Alternative developmental pathways and the propensity to migrate: a case study in the Atlantic salmon

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Abstract

Migratory behaviour with its associated phenotypic changes is generally viewed as an adaptive strategy because it incurs survival or reproductive advantages to migrants. The development of a migrant phenotype is believed to be controlled by threshold mechanisms, where individuals emigrate only after surpassing a particular body size but delay migration if below. For such a strategy to respond to natural selection, part of the phenotypic variance in the propensity to migrate must be explained by variation in additive genetic effects. Here, we use data gathered in the field and from a common rearing experiment to test for a genetic basis associated with seaward migration in Atlantic salmon (*Salmo salar* L.). We document a high heritability of the liability trait underlying the propensity to emigrate in juvenile salmon, and significant differences between offspring grouped according to their sires in body-size threshold values above which emigration takes place. The presence of additive genetic variance in both the liability and thresholds makes the onset of migration a process sensitive to selection and may therefore constitute an important explanatory mechanism for the interpopulation differences in the size at seaward migration observed in this species.

Introduction

Migration refers to the movement of individuals between widely separated and well-defined areas, including those where reproduction may occur (Landsborough Thompson, 1942; Harden Jones, 1968; Dingle & Drake, 2007). Across the many migrant animal taxa, many benefits associated with this strategy have been described, including improved feeding opportunities, avoidance of adverse environmental conditions and improved reproductive success (Northcote, 1978). Thus, migratory behaviour and the physiological and morphological changes to the phenotype that generally accompany it may be favoured

as an adaptive strategy when particular aspects of the receiving habitat enhance the survival and/or reproductive output of migrants (Salomonsen, 1955; Hutchings & Morris, 1985; Rankin, 1985; Gross, 1987; Dodson, 1997; Hendry & Stearns, 2004; Dodson *et al.*, 2009).

However, migration may also incur costs. One of these is the high energetic demands necessary to carry it out (Bernatchez & Dodson, 1987; Rankin & Burchsted, 1992; Dingle, 1996). Accordingly, measurements of energetic reserves or condition (such as body size, fat reserves or other compound traits; depending on the species) at particular ontogenetic stages have been found to be crucial physiological signals used to delay (if in depletion) or promote migration by triggering the necessary phenotypic changes to emigrate (Dingle, 1996; Ims & Hjermann, 2001; Hedenström, 2008). Within populations, a characteristic of such alternative phenotypes (i.e. migrants vs. residents) is their association with distinct

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modes in the distribution of body size, likely reflecting the internal physiological and energetic state in which migratory and resident individuals are found.

The implied prediction that emigration is controlled by threshold mechanisms, where individuals emigrate only after surpassing a particular body size but delay migration if below, has been demonstrated in several animal species (Nunes & Holekamp, 1996; Roff, 1996; Yamamoto & Nakano, 1996; Hedenström, 2008; Oliveira *et al.*, 2008). Furthermore, growth rates and body sizes at emigration have been found to be age dependent (Thériault & Dodson, 2003) and to show considerable geographic variation (Jensen & Johnsen, 1986; L'Abee-Lund *et al.*, 1989; Nicieza *et al.*, 1994). This variation can be explained by (i) different opportunities to achieve the necessary growth (because of changes in photoperiod, temperature or food availability) within periods of sensitivity and (ii) differences in the migration trade-off, so that various optimal growth rates and body sizes at emigration may be favoured by selection along particular ecological gradients (Nicieza *et al.*, 1994).

These explanations are not mutually exclusive; however, for selection to be an explanatory mechanism, part of the observed phenotypic variance in growth and/or thresholds must be explained by variation in additive genetic effects, as this is the part of the phenotypic variance that can evolve under selection (Falconer & Mackay, 1996). Additive genetic variance and the related heritability of traits associated with the propensity to migrate have been estimated for several species of insects, birds and fishes (Refstie *et al.*, 1977; Palmer, 1985; Zera, 1985; Berthold & Pulido, 1994; Roff & Fairbairn, 2001; Thériault *et al.*, 2007). However, we currently lack this knowledge for many other animal groups, as well as details on the genetic basis of the thresholds associated with these alternative developmental pathways.

In this study, we use data gathered from a natural system and from a common garden experiment to document threshold body sizes for emigration, characterize the genetic variation of migration vs. residency in the Atlantic salmon (*Salmo salar* L.) and provide evidence of genetic variation in the threshold values associated with these life-history decisions. The onset of migratory behaviour in this species involves striking physiological and morphological changes through a metamorphic process known as smoltification (after which individuals are called smolts). Readily noticeable phenotypic changes include the production of silver scales, the development of a more streamlined morphology and an increase in growth hormone concentration and $Na^+K^+ATPase$ activity, associated with osmoregulation and seawater tolerance (Tanguy *et al.*, 1994; Stefansson *et al.*, 2003).

