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The genetic basis of early-life morphological traits and their relation to alternative male reproductive tactics in Atlantic salmon

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sexual tactics.

Abstract

Although heritability estimates for traits potentially under natural selection are increasingly being reported, their estimation remains a challenge if we are to understand the patterns of adaptive phenotypic change in nature. Given the potentially important role of selection on the early life phenotype, and thereby on future life history events in many fish species, we conducted a common garden experiment, using the Atlantic salmon (*Salmo salar* L.), with two major aims. The first objective is to determine how the site of origin, the paternal sexual tactic and additive genetic effects influence phenotypic variation of several morphological traits at hatching and emergence. The second aim is to test whether a link exists between phenotypic characteristics early in life and the incidence of male alternative tactics later in life. We found no evidence of a site or paternal effect on any morphological trait at hatching or emergence, suggesting that the spatial phenotypic differences observed in the natural river system from which these fish originated are mainly environmentally driven. However, we do find significant heritabilities and maternal effects for several traits, including body size. No direct evidence was found correlating the incidence of precocious maturation with early life characteristics. We suggest that under good growing conditions, body size and other traits at early developmental stages are not reliable cues for the surpassing of the threshold values associated with male sexual development.

Introduction

Adaptive evolutionary change is caused by the heritable variation in traits linked to fitness (West-Eberhard, 2003; Lynch & Walsh, 1998; Falconer & Mackay, 1996). Even though the genes underlying most quantitative traits are likely to vary among individuals, a precise quantification of the extent to which genetic variation explains phenotypic variation, particularly at life-cycle stages where selection is known to occur, is required. In many animal species, strong viability selection may occur during the early developmental stages of life, because young individuals are more susceptible to variations in phenology-related events (e.g Feder *et al.*, 2008), fluctuations in environmental conditions (Good *et al.*, 2001), disease (Sol *et al.*, 2003), predation (Sogard, 1997) and density effects (e.g. Walker & Hamilton, 2008). In many fish species, the effects of these selective processes are often seen on body size (Sogard, 1997), with a general tendency to observe higher mortality rates for smaller individuals (Einum & Fleming, 2000). However, recent evidence has shown that this is not always the case, with some studies documenting either selection against large individuals (e.g. DiBattista *et al.*, 2007), or a significant level of temporal and spatial fluctuation in the direction of selection (e.g. Aubin-Horth *et al.*, 2005; Blanckenhorn *et al.*, 1999). Therefore, selection for viability-associated traits during juvenile stages may result in enduring spatial phenotypic differences depending on both the patterns in selective regimes and gene flow, and on the extent of the heritability of the trait(s) under selection (e.g. Blanckenhorn *et al.*, 1999; Koskinen *et al.*, 2002).

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Furthermore, events shaping these early life phenotypes are of considerable importance, because they often have significant effects on subsequent population dynamics (Armstrong *et al.*, 2003; Vigliola & Meekan, 2002) and on the characteristics of the population's mating system (e.g. Warner & Shine, 2008; West & Sheldon, 2002). At the individual level, these events may affect the future amount of resource allocation to reproductive effort and offspring quality (e.g. Hamel *et al.*, 2009; Taborsky, 2006; Lindström, 1999) and the development of individual reproductive strategies (e.g. Benton *et al.*, 2008; Letcher *et al.*, 2004; Stearns, 1992).

Indeed, for the Atlantic salmon (*Salmo salar* L.), the focal species in this study, episodes of positive selection for body size at emergence are correlated with an increase in the future frequency of the sneaker male tactic (known as mature parr) (Aubin-Horth *et al.*, 2005; Aubin-Horth & Dodson, 2004). In addition, from field observations, greater otolith sizes (and thus, assumingly, greater body sizes) are seen for offspring sired by mature parr compared to those sired by anadromous males (Garant *et al.*, 2002), suggesting that not only selection, but also geographical distribution of paternal sexual tactics may cause variation in juvenile body sizes among natal sites (even though corresponding laboratory experiments have failed to show this paternal effect on body size or have even provided evidence to the contrary; i.e. Morasse *et al.*, 2008; Garant *et al.*, 2002). These correlations have been used to suggest a causal link between body size and the development of future male sexual tactics, whereby larger sizes at emergence increase the probability of precocious maturation later in life (Aubin-Horth & Dodson, 2004).

Surprisingly, however, the genetic basis for early life traits is poorly understood, probably owing to the logistical difficulties to infer relatedness among individuals in the wild. Commonly, the evidence for the genetic basis of potentially selected traits is taken from the observation that full sib families originating from different populations display differences under common rearing conditions (e.g. Berg & Moen, 1999; Donaghy & Verspoor, 1997), even though common environmental effects are confounded with genetic inferences in these designs (Falconer & Mackay, 1996), and some of the traits measured, such as the timing of hatching and emergence are highly sensitive to small environmental perturbations (e.g. Warkentin, 1995; Balon, 1990). However, the advent of new molecular and analytic tools aimed at reconstructing genetic relationships (Garant & Kruuk, 2005; Kruuk, 2004), as well as the possibility to perform specific mating designs with some species (Lynch & Walsh, 1998), has increased our capacity to estimate quantitative genetic parameters (e.g. in salmonids, Thériault *et al.*, 2007; Perry *et al.*, 2004; Koskinen *et al.*, 2002; Heath *et al.*, 1999) and move towards a better understanding of the causes of phenotypic variation at early life developmental stages and its consequences on subsequent life-history events.

Within this framework, this study has two major objectives. The first is to determine whether the patterns of spatial variation in body size observed in the wild are genetically based and to characterize the genetic and nongenetic basis of phenotypic variation of other morphological traits likely to influence fitness. The second is to establish whether a link exists between early life phenotypic variation and the development of future male alternative reproductive tactics.

Specifically, to test for spatial, genetically based, phenotypic variation in early-life traits, we use data from the field as well as from a common garden experiment to (1) test for spatial variation in size at emergence in a natural river system, (2) determine whether the site-specific patterns of body size observed in the field are congruent with the patterns observed under common rearing conditions, (3) evaluate the effect of the paternal sexual tactic and the maternal environment on offspring phenotype at early juvenile stages (as potential sources of nongenetic variation) and (4) characterize the level of additive genetic variance for the measured traits (which in addition to size, include traits linked to swimming capacity and prey manipulation). The second objective of this study is to determine whether male reproductive tactics in this species are related to early life phenotypic traits. Therefore, we investigate whether families with large individuals at hatching or emergence (or with bigger yolk sacs) produce higher numbers of mature parr later in life.

