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Genetically based population divergence in overwintering energy mobilization in brook charr (*Salvelinus fontinalis*)

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Abstract Investigating the nature of physiological traits potentially related to fitness is important towards a better understanding of how species and/or populations may respond to selective pressures imposed by contrasting environments. In northern species in particular, the ability to mobilize energy reserves to compensate for the low external energy intake during winter is crucial. However, the phenotypic and genetic bases of energy reserve accumulation and mobilization have rarely been investigated, especially pertaining to variation in strategy adopted by different populations. In the present study, we documented variation in several energy reserve variables and estimated their quantitative genetic basis to test the null hypothesis of no difference in variation at those traits among three strains of brook charr (*Salvelinus fontinalis*) and their reciprocal hybrids. Our results indicate that the strategy of winter energy preparation and mobilization was specific to each strain, whereby (1) domestic fish accumulated a higher amount of energy reserves before winter and kept accumulating liver glycogen during winter despite lower feeding; (2) Laval fish used liver glycogen and lipids during winter and experienced a significant decrease in condition factor; (3) Rupert fish had relatively little energy reserves accumulated at the end of fall and preferentially mobilized visceral fat during winter. Significant heritability for traits related to the accumulation and use of energy reserves was found in the domestic and Laval but not in the Rupert strain. Genetic and phenotypic correlations also varied among strains, which suggested population-specific genetic architecture underlying the expression of these traits. Hybrids showed limited evidence of non-additive effects. Overall, this study provides the first evidence of a genetically based—and likely adaptive—population-specific strategy for energy mobilization related to overwinter survival.

Keywords Heritability · Non-additive effects · Energy mobilization strategy · Local adaptation · Genetic and phenotypic correlation · Fish physiology

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Introduction

Understanding the adaptive potential of populations is a central goal in evolutionary biology. While phenotypic plasticity may allow populations to adapt in the short-term, phenotypic evolution is necessary for the long-term persistence of populations (Gienapp et al. 2008; Visser 2008; Bjorklund et al. 2009; Hoffmann and Sgro 2011). This requires a sufficient genetic component of variance of fitness-related traits upon which selection may act (Falconer and Mackay 1996; Kellermann et al. 2006; Serbezov et al. 2010). While heritability of traits (h^2) is the most commonly used predictor of evolutionary potential (Falconer and Mackay 1996; Lynch and Walsh 1998), other parameters such as the coefficient of additive genetic variance of traits (CV_A) can provide further insight into the potential of organisms to respond to selection (Houle 1992; Hermida

et al. 2002). Also, the amount of additive genetic variance and heritability of traits typically differs among populations (Visscher et al. 2008) and there is thus a growing interest in investigating intraspecific variation, specifically on important physiological traits, and its underlying genetic basis (Zamer et al. 1999; Nespolo et al. 2003; Ronning et al. 2007; Tieleman et al. 2009). Such investigations are essential to assess if an adaptive response could be expected and the degree to which such response might differ among populations of a same species.

Energy mobilization during the first winter of life is an important physiological trait in populations from temperate climates since it could crucially affect survival and thus population dynamics and recruitment (Sogard 1997; Child and Laing 1998; Huss et al. 2008). Under cold climatic conditions, the annual fluctuations in temperature and food productivity create cycles in energy availability. These cycles induce periods of energy reserve accumulation and depletion in many vertebrates (Xiang and Peichao 1990; Boutilier et al. 1997; Hutchings et al. 1999; Box et al. 2010; Vollenweider et al. 2011). Because of low temperatures, short days, and limited food access, winter is a critical period for survival, especially for juvenile life stages (Finstad et al. 2004; Altwegg et al. 2005; Pelletier et al. 2007; Robles et al. 2007). To compensate for the low energy intake and to reduce mortality risk, organisms rely on their ability to mobilize endogenous energy reserves (Boutilier et al. 1997; Schultz and Conover 1999; Pelletier et al. 2007; Heermann et al. 2009). In many vertebrates, this ability to deal with winter constraints operate in a size-dependent manner, with larger individuals being favoured due to the allometry of energy metabolism (Suttie and Webster 1995; Cargnelli and Gross 1997; Schultz and Conover 1999; Hodges et al. 2006; Heermann et al. 2009).

The general pattern of energy reserve mobilization in freshwater fish is characterized by the depletion of glycogen (inducing a reduction of liver mass), followed by the use of perivisceral fat and hepatic lipids, and finally by the depletion of tissue proteins (Collins and Anderson 1995; Rios et al. 2006). A marked depletion of energy reserves can then have a critical impact on an organism's health and survival probability (Eckmann 2004; Hodges et al. 2006; Huss et al. 2008; Tattersall and Ultsch 2008). Yet, little is known about the genetic basis of such a strategy and thus on the ability of populations to physiologically adapt to different selection pressures.

Intraspecific variations in behavioural or energetic strategies to cope with winter have been documented in several species (Schultz and Conover 1997; Goto et al. 1999; Polo et al. 2007; Tattersall and Ultsch 2008; Finstad et al. 2010). In these studies, the differences in behaviour or energy storage and depletion were generally linked to local adaptations and followed latitudinal clines, with northern populations being more tolerant to winter temperatures and more efficient with regard to behaviour or energy processes (Schultz et al. 1998; Goto et al. 1999; Polo et al. 2007; Tattersall and Ultsch 2008; Finstad et al. 2010). Thus, strategies for building winter energy reserves could also result from genetically based local adaptations (Schultz and Conover 1997; Billerbeck et al. 2001; Polo et al. 2007; Finstad et al. 2010). However, since previous studies have generally been conducted in the field, the distinction of genetic versus environmental or plastic effects on these traits has remained difficult to disentangle (Hoffmann and Merilä 1999; Stelkens et al. 2009). While the few studies conducted in a common environment suggested the presence of a genetic basis for rates of energy accumulation (Schultz and Conover 1997), the actual quantitative genetic basis of energy reserve accumulation and mobilization has rarely been documented. Nevertheless, there is a growing interest in determining the heritability of body composition traits in the context of selective breeding programs in fishes (Kause et al. 2002; Neira et al. 2004; Tobin et al. 2006; Navarro et al. 2009; Saillant et al. 2009) and other economically important vertebrates (Lo et al. 1992; Hickey et al. 2007).

