Comparative Biochemistry and Physiology, Part A 159 (2011) 82–91

Contents lists available at ScienceDirect

Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa

Relationship between metabolism, sex and reproductive tactics in young Atlantic salmon (*Salmo salar* L.)

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ARTICLE INFO

Article history:
Received 15 November 2010
Received in revised form 28 January 2011
Accepted 30 January 2011
Available online 4 February 2011

Keywords:
Fish
Bimodality
Routine metabolic rate
Growth rate
Enzyme activity
Alternative reproductive tactic

ABSTRACT

Atlantic salmon can differ markedly in their growth and in the timing of reproductive maturation, leading to the dramatic contrast between the large anadromous adults and the diminutive mature male parr. This study examined the growth rates, anatomical and physiological characteristics of parr during the adoption of their discrete life histories to ascertain whether these properties can explain tactic choice. To minimise the impact of habitat differences upon these attributes, salmon were reared in the laboratory until 1.5 years of age, when the "decisions" to undergo smoltification or to mature as parr had been taken. At 1.5 years, both males and females showed bimodal size-frequency distributions. Neither the population of origin nor the paternal reproductive tactic influenced the "decision" to mature or the growth trajectories. Growth rate (% mass day^{-1} during their final 10 months) and the % male and female offspring in the upper modal group were strongly correlated and varied markedly among families. Mean growth rate per family was negatively correlated with mean metabolic rate per family at emergence. Growth rate decreased as a function of parr size in January and the growth rates of upper modal fish were displaced upwards relative to those of lower modal fish. Most males in the smaller size mode matured, whereas all other fish began smoltification. Mature male parr did not differ from similarly sized female pre-smolt in routine metabolic rate, but these smaller fish had higher metabolic rates than larger male and female pre-smolts. However, mature parr differed markedly from similarly sized females and from larger male and female pre-smolts in possessing higher oxidative and lower glycolytic capacities in muscle. Overall, these data are consistent with the interpretation that growth rates dictate the distribution of parr between upper and lower modal groups. Individuals from faster growing families would be more likely to pass the threshold for smoltification and to accelerate growth, whereas those from slower growing families would remain in the lower mode. The use of metabolic capacities, e.g. metabolic rate, was linked with modal group, whereas muscle oxidative capacity was linked with male maturity. Mean family metabolic rate at emergence was negatively linked with mean growth during the subsequent year, suggesting that metabolic efficiency facilitates growth and eventually smoltification.

1. Introduction

It is commonly thought that animal species should have a "best" reproductive strategy. Consequently, most models of fish reproduction are based on optimisation theory (Stearns, 1980). However, in many fish species alternative male reproductive behaviours have evolved. These alternative behaviours are used in competition with and coexist in the same habitat as the "normal" phenotype. While some of these alternative behaviours can be changed depending on circumstances, others are conditional choices associated with discrete life histories (Brockmann and Taborsky, 2008). This is the case of Atlantic salmon that shows a diversity of life history tactics, as mirrored by behavioural and morphological adaptations for reproduction, which have presumably evolved as an outcome of selection to maximise male reproductive success (Fleming, 1996).

The Atlantic salmon (*Salmo salar* L.) is an iteroparous anadromous species. After a freshwater juvenile stage of one to four years and a sea migration phase of one to three years, large anadromous males return to their natal rivers and fight to monopolise the anadromous females on spawning grounds (Fleming, 1996; Garant et al., 2003; Gross, 1985, 1991). Some of the males become sexually mature without migrating to sea, at a younger age and at a size five to 10 times smaller than their anadromous counterparts (Aubin-Horth and Dodson, 2004). This size difference allows them to sneak into the nests of females to fertilise eggs instead of fighting to gain access to these females (Hutchings and Myers, 1988). Mature parr reproduce at a younger age and have a greater probability of surviving before reproduction, but their fertilisation success and number of partners are smaller than those of the dominant anadromous males (Garant et al., 2002; Thomaz et al., 1997). Despite the existence of these alternative male reproductive tactics throughout the range of Atlantic salmon, size- and age-at-

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doi:10.1016/j.cbpa.2011.01.023

maturity differ markedly among populations in similar environments (Fleming, 1996; Gross, 1985, 1991; Hutchings, 2004; Metcalfe, 1998).

Both the proximal causes and the consequences of these differences in reproductive tactics are of considerable theoretical and practical interest. The conceptual framework that integrates most of the available data suggests that dominant individuals with high metabolic rates are the fastest growing members in the population and are most likely to smolt (Metcalfe, 1998). As larvae, they consume their yolk sacs and develop faster. Being larger, the newly emerged fry are able to gain access to better territories and food resources (Garant et al., 2003, 2002; Metcalfe et al., 1995; Morinville and Rasmussen, 2003; Thorpe, 1994). Additive genetic effects (potentially including paternal life history) together with environmental growth opportunity set juvenile growth rate. Juveniles whose growth is sufficiently rapid to exceed a threshold size become committed to smoltification, many months before the actual seaward migration. Presumably at a later time, male parr whose status exceeds another threshold become committed to early maturity (Páez et al., 2011; Letcher and Gries, 2003). In the wild in north-eastern North America, the large size of male parr in the spring preceding spawning favours their maturation (Prevost et al., 1992; Whalen and Parrish, 1999). When parr mature, their growth is thought to slow down, reflecting either the costs of gonadal growth or reduced feeding. The size threshold for smoltification and a mobile threshold for tactic choice seem to be the main determinants of male reproductive tactics in Atlantic salmon (Aubin-Horth and Dodson, 2004; Garant et al., 2003). Variability among river systems in the size and age-at-maturity is correlated with differences in juvenile growth opportunity (Metcalfe and Thorpe, 1990).

Under laboratory conditions, growth rates vary with genetic background, and can show an impact of paternal life history tactic (Garant et al., 2003, 2002; Morasse et al., 2008). The threshold models of smoltification of male parr suggest that families in which offspring have high growth rates should show a greater incidence of smoltification than those in which the offspring grow more slowly. However, the costs and consequences of reproductive maturation of smaller male parr complicate the picture. The dynamics of growth of female parr may help elucidate the mechanisms controlling growth of male parr, as females only undergo smoltification and eventual seaward migration. If growth rates are primarily set by the activation of a smoltification threshold, male and female parr should have similar population size structures. On the other hand, if passing the maturity threshold slows the growth of mature male parr, the size-frequency distributions of male and female parr should differ.

Juvenile growth will reflect food availability, rates of food ingestion and physiological growth efficiency and should differ with life history tactic. Metabolic differences have been invoked as an underlying cause of the eventual choice of life history tactic. High standard metabolic rates have been linked with dominance, territoriality and eventual smoltification (Higgins, 1985; Metcalfe, 1998, Metcalfe et al., 1995, 1992). Metabolic capacities could also differ due to the adoption of distinct life history tactics. Effectively, metabolic capacities in fish tissues change with energetic status, acclimation temperature, reproductive investment and size (Garenc et al., 1998; Guderley, 2004). Differences in size and reproductive investment suggest that the metabolic capacities of mature parr and smolt should differ. Mature parr are smaller than smolt. The allometry of metabolic rates and tissue metabolic capacities should lead mature parr to have higher aerobic and lower glycolytic capacities than smolt (Somero and Childress, 1990). Mature parr have a significantly greater relative ventricular mass than immature fish (Armstrong and West, 1994). In mature parr, ingested energy is shifted to gonad maturation, typical of pre-breeding changes in Atlantic salmon (Fleming, 1996). Gonads account for approximately 9% of body mass in mature male parr (Fleming, 1996). Mobilisation of tissue reserves for reproductive activities decreases muscle metabolic capacities both in Pacific salmon (Mommsen et al., 2003) and in species without terminal reproduction (Garenc et al., 1998). Both liver and muscle contain major energetic reserves in fish. Reproductive investment could lead mature parr to have reduced liver and muscle metabolic capacities compared to male or female smolt. Pyloric ceca are a major site of food absorption (Blier et al., 2007; Buddington and Diamond, 1987; Collie, 1985) and their aerobic capacity varies with growth rates in Atlantic cod (Bélanger et al., 2002). Faster growing smolt should have a greater aerobic capacity in their pyloric ceca than mature parr.