Materials and methods

Study organism and river system

Development of the early-life of the Atlantic salmon (*S. salar* L.) largely depends on the nutrients provided by the mother in the eggs. Independence from this resource is achieved after two important developmental transitions: hatching and emergence (Gorodilov, 1996). At hatching, embryos are freed from the chorion but remain hidden in the gravel environment of their natal nest absorbing the yolk sac. Several weeks later, when absorption is mostly complete, fry emerge from the gravel to live and feed exogenously in the stream environment (Fleming, 1996).

At this stage, body size is an indicator of survival, because it is positively related to the acquisition and defence of high quality nursing territories (Garcia de Leaniz *et al.*, 2007; Cutts *et al.*, 1999). Particularly under high density conditions, larger individuals are able to displace smaller fish to suboptimal habitats, likely biasing mortality towards these size classes (Nislow *et al.*, 2004; Einum & Fleming, 2000). Although reported selection differentials are generally positive (Einum & Fleming, 2000), temporal fluctuations in density dependent and

independent conditions result in the fluctuation (or even absence) of size selective mortality over time (Cutts *et al.*, 1999; Aubin-Horth *et al.*, 2005; Einum & Fleming, 2000; Good *et al.*, 2001).

The focus of this study is on a river system (The Sainte-Marguerite River, 48°20′N, 70°00′W, Quebec, Canada) for which spatial genetic and phenotypic variation is observed on an upstream–downstream gradient. First, Garant *et al.* (2000) documented, by means of microsatellites, an important level of population structure between upstream and downstream sections of the river, comparable to that reported between rivers (Dionne *et al.*, 2008). This indicates some level of reproductive isolation. Second, using an approach analogous to that of genome scans applied to the analysis of gene expression, Roberge *et al.* (2007) identified 16 outlier genes whose expression levels are likely to have evolved under the influence of directional selection between upstream and downstream sites. And finally, the incidence of precocious maturation is higher in upstream sites because of lower threshold values for maturity, presumably selected at these sites (Aubin-Horth *et al.*, 2006).

Field sampling

Data on the size of fry (post-yolk sac, swim-up stage and juvenile salmon) were collected by the Centre Interuniversitaire de Recherche sur le Saumon Atlantique (CIRSA) at six sites on both branches of the Sainte-Marguerite River (Fig. 1) for the years 1996, 1998, 2000, 2001, 2003, 2004, 2006 and 2007. Sampling was conducted in June of each year, beginning several days after emergence was first detected. Sites were unlikely to be sampled on exactly the same date across years. Once sampling commenced, all stations were sampled within the following 8 days. For all years, electro-fishing over approximately a 100 m section of each river site was conducted until 20 fry were captured. Shortly after in the laboratory, fish size was measured as length up to the fork of the caudal fin to the nearest mm, with callipers.

Common garden experiment: design and rearing conditions

For logistical reasons, capturing breeders corresponding to each site was unfeasible. Therefore, effort was focused on capturing breeders originating from upstream and downstream sites of the North-eastern branch (NE) of the Saint-Marguerite River. This branch was chosen, because in 1981, a migratory ladder was built to expand the size of suitable habitat for spawning and juvenile stages of the Atlantic salmon. Since then, anadromous males and females have established breeding grounds in the upstream sites of this river branch with mature male parr being also conspicuously present. In addition, from the field results shown later, fish in upstream and downstream sites also display significant differences in size.

Therefore, over the summers of 2003 and 2004, eight anadromous females and 29 males (13 anadromous and 16 mature parr) were captured in late August and kept in a nearby hatchery station. Anadromous progenitors captured in the migratory ladder were used to represent upstream sites, whereas those representing downstream sites were captured near a downstream spawning ground with nets (given the strong philopatric behaviour in this species, these are not unreasonable assumptions, Garant *et al.*, 2000). In turn, mature male parr progenitors representing upstream and downstream sites were electrofished near XA01 and NE06 (Fig. 1), respectively. In the late autumn of both years, the mature gametes of these individuals were used in a partial factorial mating

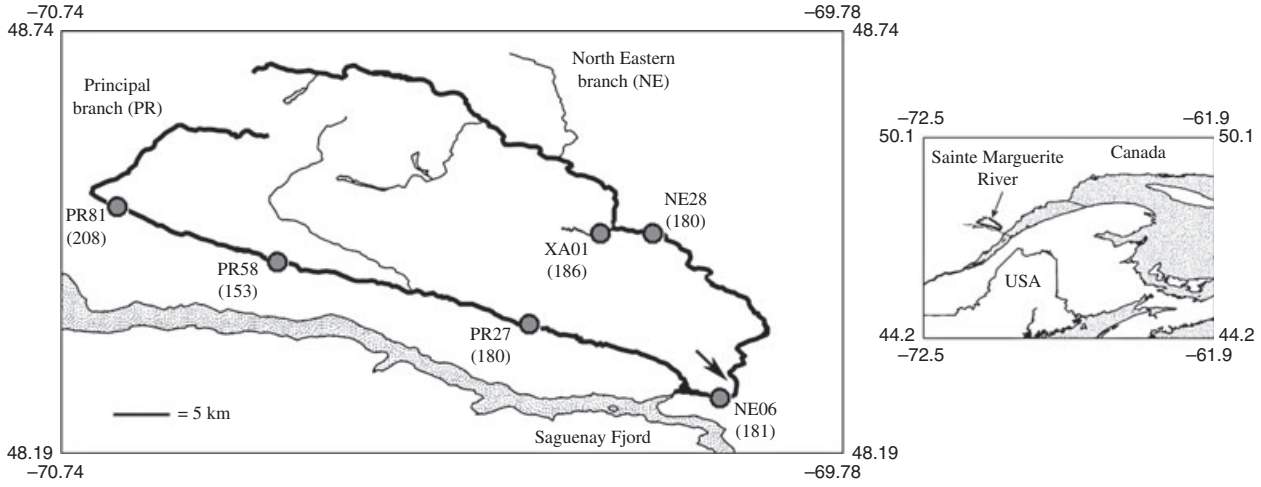

Fig. 1 The Sainte-Marguerite River system. Studied sites sampled over a period of 8 years near the date of emergence in June. The arrow represents the approximate position of the migratory ladder. Sample sizes are in parentheses.

design (Lynch & Walsh, 1998) to produce 30 and 28 families for 2003 and 2004, respectively (Table 1). Fertilization failed completely for three families in 2004, overall yielding 55 families. In addition, because of the difficulty associated with tagging individuals at these young stages, families had to be incubated in separate compartments (that is, full siblings were reared together).