Besides allowing an estimate of heritability, inter-strain hybridization can also provide important information on the genetic basis of performance. When populations are genetically closer and display significant heritabilities for traits of interest, hybrids can express additive effects and show performance levels intermediate to those of parental lines. Conversely, when populations are genetically divergent and adapted to their own environments, hybrids can express non-additive effects due to complex genetic associations that can enhance (heterosis) or reduce (outbreeding depression) performance (Falconer and Mackay 1996; Edmands 1999; Stelkens et al. 2009). Non-additive effects have been observed for different physiological traits such as growth rate, survival, and other fitness-related traits, revealing evolutionary divergence among populations (Emlen 1991; Hotz et al. 1999; Rieserberg et al. 1999; Cooke et al. 2001; Tymchuk et al. 2007) including those of brook charr (Granier et al. 2011). However, the occurrence of non-additive effects underlying energy processes has never been investigated.

In this study, we investigate intraspecific strategies of energy mobilization in three strains of brook charr (*Salvelinus fontinalis*) and their reciprocal hybrids by documenting the phenotypic and genetic bases of traits related to the accumulation of energy reserves in fall and their use during the first winter of life. More specifically, the objectives were (1) to compare energy reserve accumulation and mobilization among strains during winter in order to determine how local adaptation might have shaped this trait, (2) to estimate heritability and genetic correlations in traits related to energy reserves in a

common environment, and (3) to evaluate the importance of non-additive effects in the energy strategies.

Materials and methods

Details pertaining to strain origin, breeding design and family rearing are presented in details in Crespel et al. (2011). We thus only briefly summarize this information below.

Brook charr strains

Three genetically distinct strains of brook charr (Martin et al. 1997) were used as parental lines. The Laval strain originates from a wild population of anadromous brook charr from the Laval River (48°44′N; 69°05′W) on the north shore of the St. Lawrence estuary (QC, Canada). The fish used were from third generation breeders produced in captivity at the Station aquicole of ISMER/UQAR (Rimouski, QC, Canada). The Rupert strain originates from a northern lacustrine freshwater resident wild population inhabiting the Rupert River system (51°05′N; 73°41′W) (QC, Canada). These third generation breeders were reared in captivity at the Laboratoire Régional en Sciences Aquatiques (LARSA, Université Laval, Québec, QC, Canada). The third group was a domestic freshwater strain that has been widely used by the Québec fish farming industry for more than a hundred years. It originates from two strains (Nashua and Baldwin), and breeders were obtained from the Pisciculture de la Jacques Cartier (Cap-Santé, QC, Canada).

Breeding design

Hybrid and purebred crosses were made from mid-November 2005 until the end of December 2005 at LARSA using eggs and milt obtained from the different fish rearing locations. Three purebred strains were produced: ♀ domestic × ♂ domestic ($D_♀D_♂$), ♀ Laval × ♂ Laval ($L_♀L_♂$), and ♀ Rupert × ♂ Rupert ($R_♀R_♂$). Five reciprocal hybrids were produced: $D_♀R_♂$, $D_♀L_♂$, $L_♀D_♂$, $L_♀R_♂$, and $R_♀L_♂$. It was not possible to obtain the $R_♀D_♂$ cross because of the temporal differences in sexual maturation between these two strains (October for domestic males and December for Rupert females). All breeders were used only once. For each cross, 10 full-sib families were obtained through single-pair mating.

Family rearing

During the first 6 months, i.e., from egg incubation (January) to exogenous feeding (June), families were kept separate in recirculating fresh water and reared in seven troughs, each of which was divided into twelve units at LARSA. Water temperature was maintained at 6 °C during egg incubation and at 8 °C after hatching. In June, families were transferred to nine 3 m^3 tanks, with eight families pooled per tank. Prior to transfer, families from all cross types were randomly assigned to the different pools, with cross type randomized in pools, and were marked to allow for identification by different combinations of adipose and pelvic fin clippings. All families were brought to the same fry stage by the end of the summer and maintained at 10 °C in recirculating fresh water. The photoperiod followed the natural seasonal cycle, and fish were fed according to commercial charts. In September, fish were transferred to the Station aquicole ISMER/UQAR, where they were reared in 10 0.5 m^3 indoors tanks, with six to eight families per tank depending on the initial poolings made at LARSA, under natural temperature and photoperiod conditions in running dechlorinated fresh water. Fish were fed daily (1 % w/w ration) with commercial dry pellets until water temperature decreased to 4 °C (in January); fish were then fed twice a week. Due to the limited number of fish in some families, the number of families used for this experiment was 10 for $L_♀R_♂$, 9 for $L_♀D_♂$ and $L_♀L_♂$, 8 for $D_♀D_♂$, 7 for $D_♀L_♂$ and $D_♀R_♂$, 6 for $R_♀L_♂$, and 5 for $R_♀R_♂$. A daily record of mortalities was made throughout the winter and the relative mortality was determined for each family.

