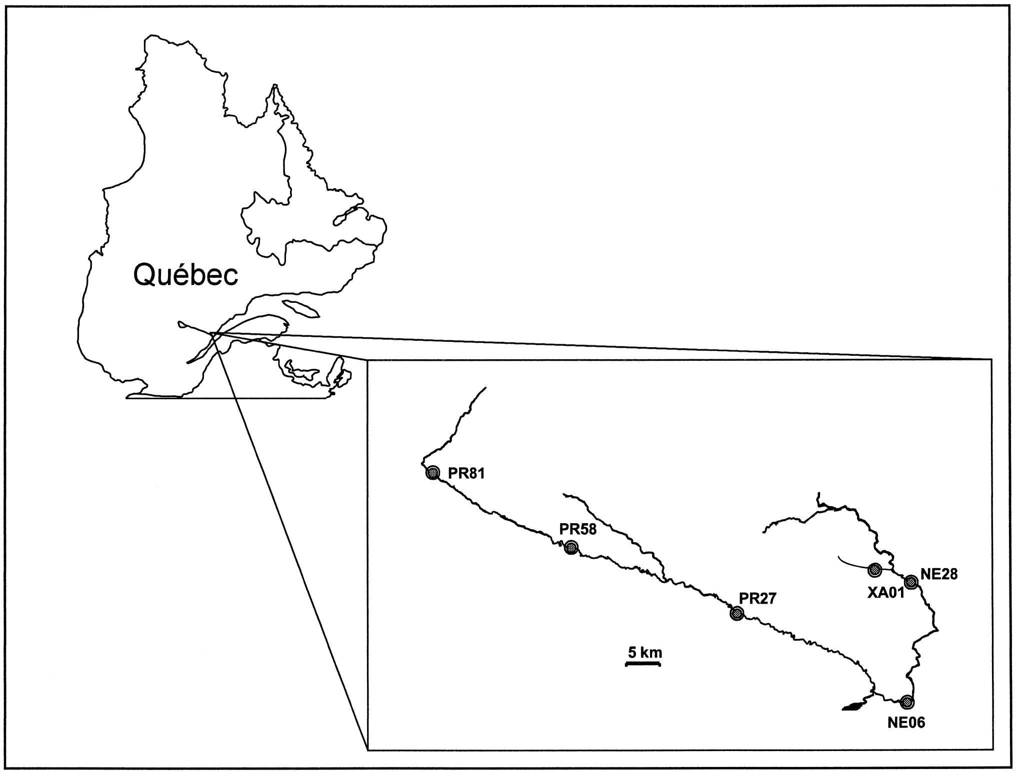

FIG. 1. Location of the six sites sampled from 1996 to 1999 in the Ste-Marguerite River system (Québec, Canada).

ies have shown the periodicity of the deposition of growth marks on the otolith and the correlation between distinct marks found on the otolith and hatching and emergence events (Wright et al. 1991; Meekan et al. 1998). determined that proportionality of otolith and somatic growth was present in juvenile Atlantic salmon aged one year, and that sexual maturation does not affect otolith-somatic size proportionality. Aubin-Horth and Dodson (2002) also performed a direct validation of the accuracy of back-calculated size estimates using the biological intercept method.

Statistical Analysis

We examined differences in size at different life stages between immature and mature males sampled at the end of their second summer of life using analyses of variance (ANOVAs). We tested whether body size, as a measure of overall condition, is correlated with the expression of alternative phenotypes in nature and we determined the life stage at which divergence in size between alternative tactics becomes apparent. Specifically, we tested for significant differences in mean back-calculated sizes at hatching, emergence, and in the spring preceding maturation between individuals that became mature parr and those that did not, from different years. We also tested for interaction between factors to verify whether the pattern observed was constant among years. We interpreted the life stage (hatching, emergence, or the following spring), when mean size differed between immature and mature males as an approximation of the life stage when condition diverges. Log-transformed data of back-calculated size were used in all ANOVAs to assure normality of the distribution, but means of untransformed data are presented in Figure 2.

To test whether an individual's early size advantage is maintained, we correlated individual size at emergence and in the spring preceding maturation of immature and mature individuals. The presence of a significant correlation would demonstrate that a size advantage of an individual at emergence was conserved until one year later in the spring. An absence of correlation would suggest that some individuals that were small at emergence gained a size advantage or vice versa, resulting in the crossing of growth trajectories.