Initially, incubation followed the natural temperature regimes found in the Sainte-Marguerite (from November to mid-March = 1.16 ± 0.62 °C). When eggs reached the eyed stage, they were transferred to the laboratory, where water temperature averaged 5.8 ± 0.7 °C, with 100% dissolved oxygen concentration. At 50% hatching, between 10 and 20 individuals per family (for a total of 933 individuals) were sacrificed and photographed using a digital camera mounted on a dissecting scope. Each image was scaled with a millimetric ruler that automatically adjusted to the magnification used. Afterwards, precise measurements on six morphological traits were obtained from these photos (Fig. 2a) to the nearest 0.01 mm (a total of 933 individuals) using the software SigmaScan Pro Version 4 (SPSS Inc., Chicago, IL, USA).

Table 1 Mating design used with sample sizes corresponding to hatching and emergence (i.e. for the family A1-F1, 18 individual were sampled at hatching and 17 at emergence). Dashes indicate unviable families. F = Anadromous dam, A = anadromous sire, P = mature parr sire. At hatching, a total of 524 and 409 individuals were sampled in 2003 and 2004, respectively; whereas 482 and 430 were sampled at emergence. The dates when the crosses were made were 28 October 2003 for F1 and F2; 20 October 2003 for F3 and F4; 11 November 2004 for F5 and F7; 24 November 2004 for F6 and 17 November 2004 for F8.

	Upstream			Downstream		
		Dam			Dam	
2003		F1	F2		F3	F4
Sire	A1	18, 17	15, 18	A4	18, 9	18, 18
	A2	18, 17	15, 18	A5	17, 9	18, 18
	A3	18, 18	18, 18	A6	18, 18	18, 18
	P1	18, 18	18, 18	A7	18, 9	18, 18
	P2	18, 18	17, 18	P5	16, 9	18, 18
	P3	17, 17	17, 18	P6	18, 9	18, 18
	P4	18, 17	18, 18	P7	18, 18	17, 18
				P8	16, 9	17, 18
2004		F5	F6		F7	F8
Sire	A8	20, 20	14, 15	A10	20, 18	14, 14
	A9	20, 20	–	A11	–	14, 14
	P9	20, 20	14, 20	A12	20, 20	14, 14
	P10	19, 20	14, 20	A13	20, 20	14, 14
	P11	–	14, 19	P13	20, 18	14, 14
	P12	20, 20	14, 20	P14	14, 14	14, 14
				P15	20, 20	14, 14
				P16	14, 14	14, 14

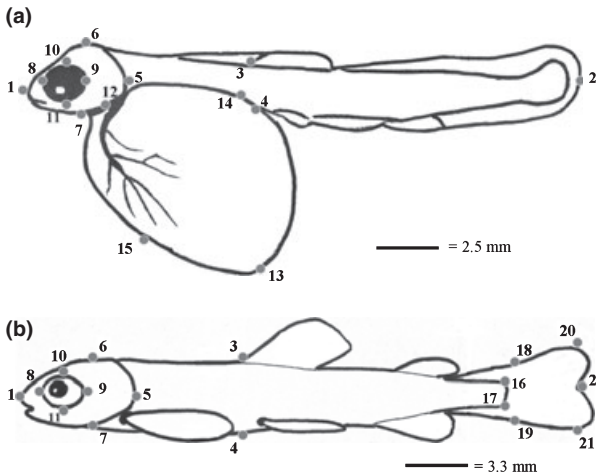

Fig. 2 Morphological traits measured at (a) hatching and (b) emergence. Traits common to both stages (measured as distances between points unless specified): 1–2 = total fork length (BL), 3–4 = body depth (BD), 1–5 = head length (HL), 6–7 = head depth (HD). To calculate the surface area of the eye (EyeA), we used: 8–9 = eye length and 10–11 = eye depth (so that EyeA = eye length × eye depth × $\pi/4$). For hatching only (a) we calculated the volume of the yolk sac (YolkV) using: 12–13, length of the yolk sac and 14–15 = depth of the yolk sac (so that YolkV = length of the yolk sac × (depth of the yolk sac)^2 × $\pi/6$). Traits measured in emergence (b) only: 16–17 = depth of caudal peduncle (Caud), 18–19 = the minimal span of caudal fin (MinCF), and 20–21 = the maximal span of caudal fin (MaxCF).

At emergence (i.e. yolk sac mostly absorbed and at least 50% of individuals in a half-sib family displaying feeding behaviour and active swimming in the water column), an additional 9–20 individuals per family were sampled (totalling 912 individuals) (Table 1). The five traits measured initially at hatching were measured once again at emergence, and an additional three traits of the fish's caudal region (not evident at hatching) were added, for a total of eight traits measured at emergence (Fig. 2b). Sampling individuals at 50% hatching and emergence, rather than on a fixed date, assures that the effect of different fertilization dates is minimized (Table 1).

Only the fish produced in 2004 (i.e. 24 families) were available to monitor patterns of male reproductive development. After the sampling at emergence, these fish were fed daily with commercial pellets dosed at 4% of their body weight. Water temperature and photoperiod regimes were also set to resemble the regimes experienced in nature; however, temperatures could not be lowered below 8 °C. Therefore, this minimum temperature was used during the winter of their first year of life (i.e. November 2005–March 2006). Mortality rates increased considerably after emergence, eliminating one family, but within the ranges commonly reported in other studies for all other families. By

November 2006 (approximately 16 months after emergence), all males within a family could be either classified as a smolt (using the characteristic streamlined body shape and silvery body colouration as indicators) or as a mature parr (using the ripe gonads, hyperextension of the ventral-anterior body and the parr markings as indicators). At this point, all fish produced in the common garden experiment were killed, and the number of males developing into each tactic within their corresponding family recorded.