Sampling

Two samplings were performed during the first winter to evaluate energy mobilization among the different crosses: one in December (water temperature at 7 °C) and the second in March (water temperature at 3 °C) (Fig. 1). For each sampling, ten fish per family were sacrificed (total number of fish sampled = 1220) by anaesthesis in MS 222 (0.16 g/L [3-aminobenzoic acid ethyl ester]) and their body mass (to the nearest 0.1 g) and fork length (0.1 cm) were measured. Condition factor was estimated according to the equation (weight/length^3) × 100. The liver was excised, weighed to determine the hepato-somatic index (HSI: liver weight/body weight × 100), rapidly frozen in liquid nitrogen, and stored at −80 °C until further analysis. Visceral fat deposits were collected, weighed, and expressed in percentage of body weight. One piece of epaxial dorsal muscle was excised, weighed, and dried for 72 h at 70 °C for the determination of water content. Liver glycogen concentration was measured using the amyloglucosidase digestion method (Carr and Neff 1984) followed by glucose concentration determination (QuantiChrom™ Glucose Assay kit, BioAssay Systems, USA); total liver lipid concentration was evaluated using the phospho-vanillin method (Frings et al. 1972); and liver protein

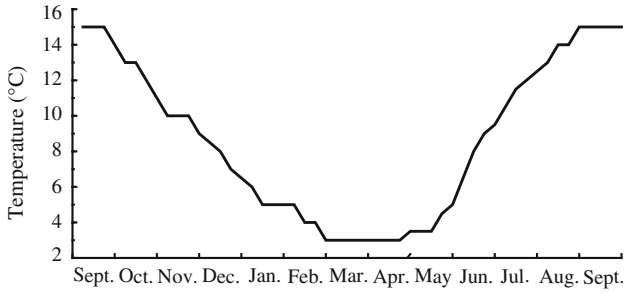


Fig. 1 Annual temperature profile of fresh water at the Station aquicole of ISMER/UQAR in Rimouski (QC, Canada)

concentration was determined using a protein dye binding method (Protein Assay kit, Biorad, USA) according to Bradford (1976). Total liver energy content was estimated after conversion of protein, total lipids, and glycogen concentrations to energy using conversion factors of 24, 38, and 17 kJ/g for proteins, lipids, and carbohydrates, respectively (Jobling 1993).

Statistical analyses

Data normality and homogeneity of variance were verified with Kolmogorov–Smirnov and Brown-Forsythe tests, respectively. Muscle water content (rank), liver total energy content (log), and survival index (arcsin) data had to be transformed to obtain normality. The different response variables were analyzed using mixed models with cross-type, sampling time, and their interaction fitted as fixed effects and full-sib families fitted as a random effect. The percentage of fish that died during winter was analyzed using one-way ANOVA with cross-type as factor ($n = 61$ families). The presence of non-additive effects was determined by the presence of significant differences between the mean trait values of each reciprocal hybrid compared to the mean traits of both parental strains according to the model results (Bryden et al. 2004). The a posteriori Tukey test was used for mean comparisons when possible or replaced by the Games and Howell test when variances were not homogenous. Analyses were made using Statistica 7.0 version for Windows (StatSoft, USA). A significance level of $\alpha = 0.05$ was used in all statistical tests.

Quantitative genetic analysis

Our breeding design was used to fit animal models (Lynch and Walsh 1998) based only on the three pure strains (not the hybrid crosses) with the software ASReml (V 2.0; Gilmour et al. 2006). Variance components for all traits in each purebred population were estimated by Restricted Maximum Likelihood (REML) using the following model:

$$y = \mu + Months + G + e$$

where y is the phenotypic observation for each population in December and March, μ is the overall mean, *Months* is the fixed effect of the sampling time, G is the random genetic effect linked to the pedigree structure (full-sib families), and e is the random residual effect. The total phenotypic variance (V_P) of each trait was decomposed into genetic variance (V_G) and residual variance (V_R). The broad-sense heritability (H^2) for each trait was estimated as the ratio of the estimated genetic variance to the total phenotypic variance ($H^2 = V_G/V_P$). A complementary analysis using calculations of evolvability (Houle 1992) was also done. Overall, heritability and evolvability estimates were comparable and positively correlated ($r = 0.74$; when assessed over all traits and strains). Consequently, only the heritability results are presented and interpreted in the manuscript.

Genetic and phenotypic correlations were also estimated in each purebred strain using bivariate models between traits for which heritability was significant (10 bivariate models in the Domestic strain, 10 bivariate models in the Laval strain, and one bivariate model in the Rupert strain) using the relationship $r_G = COV_{Ai,j}/(V_{Ai}\ V_{Aj})^{1/2}$ and $r_P = COV_{Pi,j}/(V_{Pi}\ V_{Pj})^{1/2}$, respectively. Standard errors for variance and covariance components as well as for heritabilities and genetic correlations were also estimated by the bivariate models using the ASReml software. The statistical significance of the estimated genetic variances and covariances in each population were tested by comparing the full model with a constrained model in which the (co)variance was set to zero using a likelihood ratio test (against a Chi square distribution, where $\chi^2 = -2$*difference in log likelihood). The statistical significance of estimate comparisons among populations were tested using a likelihood ratio test that compared a model including all three purebred strains, and where all variance components were estimated independently for each population, to a constrained model in which estimates were set to be equal among the three strains.

Results

Overwinter mortalities were low (mean of 2.4 % with a range from 0.32 % ± 0.12 in $D_{♀}L_{♂}$ to 5.60 % ± 3.60 in $D_{♀}R_{♂}$) and similar among crosses ($F_{1,7} = 1.61$, $P > 0.05$). However, the difference in the use of energy reserves during winter varied among cross-types (significant interactions between sampling time and cross-types for all variables measured). Tables 1 and 2 summarize the statistical results of all energy reserves. The percentage of total variance explained by the models varied from 5 %

(liver protein concentration) to 53 % (total liver energy content).

Condition factor

In December, domestic fish had a significantly higher condition factor than those of the other two pure strains (Tables 1 and 3). Condition factors in hybrids were similar to parental lines for hybrids between the Laval and Rupert lines and to the leaner parental line in hybrids issued from the domestic line ($L_♀D_♂$, $D_♀L_♂$, and $D_♀R_♂$). The condition factor in March was significantly lower than in December in almost all cross-types. The only two exceptions were the $D_♀D_♂$, and $D_♀R_♂$ crosses, where condition factors in December and March were similar (Tables 1 and 3). The strongest decrease in condition was observed in the $L_♀L_♂$ cross-type (22 % reduction in March compared to December; Table 3), whereas the decreases observed in hybrids were intermediate compared to their parental lines (Table 3).