We tested the presence of a relationship between individual size and the probability of expressing the parr maturation tactic in the Ste-Marguerite River population using a logistic regression with year as a fixed factor. This analysis not only describes the link between size and early maturation in males, but also highlights variation in thresholds in the overall population. Indeed, if the threshold is uniform in the population, the logistic regression function should show a sharp increase in probability of maturation within a narrow range of sizes (pointing to a specific size threshold). However, the effect of multiple thresholds in the population would be to broaden the relationship between size and probability of maturation, since a given size would be associated with a low maturation probability for some individuals and a high probability in others.

We also tested our hypothesis concerning the uniformity of the mean threshold value specifically among subpopulations using the covariation of mean size and the incidence of parr maturation at a given sampling site. We first assessed

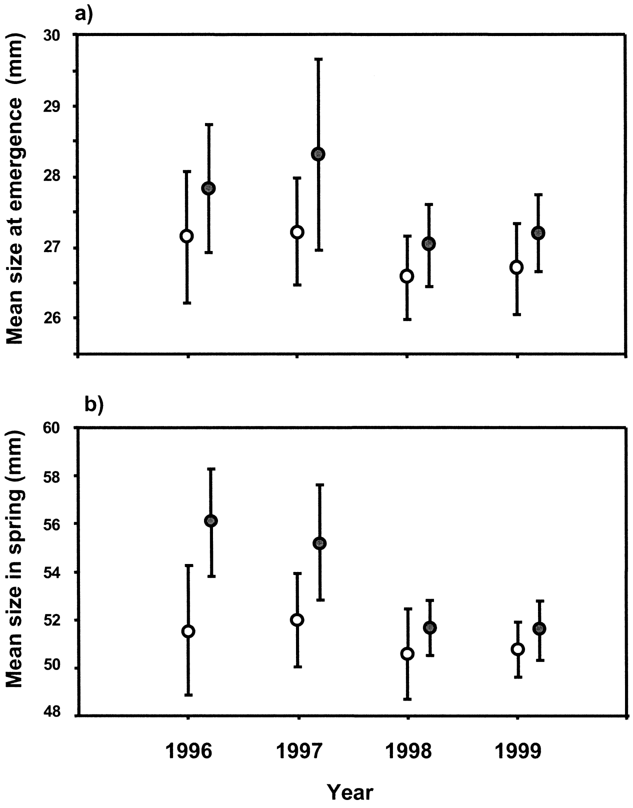

FIG. 2. Mean back-calculated size (vertical lines represent 95% confidence intervals) of immature (open circle) and mature (shaded circle) males at age one caught in autumn presented for the four years of data at (a) emergence from the nest and (b) at age one in the spring prior to maturation.

any possible differences in size among years (random factor) and sites (fixed factor) in a mixed-model ANOVA by pooling data from immature and mature males. This analysis was performed for size back-calculated at hatching, emergence, and in the spring preceding maturation. We then correlated the log of mean size with parr maturity incidence observed at each corresponding site for the four different years. Parr maturity incidence varied significantly among sites for three of the four years studied (N. Aubin-Horth and J. J. Dodson, unpubl. ms.). Calculating a Pearson correlation coefficient of these two variables tested the null hypothesis of no variability in threshold values for a given population. Since we already knew that parr maturity incidences vary significantly among subpopulations, three outcomes of this analysis were possible and they are summarized in Table 1. We correlated size at emergence and size in the spring preceding maturation, with parr maturity incidence using all sites from all years. This analysis was also performed on a year-by-year basis for size back-calculated in the spring preceding maturation only, to verify whether any patterns were repeated over time.

RESULTS

Data from the six sites were pooled in the analysis of mean size differences between immature and mature males and for the logistic regression. Differences attributable to the sampling site could not be included in this analysis because three maturity-site-year combinations were represented by only one individual with otoliths sufficiently clear for analysis, and one combination (site PR81-1997-immature males) was not represented. Size at hatching did not differ between males expressing and those not expressing the mature parr tactic later in life (Table 2). This result suggests that size at hatching does not determine the tactic, and this is stable among the four years studied (Table 2). In sharp contrast, size at emergence (Fig. 2a) varied between immature and mature males, because future mature parr were larger. There was a marginally significant effect of year on size (Table 2), suggesting that size was not uniform among years studied. In addition, the interaction term was not significant, such that this pattern of larger future mature parr than future immature males was consistent among years. In the spring preceding maturation, mean size (Fig. 2b) varied significantly depending on future maturity, since future mature parr were larger. Mean size also varied significantly among years whereas the interaction term was not significant (Table 2), suggesting that this significant size advantage of future mature parr was stable among years.

