

Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, *Salmo salar*

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Alternative reproductive tactics may be a product of adaptive phenotypic plasticity, such that discontinuous variation in life history depends on both the genotype and the environment. Phenotypes that fall below a genetically determined threshold adopt one tactic, while those exceeding the threshold adopt the alternative tactic. We report evidence of genetic variability in maturation thresholds for male Atlantic salmon (*Salmo salar*) that mature either as large (more than 1 kg) anadromous males or as small (10–150 g) parr. Using a common-garden experimental protocol, we find that the growth rate at which the sneaker parr phenotype is expressed differs among pure- and mixed-population crosses. Maturation thresholds of hybrids were intermediate to those of pure crosses, consistent with the hypothesis that the life-history switch points are heritable. Our work provides evidence, for a vertebrate, that thresholds for alternative reproductive tactics differ genetically among populations and can be modelled as discontinuous reaction norms for age and size at maturity.

Keywords: phenotypic plasticity; life-history evolution; mating systems; mature male parr; anadromous males; common-garden experiment

1. INTRODUCTION

Adaptive phenotypic plasticity represents a response by individuals to stochastic temporal and spatial environmental changes that have significant effects on fitness. Plasticity can be heuristically and graphically described by a norm of reaction—a linear or nonlinear function that expresses how the phenotypic value of a trait changes with the environment (Schlichting & Pigliucci 1998; Sultan & Stearns 2005). Reaction norms need not, however, vary continuously along an environmental gradient. This may be particularly true of those that underlie discontinuous variation in life history, such as the existence of alternative maturation phenotypes within populations.

Despite its widespread occurrence within many species of vertebrates, a fundamental question is whether alternative life histories reflect genetic variability or if they are primarily determined by environmental variables specific to each population. This dichotomy is also reflected by the two primary models used to explain the mechanism underlying alternative tactics within populations. To account for the influence of both environmental and genetic influences on age at maturity, the incidence of alternative life histories has been modelled as a threshold trait (Myers & Hutchings 1986; Hazel *et al.* 1990; Hutchings & Myers 1994; Moczek *et al.* 2002). In the quantitative genetic sense, threshold traits describe characters determined by alleles at multiple loci that can be assigned to one of two or more distinct classes (Roff 1996). For example, individuals whose growth rate, body size or condition (traits heavily influenced by local environmental conditions) exceeds a genetically determined threshold might adopt one maturation

phenotype, while those whose state falls below the threshold would adopt the alternative phenotype.

In contrast to the *threshold trait model*, the *status-dependent model* rests on the primary assumption that individuals are genetically monomorphic with respect to their ability to express an alternative life history (Shuster & Wade 2003), such that adoption of a specific maturation phenotype depends upon individuals achieving a specific condition or status (Gross 1996; Gross & Repka 1998). It is further assumed that there is additive genetic variation underlying the status of an individual (e.g. its growth rate or body size), but not the ‘decision-making mechanism’, i.e. the threshold or switch point. A corollary to this hypothesis is that the threshold does not differ among populations (Shuster & Wade 2003).

One of the most phenotypically extreme examples of alternative life histories in vertebrates is found in Atlantic salmon, *Salmo salar*. Mature male parr reproduce at sizes two to three orders of magnitude smaller (10–150 g relative to more than 1000 g) and at much less than half the age (typically 1–2 year compared with 4–8 year) of anadromous males that breed following migration to sea (Jones 1959; Hutchings & Myers 1988; Fleming 1996). Prior to spawning, parr compete physically with one another for access to a female, fertilizing eggs in competition with one or more anadromous males. As a group, parr fertilization success per egg nest can vary between 15 and 60% (e.g. Hutchings & Myers 1988; Jordan & Youngson 1992; Thomaz *et al.* 1997); at the individual level, parr fertilization success tends to be low and highly variable (Jones & Hutchings 2001, 2002).