Body reserves

Domestic fish had more visceral fat in December than the Laval and Rupert fish (Tables 1 and 3). Hybrids generally accumulated amounts of visceral fat similar to the parental line that accumulated the higher amount of fat, suggesting a possible dominance of the "fatty" phenotype. The $R_♀L_♂$ hybrid accumulated more visceral fat than either parental line, suggesting that there were non-additive effects for this trait (Table 3). The $R_♀R_♂$, $R_♀L_♂$, and $L_♀R_♂$ crosses were the only ones to significantly deplete their visceral fat during winter (Tables 1 and 3).

In both December and March, domestic fish had the lowest muscle water content, Laval fish had the highest, and Rupert fish were intermediate (Tables 1 and 3). In hybrids, muscle water content was always similar to the parental line that showed the lower muscle water content, suggesting dominance of this phenotype, except for the $D_♀R_♂$ hybrid, which was intermediate (see Table 3). December and March results were similar except for the $L_♀R_♂$ hybrid, which had higher muscle water content in March (Table 3). This increase of muscle water content in hybrids, with no change in their parental lines, indicates the presence of non-additive effects (Table 3).

In December, domestic and Laval fish had significantly higher HSI than the Rupert individuals (Tables 1 and 3). HSI in hybrids was always intermediate to that of the parental lines, suggesting additive effects for this trait (Table 3). In March, the HSI was higher than in December in the domestic strain while the reverse trend was observed in the Laval strain (Table 3). No difference was observed among sampling periods in the Rupert strain (Table 3). For hybrids, the seasonal variation was intermediate ($L_♀D_♂$, $D_♀L_♂$) or similar (hybrids issued from the Rupert line) to that of the parental lines (Table 3).

Liver reserves

In December, domestic fish had significantly more glycogen per gram of liver than those from the Laval strain with Rupert fish being intermediate (Tables 2 and 4). Hybrids had relative liver glycogen concentrations similar to their maternal line (Table 4). Non-additive effects were present in the $D_♀R_♂$ cross-type, with glycogen concentration being lower than in fish from either parental line (Table 4). Relative liver glycogen increased during winter in fish from the domestic strain while Laval fish used this energy reserve, as indicated by a significant decrease in March (Table 4). No overall change was observed in Rupert fish (Table 4). Hybrids from the Laval and the Rupert lines showed results similar to the Rupert strain, and the $D_♀L_♂$ hybrid had an intermediate response compared to its parental lines, with no difference between relative

Table 1 Summary of the mixed model statistics on sampling time × cross-type interactions for condition factor and traits related to body energy reserves (visceral fat, muscle water content, and HSI [hepato-somatic index])

	Condition factor			Visceral fat (%)			Muscle water content (%)			HSI (%)		
	df	F	*P* value	*df*	F	*P* value	*df*	F	*P* value	*df*	F	*P* value
Sampling time	1	359.7	<0.001	1	39.6	<0.001	1	0.5	0.49	1	0.1	0.92
Cross-type	7	20.6	<0.001	7	5.9	<0.001	7	16.3	<0.001	7	17.2	<0.001
Sampling time × cross-type	7	15.0	<0.001	7	6.6	<0.001	7	8.4	<0.001	7	10.4	<0.001
Family (nested in cross-type), random	53	3.4	<0.001	53	6.1	<0.001	53	3.7	<0.001	53	3.7	<0.001
Residual error	1147			1147			1147			1147		
Model R^2	0.51			0.36			0.37			0.39		
Adjusted R^2	0.48			0.33			0.34			0.35		

Table 2 Summary of the mixed model statistics on sampling time × cross-type interactions for liver energy reserve traits (glycogen, protein, lipid, and total energy)

	Liver glycogen (mg/g)			Liver protein (mg/g)			Liver lipid (mg/g)			Total energy (kJ)		
	df	F	*P* value	*df*	F	*P* value	*df*	F	*P* value	*df*	F	*P* value
Sampling time	1	2.8	0.1	1	39.7	<0.001	1	25.2	<0.001	1	0.3	0.61
Cross-type	7	13.8	<0.001	7	3.1	0.008	7	12.0	<0.001	7	25.3	<0.001
Sampling time × cross-type	7	28.3	<0.001	7	2.5	0.02	7	3.0	0.004	7	9.9	<0.001
Family (nested in cross-type), random	53	3.4	<0.001	53	0.9	0.69	53	1.5	0.02	53	5.9	<0.001
Residual error	1122			1124			1124			1121		
Model R^2	0.38			0.10			0.18			0.56		
Adjusted R^2	0.35			0.05			0.13			0.53		

glycogen concentration in December and March. The $L_{♀}D_{♂}$ and $D_{♀}R_{♂}$ hybrids had overall winter variations similar to the domestic strain, with an increase of liver glycogen (Table 4).

Relative liver protein concentrations (mg/g of liver) were similar among all cross-types in December (Tables 2 and 4). No change in relative liver protein was observed over winter for any of the purebred crosses (Table 4). However, the $D_{♀}R_{♂}$ and $L_{♀}D_{♂}$ hybrids showed a significantly lower protein concentration in March than in December (Table 4), suggesting the presence of non-additive effects. All others hybrids were similar to their parental lines (Table 4).