The hypothesis that juvenile Atlantic salmon (called parr) must attain a critical threshold body size to emigrate from freshwater systems during spring can be traced back to Elson (1957). Many subsequent studies have supported this hypothesis (Fahy, 1985; Skilbrei,

1991; Yamamoto & Nakano, 1996), suggesting that body size forms part of the physiological cue activating the thresholds involved in migratory/resident developmental pathways. The effect of a threshold body size is most evident in cases where the length–frequency distribution of juveniles becomes bimodal during autumn; fish in the upper modal group (UMG) migrate the following spring, whereas those in the lower modal group (LMG) stay as resident fish for one or several more years (Thorpe, 1977; Hirata *et al.*, 1988; Metcalfe *et al.*, 1989; Heggenes & Metcalfe, 1991; Yamamoto & Nakano, 1996; Utrilla & Lobon-Cervia, 1999). In addition, other studies have shown that the fastest growing individuals migrate at younger ages than juveniles with lower growth rates (Metcalfe & Thorpe, 1990; Jonsson & Jonsson, 1993; Økland *et al.*, 1993; Forseth *et al.*, 1999; Morita, 2001; Yamamoto & Morita, 2002), probably because they attain this threshold size faster. This is also supported by studies showing that poor growth conditions at higher latitudes result in older ages and bigger sizes at migration (Symons, 1979; Power, 1981; L'Abee-Lund *et al.*, 1989; Metcalfe & Thorpe, 1990). Note, however, that size differences between future and delayed migrants are seldom documented under natural conditions, mainly because of the logistical difficulty to monitor fish size throughout winter and early spring (but see Bohlin *et al.*, 1993 and Letcher & Gries, 2003).

Some authors argue against the existence of a threshold size at migration. Økland *et al.* (1993) rejected this hypothesis because they observed, in four populations of brown trout and in one population of Atlantic salmon, that juveniles do not migrate at their first available opportunity (i.e. the first spring following the attainment of the threshold size, estimated as the mean size of the youngest smolts). Bohlin *et al.* (1996) also rejected this hypothesis because they observed that younger smolts with faster growth rates did not migrate necessarily earlier in spring than older smolts with lower growth rates. However, mean body size at migration is strongly influenced by interannual differences in growth rate, and its variance does not reflect either the presence or the absence of a critical threshold size. Furthermore, these arguments assume that the threshold length is fixed across ages and that growth has the same developmental effect at different ages. Such assumptions are unrealistic in other species of salmonids (e.g. brook charr, Thériault & Dodson, 2003) and may not apply for the migratory/resident tactics in Atlantic salmon as evidence of threshold variation has been documented in developmental processes associated with precocial vs. delayed maturity (Aubin-Horth *et al.*, 2006; Piché *et al.*, 2008).

We use data obtained over a period of 7 years in a natural system, and a subsample of this data, where the body sizes of wild Atlantic salmon of known migratory phenotype are back-calculated to a common age to show that the onset of emigration is a size-dependant event. We then provide an estimate of the threshold body size

at which migration occurs in a main branch of the Saint Marguerite River (Québec, Canada).

Using related individuals produced from a planned mating design, we then show that the size difference observed in the field (i.e. distinguishing migrants from resident juvenile parr) also occurs under common laboratory conditions and leads to similar estimates of body-size thresholds. We then quantify the additive genetic basis explaining this propensity to migrate (Myers & Hutchings, 1986) using the threshold model of quantitative traits (Falconer & Mackay, 1996). This model assumes that the phenotypic discontinuity is caused by a polygenic liability trait (such as condition or other compound traits) that may or may not surpass a fixed threshold value of sensitivity triggering smoltification. Thus, when using this model, the additive genetic variance that is estimated is that of the liability trait associated with migration. Finally, evidence for genetic variation in threshold body sizes for migration is presented for this species by documenting how they vary across the offspring produced by the different sires used in the common rearing experiment (Falconer & Mackay, 1996).

Materials and methods

Field sampling protocol

The Sainte-Marguerite River (48°20′N, 70°00′W), Québec, Canada, is divided into two distinct branches of similar size and slope; the Principal Branch (PR, 92 km, slope: 710 m) and the North-East Branch (NE, 91 km, slope: 700 m). In this river, smolt migration occurs from mid-May until the end of June. Smolt age varies between 2 and 4, but most migrants are 3 years old (these ages are labelled as 2+, 4+ and 3+, respectively throughout the text). For 7 years (1998–2000, 2002–2005), smolts were captured during their downstream migration from the NE branch with a rotary trap, installed approximately 6 km upstream from the mouth of the river. In each year, we killed between 98 and 216 randomly selected smolts.

For all these years, resident, immature juvenile salmon (called 'parr' throughout the text) aged 2+ were also sampled by electrofishing sections of about 200 m on three sites along the NE branch in late June (as described in Aubin-Hart *et al.*, 2006). We stopped electrofishing when approximately 20, 2+ individuals had been captured at each site. Subsequently, in the laboratory, body length was measured for all fish to the nearest 0.01 mm from the most anterior region of the head to the fork of the caudal fin. Sex was determined by dissection, and individual age was established based on the formation of annual rings on scales during alternate periods of fast and slow growth (Francis, 1990).