Correlations between individual size at emergence and in the spring preceding maturation were significant in three of four years (1996: $r = 0.42$, $P < 0.001$; 1998: $r = 0.46$, $P < 0.0001$; 1999: $r = 0.39$, $P < 0.0001$) and nonsignificant in a fourth (1997: $r = 0.05$, $P > 0.7$), suggesting that size advantages are usually maintained during the year that separates these two life stages, but that crossing of growth trajectories may occur.

We found no relationship between individual size at hatch-

TABLE 1. Possible interpretations of the outcome of the correlation analysis of mean size at emergence or in the spring preceding maturation and parr maturity incidence in autumn in the corresponding site, depending on the presence or absence of significant variation in mean size among sites.

Mean size	Correlation between mean size and parr maturity incidence	Interpretation
Significant variation among sites	Significant	Fixed threshold value among sites: the same threshold is exceeded by different proportions of males depending on size attained at a site.
	Not significant	Variable threshold values among sites: an interaction between threshold value and mean size determines maturity incidence at a site.
No significant variation	Not significant	Variable threshold values among sites: the same mean size results in different proportions of males exceeding the different thresholds at each site.

TABLE 2. Effects of future maturity of males and year on mean size, and percentage difference in mean size between immature and mature males. Analyses are presented for size at hatching, at emergence, and in spring at age one.

Factor	df	F	P-value	Differences in mean size (%)
Effect on hatching size				
Future maturity	1	0.04	0.842	0.7–1.1
Year	3	0.22	0.882	
Maturity × year	3	0.18	0.909	
Effect on emergence size				
Future maturity	1	5.71	0.018	1.7–4.1
Year	3	2.57	0.055	
Maturity × year	3	0.24	0.866	
Effect on spring 1+ size				
Future maturity	1	11.95	<0.001	1.7–8.8
Year	3	4.50	0.004	
Maturity × year	3	1.54	0.204	

ing and probability of maturation with year as a fixed factor in the logistic regression analysis (all $P > 0.4$). We performed the same analysis for size at emergence. Because we found no effect of year or significant interaction on maturation probability (all $P > 0.6$), we repeated the analysis for size at emergence with all years pooled, revealing a significant effect of size at this life stage on parr maturation probability (likelihood-ratio statistics [LR], $P = 0.039$). We found that the probability of maturity increased linearly with length. We also found a significant effect of size at spring preceding maturation on parr maturation (LR, $P = 0.007$) when pooled data for all years were used (because no significant year effect or interaction was found in an analysis including year as a fixed factor; all $P > 0.4$). As with size at emergence, the probability of maturity increased linearly with length. We then included size at emergence and size in the spring preceding maturation in the analysis to show that when combined, size in the spring preceding maturation is a more important predictor of parr maturity (LR, $P = 0.033$) than size at emergence (LR, $P = 0.238$).

Mean size of the entire male population at hatching (e.g. future immature and mature males pooled) varied among sites ($P < 0.010$) and the interaction term was significant ($P < 0.01$), suggesting that the differences among sites were variable among years studied. At emergence, mean size did not vary significantly among sites ($P = 0.175$). The significant interaction term ($P < 0.0001$) indicates that the pattern of variance in size among sites was different depending on the year studied. Mean size in the spring preceding maturation varied among sites ($P < 0.0001$). The interaction term was not significant ($P = 0.6$). This suggests that the differences in mean size observed among sites were consistent over the years.

No significant correlation was observed between mean size at emergence at a given site and the incidence of mature parr observed one year later in autumn ($r = 0.174$, $P = 0.420$, $n = 24$). A marginally significant correlation was observed between mean size attained in spring at a given site and the incidence of mature parr observed in the following autumn ($r = 0.40$, $P = 0.054$, $n = 24$), when all sites and years were used in the analysis (Fig. 3). This weak correlation, however, was only due to marginally significant covariation from 1996 ($r = 0.80$, $P = 0.055$) and 1997 ($r = 0.76$, $P = 0.086$), because no significant correlation was found between these two variables in 1998 ($r = 0.28$, $P = 0.620$) and 1999 ($r = -0.01$, $P = 0.990$). Furthermore, even in 1996 and 1997, similar mean sizes at different sites also lead to different incidences of mature parr (Fig. 3).