Domestic fish had significantly higher relative total liver lipid concentration (mg/g of liver) in December than the Laval and Rupert fish (Tables 2 and 4). The relative liver lipid concentration in hybrids was generally not significantly different from those of their parental lines. The only exception was the $D_{♀}R_{♂}$ hybrids, which were closest to the paternal Rupert line (Table 4). At the end of winter, only the $L_{♀}L_{♂}$ cross-type showed a significant decrease in relative liver total lipid concentration while no change was observed in the two other purebred crosses (Table 4). The $L_{♀}R_{♀}$ hybrids also expressed a decrease in relative liver lipid concentration (Table 4). No change in liver lipid content was observed in the other hybrids.

The total liver energy content was significantly higher in December in domestic fish than in Laval and Rupert strains (Table 4). Most of the hybrids had intermediate total liver energy content compared to their parental lines, except for the $R_{♀}L_{♂}$ and $L_{♀}R_{♂}$ hybrids, which were both similar to the $R_{♀}R_{♂}$ cross-type (Table 4). The pure Laval strain was the only strain for which the liver energy content was lower in March than in December (Table 4). All other pure and hybrid cross-types showed no change in their liver energy content, suggesting dominance of the "high energy" phenotype in hybrids.

Genetic effects and heritability

Significant genetic variances were observed for all traits (Table 5) except for liver protein and lipid concentrations. However, there were notable differences among strains. In the domestic strain, genetic variances for visceral fat, muscle water content, HSI, and liver total energy content were all significant and showed medium to high values of heritability (see Table 5). In the Laval strain, there was a significant genetic variance with medium heritability for the condition factor ($H^2 = 0.32$), visceral fat ($H^2 = 0.31$), HSI ($H^2 = 0.26$), and relative liver glycogen concentration ($H^2 = 0.42$) (Table 5). In contrast, condition factor for the Rupert strain was the only trait for which a significant genetic component of variance was found and for which heritability was high ($H^2 = 0.50$) (Table 5). Finally, the parameters for visceral fat and liver total energy content were significantly different among strains (Table 5).

Genetic and phenotypic correlations

Significant genetic covariances and phenotypic correlations were present between fish body mass and energy reserves, but again these differed among strains (Table 6). In domestic fish, significant genetic covariances and strong correlations were obtained between body mass and two energy reserve indices—visceral fat ($r_G = 0.75$) and total liver energy content ($r_G = 0.99$) (Table 6). These two energy reserves were also highly correlated to each other ($r_G = 0.69$; Table 6). No significant genetic covariances were detected between body mass and any of the energy reserve traits in the Laval strain (Table 6). However, in the same strain, significant genetic covariances and high genetic correlations ($r_G > 0.90$) were observed between condition factor and two energy reserve indices, i.e., visceral fat and relative liver glycogen (Table 6). These two energy reserve indices were also highly correlated with

Table 3 Body condition and energy reserves measured as condition factor, visceral fat (%), muscle water content (%), and HSI (hepato-somatic index; %) in the three purebred strains (bold) and their hybrids in December and March

Cross	December					March				
	n	Condition factor	Visceral fat (%)	Muscle water (%)	HSI (%)	n	Condition factor	Visceral fat (%)	Muscle water (%)	HSI (%)
$D_{♀}R_{♂}$	70	1.02 ± 0.01^{fg}	2.50 ± 0.12^{cde}	78.5 ± 0.14^{bcd}	1.35 ± 0.03^{c}	68	0.98 ± 0.02^{cdef}	2.41 ± 0.14^{cde}	78.0 ± 0.12^{ab}	1.47 ± 0.05^{c}
$D_{♀}D_{♂}$	**80**	**1.11 ± 0.01^{h}**	**2.84 ± 0.12^{de}**	**78.2 ± 0.11^{abc}**	**1.64 ± 0.03^{d}**	**80**	**1.07 ± 0.01^{gh}**	**2.32 ± 0.11^{cd}**	**77.8 ± 0.10^{a}**	**1.84 ± 0.05^{e}**
$D_{♀}L_{♂}$	70	1.05 ± 0.01^{fg}	2.90 ± 0.12^{e}	78.1 ± 0.07^{ab}	1.57 ± 0.03^{d}	70	0.94 ± 0.01^{cd}	2.39 ± 0.15^{cde}	78.3 ± 0.10^{abcd}	1.61 ± 0.04^{d}
$L_{♀}D_{♂}$	90	1.04 ± 0.01^{fg}	3.01 ± 0.31^{cde}	78.6 ± 0.12^{cde}	1.66 ± 0.04^{de}	90	0.93 ± 0.01^{c}	2.92 ± 0.15^{de}	78.3 ± 0.11^{abcd}	1.66 ± 0.04^{de}
$L_{♀}L_{♂}$	**90**	**0.99 ± 0.02^{def}**	**1.71 ± 0.11^{ab}**	**80.0 ± 0.31^{g}**	**1.63 ± 0.03^{d}**	**89**	**0.77 ± 0.01^{a}**	**1.62 ± 0.11^{ab}**	**79.9 ± 0.27^{g}**	**1.37 ± 0.02^{c}**
$L_{♀}R_{♂}$	100	0.98 ± 0.01^{de}	2.25 ± 0.09^{c}	78.7 ± 0.16^{cde}	1.35 ± 0.02^{c}	99	0.85 ± 0.01^{b}	1.40 ± 0.09^{a}	*79.2 ± 0.10^{fg}*	1.29 ± 0.02^{bc}
$R_{♀}L_{♂}$	60	1.00 ± 0.02^{def}	*2.71 ± 0.13^{de}*	78.6 ± 0.06^{ef}	1.33 ± 0.03^{bc}	60	0.87 ± 0.01^{b}	2.10 ± 0.15^{bc}	78.9 ± 0.14^{ef}	1.29 ± 0.04^{abc}
$R_{♀}R_{♂}$	**50**	**1.02 ± 0.01^{ef}**	**2.02 ± 0.14^{bc}**	**78.7 ± 0.27^{def}**	**1.18 ± 0.04^{a}**	**50**	**0.94 ± 0.01^{cd}**	**1.33 ± 0.10^{a}**	**78.7 ± 0.19^{cdef}**	**1.16 ± 0.03^{a}**