Statistical analyses

Field data and common garden experiment

Given the interest in comparing the size of recently emerged fish among sites, we fitted a linear mixed model (LMM) to the data, with river site (six levels) as a fixed effect, and the year of sampling (eight levels) as a grouping random effect. Overall significance of the site effect was assessed using *F*-tests. Following this, multiple *t*-tests were used to compare sites. The *P*-values returned in this procedure were corrected using the Benjamini & Hochberg (1995) method implemented in R (R Development Core Team, 2008) for multiple comparisons. In addition, because an appropriate parametric distribution for the null distributions under *F* and *t* tests is not well known in LMMs, *P*-values for these tests were cross-checked with those generated through a 5×10^4 iteration Markov-Chain-Monte-Carlo sampling procedure (Baayen, 2008). However, because both methods returned very similar *P*-values, we only present those associated with the *F* and *t*-tests.

Specific to the data obtained from the common garden experiment, we also used linear mixed modelling to evaluate the effect of the site of origin, the sire's sexual tactic (i.e. anadromous fighter male or mature parr) and their interaction on each morphological trait. Therefore, for each trait, these three parameters were added as fixed effects in the model. The fixed structure of the model was completed by adding the year of sampling, the average number of days up to hatching and to emergence and an index of the average density experienced by individuals within their families. This index ranged from 1 to 7, where a value of 1 was assigned to families which had < 250 individuals, a value of 2 assigned to families between 251 and 500 individuals and so on, to a maximum index of 7 for families numbering between 1501 and 1750 individuals.

The random structure of these models included the rearing tank, and the sire and dam's identity. If a significant interaction between the site and the paternal sexual tactic was detected after correcting for multiple comparisons, *a posteriori* pairwise comparisons (i.e. Upstream – Fighter sire vs. Downstream – Sneaker sire, etc.) were performed. If no significant effects from the interaction were observed, this term was removed from the model to assess individually the main effects.

Quantitative genetic analyses

Sensitivity and power analyses based on the pedigree design. The first step in the quantitative genetic analyses was to determine the power to detect unbiased heritabilities from the pedigree design. As maternal effects are assumed to be very important at these early juvenile stages (as all the nutriments for development are used from the yolk sac), PEDANTICS (Morrissey *et al*., 2007) was used to simulate data for heritabilities ranging from 0 to 0.35 at 0.05 intervals under different combinations of maternal environmental effects, also ranging from 0 to 0.35 at 0.05 intervals. Five hundred data sets were simulated for each of the 64 combinations (e.g. first combination: when $h^2 = 0.0$ and $m^2 = 0.0$; second combination: when $h^2 = 0.0$ and $m^2 = 0.05$, etc.) and then analysed in an animal model with an effect of the maternal environment, i.e.

$$y = \mu + Z_1 a + Z_2 m + e$$

where y is a vector of simulated observations, μ is the sole fixed effect, i.e. the estimated population mean, a is a vector of direct additive effects, m is a vector of maternal effects, and e is a vector of random errors. The incidence matrices, Z_1 and Z_2, relate individual observations to a and m, respectively. These models were fit by restricted maximum likelihood using the software WOMBAT (Meyer, 2007). Following this, the apparent power to detect significant heritabilities was calculated as the number of significant tests divided by the total number of tests, whereas estimation biases were assessed with the level of deviation of simulated values from their true value (Morrissey *et al*., 2007).

Estimation of variance components based on the phenotypic measurements. As described previously, the year of sampling, the index of family density and the average days up to hatching or emergence always had a significant effect on the measured traits. Therefore, these variables were included as fixed effects in the animal models. The rearing tank was also added as an additional random effect (in addition to the animal and maternal identities) to account for other common environmental effects, such that the structure of the animal model for each trait was as follows:

$$y = X\beta + Z_1 a + Z_2 m + Z_3 ec + e$$

where β is the vector of fixed effects, X is the design matrix relating the fixed effects to the observations, a, m and ec are vectors of additive, maternal and common environmental effects, respectively, with the appropriate incidence matrices Z_1, Z_2 and Z_3. Afterwards, narrow-sense heritability and the contribution of maternal effects were calculated as the ratio between their estimated variances (V_A, and V_m, respectively) to total phenotypic variation (V_p). We also used the coefficient of variation (CV), which adjusts variation relative to the mean of the

trait, to assess the relative magnitude of variation across traits and developmental stages (Houle, 1992).

Link between early morphological traits and future sexual tactics

To test the prediction that patterns of male reproductive maturity are influenced by phenotypic characteristics at early ages and/or by the level of maternal investment in young, we fitted a generalized LMM with binomial errors to the data. In this model, we used the proportion of sneaker males per family, as the response variable, and the dam and sire's identity as grouping random effects. Initially, we specified the simplest model solely with the proportion of mature parr as the response variable and the intercept. We then sequentially added, as fixed effects, the family means of phenotypic variables likely to influence the incidence of male sexual maturity, with the objective to retain only those that had a significant effect. The variables used were (1) mean family size at hatching, (2) family variance in size at hatching, (3) mean family yolk volume, (4) family variance in yolk volume, (5) mean family size at emergence, (6) family variance in size at emergence and (7) mortality rate per family. We used Wald *z*-tests and Akaike information criteria (AIC) to assess the significance of these effects (Bolker *et al.*, 2009).

Results

Field survey

Overall, we detected significant size differences among recently emerged alevins specific to their sampling sites (LMM: $F_{5,1194} = 9.76$, $P < 0.001$). We found that fish sampled at XA01 were the biggest (estimated mean = 30.04 mm with a standard error of 0.64), whereas those sampled at PR27 were the smallest (estimated mean = 28.71 mm, standard error = 0.64). Smaller but significant differences in size were found for most other pairwise comparisons (Table 2). However, no differences were observed when comparing the most upstream sites within each river branch (i.e. between XA01 and NE28 and PR58 and PR81) and when comparing the sites NE06 with both PR58 and PR81, and NE28 with PR58. These results reveal an upstream–downstream gradient in alevin size as well as an overall difference between river branches.