To examine these questions, this study examined how mature male parr, male pre-smolts and female pre-smolts of the same age differ in their growth rates and in anatomical and physiological characteristics. To minimise the impact of habitat differences upon the growth and physiological capacities of these individuals, salmon were reared in the laboratory until approximately 1.5 years of age, when the "decisions" relative to smoltification and maturation had been taken. To evaluate the impact of originating from populations with different proportions of mature male parr, we examined juvenile salmon produced from crosses of broodstock from two spawning populations in the Ste. Marguerite River. To assess the impact of the paternal reproductive tactic, we used both anadromous male and mature male parr from each population as fathers. We examined individual growth of juveniles between 10 and 20 months after emergence and assessed the links between size at age 10 months and subsequent growth as well as the influence of family origin upon growth rates. We then evaluated the routine metabolic rate, tissue indices and the metabolic capacities of muscle, liver and pyloric ceca in a sub-set of the 20 month old juveniles, sampling approximately equal numbers of mature male parr, male pre-smolt and female pre-smolt. We hypothesised that mature parr would have higher routine metabolic rates and higher tissue aerobic capacities than male or female pre-smolts. We predicted that the slowed growth of mature male parr would be reflected in decreased metabolic capacities in liver and pyloric ceca, given the likely diversion of energy and materials to gonadal growth. To evaluate these hypotheses, we assessed tissue aerobic capacity by measuring the levels of three mitochondrial enzymes: citrate synthase (CS; EC 2.3.3.1), cytochrome C oxidase (CCO; EC 1.9.3.1) and glutamate dehydrogenase (GDH; EC 1.4.1.3). Glycolytic capacity was assessed by measuring lactate dehydrogenase (LDH; EC 1.1.1.27). Creatine kinase (CK; EC 2.7.3.2) activity indicated the capacity for buffering ATP levels. By evaluating whether the reproductive tactics of paternal males influence the growth, metabolic capacities and choice of reproductive tactic of their offspring, this study makes a unique contribution. Comparing the growth trajectories and physiological characteristics of female and male juveniles allowed us to evaluate whether the "choice" of reproductive tactic was the cause or the consequence of differences in growth and metabolic characteristics.

2. Materials and methods

2.1. Habitat characteristics, breeding and holding conditions, sampling times

The Ste. Marguerite River (48°20′N, 70°00′W) lies 250 km northeast of Quebec City, Canada and is divided into two branches. Access to salmon in the northeast branch is limited to the first 35 km because of waterfalls, and was restricted to the lower 6.5 km until a fish ladder was installed at the first waterfall in 1981. Partial reproductive isolation between the upstream and downstream populations, as indicated by differentiation at microsatellite loci, was apparent in 1997 (Garant et al., 2002). The upstream site has a higher proportion of mature male parr and a smaller size threshold for maturation than the downstream site (Aubin-Horth et al., 2006).

During the summer of 2004, anadromous males and females as well as mature parr were collected at the fish ladder and well downstream of the fish ladder. Because this species displays strong

philopatry, samples collected from the fish ladder were considered as representative of the upstream population. Individuals collected downstream of the ladder were taken to represent the downstream population. We collected 4 anadromous males, 2 anadromous females and 4 mature male parr as broodstock for each population. Unfortunately 2 of the anadromous males from the upstream population died at the hatchery. These fish were kept in tanks at a government fish hatchery in Tadoussac (15 km from the Ste. Marguerite River). The length and mass of the parental fish were measured before obtaining the eggs and sperm in November 2004. Crosses within each population were performed to yield full-sib, half-sib and unrelated offspring. Essentially, eggs from both females in each population were crossed with sperm from each anadromous male and each mature parr. The crosses were done in individual buckets. The fertilised eggs were maintained in darkness in drawers in the stream-fed incubator, except that after 24 h, non-fertilised eggs were removed. Fertilised embryos were maintained in these incubators until the eyed stage (mid-March 2005) when they were transferred to the Laboratoire Régional des Sciences Aquatiques (LARSA) at Université Laval, Québec to complete their development. Accidental mortalities in the early stages led to the loss of 3 families. In the end, we had 24 families; 9 from the upstream population (2 anadromous males and 4 mature parr crossed with 2 females) and 15 families (4 anadromous males and 4 mature parr crossed with 2 females) from the downstream population.

At the LARSA, the fertilised eggs were placed in a long rectangular raceway. The embryos from each family were placed in a compartment, separated from the other families by netting, until hatching and emergence. Well-aerated water (110% dissolved oxygen; 5.8 ± 0.7 °C) circulated through the raceway, assuring equivalence of the physiochemical conditions. After emergence and until the age of 10 months (January 2006), the alevins were held in separate tanks at densities adapted to their size and fed with commercial food at 4% of their body mass. As we could not cool the water below 8 °C, the fish were maintained at 8 °C during their first winter after emergence. In January 2006, when the fish had reached a sufficient size, they were anaesthetised (eugenol, 10%), measured, weighed and marked with passive integrated transponder (PIT) tags, (Gibbons and Andrews, 2004). Subsequently, the fish were held in two tanks, each containing fish randomly selected from all the families. The amount of food provided to the fish was adjusted as a function of their density. The fish were maintained at 10 °C (9.9 ± 0.016) and the natural photoperiod was followed until the end of the experiment (November 2006), when we could separate pre-smolt and mature parr (using silvery body coloration or hyperextension of the ventral anterior body as classification criteria). We consider these salmon pre-smolts because, although smoltification had begun, they were still in fresh water. The thermal differences between the laboratory and the natural habitat make it difficult to establish the corresponding age of wild fish in the Ste. Marguerite River system.

In November 2006, all fish reared in this experiment were sacrificed and all data were collected. We measured the mass and length of all the fish ($N = 1147$). For the physiological and metabolic characterisation, we sampled approximately equal numbers of mature male parr and immature pre-smolts per family, attaining a total of 40 mature male parr and 100 male and female pre-smolts from all the families. The silvery colouration of the smaller pre-smolts was less pronounced than that of the larger pre-smolts. During reproduction, rearing, characterisation, tagging and sampling, we followed procedures established by the Canadian Council for Animal Care and our local animal care committee (Comité de Protection des Animaux de l'Université Laval).