Adoption of one of the maturation phenotypes is associated with significant life-history trade-offs. The fitness benefits accrued by parr of maturing at an earlier age—increased probability of surviving to reproduce,

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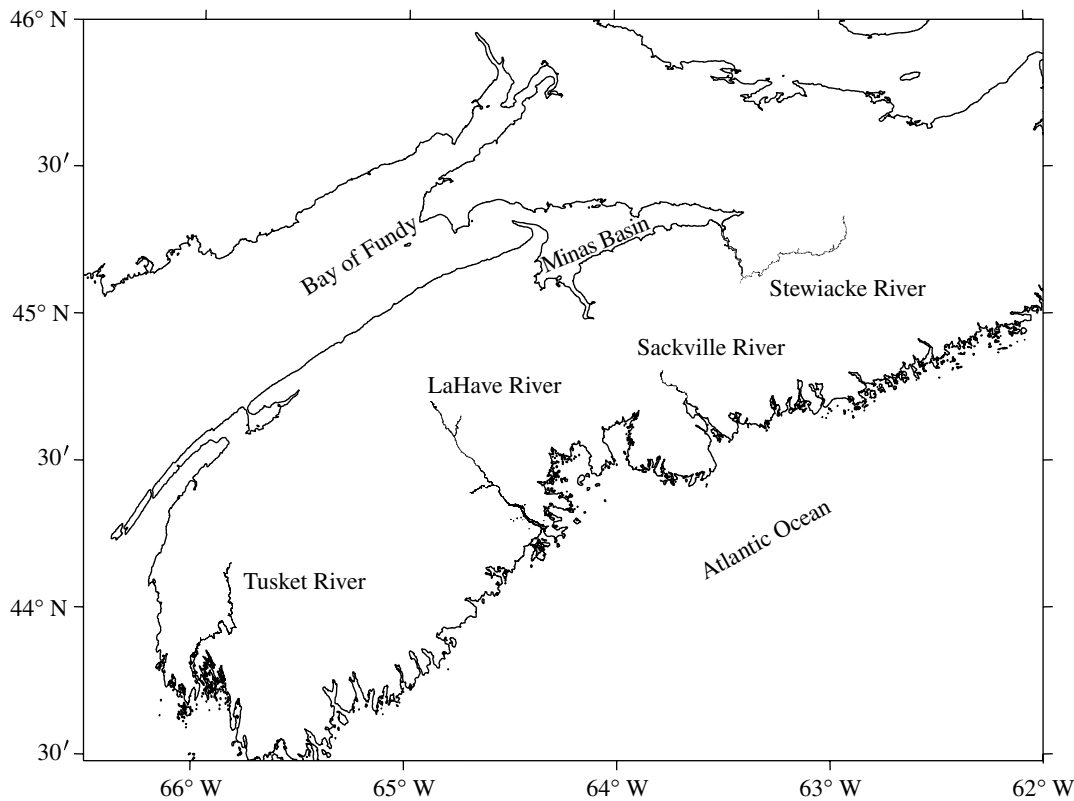


Figure 1. Map of Nova Scotia, Canada, showing the locations of the rivers from which the Atlantic salmon used in pure- and mixed-population crosses were obtained.

increased rate of gene input into the population—are offset by reduced post-reproductive survival (Myers 1984; Hutchings & Jones 1998) and reduced fertilization success (Jones & Hutchings 2001, 2002). By contrast, the higher fertilization success among anadromous males is offset by the low probability of surviving the migration to and from the ocean (Hutchings & Myers 1994). The persistence of alternative reproductive tactics in general has been explained as a product of negative frequency-dependent selection (Partridge 1988), a hypothesis for which there is support in Atlantic salmon (Hutchings & Myers 1994).

The threshold trait and status-dependent models for alternative tactics share the assumptions that adoption of a given maturation phenotype is triggered by the attainment of a threshold and that the liability trait that triggers the threshold is heritable. The primary difference between the models pertains to the threshold itself. In contrast to the status-dependent model, the threshold trait model incorporates the assumptions that the threshold differs genetically among individuals within a population, that it is heritable, and that it differs genetically among populations (Hazel *et al.* 1990; Hutchings & Myers 1994; Shuster & Wade 2003; Tompkins & Hazel 2007).

To compare the predictions of the threshold trait and status-dependent models, we reared pure- and mixed-population crosses of Atlantic salmon in a common environment. Our objectives were twofold. The first was to determine whether there are genetic differences among populations in the incidence of male parr maturity. Our second objective was to examine whether there was evidence for thresholds (reflected by size at age and a metric of growth rate) for parr maturity and, if so, whether the thresholds differ genetically among populations.