Thus, to explicitly test for differences between upstream and downstream sites and between river branches, we repeated our analysis, grouping the data according to river branches and upstream or downstream positions (such that XA01 and NE28 and PR81 and PR58 were pooled together and considered as upstream sites). With this test, we find a statistically significant effect of both the branch and site location, but not for the interaction between these terms (Table 2), demonstrating that upstream fish are bigger (estimated mean size = 29.61 mm, standard error = 0.13) than downstream fish (mean size = 28.96 mm, standard error = 0.63) and fish from the North-Eastern branch are bigger (estimated mean size = 29.66 mm, standard error = 0.63) than individuals from the Principal branch (mean size = 29.1, standard error = 0.12). Finally, variation among years explained 44.3% of the variation in size [Log-likelihood ratio test (LRT) = 537.41, d.f. = 1, $P < 0.001$].

Common garden experiment

Low mortality rates were recorded between hatching and emergence, and no differential mortality in terms of the site of origin or the sire's sexual tactic occurred (mortality rate averaged 1.7% with a median of 1.3%). The means and standard deviations for the traits measured on individuals from the common garden experiment are presented in (Table 3). However, no significant interactions between the site of origin and the sire's sexual tactic

Table 2 Body length (BL) (in mm) comparisons between the sampled sites from the Sainte-Marguerite River. Above: the diagonal represents the estimated BL with standard errors in parentheses. The off-diagonal elements are the *t*-values obtained from the comparisons with corrected *P*-values in parentheses. Below: analysis of variance table showing the upstream vs. downstream site effect, NE vs. PR branch effect and the interaction between branch and site. Significant *P*-values (at $\alpha < 0.05$) are in bold.

Site	NE06	NE28	XA	PR27	PR58	PR81
NE06	29.21 (0.64)	**2.48 (0.025)**	**−4.69 (< 0.001)**	**−2.38 (0.029)**	0.73 (0.54)	0.26 (0.80)
NE28		29.72 (0.64)	−1.61 (0.15)	**−4.85 (< 0.001)**	−1.52 (0.16)	**−2.21 (0.019)**
XA			30.05 (0.64)	**−6.43 (< 0.001)**	**−2.98 (0.009)**	**−3.81 (< 0.001)**
PR27				28.72 (0.64)	**2.88 (0.01)**	**2.63 (0.019)**
PR58					29.37 (0.65)	0.49 (0.67)
PR81						29.26 (0.64)

Analysis of variance table

Effect	$F_{1,1196}$	*P*
Site (upstream vs. downstream)	26.05	**< 0.001**
Branch	19.75	**< 0.001**
Site × branch	0.11	0.74

Table 3 Raw means of the measured morphological traits at hatching and emergence with standard deviations in parentheses.

Trait	Overall mean	U-A	D-A	U-P	D-P
Hatching					
BL	18.99 (1.29)	18.91 (1.25)	18.80 (1.16)	18.88 (1.49)	19.34 (1.15)
BD	1.76 (0.186)	1.73 (0.16)	1.75 (0.17)	1.71 (0.19)	1.84 (0.18)
HL	3.34 (0.25)	3.34 (0.20)	3.26 (0.29)	3.32 (0.24)	3.44 (0.20)
HD	2.55 (0.177)	2.55 (0.13)	2.57 (0.26)	2.53 (0.15)	2.56 (0.10)
EyeA	1.27 (0.182)	1.25 (0.17)	1.26 (0.17)	1.23 (0.20)	1.33 (0.17)
YolkVol	172.62 (38.77)	172.34 (38.99)	169.12 (39.61)	180.39 (35.51)	168.64 (39.92)
Emergence					
BL	28.78 (1.14)	28.8 (1.20)	28.75 (1.06)	28.66 (1.25)	28.92 (0.99)
BD	3.69 (0.51)	3.59 (0.52)	3.68 (0.50)	3.68 (0.51)	3.76 (0.50)
HL	6.59 (0.26)	6.56 (0.26)	6.58 (0.28)	6.56 (0.27)	6.64 (0.24)
HD	4.06 (0.162)	4.02 (0.16)	4.07 (0.17)	4.05 (0.17)	4.09 (0.14)
EyeA	2.90 (0.26)	2.92 (0.25)	2.88 (0.25)	2.88 (0.25)	2.93 (0.26)
Caud	1.80 (0.155)	1.79 (0.17)	1.78 (0.15)	1.79 (0.15)	1.83 (0.16)
MinCF	3.41 (0.177)	3.44 (0.14)	3.38 (0.19)	3.41 (0.17)	3.40 (0.20)
MaxCF	5.02 (0.34)	4.96 (0.26)	5.00 (0.40)	5.07 (0.30)	5.01 (0.36)

All measurements are in mm except EyeA and YolkVol which are in mm^2 and mm^3, respectively U-A, upstream anadromous sire; U-P, upstream mature parr sire; D-A, downstream anadromous sire; D-P, downstream mature parr sire; BL, body length; BD, body depth; HL, head length; HD, head depth; EyeA, area of the eye; YolkVol, volume of the yolk sac; Caud, depth of the caudal peduncle; MinCF, minimal span of the caudal fin and MaxCF, maximal span of the caudal fin.

were found for any trait at either hatching or emergence (Table 3). Furthermore, removing the interactions from the models did not render the main effects statistically significant (results not shown), such that neither the site of origin nor the paternal sexual tactic had an effect on the measured phenotypic traits.

Variance component estimates

Our study design provides substantial power (i.e. $1 - \beta > 0.8$, where β is the probability of failing to reject the null hypothesis when it should be rejected) to detect heritabilities over 0.30, and modest power to detect heritabilities as low as 0.15 (Fig. 3a). Power to detect maternal effects was very high for effects accounting for as little as 10% of the phenotypic variance but was substantially compromised by the segregation of additive effects (Fig. 3c). For practical analytical purposes, animal model-based estimates of genetic and maternal effects are largely unbiased (Fig. 3b,d), although a general trend is apparent for both to be underestimated. Most importantly, our models were effectively able to distinguish between direct genetic and maternal sources of variation, because neither the bias in V_A or V_m changed among the different simulated combinations (Fig. 3c,d). Finally, power and sensitivity analyses conducted on other models (i.e. using a sire model) yielded virtually the same results as the animal model (results not shown), suggesting that the animal model is adequate for the quantitative genetic analyses on the real data.