2.2. Determination of routine metabolic rate

We measured the routine metabolic rate of 4–9 fish per family at hatch, emergence and at the end of experiment. At hatch and emergence, the methods and results are given in Rossignol et al. (2010). In November 2006, the size of the fish suggested which fish were pre-smolts, but the sex and reproductive status were only determined after the sacrifice of the fish. In families with few offspring, we were forced to reduce the number measured. Individual plastic respirometry tunnels (2600 ml) were equipped with a water pump that circulated water continuously. The chambers were placed above the holding tanks and water from these tanks circulated through the respirometry chambers. Individual fish that had not been fed for 24 h were gently transferred to and habituated in the open respirometry chambers for one hour, before closing the chambers with the polarographic electrodes and continuously monitoring oxygen uptake during an additional hour. These routine metabolic rates were stable during the measurement period. The oxymeter (OM200 Oxygen Analyzer, Cameron Instruments Company) was calibrated to 100% saturation by using the aerated water from the incubator and sodium hydrosulphite was added to obtain 0% oxygen saturation. The calibration was carried out at the start and end of each day. All respirometry measurements were carried out during the light period of the day. To control for microbial O_2 uptake and O_2 uptake by the electrodes, we determined the oxygen consumption of empty chambers for one hour before and after each sampling period. These rates remained negligible throughout the experimental period. The water temperature in the respirometry chambers was 10 °C. The atmospheric pressures for the sampling days were obtained from the "Service Météorologique du Québec".

2.3. Determination of anatomical parameters and enzyme activity

In November 2006 (at 1.5 years old), salmon were killed by a blow to the head, measured and weighed after being patted with paper towelling to remove excess water. Immediately after weighing, the salmon were dissected to determine their sex and reproductive tactic. Gonads and organs were weighed and the rest of the bodies were frozen at −80 °C until enzyme assays. We calculated a condition factor as follows:

$$\text{Condition factor} = \left[\text{whole body mass (g)} * \text{total length (cm)}^{-3}\right] * 100.$$

To estimate the relationship between muscle mass and the mass of the carcass (left posterior half including the muscles, fins and bones), we used 15 fish. They were randomly chosen in the common tank to cover the overall size range of the fish. These fish were weighed and then carefully dissected to obtain all the muscles. The following relationship between carcass mass and muscle mass in the fish ($R^2 = 0.998$) was used to estimate the muscle mass of the other fish sampled:

$$\text{Muscle mass} = 0.7498\ \text{carcass mass} - 2.0101$$

This relationship showed no change in slope over the fish size range examined (54.41 g–164.47 g).

Individual growth rates were calculated using the following equation:

$$\text{Growth rate} = [(\ln W_2 - \ln W_1)/t] * 100,$$

where growth rate is measured in $\%\,\text{day}^{-1}$, W_1 represents the mass (g) or length (mm) in January, W_2 the mass or length in November and t the number of days between these periods.

2.4. Preparation of tissue extracts

Throughout preparations for enzymatic assays, fish and samples were preserved on ice. Muscle samples were always taken below the dorsal fin, on the left side, free of red muscle. After weighing the liver and pyloric ceca, a sample of both was taken. These samples were

rapidly homogenised. Additional samples of muscle, liver and ceca were weighed and placed at 75 °C for 48 h to obtain their dry mass and water content. Samples for enzyme assays were immediately homogenised in ten volumes of ice-cold KH_2PO_4/K_2HPO_4 (100 mM), Triton X-100 (0.1% v/v) and EDTA (5 mM), pH = 7.0. The pH of all solutions was adjusted at room temperature (20 °C). After homogenisation, 50 μL of the homogenate was frozen at −20 °C for protein determinations. Protein concentration was measured using bicinchoninic acid (Smith et al., 1985). The remaining homogenates were centrifuged for 10 min at 500×*g* (Micromax, IEC) and the supernatants were used for enzymatic tests.

Enzymes were assayed using a microplate UV/VIS spectrophotometer (SpectraMax 190, Molecular Device) coupled to the Softmax Pro software for data recovery (version 4.6 Molecular Device). Assays were carried out at 20 °C. CS activity was measured at 412 nm to detect the transfer of sulfhydryl groups to 5,5′dithiobis-2-nitrobenzoic acid (DNTB) (micromolar extinction coefficient = 13.6). CCO activity was measured at 550 nm to follow the oxidation of reduced cytochrome C (micromolar extinction coefficient = 19.1). GDH, LDH and CK activity were measured by following NADH and NADP at 340 nm (micromolar extinction coefficient = 6.22).

These assays were based on Guderley et al. (2001) and Kuo et al. (1994) as presented in Rossignol et al. (2010). All enzymes were measured, in triplicate, in the three organ samples. Enzyme activities were expressed in international units (one unit is the amount of enzyme producing 1 μmol of product per minute at 20 °C). Biochemicals were purchased from Sigma Chemicals Co., Roche Diagnostics and Fisher Scientific Co.

2.5. Statistical analysis

For statistical analysis, the normality of the residuals was tested with the Shapiro–Wilk test and the homogeneity of variances with the Levene test. A mixed model containing both fixed and random effects was used to evaluate the influence of the different parameters in our experimental design. The design used randomised blocks with fixed treatment effects and random block effects (SAS system for mixed models, 2002). For each variable, the fixed effects in the model were paternal reproductive phenotype (PRT) (anadromous or mature parr) and the population of origin of the parents. Given the bimodality of the length-frequency distributions of the parr (see below), another fixed effect was the modal group, or the tactic chosen (lower mode female pre-smolt, upper mode female pre-smolt, male parr and male pre-smolt). We included mass as a fixed effect in the models examining enzyme activities. The models included interaction terms between these effects (population*PRT, modal groups*population, modal groups*PRT and modal groups*population*PRT). We also included maternal identity, paternal identity and their interaction (e.g. family) as random effects. The level of significance was a = 0.05. Computations were carried out with SAS 9.0 statistical software. When we analysed proportional data, we used a generalised linear model with binomial errors and a logit link function executed in R (Baayen, 2008).

3. Results

3.1. Bimodality in length frequency distributions

In January 2006, the overall length frequency distribution of the parr presented a single mode. When the parr were separated according to future modal group (mature parr, future male pre-smolt, future lower mode female pre-smolt and future upper mode female pre-smolt), a slight separation of sizes became apparent, with future mature parr and future lower mode females being slightly smaller than their counterparts in the future upper modes (Fig. 1). In November 2006, marked bimodality in the length frequency distribution was apparent for both males and females (Fig. 1). Female pre-smolts in the lower modal group were similar in size to mature parr, whereas the female pre-smolt in the upper modal group covered the same size range as the male pre-smolt.

3.2. Proportions of mature parr and of lower modal group females

The proportion of mature male parr varied markedly between families (8–82%), as did the proportion of females in the lower modal group (9–75%). Neither the population of origin, paternal reproductive tactic nor the interaction between population and paternal reproductive tactic affected the distribution of males and females between the two size modes (e.g. choice of reproductive tactic among males, statistical results not shown). Families with higher proportions of mature male parr also had higher proportions of lower mode females ($R^2 = 0.20$, $p = 0.0321$). We reasoned that this common relationship could be based on differences in growth rate. Effectively, families differed considerably in mean growth rates (for females: $z = 6.453$, $p < 0.0001$; for males: $z = 9.297$, $p < 0.0001$), and mean growth rates, in turn, were positively correlated with the % offspring in the upper mode. This relationship was similar for males and females (Fig. 2), but the range of growth rates was broader for male than female siblings.

3.3. Anatomical parameters

When they were measured in January (age 10 months) future mature parr were shorter and lighter than future male pre-smolts, but did not differ in condition factor (Table 1, statistical results in Tables 1 and 2). Similarly, future lower mode females were lighter and shorter than future upper mode females, and did not differ in condition factor. Thus, although the overall distribution of the fish was not significantly bimodal in January, the future mature male parr and the future lower mode females were already significantly smaller than the fish that would compose the larger size mode.