2. MATERIAL AND METHODS

Wild anadromous Atlantic salmon were obtained from four rivers in Nova Scotia (NS), Canada, and transported to a federal government hatchery at Coldbrook, NS, where gametes were obtained from anaesthetized individuals. The populations included in the breeding crosses were from Tuskent River, LaHave River, Sackville River and Stewiacke River (figure 1). The gametes were transported, on ice, to the Aquatron facility at Dalhousie University, where the pure- and mixed-population crosses were made (table 1). We had a sufficiently high number of adults to produce three pure-population crosses (7–10 full-sib families per cross) and four mixed-population crosses (5–10 full-sib families per cross) in late November and early December. Beginning with an initial sample of 250 eggs per family, individuals were reared separately (one family per tank) in 1 of 60, 45 l tanks, each of which received 2 l min⁻¹ of filtered fresh water. The eggs were incubated at 4–6°C in darkness and examined daily to record and remove embryonic mortalities. Upon hatching, the developing young were exposed to ambient photoperiod until the end of the experiment. At the beginning of exogenous feeding in May, individuals were fed dry pellets (Corey Aquafeeds High-Pro Starter and Fry feed) three to four times daily. In July, individuals were randomly removed from each tank until the number of fish per tank equalled 150.

In November, 20 individuals from each family were sampled at random to determine their sex and state of maturity. Male parr were recorded as being mature if their gonads were large (exceeding the size of the intestine), opaque and white (thus containing milt). Immature males were distinguished by clear thin gonads that were neither white nor opaque. None of the female parr was mature.

Table 1. Summary information on the population crosses of Atlantic salmon. (The number of males examined is different from the number of males measured; weight and length measurements were recorded for the first 15 out of 20 randomly sampled individuals in each family.)

population cross	no. of families	no. of males examined	incidence of male parr maturity ^a (%)	no. of males	mean weight \pm s.d.	mean length \pm s.d.
Stewiacke \times Stewiacke	10	105	21.0	79	4.1 \pm 2.0	7.0 \pm 0.9
Stewiacke \times LaHave	10	107	20.6	80	4.6 \pm 2.5	7.2 \pm 1.1
LaHave \times LaHave	7	80	10.0	57	5.6 \pm 3.2	7.7 \pm 1.1
Sackville \times LaHave	9	94	12.8	73	4.6 \pm 1.5	7.2 \pm 0.7
Sackville \times Sackville	7	75	29.3	51	5.5 \pm 2.2	7.6 \pm 0.9
Tusket \times Stewiacke	5	53	39.6	40	4.3 \pm 1.3	7.1 \pm 0.6
Tusket \times LaHave	5	68	10.3	54	4.5 \pm 1.2	7.2 \pm 0.6

^a Based on the number of males examined.

Given that the incidence of maturity is a binary variable, a generalized linear mixed model was performed to assess the effect of body size (length and weight) and population cross on male parr maturity while accounting for family origin. A generalized linear mixed model (binomial regression) was fit using the lmer function obtained from the R package lme4 that uses maximum likelihood to estimate model parameters. Given the difficulty in calculating likelihoods directly for non-Gaussian mixed models, the procedure uses a Laplace approximation (Diggle *et al.* 2002). The Akaike's information criterion (AIC) was used to assess model performance. Fisher's least significant difference method was applied to test whether the growth-rate thresholds for male parr maturity, defined as the size at age at which the probability of parr maturity was 50%, differed among crosses.

3. RESULTS

The dates of hatching and the initiation of exogenous feeding overlapped considerably among families (both encompassing a 2.5-week period; $p > 0.05$), indicating that individuals did not differ in age. The incidence of male parr maturity differed significantly among crosses ($\chi^2_6 = 18.06$, $p = 0.006$), ranging from a high of 40% among parr from the Tusket \times Stewiacke cross to a low of 10% for parr from the LaHave \times LaHave and Tusket \times LaHave crosses (table 1). Comparing the pure crosses, maturity differed almost threefold among parr from LaHave River (10%) and Sackville River (29%; $\chi^2_1 = 7.72$, $p = 0.005$). Comparing mixed with pure crosses, incidence of maturity among LaHave \times Sackville parr (13%) was intermediate to those of the pure Sackville (29%) and LaHave (10%) crosses, being significantly less than the former ($\chi^2_1 = 3.90$, $p = 0.048$). Maturity among Stewiacke \times LaHave parr (21%) was greater than that of LaHave parr (10%; $\chi^2_1 = 3.28$, $p = 0.070$), albeit not significantly so, and equal to that of Stewiacke parr.