Mean ± SEM; n is the number of individuals. The different letters indicate significant differences among cross-types in December and March ($\alpha = 0.05$). In December, italic indicates hybrids that had significantly more or less energy reserves than both parental lines (non-additive effects). In March, italic indicates hybrids that used significantly more or less energy reserves than both parental lines during winter (non-additive effects)

Table 4 Liver energy reserves measured as glycogen (mg/g), protein (mg/g), lipid (mg/g), and liver total energy (kJ) in the three purebred strains (bold) and their hybrids in December and March

Cross	December					March				
	n	Glycogen (mg/g)	Protein (mg/g)	Lipid (mg/g)	Total energy (kJ)	n	Glycogen (mg/g)	Protein (mg/g)	Lipid (mg/g)	Total energy (kJ)
$D_{♀}R_{♂}$	67	*45.5 ± 2.1*^{bc}	58.7 ± 2.1^{c}	25.7 ± 1.2^{cde}	0.92 ± 0.06^{de}	66	71.2 ± 4.3 ^{fg}	*48.5 ± 1.7*^{ab}	26.1 ± 1.3^{cdef}	1.49 ± 0.14^{ef}
$D_{♀}D_{♂}$	**80**	**61.4 ± 2.1**^{ef}	**54.9 ± 1.6**^{abc}	**31.9 ± 1.1**^{f}	**1.72 ± 0.13** ^{fg}	**79**	**91.2 ± 4.3** ^{g}	**48.6 ± 1.6**^{ab}	**31.4 ± 1.5**^{ef}	**2.53 ± 0.19** ^{g}
$D_{♀}L_{♂}$	67	56.8 ± 2.3^{def}	60.5 ± 1.9^{c}	27.2 ± 1.3^{cdef}	1.13 ± 0.08^{e}	69	65.3 ± 4.4^{def}	53.5 ± 1.6^{abc}	25.6 ± 1.2^{cde}	1.63 ± 0.18^{ef}
$L_{♀}D_{♂}$	88	50.1 ± 1.7 ^{cd}	57.5 ± 1.4^{c}	30.4 ± 1.3^{def}	1.21 ± 0.08^{e}	89	67.4 ± 3.5^{f}	*47.7 ± 1.4*^{a}	25.8 ± 1.1 ^{cd}	1.47 ± 0.12^{ef}
$L_{♀}L_{♂}$	**87**	**48.8 ± 2.2** ^{cd}	**54.8 ± 1.4**^{abc}	**25.6 ± 1.1**^{cde}	**0.44 ± 0.02**^{b}	**87**	**19.8 ± 2.1**^{a}	**55.5 ± 1.6**^{bc}	**18.6 ± 0.8**^{a}	**0.26 ± 0.02**^{a}
$L_{♀}R_{♂}$	99	44.4 ± 1.6^{bc}	58.3 ± 1.5^{c}	24.9 ± 0.8^{c}	0.64 ± 0.03^{c}	97	35.0 ± 2.6^{b}	53.8 ± 1.7^{abc}	19.0 ± 0.8^{ab}	0.56 ± 0.05^{bc}
$R_{♀}L_{♂}$	59	61.1 ± 2.8^{def}	57.6 ± 1.7^{bc}	26.9 ± 1.4^{cdef}	0.72 ± 0.06 ^{cd}	59	48.8 ± 4.7^{bcde}	54.5 ± 1.9^{abc}	23.9 ± 1.3^{bc}	0.69 ± 0.07^{bcd}
$R_{♀}R_{♂}$	**49**	**57.4 ± 3.3**^{def}	**59.1 ± 2.4**^{c}	**24.2 ± 1.4**^{abcd}	**0.48 ± 0.04**^{bc}	**49**	**46.6 ± 4.0**^{bcde}	**55.2 ± 2.2**^{abc}	**22.7 ± 1.2**^{abc}	**0.48 ± 0.04**^{bc}

Mean ± SEM; n is the number of individuals. The different letters indicate significant differences among cross-types in December and March ($\alpha = 0.05$). In December, italic indicates hybrids that had significantly more or less energy reserves than both parental lines. In March, italic indicates hybrids that used significantly more or less energy reserves than both parental lines during winter (non-additive effects)

each other and with HSI (r_G of 0.94, 0.88, and 0.83 for relative liver glycogen vs. visceral fat, visceral fat vs. HSI, and HSI vs. relative liver glycogen, respectively) (Table 6). In the Rupert strain, covariance between body mass and condition factor was not significant ($COV_A = -0.01$).

Discussion

The main objective of this study was to test for the existence of genetically based differences in energy accumulation and mobilization among strains of brook charr. Winter survival was comparable among strains, although each of them coped with winter conditions using different energy strategies (Fig. 2). A genetic basis was detected for traits related to body condition and energy storage/use in the domestic and Laval strains but not in the Rupert. Genetic and phenotypic correlations also varied among strains, which was therefore suggestive of population specific genetic architecture underlying the expression of these traits. Hybrids showed limited evidence of non-additive effects. Overall, this study provides strong evidence for a genetically based—and likely adaptive—population-specific strategy for energy mobilization related to overwinter survival.