In November the four groups were quite distinct in mass and length, with the mature male parr having the lowest mean values followed by the lower mode females, then the male pre-smolt and finally the upper mode females (Fig. 1; Table 1). This size differentiation according to modal group affected all anatomical parameters. Neither the population of origin, paternal reproductive tactic nor the interaction between population, paternal reproductive tactic and modal group affected the body mass, length, condition factor, muscle mass, liver mass, ceca mass, gonad mass, or the hepatosomatic and gonadosomatic indices. As the modal group significantly affected all of these parameters (Tables 2 and 3), the modal size group to which individuals belonged was the primary determinant of their anatomic characteristics. Nonetheless, the proportions of muscle and pyloric ceca over the total body mass were significantly smaller in mature parr than in the other modal groups (Tables 1–3).

As we determined the mass and length of the fish during tagging in January, we were able to assess the relationship between these external characteristics in January and subsequent growth (% mass - day^{-1}). As could be predicted from the marked size differences between the upper and lower mode fish in November, the relationship between length in January and growth (% mass day^{-1}) between January and November varied considerably between fish in these modes (Fig. 3). Similar relationships were obtained for % length day^{-1}. For both males and females, two virtually parallel relationships were found for the growth of individuals in the upper and lower modes, despite the substantial overlap of their lengths in January. All growth rates decreased as a function of length in January. The slope of these relationships was similar between the upper and lower modal groups (−0.0042 to −0.0062% day^{-1} mm^{-1}), but growth rates were systematically greater for fish in the upper modal groups.

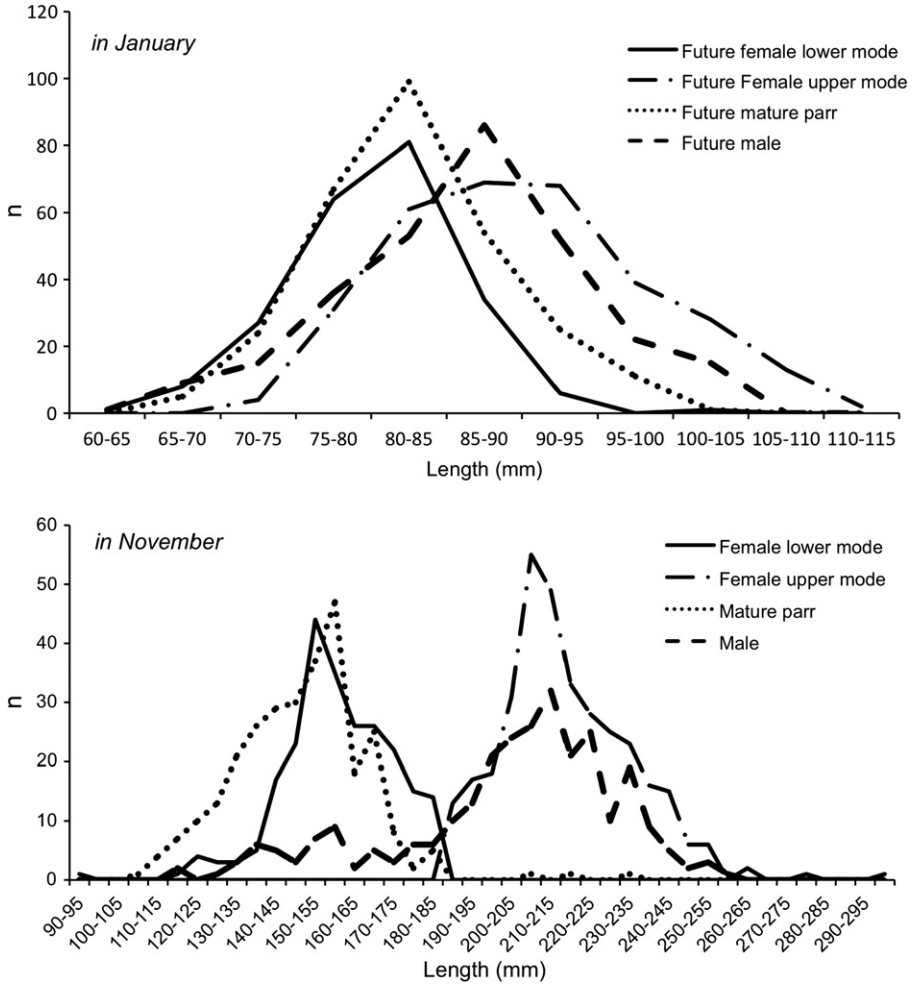

Fig. 1. Length–frequency distributions in January and in November for each modal group, mature parr (N = 286), female pre-smolt lower mode (N = 239), female pre-smolt upper mode (N = 339) and male pre-smolt (N = 289).

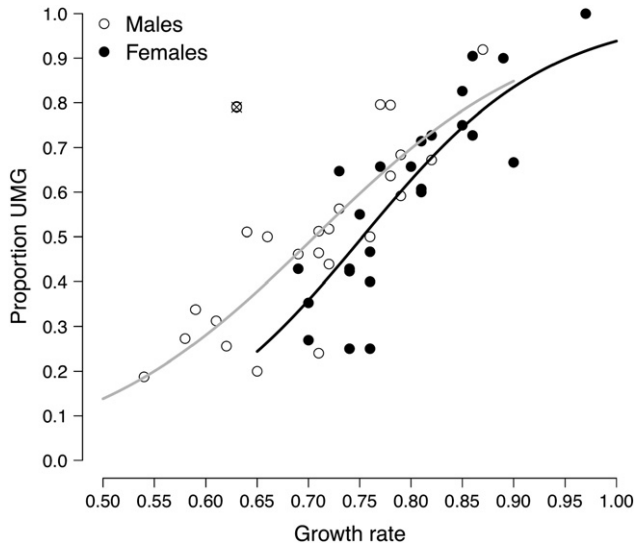

Fig. 2. Relationships between mean growth rate (% mass day^{-1}) per family and the percentage of pre-smolt in the upper mode. Values are separated by sex with males shown as open circles and females with black circles. We used a generalised linear model with binomial errors and a logit link function to generate these curves. The data point with a cross through it is an outlier and was removed from the data.

3.4. Routine metabolic rate

We compared mass specific metabolic rates (μmol O_2 h^{-1} g^{-1}) of our samples because total metabolic rate would have directly reflected offspring size. Neither the population, the paternal reproductive tactic nor their interaction with modal group, influenced offspring metabolic rate (Table 3). Modal group significantly influenced metabolic rate ($p = 0.010$). Mature parr had higher metabolic rates than male and female pre-smolt in the upper mode, but exhibited similar metabolic rates as the female pre-smolt in the lower mode (Fig. 4). Mean routine metabolic rate per family in November was not correlated with the growth rate ($p = 0.535$), partly due to the considerable variability within families with offspring in both size modes. However, the mean metabolic rate at emergence (June 2005) of offspring from these families (reported in Rossignol et al., 2010), was negatively correlated with the mean growth rate of their offspring between January and November 2006 (Fig. 5; $R^2 = 0.34$, $p = 0.0013$). In other words, comparison of our 24 families showed that mean offspring growth between January and November declined as a function of mean offspring metabolic rate at emergence.