For all analyses, body size, expressed as length between the snout and the fork of the caudal fin, was considered a surrogate measure of an individual's overall condition.

From the captures in 2002 and 2003, scales were prepared, read and validated according to standard protocols (Bagenal & Tesch, 1978; Francis, 1990) to back-calculate the body sizes of smolts aged 3+ in 2003 and both smolts and parr aged 2+ in 2002, to the start of the growing season of their second year of life (that is, to a common time when all fish were 2-year-old parr). Back-calculating individual size to this time allowed us to remove the effect of differential growth because of the different dates of capture. All back-calculations were based on the body proportional scale hypothesis method (Francis, 1990). This approach resulted in fifty-four 3+ smolts (of 143 captures), thirty-seven 2+ smolts (of 74 captures) and twenty-three 2+ resident parr (of 60 captures) with suitable scales for the back-calculation procedure. These fish were also verified to be immature by dissection. None of the smolts had evidence of spent gonads that would be expected if sexual maturity had occurred before migration to sea.

Field data statistical analyses

We used linear mixed modelling (LMM) to compare the size at capture between (i) 3+ smolts and 2+ smolts and (ii) 2+ smolts and 2+ parr. For the latter, a difference in body size would indicate that migration and/or residency are size-dependant events. Furthermore, a large difference in body size between 3+ and 2+ smolts at capture would strongly suggest different size thresholds at which migration occurs. Although resident fish were sampled at a later date than smolts (1–3 weeks), larger body sizes in the smolts would be consistent with the hypothesis that by the end of the preceding autumn (i.e. while still parr), they were the largest fish, as very little opportunity to grow occurs during winter at these latitudes (Metcalfe & Thorpe, 1990).

Thus, specific to (i), body length was fitted as a function of smolt age and sex that were added as fixed effects in the LMM. In a similar fashion, in (ii), the fixed effects were life-history state (i.e. smolt or resident) and sex. In both (i) and (ii), we tested for a significant interaction between the fixed effects to determine whether the life-history state or age structure had different effects on the body length of the two sexes. The random structure of both models consisted of the date of sampling nested within year, such that the variation in body length explained by the year term would reflect temporal variation in size, independent from the date when fish were captured. In all cases, the significance of the fixed effects was assessed using F-tests (Baayen, 2008), whereas that of the random effects was assessed using log-likelihood ratio tests (LRT) (Pinheiro & Bates, 2000).

The back-calculated body lengths of individuals that were subsampled for scale analysis were not different from the remaining captured individuals of the same age and life-history state (3+ sampled vs. the remaining captured 3+ smolts: $t\text{-}test_{114.01} = -1.16$, $P = 0.25$;

2+ sampled vs. the remaining captured 2+ smolts: t-test$_{560.7}$ = 0.28, P = 0.78; 2+ sampled vs. the remaining captured 2+ resident parr: t-test$_{31.4}$ = 1.25, P = 0.22). This indicates that individuals sampled for scale analysis are an unbiased sample of their corresponding data sets. Therefore, we compared the lengths of smolts aged 3+ and 2+ and resident parr aged 2+, all back-calculated to the start of the growing season of the second year of life, when all were parr. In this case, we used an ANOVA and a Tukey test to correct for multiple comparisons to test our prediction that 2+ resident fish and future 3+ smolts (i.e. parr that migrated a year later) are significantly smaller than 2+ fish that became smolts and migrated in that year (we also performed nonparametric Welch and Kruskal–Wallis tests, which are not presented as the results obtained were identical to the ANOVA).

We also used these data to estimate the minimal threshold body size at which migration occurs. This threshold size is presumably surpassed by the third year of life because the great majority of smolts in this river are 3+, and 3+ parr (both mature and immature) are rare (Centre interuniversitaire de recherche sur le saumon atlantique, *unpublished* results). However, many smolts are 2+ (see results), suggesting that between the first and second year of life, many fish grow sufficiently to surpass this threshold. Based on this logic, we estimated the minimal threshold size for migration using body lengths, calculated at the formation of the second annulus, of 2+ smolts and 2+ resident parr. To these data, we fitted a logistic regression model using general linear modelling (GLM), where the binary response variable was smoltification and residency (coded as 1 and 0, respectively), and the body length was the sole continuous explanatory variable. Rather than assuming that the size threshold occurs at the 50% incidence point, we used a receiver operating characteristic (ROC) procedure to calculate the incidence cut-off point at which the error of misclassifying an individual as a smolt or a resident parr is minimized (Hosmer & Lemeshow, 2000). The body length corresponding to the cut-off point was then interpreted as the threshold size above which migration occurs (Aubin-Horth *et al.*, 2006).