Table 4 shows the estimated heritabilities and maternal effects for the measured traits. As expected from the preliminary simulations, point estimates lower than 0.2 were usually nonsignificant, probably owing to the low power to detect such values with precision from our pedigree design. Despite this, we found significant maternal and additive genetic effects at both developmental stages. At hatching, strong maternal effects were found for volume of the yolk sac (YolkVol), head depth (HD) and body length (BL), whereas at emergence, these effects were the strongest on caudal structures (Table 4). Both maternal and additive genetic effects were particularly important in explaining phenotypic variation in body size at both developmental stages (as seen for BL) (Table 4). In agreement with previous observations (Kruuk, 2004), excluding either maternal or common environmental effects from the models inflated the heritability estimates considerably. In addition, failing to condition the estimation of variance components on mean family densities and on the family average date of hatching and emergence caused a downward bias in the estimation of heritability by increasing residual and common environmental effects (not shown).

The strongest additive genetic effect on phenotypic variance was observed on area of the eye (EyeA) at hatching and the weakest on both YolkVol and on the HD at both developmental stages. Heritability point estimates of the caudal structures were moderately low and nonsignificant. Finally, the CV suggests that phenotypic variation decreases between hatching and emergence for all traits (Table 4). Overall, this decrease tends to correspond to a decrease in all variance components. HD is the only trait for which CV_m tends to increase from hatching to emergence.

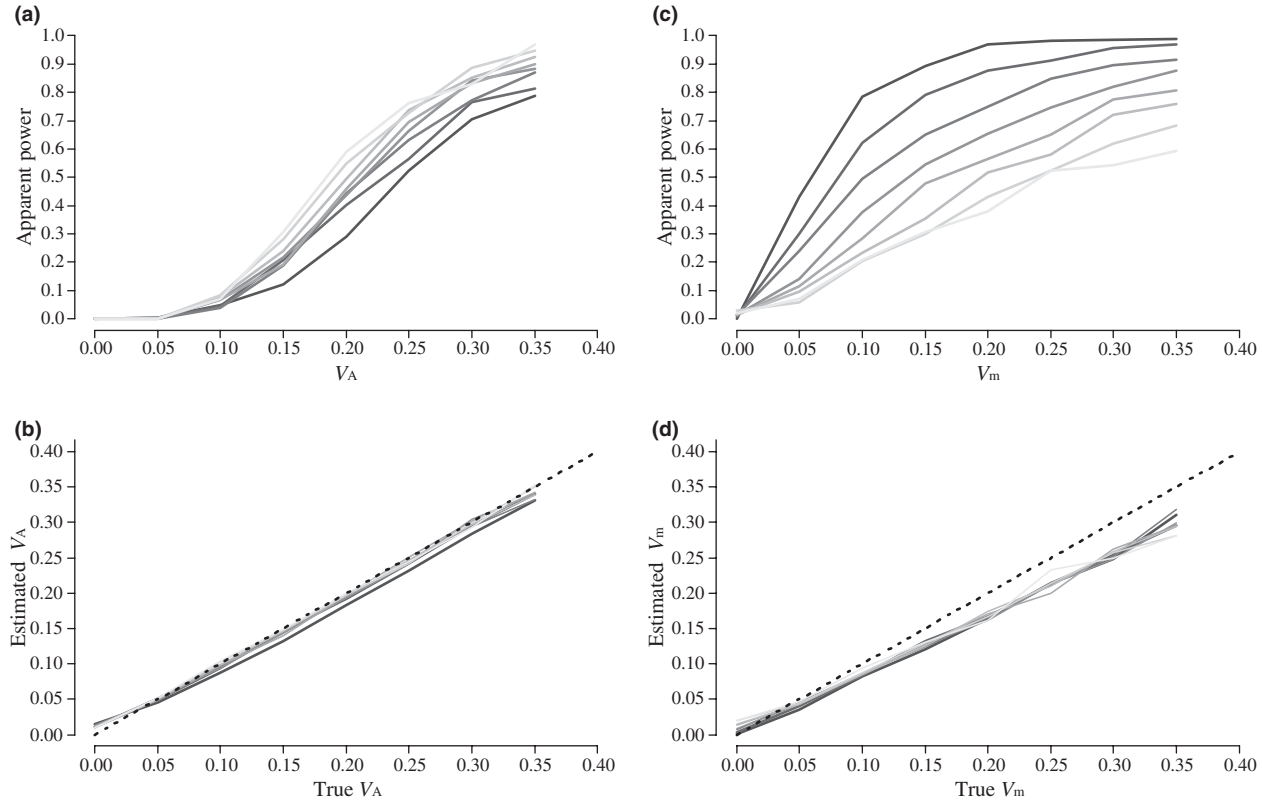

Fig. 3 Power (top panels) and bias (bottom panels) analyses for additive genetic variance and maternal environmental effects using an animal model based on our pedigree design. The left panels are (a) V_A power and (b) V_A bias; whereas the right panels are (c) V_m power and (d) V_m bias. Consider the upper left plot. Each line represents the power to detect V_A under a particular value of V_m. The different grey intensities represent the range of V_m values under which V_A was simulated, with lighter shadings attributed to higher V_m values such that: ● V_m = 0.0; ● V_m = 0.05; ● V_m = 0.10; ● V_m = 0.15; ● V_m = 0.20; ● V_m = 0.25; ○ V_m = 0.30; ○ V_m = 0.35. This same interpretation applies to the other plots except that in panels c and d, the different grey intensities represent the range of V_A values under which V_m was simulated. In the bias plots (bottom panels), the dotted line represents the 1 : 1 expectation of no bias. Deviations from this line thus represent over-estimation (if above) or under-estimation (if below) of the variance components.

Link between early morphological traits and future sexual tactics

Great variation was observed in the proportion of male alternative tactics between families (ranging from 0.08% to 80% of male precocious maturation per family, with a median of 0.49%). However, contrary to the predictions, no association was found between the trait values at early developmental stages and the number of fish in a family developing as mature parr (Table 5). Furthermore, no association between the level of maternal investment, as measured with the YolkVol, and male reproductive tactics was found. In fact, the model that fitted best the data (based on AIC) at both hatching and emergence consisted only of the intercept as the sole fixed effect, and the dam and sire's identity as grouping random effects (Table 5).