3.5. Enzyme activity

Neither the population of origin, paternal reproductive tactic nor the interaction between populations, paternal reproductive tactic and modal group affected the measured enzyme activities (Fig. 6). Only the modal group consistently had a significant impact on the enzyme activities (results of statistical comparisons Table 3). Size only affected

Table 1
Morphological parameters in January and November. N represents the number of individuals per morph for each parameter. Values are mean ± standard error. N.A. indicates unavailable values. When lines have different letters, they differ significantly (*a posteriori* tests, $p<0.05$).

	Mature parr				Female pre-smolt lower mode				Female pre-smolt upper mode				Male pre-smolt			
	N	Mean		S.E.	N	Mean		S.E	N	Mean		S.E	N	Mean		S.E
January																
Body mass (g)	286	6.1	±	0.09 a	239	5.2	±	0.07 b	338	7.6	±	0.11 c	279	6.9	±	0.13 d
Length (mm)	286	82.6	±	0.38 a	222	80.4	±	0.37 b	316	89.9	±	0.46 c	279	86.4	±	0.52 d
K	286	1.06	±	0.01 a	239	1.01	±	0.01 b	338	1.03	±	0.01 ab	279	1.06	±	0.01 a
November																
Body mass (g)	269	38.7	±	0.76 a	221	43.9	±	0.82 b	316	111.2	±	1.48 c	265	95.7	±	2.18 d
Length (mm)	286	149.1	±	0.99 a	239	158.3	±	0.91 b	338	216.1	±	0.90 c	279	201.9	±	1.69 d
K	269	1.14	±	0.01 a	221	1.08	±	0.01 b	316	1.09	±	0.01 c	265	1.11	±	0.01 d
Gonads (g)	270	3.9	±	0.14	223	0.16	±	0.003	316	0.26	±	0.003		N.A.		
Muscle/body mass (%)	39	63.8	±	4.8 a	23	71.8	±	2.4 b	26	76	±	8.2 b	41	73.4	±	9.6 b
Muscle protein (g/g wet mass)	23	0.15	±	0.005	22	0.16	±	0.007	19	0.16	±	0.006	25	0.15	±	0.008
Muscle water content (%)	40	73.2	±	3.1	24	72.1	±	1.7	25	68.8	±	6.5	40	70.8	±	4.2
Hepatosomatic index (%)	39	0.96	±	0.04 a	23	1.27	±	0.16 b	26	1.23	±	0.07 ab	41	1.33	±	0.06 ab
Liver protein (g/g wet mass)	31	0.12	±	0.006	24	0.11	±	0.005	21	0.12	±	0.005	36	0.10	±	0.006
Liver water content (%)	40	76.2	±	7.9	24	74.7	±	11.8	25	71.5	±	4.8	40	73.5	±	4.4
Ceca/body mass (%)	39	1.03	±	0.08 a	23	1.53	±	0.07 b	26	1.82	±	0.10 b	41	1.93	±	0.07 b
Ceca protein (g/g wet mass)	31	0.10	±	0.007	23	0.12	±	0.008	23	0.11	±	0.005	31	0.10	±	0.007
Ceca water content (%)	40	53.5	±	18.0	24	39.9	±	8.5	25	43.7	±	9.8	40	46.9	±	8.5

the activity of LDH in muscle and the activity of CK in pyloric ceca (Table 3). In muscle, the mitochondrial enzymes, CCO, CS and GDH, had significantly higher activities in mature male parr than in male or female pre-smolt (lower and upper mode) (Fig. 6a,b,c), whereas LDH activity was higher in male and female pre-smolt than in mature male parr (Fig. 6e). CK activity in muscle did not differ between the modal groups (Fig. 6d). In liver, mitochondrial enzyme activities differed less, with mature parr having slightly higher CS and GDH activities than female pre-smolt (both modes) and male pre-smolt. Hepatic CK was lower in male pre-smolt than female pre-smolt in the lower mode. For hepatic CCO and LDH activities, modal group did not have a significant effect. In the pyloric ceca, male pre-smolt had significantly higher activities than female pre-smolt or mature male parr for GDH and CK. For the other activities (CCO, CS and LDH) in the pyloric ceca, modal group had no significant effect. As the protein and water contents of muscle, liver and pyloric ceca did not differ between the four modal groups (Table 1), the differences in metabolic capacities between the modal groups are not due to a generalised protein mobilisation due to reproductive investment.

In muscle, but not in liver or pyloric ceca, the activities of the three mitochondrial enzymes, CCO, CS and GDH, were negatively correlated ($R^2 \leq 0.25$) with LDH activity. On the other hand, in the pyloric ceca all enzyme activities increased in parallel. In liver, when significant correlations were observed between enzyme activities, they too showed

Table 2
Results (*p*-values) of mixed models for morphological parameters of the overall sample (N = 1142) and of the samples used for metabolic and physiological characterisation (N = ~130) in January and November. All models contained double and triple interactions, none of which were significant. The results of these interactions have been omitted to simplify the presentation. Population refers to the upstream or downstream populations from which the parental salmon originated. PRT refers to the paternal reproductive tactic. Modal group refers to whether the salmon were mature parr, male pre-smolt or female pre-smolt (lower and upper mode) when sampled in November. The degree of freedom of the fixed factors is indicated in the subscript. *, ** and *** represent significance levels (<0.05; <0.01 and <0.001).

	N	Population	PRT	Modal group
Overall sample				
January				
Body mass	1142	$0.971_{(1)}$	$0.482_{(1)}$	$<0.0001^{***}{}_{(3)}$
Length	1142	$0.810_{(1)}$	$0.309_{(1)}$	$<0.0001^{***}{}_{(3)}$
K	1142	$0.697_{(1)}$	$0.362_{(1)}$	$<0.0001^{***}{}_{(3)}$
November				
Body mass	1070	$0.762_{(1)}$	$0.653_{(1)}$	$<0.0001^{***}{}_{(3)}$
Length	1142	$0.886_{(1)}$	$0.901_{(1)}$	$<0.0001^{***}{}_{(3)}$
K	1070	$0.695_{(1)}$	$0.957_{(1)}$	$<0.0001^{***}{}_{(3)}$
Samples used for metabolic characterisation				
January				
Body mass	129	$0.979_{(1)}$	$0.619_{(1)}$	$<0.0001^{***}{}_{(3)}$
Length	129	$0.697_{(1)}$	$0.146_{(1)}$	$<0.0001^{***}{}_{(3)}$
K	129	$0.360_{(1)}$	$0.014_{(1)}$	$<0.0001^{***}{}_{(3)}$
November				
Body mass	129	$0.320_{(1)}$	$0.465_{(1)}$	$<0.0001^{***}{}_{(3)}$
Length	113	$0.626_{(1)}$	$0.897_{(1)}$	$<0.0001^{***}{}_{(3)}$
K	113	$0.562_{(1)}$	$0.752_{(1)}$	$0.004^{**}{}_{(3)}$

Table 3
Results (*p*-values) of mixed models for enzyme activities and metabolic rate of salmon sampled in November. Population refers to the upstream or downstream populations from which the parental salmon originated. PRT refers to the paternal reproductive tactic. Modal group refers to whether the salmon were mature parr, male pre-smolt or female pre-smolt (upper and lower mode) when sampled in November. The degree of freedom of the fixed factors is indicated in the subscript. *, ** and *** represent significance levels (<0.05; <0.01 and <0.001).