Common rearing experiment

A detailed account of the materials and methods used in the pedigree design, rearing conditions and on the power and sensitivity to estimate quantitative genetic parameters is described in Páez *et al.* (2010, focusing on early life stages) and can be obtained upon request from the authors (for later life stages). Briefly, 24 maternal and paternal half-sib families were produced from the crosses between 14 sires (eight mature parr and six anadromous males) and four anadromous dams. The fish thus produced were surgically Passive Integrated Transponder–tagged approximately 8 months after hatching (January 2006), allowing to monitor individual growth

thereafter. The fork length and body mass of all individuals were measured on four occasions (January 2006, April 2006, July 2006 and November 2006). The linear regression of log body length on log body mass was very similar across developmental stages (smolts: intercept = 3.954 ± 0.014, slope = 0.299 ± 0.005; parr: intercept = 3.824 ± 0.009, slope = 0.321 ± 0.005), indicating that using either variable for our analyses would lead to the same conclusions. By November 2006, 1147 fish were killed, sexed and classed as either a male mature parr (N = 281), or male (N = 290) and female smolt (N = 576). All mature parr were excluded from these analyses. No difference in the body length between males and females within the LMG and UMG was observed at any date (linear mixed model with repeated measures (LMM): UMG females vs. males, $F_{1,2040}$ = 0.70, P = 0.39; LMM: LMG females vs. males, $F_{1,1132}$ = 0.30, P = 0.59). Thus, sexes were pooled together to examine how body length changes through time in the LMG and UMGs.

Statistical analyses for the common rearing experiment

Bimodality in the body length frequency distribution of juveniles was apparent as early as July 2006. By the end of the experiment, however, the same silvery phenotype had also developed in the LMG fish, showing that the extended period of high growth in the laboratory leads to the eventual smoltification of all immature individuals. A *k*-means cluster analysis, specifying two groups (Crawley, 2007), was used to determine the maximal body size at which individuals could be clustered unambiguously into the LMG in November 2006 (when the strongest bimodality was observed). Because we had individual records for all fish, we could then trace back the corresponding LMG and UMG size distributions to January 2006, when fish were first marked individually and life-history states were much more difficult to determine. We used a dip-test that measures multimodality in a sample (Hartigan & Hartigan, 1985) to determine when, across the sampling dates, the hypothesis of a unimodal size distribution could be rejected.

To estimate the heritability of the LMG and UMG life-histories, we first determined the fixed effects structure of the animal model by assessing the effect of seven variables on the probability of classifying fish into the LMG or UMG (coded as 0 and 1, respectively). This was performed through generalized linear mixed modelling (GLMM, with binomial errors). Based on these results, we conditioned the estimation of quantitative genetic parameters (Wilson, 2008) on individual sex, the timing up to emergence (which is when 50% of individuals in a family first swim-up from their nests and show active feeding behaviour) and the average densities at both the early and late life rearing tanks (see Supporting information). The random effect structure of the GLMMs always consisted of the sire and dam identity, as well as the effects of tanks before and after individual tagging. Once the fixed structure was established, we used

WOMBAT (Meyer, 2007) to fit a full animal model of the form:

$$y = X\,u + Z_1\,a + Z_2\,m + Z_3\,EC_1 + Z_4\,EC_2 + e$$

where y is a vector of phenotypic observations (in this case consisting of 0s and 1s) and u represents a vector of the fixed effects related to y by the incidence matrix X. The vectors a, m, EC_1 and EC_2 contain the additive genetic, maternal (i.e. environmental) and tank effects before and after tagging, respectively. These vectors are related to y through the incidence matrices Z_1, Z_2, Z_3 and Z_4. The vector e contains the residual errors. We considered the random effects as contributing to the variation in y, if their removal significantly decreased the log-likelihood ratio score compared with that of a more saturated model (Kruuk, 2004).

Based on this approach, the best model consisted only of the random effect described by the animal as the LRT results for the dam and tank environments were not significant (dam LRT: $\chi^2 = 0$, d.f. = 1, $P > 0.9$; Early-life tank LRT: $\chi^2 = 2.01$, d.f. = 1, $P = 0.16$; post-tagging tank LRT: $\chi^2 = 0$, d.f. = 1, $P > 0.9$). Narrow sense heritability (h^2) was then calculated as the ratio of V_A/V_P, representing the additive genetic variance and the total phenotypic variance, respectively. The heritability thus calculated assumes that the underlying response variable (i.e. the 'liability') is normally distributed but is based on measures taken on a 0, 1 scale. We corrected this estimation and its standard error by taking into account the proportion of individuals in the UMG and LMG as described in Roff (1997).

The estimation of body length threshold values from the common garden experiment differed from the method used in the field data in the following ways. First, 22% of male and 58% of female smolts were classed in the LMG. The lower incidence of males in the LMG was likely due to the precocious sexual development of the majority of males in this group but may have also resulted from different body-size thresholds between the sexes. Therefore, using only the measurements made in January 2006, we first fitted a GLMM including body length and sex as fixed effects predicting the incidences in LMG and UMG. As aforementioned, the random structure of this model consisted of the sire and dam identities and the tank environments before and after tagging. Because the sex term was significant (see Results), we then proceeded to determine whether the size thresholds between males and females were different. For this, we refitted the GLMM on sex-specific data, estimated the threshold values and then compared these estimates using a two-tailed z-test. A nonsignificant difference between these estimates would justify the estimation of a threshold body size common to both sexes.