Different strains exhibited different genetically based energy strategies to cope with constraints imposed by low winter temperature (see also Crespel et al. 2013). Domestic fish accumulated high amount of energy reserves before winter and kept accumulating liver glycogen during winter despite the lower amount of food being available compared to other seasons. Hepatic glycogen reserves play an important role in fish metabolism, and glycogen is the first form of energy that is accumulated after starvation (Rios et al. 2006; Heermann et al. 2009). Therefore, the domestic strain seemed to be relatively unaffected by low winter temperature conditions. Laval fish had low energy reserves at the onset of winter and seemed to have suffered energy costs during the coldest months since their condition factor was the most reduced by March. Anadromous Laval fish, like most anadromous salmonids, have a low condition factor and are more streamlined than their freshwater counterparts (Morinville and Rasmussen 2008). Therefore, the observed decrease in condition factor during winter may reflect the cost related to limited energy storage prior to winter. Anadromous fish overwinter away from their main feeding area and therefore may not be adapted to feed and accumulate energy during winter. Yet, mortality was no greater in Laval fish than in the other cross-types surveyed. During winter, the strategy of the Laval fish was thus to mobilize liver glycogen and lipids, which is similar to the general pattern of energy mobilization during starvation or limited energy intake in other fishes (golden perch, *Macquaria ambigua*, Collins and Anderson 1995; Traira, *Hoplias malabaricus*, Rios et al. 2006). In contrast, the strategy of Rupert brook charr, which also had relatively low energy reserves accumulated by the end of autumn, was to mobilize visceral fat during winter, which is compatible with the fact that these non-migratory fish overwinter in their main feeding area which could be used during the winter. A similar preferential use of visceral fat has been seen in starved gilthead seabream (*Sparus auratus*; Ibarz et al. 2010). To our knowledge, such difference in energy mobilization strategies among populations has never been documented previously in fishes. For aquatic organisms, perhaps the most comparable study to ours was performed in oysters, whereby it was observed that one species (*Ostrea edulis*) preferentially used lipids while the

Table 5 Estimates of the broad-sense heritability ($H^2 \pm$ SE) and genetic variance ($V_G \pm$ SE) for condition factor and the different traits related to energy reserves in the three purebred populations

	Domestic		Laval		Rupert		Difference
	H^2	V_G	H^2	V_G	H^2	V_G	*P* value
Condition factor	0.09 ± 0.10	0.001 ± 0.001	**0.32 ± 0.17**	**0.005 ± 0.003**	**0.50 ± 0.31**	**0.004 ± 0.004**	0.065
Visceral fat	**0.56 ± 0.25**	**0.481 ± 0.290**	**0.31 ± 0.17**	**0.340 ± 0.217**	0	0	0.033
Muscle water	**0.29 ± 0.18**	**0.256 ± 0.178**	0.03 ± 0.06	0.188 ± 0.472	0	0	0.28
HSI	**0.20 ± 0.14**	**0.024 ± 0.019**	**0.26 ± 0.15**	**0.021 ± 0.014**	0.05 ± 0.11	0.003 ± 0.006	0.21
Liver glycogen	0.08 ± 0.09	74.83 ± 88.07	**0.42 ± 0.20**	**164.90 ± 98.71**	0.11 ± 0.14	71.48 ± 96.78	0.42
Liver protein	0	0	0.01 ± 0.06	2.50 ± 11.63	0	0	0.81
Liver lipid	0.06 ± 0.08	8.46 ± 11.98	0.13 ± 0.11	10.18 ± 9.01	0	0	0.18
Total energy	**0.90 ± 0.29**	**1.97 ± 1.12**	0.04 ± 0.07	0.001 ± 0.002	0.06 ± 0.11	0.004 ± 0.008	<0.001

Significant values are in bold. Null estimates represent parameters being constrained. Significance of differences (Difference) in genetic variance among strains was obtained from a likelihood ratio test (see text for details)

other (*Crassostrea* gigas) used protein reserves at low winter temperatures (Child and Laing 1998). However, the genetic basis of those differences was not documented.

Our results suggest that brook charr could potentially adapt their energy mobilization strategy in the long-term by evolutionary adjustments. The significant correlation observed between heritability and evolvability estimates strengthen our conclusions. Studies on other animal species have also revealed the presence of a significant genetic basis underlying energy mobilization as well as substantial levels of additive variance in energy traits (H^2, Jones et al. 1992; H^2, Ronning et al. 2007; narrow-sense heritability (h^2), Tieleman et al. 2009; H^2, Jumbo-Lucioni et al. 2010). In fishes in particular, our heritability values for condition factor, muscle water content, and visceral fat were generally in the upper range of estimates documented in species (condition factor: 0.10–0.40; muscle water content: 0.06–0.36; visceral fat: 0.18–0.68; h^2, Kause et al. 2002; H^2, Neira et al. 2004; H^2, Tobin et al. 2006; h^2, Navarro et al. 2009; h^2, Saillant et al. 2009). Admittedly, such high values could be partially due to our full-sib design, which can overestimate the genetic variance by including other variance sources (common environment and/or maternal variance, and some portion of dominance variance) in addition to the additive variance (Falconer and Mackay 1996; Perry et al. 2004). However, it is noteworthy that most previous studies mentioned above also used full-sib families to estimate heritabilities. Our study is however the first to report heritability values for liver energy reserves which varied widely among strains. In addition, genetic correlations for some of the traits measured here were consistent with those previously observed for other species, such as the rainbow trout (*Oncorhynchus mykiss*), gilthead seabream, and sea bass (*Dicentrarchus labrax*), for which estimates varied from low to highly significant depending on the traits (r_G between condition factor and muscle water content: −0.27 to 0.51; r_G between condition factor and visceral fat: 0.19–0.87; r_G between muscle water content and visceral fat: 0.08–0.41; Kause et al. 2002; Navarro et al. 2009; Saillant et al. 2009). Such correlations reflect the potential for the partially dependent evolution of these traits.