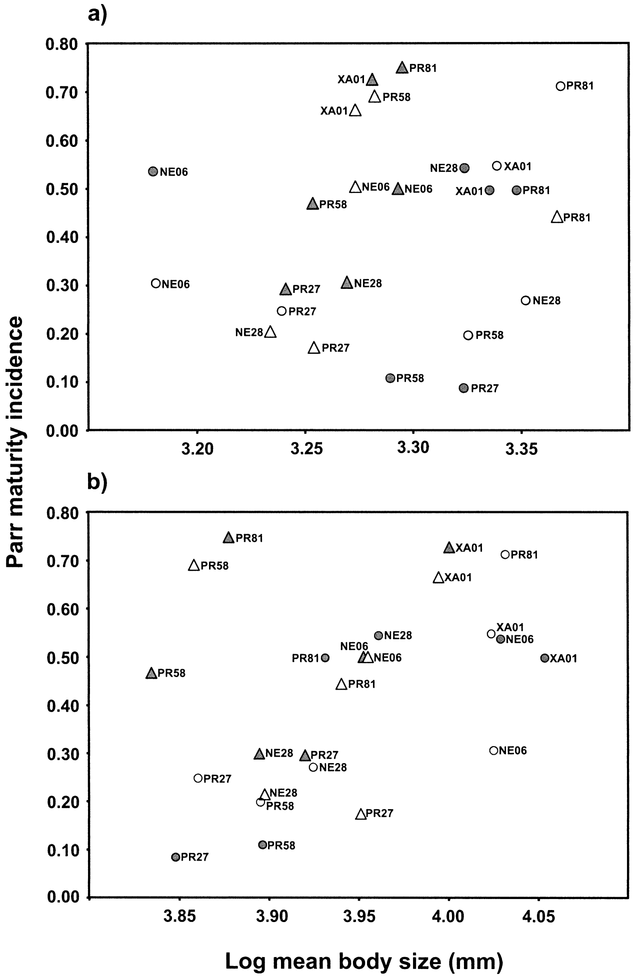

FIG. 3. Covariation of the incidence of mature parr observed at a site in autumn and log-transformed mean back-calculated size at (a) emergence and (b) in the spring of Atlantic salmon males aged one year from that site for samples taken from 1996 to 1999 in six subpopulations of the Ste-Marguerite River. Each year is represented by a different symbol: 1996, shaded circle; 1997, open circle; 1998, shaded triangle; 1999, open triangle. Each subpopulation is indicated.

DISCUSSION

Parental and Environmental Components of Expression of the Mature Parr Phenotype

Our study is, to our knowledge, one of the first to determine directly in the wild and for different cohorts the growth trajectories from hatching to maturation of individual fish that express a conditional reproductive strategy based on size. We present direct evidence for the existence of a divergent size between salmon males that express the mature and those that express the immature phenotypes as early as emergence from the nest, a difference that is maintained until the development of gonads a year later. However, the parental effect on size advantage of an individual suggested by this result is partly offset by environmental effects that vary over years.