	N	Population	PRT	Modal group	Body mass
MO_2	92	$0.523_{(1)}$	$0.678_{(1)}$	$0.01^{**}{}_{(3)}$	/
% muscle/body mass	129	$0.674_{(1)}$	$0.632_{(1)}$	$0.0001^{***}{}_{(3)}$	0.032^{*}
% liver/body mass	129	$0.938_{(1)}$	$0.337_{(1)}$	$0.040^{*}{}_{(3)}$	0.218
% ceca/body mass	129	$0.610_{(1)}$	$0.802_{(1)}$	$<0.0001^{***}{}_{(3)}$	0.307
g protein/g muscle	86	$0.297_{(1)}$	$0.265_{(1)}$	$0.231_{(3)}$	0.058
g protein/g liver	108	$0.823_{(1)}$	$0.956_{(1)}$	$0.145_{(3)}$	0.326
g protein/g ceca	105	$0.960_{(1)}$	$0.774_{(1)}$	$0.136_{(3)}$	0.938
CCO muscle	129	$0.886_{(1)}$	$0.430_{(1)}$	$0.004^{**}{}_{(3)}$	0.826
CS muscle	129	$0.617_{(1)}$	$0.980_{(1)}$	$<0.0001^{***}{}_{(3)}$	0.950
GDH muscle	129	$0.560_{(1)}$	$0.763_{(1)}$	$0.063_{(3)}$	0.480
CK muscle	129	$0.833_{(1)}$	$0.340_{(1)}$	$0.063_{(3)}$	0.249
LDH muscle	129	$0.444_{(1)}$	$0.521_{(1)}$	$0.010^{**}{}_{(3)}$	0.0002^{**}
CCO liver	129	$0.727_{(1)}$	$0.843_{(1)}$	$0.796_{(3)}$	0.095
CS liver	129	$0.466_{(1)}$	$0.571_{(1)}$	$0.031^{*}{}_{(3)}$	0.301
GDH liver	129	$0.994_{(1)}$	$0.150_{(1)}$	$0.020^{*}{}_{(3)}$	0.390
CK liver	129	$0.731_{(1)}$	$0.915_{(1)}$	$0.034^{*}{}_{(3)}$	0.067
LDH liver	129	$0.743_{(1)}$	$0.117_{(1)}$	$0.442_{(3)}$	0.759
CCO ceca	129	$0.262_{(1)}$	$0.792_{(1)}$	$0.137_{(3)}$	0.202
CS ceca	129	$0.811_{(1)}$	$0.791_{(1)}$	$0.823_{(3)}$	0.087
GDH ceca	129	$0.627_{(1)}$	$0.247_{(1)}$	$0.043^{*}{}_{(3)}$	0.471
CK ceca	128	$0.954_{(1)}$	$0.797_{(1)}$	$0.003^{**}{}_{(3)}$	0.002^{**}
LDH ceca	126	$0.808_{(1)}$	$0.666_{(1)}$	$0.107_{(3)}$	0.118

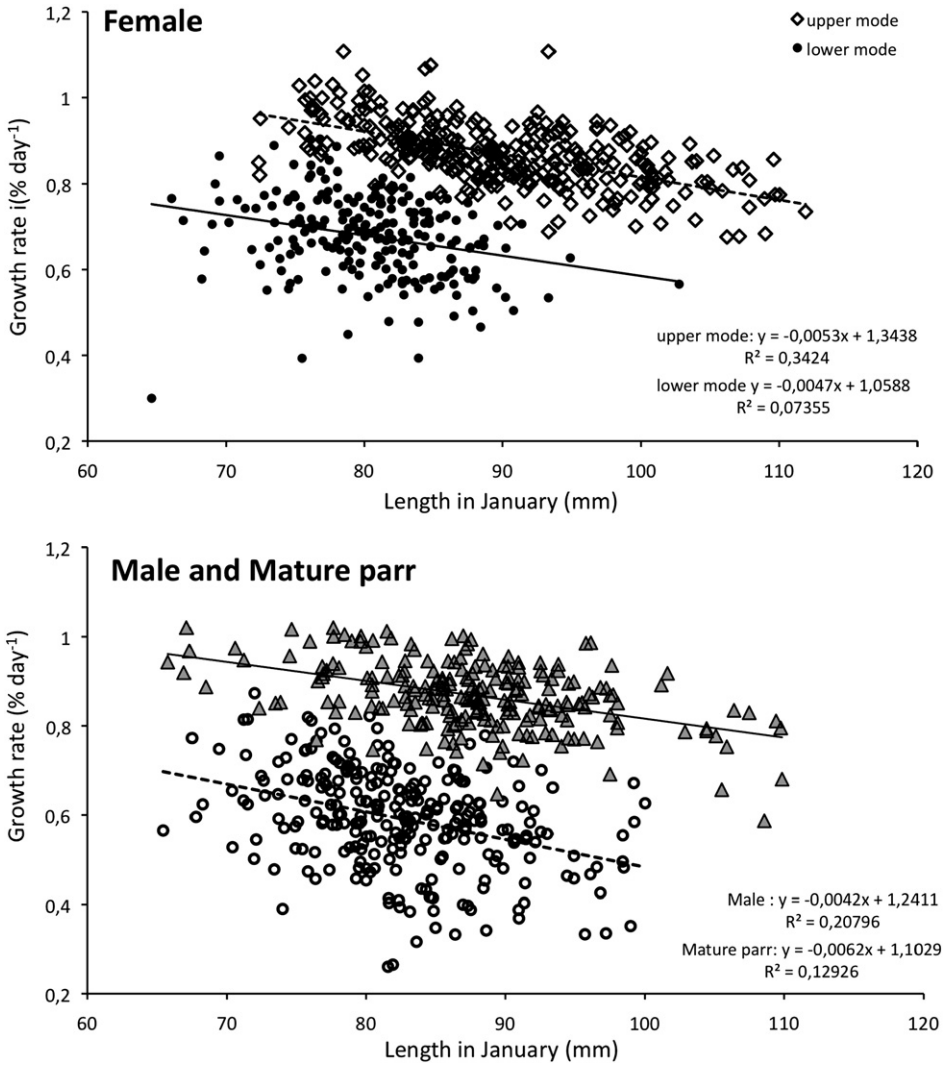

Fig. 3. Relation between length in January and growth rate in % mass day^{-1}. Values are shown by modal group; females ($n_{upper\ mode} = 239$; $n_{lower\ mode} = 339$), males ($n_{upper\ mode} = 236$; $n_{lower\ mode} = 285$).

parallel increases, with LDH and CK positively correlated with the activities of mitochondrial enzymes. While most of these correlations were highly significant ($p \leq 0.0009$), the portion of the variance they explained was limited.

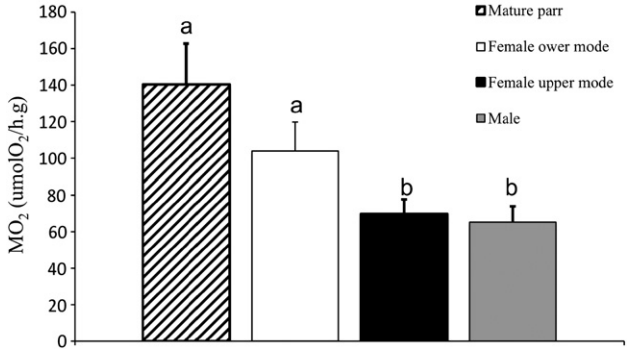

Fig. 4. Metabolic rate according to modal group; mature parr (cross-hatched bars, N = 18), male pre-smolt (grey bars, N = 21), female lower mode (white bars, N = 28) and female upper mode (black bars, N = 24). Values are means ± S.E. and are shown as μmol O_2 h^{-1} g^{-1}. The individuals used for these measurements were randomly chosen among the different families sampled in November 2006. When columns have different letters, they differ significantly (*a posteriori* tests, $p < 0.05$).