Discussion

This study provides some of the first data on sources of among- and within-population variation in early life traits in salmonids. Contrary to the observed levels of phenotypic variation in the wild, we failed to detect any genetically based spatial variation in body size. We did, however, detect significant additive genetic variation within populations, suggesting that future phenotypic change is not constrained, at least for body size. Furthermore, the variation in additive genetic effects among the measured traits is likely to have individual- and population-level evolutionary consequences. In addition, maternal but not paternal effects (related to the sire's sexual tactic) were found to contribute to phenotypic variation. Finally, and contrary to some published reports, we found no evidence for relationships between reproductive tactics and early life traits.

Atlantic salmon living in the Sainte-Marguerite River display significant phenotypic differences at different life-cycle stages which are specific to the site of birth and which affect life-history events (Aubin-Horth *et al.*, 2006; Roberge *et al.*, 2007; see also Baum *et al.*, 2004 for an example in a different river system). We demonstrated,

Table 4 Variance components and corresponding coefficients of variation (CV) estimated for traits measured at hatching and emergence using an animal model. For illustration purposes, all variance estimates, excepting BL (at hatching and emergence) and YolkVol, were multiplied by 100. Values in parentheses are the standard errors of the estimate. Bold values are considered significant m^2 and h^2.

Trait§	V_P	V_R	V_{EC}	V_m	V_A	m^2	h^2	CV_P	CV_R	CV_{EC}	CV_m	CV_A
Hatching												
BL	0.85 (0.24)	0.30 (0.065)	0.038 (0.021)	0.29 (0.25)*	0.22 (0.12)†	**0.34 (0.2)**	**0.26 (0.17)**	4.85	2.88	1.02	2.83	2.49
BD	2.28 (0.4)	1.31 (0.23)	0.25 (0.11)	0.31 (0.42)	0.42 (0.44)	0.14 (0.17)	0.18 (0.2)	8.59	6.51	2.81	3.15	3.67
HL	5.05 (1.34)	1.79 (0.75)	1.13 (0.42)	1.14 (1.4)	0.99 (1.48)	0.23 (0.23)	0.2 (0.3)	6.72	4.01	3.18	3.19	2.98
HD	6.59 (3.19)	0.81 (0.44)	0.64 (0.24)	4.51 (3.21)*	0.63 (0.87)	**0.68 (0.16)**	0.095 (0.14)	10.07	3.53	3.15	8.33	3.11
EyeA	2.35 (0.38)	0.65 (0.33)	0.12 (0.07)	3×10^{-4} (0.41)	0.65 (0.33)*	0.0 (0.18)	**0.67 (0.27)**	12.06	6.36	2.68	0.14	9.89
YolkVol	1624.6 (553.3)	574.5 (126.7)	216.8 (79.8)	833.3 (552.9)*	0.02 (247.5)	**0.513 (0.17)**	0.0 (0.15)	23.35	13.88	8.53	16.72	0.07
Emergence												
BL	1.02 (0.33)	0.31 (0.06)	0.04 (0.02)	0.45 (0.33)*	0.22 (0.12)*	**0.44 (0.18)**	**0.22 (0.13)**	3.51	1.95	0.67	2.33	1.63
BD	4.34 (1.28)	1.59 (0.31)	0.16 (0.1)	1.52 (1.29)*	1.07 (0.58)*	**0.35 (0.2)**	**0.25 (0.15)**	5.65	3.42	1.07	3.35	2.80
HL	5.24 (0.61)	3.41 (0.53)	0.44 (0.24)	0.00 (0.62)	1.39 (0.98)	0.0 (0.12)	0.27 (0.18)	3.47	2.80	1.01	0.015	1.79
HD	2.27 (0.23)	1.68 (0.27)	0.44 (0.17)	0.16 (0.23)	0.0 (0.51)	0.07 (0.1)	0.0 (0.23)	3.71	3.19	1.63	0.98	0.03
EyeA	4.84 (1.00)	2.38 (0.35)	0.15 (0.12)	1.08 (0.99)‡	1.24 (0.65)*	**0.22 (0.16)**	**0.26 (0.14)**	7.59	5.32	1.33	3.58	3.84
Caud	1.84 (0.77)	0.41 (0.11)	0.12 (0.06)	1.1 (0.76)*	0.22 (0.21)	**0.6 (0.17)**	0.12 (0.12)	7.54	3.56	1.90	5.82	2.6
MinCaud	3.39 (1.35)	0.87 (0.17)	0.12 (0.07)	1.92 (1.34)*	0.48 (0.32)	**0.57 (0.17)**	0.14 (0.10)	5.4	2.73	1.02	4.06	2.03
MaxCaud	13.15 (3.22)	6.74 (0.98)	1.03 (0.5)	4.05 (3.27)*	1.33 (1.82)	**0.31 (0.18)**	0.10 (0.14)	7.22	5.17	2.02	4.01	2.30

V_P, phenotypic variance; V_R, residual variance; V_{EC}, variance because of common environmental effects; V_m, variance because of maternal effects; V_A, additive genetic variance; m^2, ratio of V_m over V_P; h^2, narrow sense heritability; BL, body length; BD, body depth; HL, head length; HD, head depth; EyeA, area of the eye; YolkVol, volume of the yolk sac and Caud, depth of the caudal peduncle.
*$P < 0.05$; †$P = 0.0503$; ‡$P = 0.056$.
§See Fig. 2.

Table 5 Relationship between traits measured at hatching and emergence and future reproductive tactics in male Atlantic salmon.

	Estimate	SE	AIC	Wald *Z*	*P*
Fixed effect added*			68.4		
Mean family length at hatching	0.15	0.23	70.0	0.65	0.51
Family variance in length at hatching	−0.66	0.43	68.2	−1.57	0.12
Mean family yolk sac volume	−0.012	0.013	69.5	−0.98	0.33
Family variance in yolk sac volume	-2.34×10^{-5}	7.35×10^{-4}	70.4	−0.03	0.97
Mean family length at emergence	0.096	0.30	70.3	0.32	0.75
Family variance in length at emergence	−0.18	0.53	70.3	−0.34	0.73
Per cent mortality per family	−1.29	1.01	69.0	−1.28	0.20

*Each trait was added sequentially to a model consisting only of the intercept, setting the AIC at 68.4.

using measurements of body size, that recently emerged individuals from upstream sites are bigger than those emerging at downstream sites of this river system.