In our half-sib pedigree design, threshold variation across the sires would reflect additive genetic variation for developmental thresholds (Falconer & Mackay,

1996). To examine this, we fitted another GLMM with the incidence of LMG and UMG depending on both body length and the sire identity. Because the sire had a significant effect (see Results), we then estimated the threshold values and corresponding standard errors for offspring of each sire by fitting GLMs.

Results

Field results

Over the seven sampling years, 300 age 2+ parr and 1109 smolts were captured. Among smolts, 71%, 26% and 2.6% were 3+, 2+ and 4+ smolts, respectively (Table 1). At capture, 3+ smolts were not much bigger than 2+ smolts (after controlling for sampling date) even though these fish remained in freshwater for an additional year (estimated body length of 2+ and 3+ smolt = 119.55 ± 2.39, and 121.66 ± 3.42 mm, respectively. LMM: $F_{1,1077} = 3.87$, $P = 0.05$).

Overall, the 2+ smolts were bigger than 2+ parr (estimated body length 2+ smolts = 119.1 ± 4.41 mm; estimated body length 2+ parr = 87.15 ± 2.36 mm; LMM: $F_{1,587} = 254.3$, $P < 0.001$), and a marginally non-significant interaction between the life-history state and individual sex was observed (LMM: $F_{1,586} = 3.34$, $P = 0.07$). However, we found a significant effect of sex (LMM: $F_{1,587} = 6.95$, $P = 0.009$) whereby female smolts were larger than male smolts (estimated body length 2+ females and males = 120.37 ± 2.48 and 115.73 ± 4.27 mm, respectively. LMM: $F_{1,288} = 6.76$, $P = 0.01$). This relationship was not observed among resident parr (estimated body length female and male 2+ parr = 88.10 ± 1.76, and 87.22 ± 2.78 mm, respectively. LMM: $F_{1,298} = 0.73$, $P = 0.39$). Finally, variation between sampling years explained 12% of the variation in body length (LRT = 60.7, d.f. = 1, $P < 0.001$).

The ANOVA indicated that the back-calculated body lengths were different between the age groups (ANOVA: $F_{2,112} = 101.99$, $P < 0.001$). Specifically, we found that 2+ future smolts were significantly bigger than both 3+ future smolts (size difference = 32.3 ± 3.72 mm, adjusted $P < 0.001$) and 2+ resident parr (size difference = 51.9 ± 4.65 mm, adjusted $P < 0.001$) at the formation of the second annulus (Fig. 1). We also found that future 3+ smolts were significantly bigger than 2+ resident parr (size difference = 19.6 ± 4.35 mm adjusted $P < 0.001$).

The logistic regression analysis between future 2+ smolts and 2+ resident parr suggests that body length (at the start of the growing season of the second year of life) is a significant predictor of smoltification at 2+ (GLM: $\chi^2 = 70.94$, d.f. = 1, $P < 0.001$; overdispersion parameter = 0.15). Thus, for any 1-mm increase in body length, the odds of migrating vs. remaining as parr that year increased by a factor of 1.53. Furthermore, the area under the ROC curve suggested that the specified model has an excellent fit to the data (ROC = 0.996). The best

Table 1 Summary statistics of the smolt captures over a period of 7 years in the North-Eastern Branch of the Sainte-Marguerite River.

| Year | | Smolt age | | | | | | Total |
| | | 2+ | | 3+ | | 4+ | | |
		Male	Female	Male	Female	Male	Female	
1998	*N*	32	55	30	53	4	6	180
	Length	125 (13.6)	130.8 (12.2)	131.1 (6.1)	130.3 (11.6)	136.3 (12.9)	138 (11.5)	
1999	*N*	14	33	71	93	5	0	216
	Length	112.1 (18.9)	124.3 (16.3)	120.4 (10.5)	120.8 (14.3)	120 (5.7)	–	
2000	*N*	9	8	50	54	4	1	126
	Length	114.1 (18.9)	126.1 (23)	120 (10.5)	116.3 (8)	126.8 (5.7)	110	
2002	*N*	22	48	38	58	0	0	166
	Length	120.5 (14.2)	126.1 (35.3)	121.1 (8.8)	130.6 (19.5)	–	–	
2003	*N*	11	15	61	75	1	1	164
	Length	110.3 (6.8)	109 (8.1)	116.1 (11.8)	118.5 (13.8)	121	139	
2004	*N*	7	13	33	41	1	3	98
	Length	112.3 (13)	113.7 (18.2)	112.5 (8.6)	114 (9.1)	124	118.7 (5)	
2005	*N*	11	13	47	85	2	1	159
	Length	115.8 (10.3)	114.7 (9.2)	115.2 (7.1)	116.3 (11.6)	117.5 (3.5)	114	
Overall	*N*	106	185	330	459	17	12	1109
	Length	118.1 (13.9)	124.1 (22.5)	118.9 (10.7)	120.8 (14.4)	125.4 (10.7)	128.7 (14)	