4. Discussion

The variety of life histories available to Atlantic salmon is mirrored in the growth trajectories they can follow during the freshwater

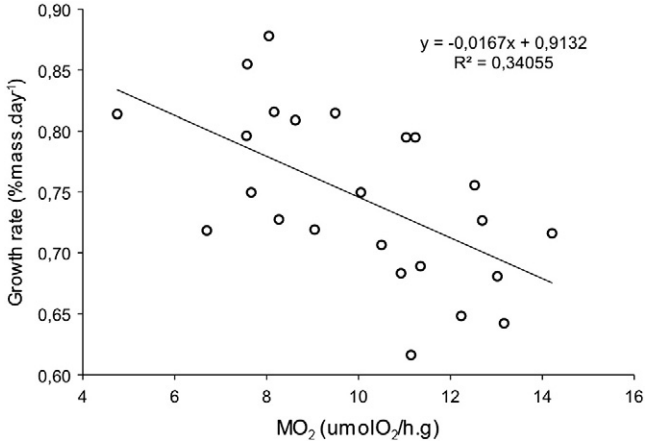

Fig. 5. Relation between mean growth rate by family (January 2006–November 2006) and mean metabolic rate of these families at emergence (June 2005), $p = 0.0013$.

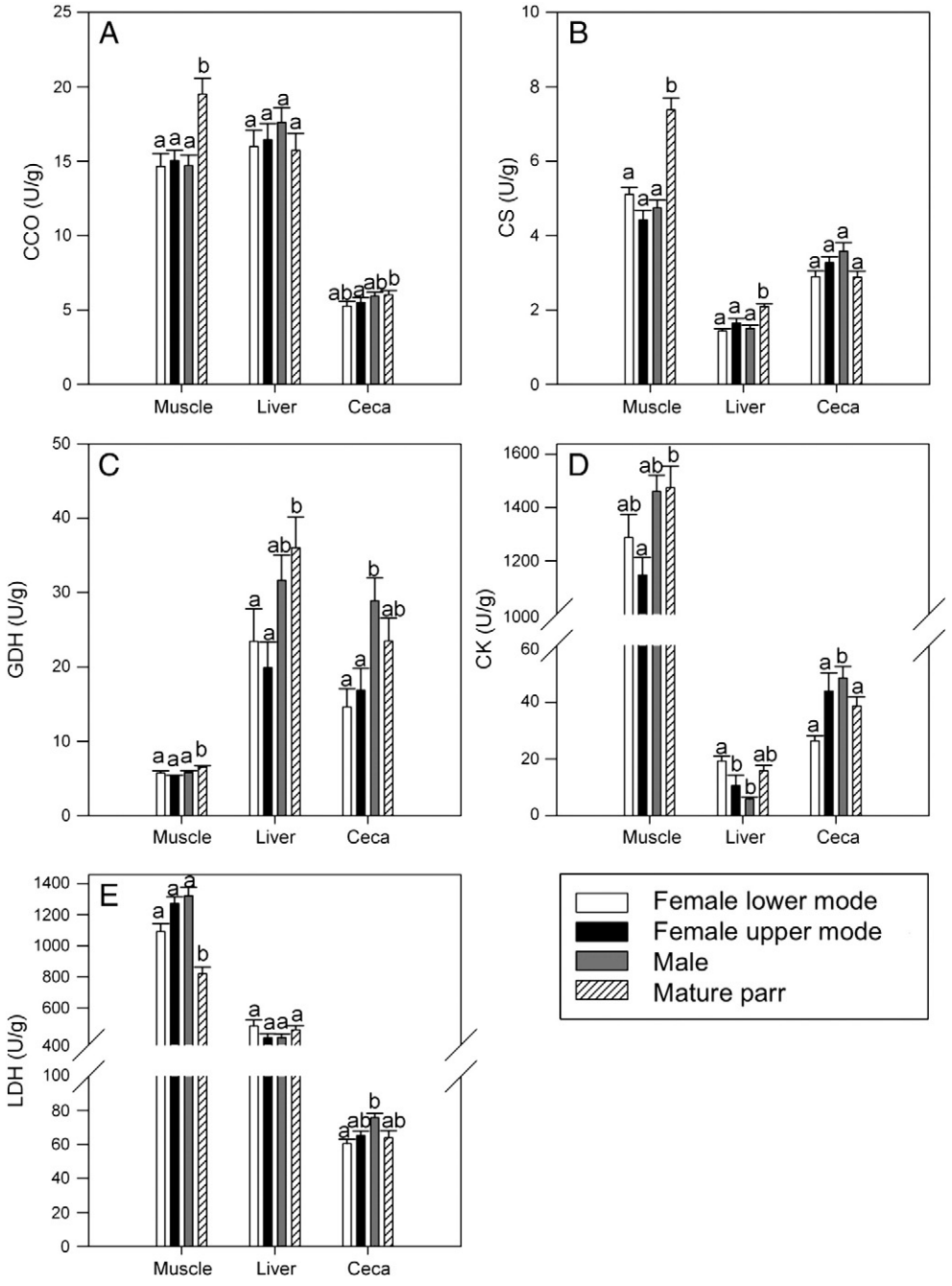

Fig. 6. Specific enzyme activities in muscle, liver and pyloric ceca according to modal group; mature parr (black bars, N = 39), male pre-smolt (pale grey bars, N = 40) and female smolt lower pre-mode (light grey) and female upper mode (medium grey bars, N = 51). Values are means ± S.E. Enzyme activities, CCO (A), CS (B), GDH (C), CK (D) and LDH (E), are shown as U/g wet mass. Samples used for these measurements were randomly chosen among the families (Fig. 2). When columns have different letters, they differ significantly (*a posteriori* tests, $p<0.05$). When there are no letters, the modal group did not have a significant effect on enzyme activities.

portion of their life cycle. Marked bimodality of the length frequency distributions of Atlantic salmon reared under artificial conditions (Metcalfe et al., 1989; Villarreal and Thorpe, 1985) indicates that salmonid growth is highly regulated. Our comparison of the growth of male and female parr suggests that the "decision" to undergo smoltification is the primary driver of growth rates and that reproductive maturation plays a secondary role. In January 2006, at 10 months after hatching, future male pre-smolts were only slightly larger than future mature male parr, with the same holding true for the upper and lower mode females. By November 2006, bimodality was pronounced for females and males. The relationships between length in January and growth rates of the individuals in the upper and lower modes were parallel, suggesting regulated suppression of growth in the fish in the lower mode, rather than a passive response to differing access to food. Smoltification increases the day-length sensitivity of the cortisol and growth hormone pathways, as well as modifying circulating levels of cortisol, growth hormone, prolactin, thyroxin, insulin and insulin-like growth factor 1 (McCormick, 2009). Such hormonal changes presumably accelerate growth. Clearly, the slowed growth of fish in the lower mode was not due to reproductive maturation, since females in the lower mode did not mature. Nonetheless, in families with a high proportion of offspring in the lower modal group, growth of mature male parr was slower than that of the lower modal group females. Families varied markedly in the proportion of female pre-smolt in the lower mode, in the proportion of mature male parr and in growth rates, suggesting heritability of the

growth and maturation characteristics of Atlantic salmon (Páez et al., 2011). Inter-family differences in growth rate would influence the probability of the offspring reaching the threshold for smoltification.