In addition, important differences were seen between river branches and between the types of habitats sampled (i.e. whether the site was a creek or part of the main river, in agreement with Garant *et al.*, 2003). However, the results of the common environment experiment did not reflect the patterns observed in the field. When reared together, no differences in any morphological trait was observed between individuals originating from the different sites. We interpret these results as indicating that the patterns observed in the wild are mainly driven by differential growth opportunities enhanced by local environmental conditions, such as micro-environmental variations in temperatures across sites or fluctuating patterns of selective mortality. As access to nutrients during these developmental stages depends exclusively on the quantity and quality of yolk reserves, the differences in size between upstream and downstream sites could also be explained if migration to upstream spawning grounds is more likely achieved by larger females (as indirectly suggested by Aubin-Horth *et al.*, 2006).

Furthermore, we found no effect of the paternal sexual tactic on any of the measured traits. Considering that, at least for this species, no additional contributions to offspring development are known to be stored in sperm (that is, other than the breeding value, which is a genetic effect), it is difficult to hypothesize on the nature of any additional nongenetic paternal effects (e.g. Garant *et al.*, 2002). In our sampling design, we have used an adequate number of male progenitors to separate the effects of a sire's sexual tactic and its genotype on offspring

development. Furthermore, using a similar sampling design, Rossignol *et al.* (in press) came to the same conclusions when examining differences in metabolic capacities and other physiological traits between offspring sired by males of both sexual tactics.

However, we detected significant additive genetic effects on phenotypic traits. The heritability of size was significant at both developmental stages, explaining about 20–25% of total phenotypic variation, and suggesting that the future evolution of body size is not constrained by low levels of additive genetic variance. Significant heritabilities were also found for body depth and the EyeA. Moderately, high point estimates, even though nonsignificant, were found for head length. Similarly, lower, nonsignificant point estimates of heritability were found for the caudal fin structures at emergence, and point estimates close to 0 were observed for the YolkVol and the depth of the head. Of all of these traits, the additive CV was higher for the EyeA at emergence, suggesting that this trait is likely to display the strongest response to selection. Although we do not fully understand the biological significance, phenotypic variation in eye dimensions may be correlated with variations in foraging capabilities and predator avoidance behaviours, which contribute to the survival of inexperienced individuals as they emerge from the gravel. If individuals with larger eyes are favoured, we would expect lower levels of additive genetic variance for this trait. The high levels observed, however, may be attributed to negative genetic covariances with other traits or with maternal genotypes. In fact, these pleiotropic effects may be involved in the maintenance of additive genetic variance for all traits (Stearns, 1992).

Even though statistical tests are not designed to demonstrate the absence of variation, low additive genetic (co)variation has been demonstrated in multivariate contexts (Mezey & Houle, 2005; Wilson *et al.*, 2003; Kirkpatrick & Lofsvold, 1992). Therefore, it is possible that low levels of additive genetic variance are characteristic of traits such as the depth of the head and certain caudal structures at these developmental stages. These small values may represent a genetic constraint to future adaptation, thus having important evolutionary and conservation implications (see below).

We also revealed a significant effect of the maternal environment on offspring phenotype at early juvenile stages. As individuals completed nutrient absorption prior to emergence, these effects seemed to increase in their importance, particularly for traits developing in the period between hatching and emergence (such as the caudal structures, which were not evident at hatching, and body depth, which increased four times in magnitude following hatching). Although the change in maternal-based variation between hatching and emergence seems to be trait specific (as it can increase, decrease or remain the same for different traits), the overall significant influence on body size and the caudal structures, which are associated with swimming capacities, indicates that maternal investment in egg quality is likely to influence important aspects determining early life fitness.

Maternal effects are likely to influence the amount of heritable variation in ways that remain unknown in this study because of insufficient data to partition such effects into genetic and permanent environmental variation. Estimates of these genetic effects generally require elaborate pedigree designs (see Roff, 1997; Thompson, 1976), which up to now are rarely attainable in wild animal studies (but see Wilson & Réale, 2006; Wilson *et al.*, 2005; Perry *et al.*, 2004). Therefore, future work should be directed at obtaining multi-generational pedigrees to evaluate the indirect genetic contribution of maternal effects to total heritable variation (e.g. Wilson & Réale, 2006). Nevertheless, as ontogeny progresses and individuals depend more on their own capabilities to obtain food, the maternal sources of variation (both genetic and environmental) are expected to decrease rapidly, as documented for Atlantic salmon (Garant *et al.*, 2003) and for other animal species (e.g. Wilson *et al.*, 2005; Lindholm *et al.*, 2006; Heath *et al.*, 1999).

Similar to other threshold traits, the expression of male alternative reproductive tactics depends on whether or not a cue, such as individual body condition, is sufficient to surpass a genetically determined switch point (that varies among individuals) at an appropriate time (Hazel *et al.*, 1990). In the case of Atlantic salmon, evidence from field studies is interpreted as suggesting that body size at emergence is directly related to attaining the critical size for precocious maturity. However, because of optimal feeding conditions in the laboratory, its role in the present experiment is of little consequence. Under field conditions, larger individuals at emergence might out-compete smaller individuals, gaining access to higher quality resources and therefore augmenting future growth opportunities. These early effects on growth may be amplified by subsequent growth opportunities critical for sexual development. Indeed, the correlation between body size and parr maturity increases with time, so that the size in spring is a stronger predictor of future maturity than the size at emergence (Aubin-Horth & Dodson, 2004).

In conclusion, our results quantify some of the causes and effects of phenotypic variation in early life morphological traits and are a first attempt at a comprehensive understanding of the genetic capacity to respond to selection in juvenile Atlantic salmon. Although point estimates of heritability of body size are significant, they are low for other measured traits and in some cases close to zero. We cannot exclude the possibility that this is an outcome of statistical limitations in our analyses. However, the absence or very low levels of additive genetic variance implies that some aspects of the early-life phenotype are genetically constrained and thus may represent a barrier for the future adaptation of this species (Gomulkiewicz & Houle, 2009; Mezey & Houle,

2005). This has important conservation implications if we consider the world-wide decline of population sizes in salmon and other commercially important fish species (Parrish *et al.*, 1998; Hutchings & Reynolds, 2004; Myers & Worm, 2003), and recent theoretical evidence showing that, for small populations, higher levels of additive genetic variance are needed to respond adaptively to selective pressures and avoid extinction (Gomulkiewicz & Houle, 2009).

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