The individuals that have a larger size in the spring preceding maturation tend to mature as parr in the population under study, which is in accordance with other reports (Prévost et al. 1992; Whalen and Parrish 1999). Our study is unique in that the use of otoliths allowed us to determine the size of each individual as far back as hatching and emergence. As such, we reconstructed the timing of divergence between individuals expressing the two alternative phenotypes. Since future reproductive phenotype cannot be predicted on the basis of size at hatching in our study, we can take this as an indication that the future phenotype of the individual is not determined or expressed at this moment or that a size difference cannot be detected with our sample size and methodology. Our longitudinal analysis also reveals that size difference is already apparent before the first external feeding (at the time of emergence). Certain individuals therefore may have an intrinsic advantage in size, since all growth between hatching and emergence from the nest relies on use of endogenous energy reserves from the yolk sac. In the context of a conditional strategy, they are thus *predisposed* to mature as parr before exposure to external environmental conditions. This direct demonstration in a natural population of a link between intrinsic size advantage and conditional reproductive tactic expressed more than a year later is novel in a species without parental care, although a similar phenomenon has been observed in care-giving species (Wiegmann et al. 1997; Hunt and Simmons 2000). In the case in which direct parental care is absent, this intrinsic size advantage of endogenous feeding individuals may be linked to a direct maternal effect, or an indirect parental genetic identity effect (Travis 1981; Garant et al. 2002). Both causes are plausible but have different implications, because phenotypic variance among offspring may or may not have a genetic basis depending on the case. Parental identity effects could be reflected in any factor leading to higher growth such as genetically based differences in immunocompetence, rate of development, metabolism, or efficiency of energy transformation whereas maternal effects may act through direct superior energy reserves (egg size) or prehatching environmental conditions associated with nest site choice by the mother (Bernardo 1996; Einum and Fleming 2000). However, it is not possible to confirm or reject the presence of a parental identity or maternal effect in our study. Interestingly, in a study of Atlantic salmon in which the maternal effect was eliminated by using the same females in experimental crosses with different male phenotypes, a paternal identity effect was demonstrated: the offspring of mature parr were larger than anadromous males' offspring (Garant et al. 2002). Such a paternal effect can be hypothesized to exist in the present case, but this cannot be verified because pedigrees are not known. Although controlled crosses eliminated all maternal effects in the study by Garant et al. (2002), these effects might be randomly distributed among individuals in our natural population. This could explain the difference in size between emerging future mature and immature males, which was about 1.7–4.1% depending on the year in our study, compared to 9.6% in offspring of fathers of these two phenotypes in Garant et al. (2002) in laboratory conditions. If the hypothesis of paternal identity was retained over the maternal effect hypothesis, this would suggest that mature parr could provide a size advantage to their sons, who in turn would be more likely to reach the size threshold and develop as mature parr.

Although this is in accordance with an earlier report of a larger proportion of mature parr in the progeny of mature parr than of anadromous sires in experimental crosses (Glebe and Saunders 1986), this putative correlation of tactics across generations will be realized only if the size advantage at emergence of future mature parr is maintained later in life. It must be emphasized that this is linked to a central assumption in the conditional strategy theory and that other studies, along with our results, suggest that this may not always be the case under natural conditions. For example, significant maternal effects present at birth have been shown to become undetectable over the course of juvenile life in Chinook salmon (*Oncorhynchus tshawytscha*; Heath et al. 1999). Furthermore, heritability estimates of quantitative traits have been shown to vary depending on environmental conditions, with some traits having a lower heritability in unfavorable habitats (Merilä 1997; Hoffmann and Merilä 1999). In the present study, we show a significant covariation for three of the four years studied between size at emergence and in the spring preceding maturation, but with different correlation coefficient values. This suggests that individuals tend to keep their size advantage during this first year, but that environment effects are present and some small individuals will grow faster and reach large size at age one, equivalent to the largest individuals of the population at emergence. Our study therefore provides an example of the interaction of genotype and environment (or maternal effect and environment) on body size. Unpredictable events that may happen between emergence and the following spring include changes in abiotic or biotic factors such as displacement by a flood event, a drought, new predation/infection risks, the gain of a feeding territory, the lowering of feeding opportunities, or a rise in metabolic expenses, all possibly leading to lower or higher individual growth during a certain period. Changes in habitat during the lifetime of a juvenile may also result in a genotype becoming less favorable in the new conditions with a subsequent reduction in growth. Our study is novel in that we determine how the interaction of genotype and environment (or maternal effect and environment) on size affects the determination of the reproductive phenotype in the conditional strategy. We hypothesize that this interaction will result, in some instances, in anadromous males having offspring that will become large enough to express the mature parr phenotype and vice versa. Our results therefore support an essential condition for the evolution of a conditional strategy: the environment faced by a male and his condition at the moment of reproduction do not always predict the reproductive environment faced by his offspring nor the fitness they will obtain by expressing the same tactic as their father (Roff 1996).