The AIC yielded two candidate models: the model including the effect of population cross and weight (model 5) and population cross and length (model 6; table 2). This is not surprising given that body weight and (fork) length are highly linearly related (Pearson's, $r = 0.96$). Given that length and weight are qualitatively the same, and that weight is more frequently used as a metric for physiological processes (Wootton 1998), model 5 (Cross + WT) was selected to be the best model. Therefore, only weight-related results will be reported and discussed further.

Table 2. Generalized linear mixed model using family as the random effect (i.e. family nested in cross). (WT, weight; FL, fork length; AIC, Akaike's information criterion; models with the lowest AIC are in italics.)

models	AIC	<i>pseudo R</i> ^{2a}
1. Intercept	471.7	—
2. Intercept + Cross	470.2	0.223
3. Intercept + WT	459.2	0.238
4. Intercept + FL	459.9	0.229
5. <i>Intercept + Cross + WT</i>	454.8	0.441
6. <i>Intercept + Cross + FL</i>	454.8	0.441
7. Intercept + FL + WT	461.2	0.238
8. Intercept + Cross + WT + FL	456.5	0.445
9. Intercept + Cross + WT + Cross : WT	461.1	0.497
10. Intercept + Cross + FL + Cross : FL	462.8	0.481
11. Intercept + Cross + WT + FL + Cross : WT	463.0	0.499
12. Intercept + Cross + WT + FL + Cross : FL	464.4	0.485
13. Intercept + Cross + WT + FL + Cross : WT + Cross : FL	470.5	0.539

^a *Pseudo R*² (Cox & Snell 1989).

Growth rate, reflected by the weights of individuals at the same age, had a significantly positive influence on the incidence of male parr maturity ($\chi^2_1 = 17.44$, $p < 0.0001$; Cohen $f^2 = 0.389$). There was also a significant effect of population cross on the threshold for parr maturity ($\chi^2_6 = 16.41$, $p = 0.0117$, Cohen $f^2 = 0.363$). Predicted weight at 50% maturity was greater among LaHave parr (14 g) than it was among either Tusket \times Stewiacke parr (6 g) or Sackville parr (8 g); predicted weight at 50% maturity was also significantly higher among Sackville \times LaHave (12 g) parr than that of Tusket \times Stewiacke parr (table 3). Fitted relationships between growth rate and incidence of parr maturity for the mixed crosses were intermediate to those of the pure crosses from the LaHave River, Sackville River and Stewiacke River, although these differences in maturity thresholds were not significant (figure 2).

4. DISCUSSION

Maturity in male Atlantic salmon can be modelled as a threshold trait, such that maturation is dependent upon the attainment of a critical growth rate, body size or some combination thereof (Leonardsson & Lundberg 1986;

Table 3. Differences in size thresholds for male parr maturity among population crosses of Atlantic salmon. (Thresholds are defined as the estimated body size (g), six months after the initiation of exogenous feeding, corresponding to a 50% incidence of maturity (95% CIs are in parentheses).)

population cross	estimated weight (g) at 50% maturity
Stewiacke × Stewiacke	9.4 (6.0,12.8)
Stewiacke × LaHave	9.7 (6.4,13.1)
LaHave × LaHave	14.4 (9.2,19.6)
Sackville × LaHave	12.1 (7.6,16.5)
Sackville × Sackville	7.9 (5.1,10.7)
Tusket × Stewiacke	6.1 (3.1,9.1)
Tusket × LaHave	12.4 (7.3,17.4)

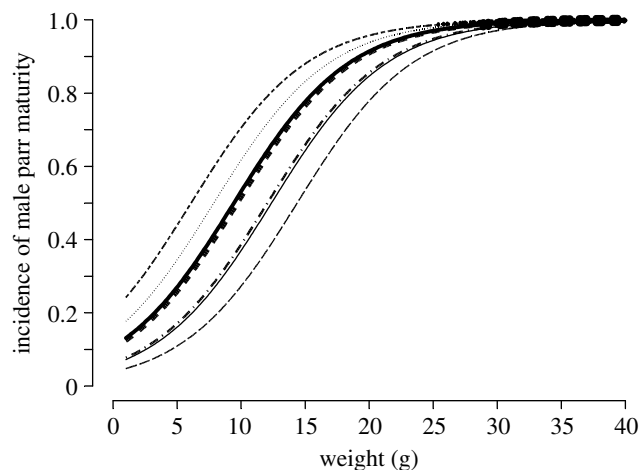


Figure 2. Threshold norms of reaction between incidence of parr maturity and individual growth rate (body weight at seven months) in male Atlantic salmon. Left to right, the reaction norms are for the following population crosses: Tusket × Stewiacke; Sackville × Sackville; Stewiacke × Stewiacke; Stewiacke × LaHave; Sackville × LaHave; Tusket × LaHave; LaHave × LaHave.