Several authors connect bimodality in salmon size structure to variation in the year of smoltification within sibling groups kept under similar conditions (Metcalfe et al., 1989). The decision of whether or not to smolt the following spring is made in the summer (Metcalfe et al., 1989; Metcalfe and Thorpe, 1990; Thorpe et al., 1982; Villarreal and Thorpe, 1985). The separation of males into two groups according to reproductive tactic markedly reduced the abundance of future male pre-smolts in the lower size mode making it impossible for us to obtain sufficient individuals for a systematic physiological analysis. Bailey et al. (1980) found high proportions of mature male parr among the lowest modal length group in November of their first year, and a few mature fish in the upper modal groups (Bailey et al., 1980). Thorpe and Morgan (1980) found mature male parr only in the lowest modal groups at the end of their second year (Thorpe and Morgan, 1980). In other words, mature parr are generally from the lower mode and larger parr become pre-smolts. The marked bimodality of females indicates that delayed somatic growth is not a consequence of gonadal development. Rather, growth of lower mode females would have been suppressed after they did not attain the threshold for smoltification. These conditional thresholds are thought to be active during specific developmental periods (Thorpe et al., 1998). That the sizes of the future upper and lower mode fish were already separated in January suggests that the window for future smoltification was open at or near that time.

The physiological differences we observed between mature male parr and the pre-smolts were likely the consequence rather than the cause of their reproductive tactic. Routine metabolic rates were higher in males and females from the lower mode than in the larger pre-smolts, as expected with the size dependence of metabolic rates. Ontogenetic increases in size systematically lead mass specific metabolic rates to decrease, partly due to a decrease in the proportion of metabolically demanding tissues (Goolish, 1995). Differences in rates of protein synthesis and breakdown (Morgan et al., 2000) are likely to underlie the differing growth rates and are probably under hormonal control. Muscle metabolic capacities point to a higher aerobic capacity for muscle of mature male parr relative to similarly sized females. Here, a specific response to the reproductive tactic seems likely. The other differences in tissue metabolic capacities measured at 1.5 years of age did not reveal a mechanism leading to the different modal groups.

High routine metabolic rates can decrease metabolic efficiency and slow growth. Thus the higher the mean routine metabolic rates of offspring from our families, measured at emergence, the lower the future growth of offspring in these families. In laboratory rearing with its high food availability, obtaining food does not require as much effort as prey capture in the natural environment. Our results indicate that in the laboratory rearing, the costs of high routine metabolic rates outweigh the advantages, leading to slower growth by the offspring from families with higher routine metabolic rates. On the other hand, recently emerged Atlantic salmon alevins that are dominant in paired interactions have higher standard metabolic rates than the subordinates (Metcalfe et al., 1995). Dominance can bring many advantages, including territory possession and improved feeding opportunities, but the costs of high metabolic rates, be they standard or routine, can reduce growth rates. Accordingly, we found inter-family differences in metabolic rates (at emergence) explained a considerable portion of the interfamily variability in future growth.

Although the upstream and downstream populations of Atlantic salmon in the Ste. Marguerite River have diverged genetically (Garant et al., 2002) and although the upstream populations show a greater incidence of mature male parr (Aubin-Horth et al., 2006), neither the population of origin nor the paternal reproductive tactic influenced the reproductive tactic or the proportion of females in the upper or lower mode. Furthermore, population and paternal reproductive tactic did not influence the physiological capacities of salmon, either at hatching, emergence (Rossignol et al., 2010) or after 1.5 years (this study). At 1.5 years, metabolic and enzymatic traits were only influenced by the modal group. The reproductive tactic of fathers was suggested to influence that of his male offspring (Glebe and Saunders, 1986) and such an influence seemed apparent early during ontogeny in the field (Garant et al., 2002). But, in our study of the actual choice of reproductive tactic by offspring, this hypothesis was not supported. In the families of the 6 anadromous fathers, 53% ± 16 of their male offspring became pre-smolts and 47% ± 16 became mature parr, whereas for the 8 fathers that were mature parr, 46% ± 20 of their male offspring became pre-smolts and 54% ± 20 became mature parr. Thus there was no significant relationship between the paternal reproductive tactic and the reproductive tactic "chosen" by their offspring. However, the marked inter-family differences in reproductive tactic, metabolic rate, protein content, juvenile mass and tissue metabolic capacities suggest considerable heritability. Complementary studies on estimated heritability are underway.

The causes of slower growth by the salmon in the lower mode may include reduced food intake, social stress, high metabolic rate or lack of hormonal stimulation of growth. Whereas the existence of two size modes among the female pre-smolts indicates that reproductive maturation, per se, is not the only cause of slow growth, the lower hepatosomatic index and ceca index of the mature parr relative to the lower mode females suggest that maturation reduced the capacity for food assimilation. Gonadal development would logically be detrimental to muscle growth in the mature male parr. Indeed, the muscle mass (and proportion of muscle) in mature male parr was lower than that of lower mode females. The markedly higher specific activities of mitochondrial enzymes in muscle of mature parr than in the other modal groups, suggest a higher aerobic capacity in axial muscle of mature parr. The greater swimming activity of mature parr may be facilitated by these higher activities (Morasse et al., 2008; Tucker and Rasmussen, 1999). Organ proportions indicate that reproductive maturation not only diverted ingested food to gonad growth but also decreased the capacity for food digestion and assimilation and led to a more aerobic metabolic profile in swimming muscle. Systematic differences in tissue metabolic capacities between upper and lower mode pre-smolts were not apparent, taking a back seat to sex differences that were not linked with growth trajectory.

In conclusion, the growth trajectories of juvenile Atlantic salmon differed among families, leading to marked variation in the proportion of offspring in the upper and lower growth modes and thus in the proportion of mature parr. These different trajectories led routine metabolic rate to vary between fish in the lower and upper modes, following the allometry typical of metabolic rates. Reproductive maturation was linked with differences in tissue metabolic capacities, with mature male parr having higher muscle aerobic capacities and lower glycolytic capacities than similarly sized females. As male and female juveniles in the lower modal group both suppressed growth, reproductive maturation was not the primary cause of slowed growth. We suggest that family differences in the penetration of offspring into the upper modes reflect inter-family variation in growth and in routine metabolic rate during early life. Fry with low metabolic rates would grow more quickly and would be more likely to exceed the size threshold for smoltification than those with high metabolic rates. Reproductive maturation subsequently would cause differences in anatomic proportions (e.g. muscle and ceca mass) and tissue metabolic capacities between lower mode females and mature male parr. The combined operation of the "decisions" for smoltification and reproductive maturation would dictate the physiological capacities of Atlantic salmon, with interfamily differences in routine metabolic rate at early stages being one factor that underlies the differences in growth rate that influence the passage of these thresholds.

Acknowledgements

We thank the staff at La Station Piscicole at Tadoussac (Qc), Serge Higgins and Jean Christophe Therrien at the Laboratoire de Recherche en Siences Aquatiques (LARSA), Université Laval (Qc), for their help in raising the fish. We also thank Nicolas Martin and Marie-Claude Lamarche for help. We give special thanks to David Páez for his help with the experiments, the statistical analysis and for his insightful and constructive comments. We also thank Prof. Neil Metcalfe for his constructive comments. This work was funded by a research grant from an NSERC grant (Strategic programme) awarded to L. Bernatchez., J.J. Dodson, and H. Guderley and is part of the research activities of CIRSA and RAQ (Reseau d'aquaculture du Québec).

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