Divergence in Threshold Value

We also tested the prediction that threshold values that must be exceeded for an individual to express the mature parr tactic will vary within a natural population, and that this may be in relation to different environments, and we present empirical support for this hypothesis. The significant linear relationship we found in the logistic regression analysis between size at emergence and size in the spring and maturation probability the following autumn with all years and sites pooled supports our hypothesis of the presence of variable thresholds in the population. Indeed, a single threshold would have resulted in all individuals above a given size (the threshold) exhibiting a high probability of maturation. However, we observed individuals of the same size that may or may not be mature, which is the signature of the presence of several thresholds in the population. The fact that mean size did not vary significantly among subpopulations at emergence but that later parr maturity did is in accordance with the alternative hypothesis that the threshold for parr maturation is not uniform but varies spatially among the subpopulations (see Table 1). Furthermore, the weak correlation between mean size attained in the spring and percentage of maturing males in the following autumn also indicates that these different thresholds present in the population may not be randomly spatially distributed in the population. However, our interpretation of the presence of dissimilar mean threshold values in the different sites sampled requires caution because it is based on the absence of detection of a significant covariation. Further support that threshold values vary among habitats comes from the variance around the relationship in the years when there was a significant covariation between size and parr maturation and from the departure of some sites from the major correlation. However, it could also indicate that size is not the only variable determining the expression of alternative tactics. This proposal of threshold variability among environments must be further examined using an experimental method that decouples genotype and environment effects on the expression of maturity. Common-environment and reciprocal transplant experiments would allow this. Individuals from each subpopulation (genotype) could be raised together in several different conditions affecting growth (environment). The phenotypes expressed by individuals from each subpopulation in each condition (reaction norm) would allow one to estimate a threshold value and empirically test the null hypothesis of threshold uniformity.

With this caution in mind, we propose that the difference in genotypes among different habitats results in different thresholds and that they may represent local adaptations. When variable environment and patterns of genetic differentiation are superimposed spatially, a favorable system for the emergence of local adaptation is produced. The local adaptation hypothesis (for a review on salmonids see Taylor 1991) implies that the expression of a particular reproductive phenotype is consistently favored in some habitat conditions but not in others. Conditions faced by juvenile salmon can be very different for members of the same population that live in different parts of the river system, since local conditions in river habitats are highly heterogeneous and juveniles are largely sedentary. Furthermore, philopatry is important in Atlantic salmon (Stabell 1984). Adults return to their birth site in their natal river to spawn, as established by the spatial structuring of genetic differentiation observed among (Ståhl 1983; King et al. 2000) and within (Verspoor and Jordan 1989; Spidle et al. 2001) rivers. As a consequence, locally advantageous genetic differences can accumulate at a scale that is smaller than the entire river drainage. In accordance with this hypothesis, adaptive functional differences among populations using different streams have been found in this species (Riddell et al. 1981; Verspoor 1986) as well as at a smaller spatial scale (Verspoor and Jordan 1989; Verspoor et al. 1991). Specifically, in the Ste-Marguerite River, this type of spatial structuring of genetic differentiation has been observed at neutral loci among the same sites sampled in the present study (Garant et al. 2000). Spatial genetic variation was weak but significant with some sites showing temporal stability in allelic frequencies among years whereas others did not. The distribution of genotypes is therefore neither uniform nor random in this river. More importantly, functional gene differentiation among the same sites sampled in the present study have been shown at the major histocompatibility complex, which is an important component of immune defense in fishes, and this variation has been attributed to selection rather than drift (Landry and Bernatchez 2001). These studies confirm that salmon juveniles are structured in subpopulations and are subjected to divergent selection pressures among environments in the Ste-Marguerite system. Superimposing our results on findings from these two studies allows us to propose that threshold values could be among those traits that are differentially selected among these subpopulations.

In other species, the constraints acting on age at maturation or determining the adoption of an alternative feeding or reproductive tactic are directly linked to the probability of succeeding by using a given tactic, as well as to the trade-off between reproduction, survival, and growth potential, which varies among populations and individuals according to habitat and differences in condition (Hutchings 1993; Roff 1994; Godin 1995; Bertschy and Fox 1999; Johnson and Belk 2001; Frankino and Pfennig 2001). Such among-habitat differences in the relationship between size and reproductive success as a parr, or between size and survival, or other variables such as distance from the mouth of the river to the spawning sites, could be present in the highly heterogeneous habitat faced by salmon. Interestingly, in our study system, the sites that are farther upstream (PR81, XA01) are the ones that usually exhibit the highest proportion of mature parr when compared to downstream sites on the same river branch for a given year, and also exhibit the least variation in parr maturation among years (N. Aubin-Horth and J. J. Dodson, unpubl. ms.), although they are not always the sites with the highest mean size in the spring (data not shown). Since this suggests a lower threshold value upstream, this could mean that parr maturity is either favored at these sites, or not favored at downstream sites. Although knowledge of the environmental variables that act to modify the profitability of being mature as a parr would help to test this hypothesis, this was beyond the scope of this study and further investigations are needed. In summary, our small-scale approach in the wild allows us to conclude that the genotype determining the threshold value, the size at emergence, and the intrinsic characteristics of the individual interacts with environmental conditions in determining the reproductive phenotype expressed by an individual in this conditional strategy.

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