Number (*N*) and mean body length (mm) of male and female smolts 2+, 3+ and 4+ years old. The values in parentheses are standard deviations.
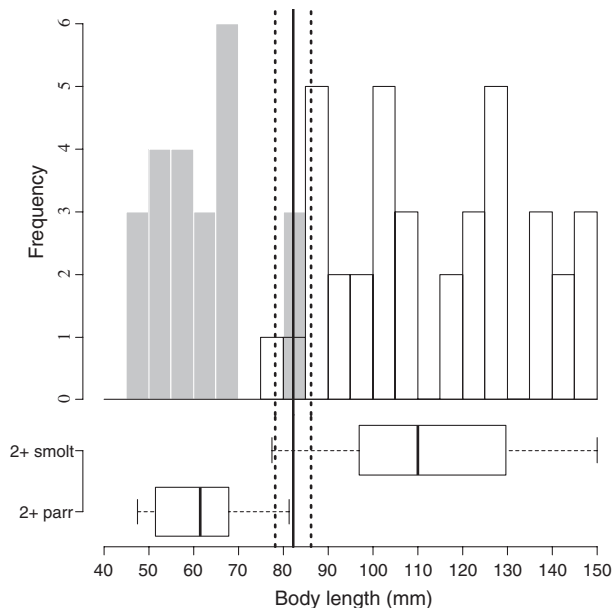
Fig. 1 Back-calculated body length frequency distribution (above) at the start of the growing season of the second year of life of 2+ smolts (white bars) and 2+ resident parr (grey bars). The box plots (below) show the median body lengths, 25th and 75th percentiles and the interquartile range (whiskers). The threshold body size and its 95% confidence intervals above which individuals become smolts are depicted by the solid and dotted black lines, respectively.

compromise between the probability of correctly, and incorrectly, classifying a fish as a smolt was found at an incidence of 63.2%. This cut-off point, which minimizes

the two types of errors, corresponded to a minimal threshold body size of 82.23 ± 2.01 mm, above which fish migrate (Fig. 1). When this analysis was performed on the body length data at capture, an upward bias in the threshold body size was found (threshold = 101.7 ± 1.34 mm).

Common garden results

The cluster analyses performed on the measurements made at November 2006 indicate that fish below 187 mm clustered in the LMG and those above in the UMG. The centres of the two modes occurred at 158.35 mm for the LMG and 215.32 mm for the UMG; no individuals were misclassified. A total of 556 individuals (331 females and 225 males) were thus classed in the UMG, whereas 310 (245 females and 65 males, not including mature male parr) were classed in the LMG. Although size differences between LMG and UMG were already apparent by January 2006 (Fig. 2), rejection of the hypothesis of a unimodal distribution occurred only from July 2006 (Dip = 0.0183, $0.05 < P > 0.01$) and was stronger in November 2006 (Dip = 0.0264, $P < 0.01$).

The estimated heritability on the underlying continuous scale was strong ($h^2 = 0.77 \pm 0.33$), showing that additive genetic variance explains an important portion of the variation in the liability trait associated with these life-history trajectories (LRT = 40.55, d.f. = 1, $P < 0.001$) (Table 2a). We found that both body length and individual sex significantly explained the incidence in the LMG and UMG (GLMM: body length, $\chi^2 = 371.8$, d.f. = 1, $P < 0.001$; sex, $\chi^2 = 24.1$, d.f. = 1, $P < 0.001$). Thus, an increase of one mm in body length increases the odds
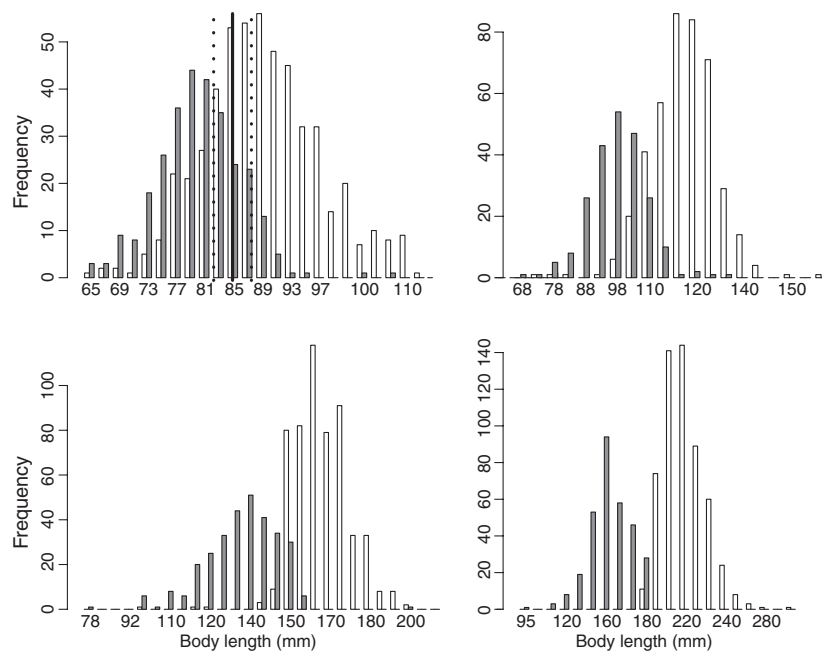
Fig. 2 Frequency distributions of body length at January (upper left), April (upper right), July (lower left) and November (lower right) obtained from the common rearing experiment. Grey bars indicate individuals classed in the lower modal group, whereas white bars indicate individuals classed in the upper modal group. The solid and dotted black lines depicted in the upper left histogram show the estimated threshold value with its 95% confidence intervals, respectively.