Thorpe 1986; Hutchings & Myers 1994; Aubin-Horth & Dodson 2004). Our work contributes empirical data that may inform a fundamental question concerning the evolution of alternative mating phenotypes. Namely, are thresholds for alternative reproductive tactics heritable (Hazel *et al.* 1990; Hutchings & Myers 1994), or is the probability of attaining the threshold, or switch-point, purely a function of an individual's status (Gross 1996)?

Our results do not appear to support the status-dependent selection model for alternative maturation phenotypes. Firstly, the incidence of male parr maturity differed among pure- and mixed-population crosses in a common environment, indicating that there is a genetic basis to the probability with which a male adopts the mature parr phenotype. This finding is consistent with previous reports of a genetic basis for alternative reproductive tactics in salmonid fish (Glebe & Saunders 1986; Heath *et al.* 1994; Garant *et al.* 2003). Secondly, among-cross differences in growth-rate switch points indicate the presence of among-population genetic variability in threshold reaction norms for alternative male phenotypes, suggesting that thresholds may vary among genotypes within populations (Hazel *et al.* 1990) and respond to natural and anthropogenic selection.

The considerable differences in male parr maturity reported in our common-garden experiments are consistent

with the observations from natural populations for which the incidence of maturity has been reported to range from less than 10% to more than 90% (Hutchings & Jones 1998). Thresholds for parr maturity are predicted to vary considerably among populations owing to the substantive demographic consequences of population differences in density, individual growth and stage-specific survival probabilities (Hutchings & Myers 1994). Indeed, Aubin-Horth *et al.* (2006) provided evidence that thresholds differ among sub-populations of Atlantic salmon within a single river. Additional work has explored how factors such as density, altitude and freshwater migration distance can affect parr maturity thresholds within and among populations (Aubin-Horth & Dodson 2004; Baum *et al.* 2004).

The existence of genetic variability for growth-rate thresholds suggests that switch points for alternative tactics need not be constant within populations and that they can evolve. The proportional representation of mature male parr and anadromous males within a population of Atlantic salmon will depend, in part, on the distribution of individual growth rates. Factors that may change individual growth, such as density or food supply, can be expected to generate a selection response in the position of the parr maturity threshold. Similarly, changes in the survival probabilities of salmon either at sea or in fresh water can also be expected to effect a genetic response in the parr maturity switch point. For example, increased mortality among anadromous males at sea would be expected to increase the fitness associated with the parr tactic, leading to a shift in the inflection points of the reaction norms to lower growth-rate thresholds. Such a shift could represent an evolutionary response to increased commercial or recreational fishing mortality (Myers *et al.* 1986; Hutchings & Fraser 2008; Thériault *et al.* 2008) or to increased predator-induced mortality resulting from ecosystem-based shifts in community structure.

The present study suggests that among-population differences in the incidence of alternative reproductive tactics can reflect heritable genetic variability in an environmentally influenced threshold trait. To our knowledge, this work is the first to document such genetic variation in a vertebrate. The only other vertebrate for which genetic variability in a threshold trait has been documented appears to be the salamander *Ambystoma talpoideum*, for which Semlitsch & Wilbur (1989) reported variation in the phenotypic switch between metamorphosis and paedomorphosis in two populations. Among invertebrates, there is evidence that polyphenisms can be genetically variable in several species of insects (Moczek *et al.* 2002 and references therein; Unrug *et al.* 2004), suggesting that heritable differences in threshold norms of reaction may not be uncommon. Our work underscores the assertion that the theoretical and empirical constructs encompassed by threshold norms of reaction provide an appropriate framework in which to address questions pertaining to the evolutionary stability of alternative reproductive tactics (Hazel *et al.* 1990; Hutchings & Myers 1994; Tompkins & Hazel 2007).

The research protocol was approved by the Dalhousie University's Committee on Laboratory Animals, in accordance with the guidelines provided by the Canadian Council on Animal Care.

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