of belonging to the UMG by a factor of 1.20 and 1.32 in males and females, respectively. The paternal sexual tactic did not have a significant effect on this probability ($\chi^2 = 0.29$, d.f. = 1, $P = 0.59$).

The estimated thresholds specific to each sex were not significantly different (estimated threshold in males = 79.82 ± 2.48 mm; in females = 84.96 ± 2.02 mm; two-tailed z-test = 1.52, $P = 0.13$). We therefore proceeded to estimate a common threshold for both males and females. The incidence cut-off point was found at 69.6%, and the model provided an excellent fit to the data (ROC = 0.83). These analyses revealed an overall threshold value of 84.94 ± 2.02 mm separating the LMG from UMG (Fig. 2). This threshold value is not significantly different from that observed in the field (two-tailed z-test = 0.34, $P = 0.95$). Finally, additive genetic variance is also likely to explain variation in threshold body sizes as sire groups were found to influence significantly the incidence in LMG and UMG ($\chi^2 = 33.66$, d.f. = 13, $P = 0.0014$) and show variation in their estimated threshold values (Table 2b).

Discussion

This study provides empirical evidence that the propensity to migrate has a strong genetic basis in a vertebrate. Based a common rearing experiment, in which environmental variability is kept to a minimum, we document a high heritability of the liability trait and differences between offspring grouped by their sire in threshold values above which migration takes place. The presence of additive genetic variance in both the liability and thresholds makes the onset of migration a process prone to changes via selection (as hypothesized by Myers & Hutchings, 1986). The high capacity of the liability and possibly of thresholds to respond to selective processes may therefore explain the noticeable variation in the size at emigration (and other life-history characteristics) observed among populations in this species (Jensen & Johnsen, 1986; Hutchings & Myers, 1994; Nicieza *et al.*, 1994; Piché *et al.*, 2008).

In Atlantic salmon, several interrelated behavioural and physiological processes, including growth rate, are hypothesized to contribute to smoltification (Tanguy *et al.*, 1994; McCormick *et al.*, 1998; Stefansson *et al.*, 2003). In this study, we show that variation in the compound effect of these traits is largely explained by additive genetic effects resulting in a high heritability of 0.76. Furthermore, the estimated heritability is at least three times greater than the heritability of the proportion of 1-year-old smolts reported in Norwegian populations by Refstie *et al.* (1977). Although caution should be made when comparing and interpreting the adaptive value of univariate estimates of heritability (Walsh & Blows, 2009), this difference suggests that the capacity to respond to selection of migratory strategies may

Table 2 Variance components of the liability trait influencing migration (a) and threshold estimation on offspring data grouped by sires using a general linear model (b).

(a) Variance components of the liability trait influencing migration

V_P	V_R	V_A	h^2	$h^2_{Adjusted}$
0.26 (0.03)	0.14 (0.04)	0.12 (0.07)	0.46 (0.20)	0.77 (0.33)

(b) Threshold estimation on offspring data grouped by sires using a general linear model

	Number of fish					Confidence intervals	
Sire ID	LMG	UMG	χ^2 test (*P*-value)	Goodness of fit (ROC)	Threshold estimate	Lower	Upper
1010A	31	69	**72.51 (<0.001)**	0.82	82.25	79.13	85.36
1020A	3	27	1.08 (0.30)	–	–	–	–
1030P	37	49	**59.56 (<0.001)**	0.92	85.62	83.93	87.31
1040P	30	27	**39.1 (<0.001)**	0.92	84.45	81.96	86.93
1050P	19	30	**16.78 (<0.001)**	0.83	89.16	85.97	92.35
1060P	4	6	**7.77 (0.005)**	0.96	77.39	74.92	79.85
1070A	30	61	**37.91 (<0.001)**	0.86	84.86	83.18	86.54
1080A	20	18	**16.47 (<0.001)**	0.85	90.05	86.08	94.02
1090A	23	12	**16.03 (<0.001)**	0.84	88.67	84.03	93.30
1100A	26	43	**24.20 (<0.001)**	0.82	84.84	81.38	88.31
1110P	18	93	**18.91 (<0.001)**	0.76	74.81	68.70	80.92
1120P	27	36	**38.37 (<0.001)**	0.91	84.45	82.43	86.47
1130P	13	46	**17.26 (<0.001)**	0.85	82.31	78.88	85.74
1140P	29	39	**12.48 (<0.001)**	0.76	85.33	81.15	89.51
Total	310	556					

All values in parenthesis are standard errors of the estimates. The letter next to the sire ID represents anadromous (A) and mature parr (P) sires. LMG, lower modal group; ROC, receiver operating characteristic; UMG, upper modal group; V_P, phenotypic variance; V_R, residual variance; V_A, additive genetic variance; h^2, narrow sense heritability; $h^2_{Adjusted}$, narrow sense heritability on the underlying continuous scale. Bold values are significant estimates as represented by their *P*-value.

be different between European and North American populations.

However, to better understand the evolution of these life-histories, characterization of patterns of covariation between threshold and status-related traits (or other such compound traits) is needed (Thériault *et al.*, 2007; Páez DP, Bernatchez L, Dodson JJ, unpublished). On the one hand, strong correlations between the liability trait and thresholds would indicate that a selective effect on one of these traits would influence the evolution of the other and impose constraints (Lande, 1979). On the other hand, weak genetic correlations between these traits would indicate that thresholds and liability traits could evolve somewhat independently from one another. Given the widely recognized phenotypic relationships between growth and size at migration in many species of salmonids, such patterns of covariation at the genetic level are likely to occur (Roff, 1997).

The migratory behaviour of the Atlantic salmon is clearly a size-dependant event, as confirmed by our results and by the observations in several independent studies (e.g. Letcher & Gries, 2003). Future migrants were larger than residents in the field, with bimodality in body size similar to that commonly observed under laboratory conditions. In addition, we show that individuals bigger than approximately 85 mm become smolts at age 2+, whereas smaller individuals of the same age remain in freshwater.

Unlike observations on brook charr (Thériault & Dodson, 2003) and a Norwegian population of Atlantic salmon (Økland *et al.*, 1993), threshold body sizes for migration seem to be stable across age groups in our study system; 3-year-old smolts were the same size as smolts migrating at 2 years old. When we compare the body length of these age groups to a length calculated when fish were the same age, we observe that future 2+ smolts are bigger, suggesting that the failure to migrate at 2+ results from the incapacity to grow sufficiently to surpass approximately 85 mm within a developmentally sensitive time interval. Although 4-year-old smolts appear to be somewhat bigger, they represent such a small proportion of migrating fish that it is difficult to interpret this observation.

Within populations, differential growth capacities among individuals have generally been attributed to social status or competitive inequality (Metcalfe *et al.*, 1989; Metcalfe, 1991). While these are important factors, it is important to note that in our laboratory experiment, fish were reared under conditions both favouring growth (as they were fed at 4% of their body weight and at relatively high temperatures) and limiting the formation of dominance hierarchies or territories (as they were

reared in radial tanks, at high densities). Yet, marked variation in size developed quickly and was maintained even when all immature individuals smoltified (i.e. by November 2006). Future investigation into the proximal causes of this size bimodality leading to the alternative life-histories is therefore warranted, particularly because it is a characteristic in several other migratory salmonid species (Masu salmon, *Oncorhynchus masou*, Hirata *et al.*, 1988; white-spotted charr, *Salvelinus leucomaenis*, Yamamoto & Nakano, 1996) but not in others (brown trout, *Salmo trutta*, Tanguy *et al.*, 1994).

The body-size threshold at emigration in the Atlantic salmon has generally been considered as the size at which the compromise between the costs and the benefits of migration is minimized. Thus, sizes above this threshold are hypothesized to reduce transportation costs (as these are inversely related to fish size, Peters, 1993), increase salinity tolerance or osmoregulatory capacities (McCormick & Saunders, 1987) and potentially discourage attack from fish predators (Salminen *et al.*, 1995).

Alternatively, the threshold size could also be viewed as the minimal size above which survival decreases in fresh water because resource acquisition becomes more risky as seasons change (Angilletta *et al.*, 2003). To our knowledge, evidence for either of these predictions is scarce, and no study has documented how these trade-offs vary across the distribution of the Atlantic salmon. Nevertheless, laboratory experiments have shown that threshold sizes and growth rates differ between populations reared under identical conditions (Nicieza *et al.*, 1994). This suggests that variable selection pressures for growth may be acting across the distribution of this species. Our study demonstrates that a response to such selective regimes is possible and likely to be strong. Because growth is an integral part of the liability explaining the propensity to migrate, such selective effects would cause variation in the migratory strategies of the Atlantic salmon.

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Author contributions

C.B., D. J. P. and O.R. participated in the design of the study and performed field and laboratory sampling. J.J.D., H. G. and L. B. conceived and initiated the project. D. J. P., C. B. and J. J. D. analysed the data and wrote the manuscript. All authors contributed to the final version of the manuscript.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Description of the variables used as fixed effects in the conditioning of the estimation of heritability.

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