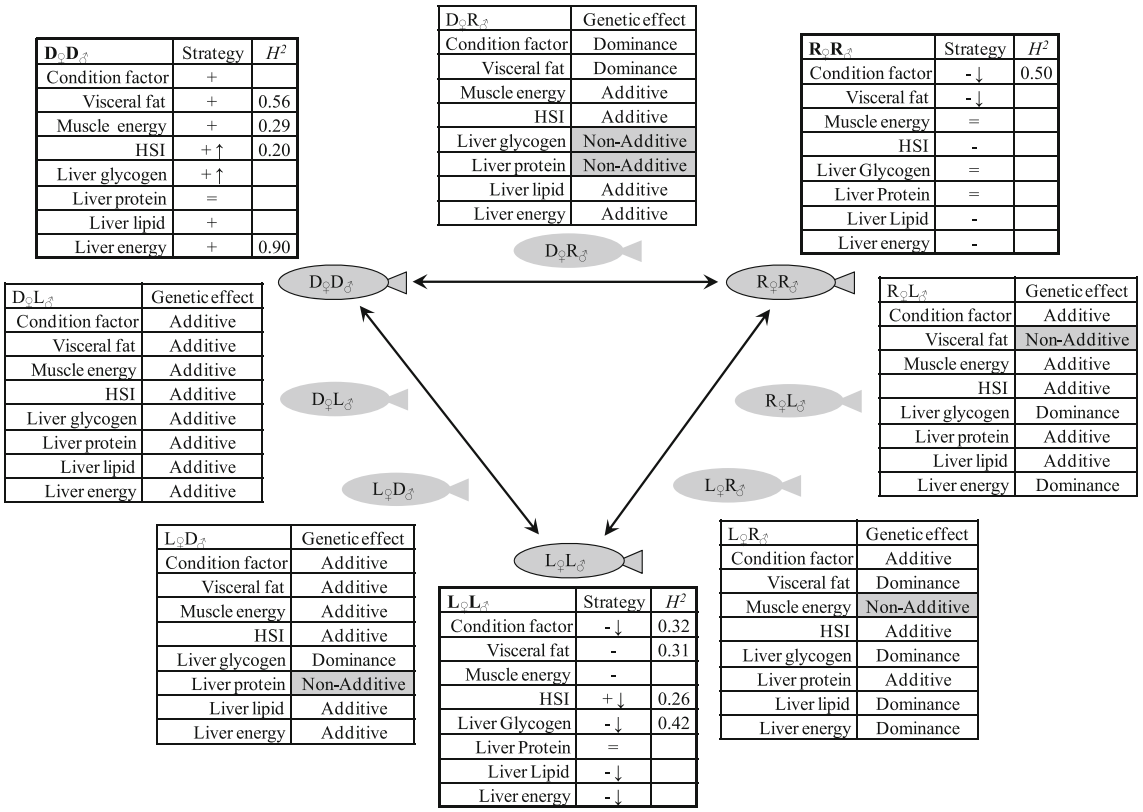
Traits related to energy reserves were generally heritable in brook charr, although each strain seemed to have its own characteristics. In the domestic and Laval strain strategies, energy reserves had heritable genetic bases while the strategy of the Rupert strain did not. Moreover, two traits related to energy reserves (visceral fat and total liver energy) had significantly different heritabilities among the strains, revealing a major divergence in the underlying genetic basis of these traits. The three strains also showed distinct patterns of genetic correlations among the heritable traits measured, which is suggestive of differences in their genetic architecture related to energy mobilization (Jensen et al. 2003; Robinson et al. 2009). The genetic basis for energy strategy thus seems to be population-specific and cannot be extrapolated to other populations. Our results also indicate that the three strains have distinct potential of physiological, and possibly adaptive response to selective pressures associated with overwintering in a cold environment. This is in contrast with the other few studies that compared the genetic basis of energy-related traits. For instance, no difference in heritability or genetic correlation for energy related-traits was observed among populations of coho salmon, *Oncorhynchus kisutch,* produced for aquaculture (H^2, Neira et al. 2004) or among wild populations of stonechats, *Saxicola torquata*, (h^2, Tieleman et al. 2009).

We found no evidence for a genetic basis related to the use of energy reserves in the Rupert strain, suggesting that environmental effects are mainly involved in the observed phenotypic variation of this strain. Traits submitted to

Table 6 Estimates of genetic (below diagonal) and phenotypic (above diagonal) correlations with standard error (±SE) and genetic covariance (in italic below diagonal and genetic correlations) for body mass, condition factor, and the different energy reserves for which heritabilities were significant in all the purebred strains using bivariate analyses

	Mass	Condition factor	Visceral fat	Muscle water	HSI	Liver glycogen	Total energy
Domestic							
Mass	–		**0.55 ± 0.11**	−0.42 ± 0.10*	0.20 ± 0.11		**0.90 ± 0.03**
Visceral fat	**0.75 ± 0.19**		–	−0.52 ± 0.08*	0.29 ± 0.10		**0.52 ± 0.10**
	(***4.56 ± 3.09***)						
Muscle water	−0.65 ± 0.27*		−0.62 ± 0.29*	–	−0.17 ± 0.09		−0.42 ± 0.09*
	(*−2.91 ± 2.29*)		(*−0.11 ± 0.09*)				
HSI	0.53 ± 0.36		0.15 ± 0.48	−0.46 ± 0.45	–		0.54 ± 0.08
	(*0.73 ± 0.70*)		(*0.01 ± 0.02*)	(*−0.02 ± 0.02*)			
Total energy	**0.99 ± 0.01**		**0.69 ± 0.22**	−0.66 ± 0.27*	0.67 ± 0.28		–
	(***13.11 ± 7.35***)		(***0.38 ± 0.24***)	(*−0.23 ± 0.18*)	(*0.07 ± 0.06*)		
Laval							
Mass	–	0.24 ± 0.08	0.58 ± 0.07		0.04 ± 0.08	−0.04 ± 0.09	
Condition factor	0.06 ± 0.65	–	**0.31 ± 0.09**		0.19 ± 0.09	**0.38 ± 0.08**	
	(*0.01 ± 0.02*)						
Visceral fat	−0.52 ± 0.76	**0.90 ± 0.16**	–		**0.43 ± 0.07**	**0.27 ± 0.09**	
	(*−0.12 ± 0.15*)	(***0.02 ± 0.01***)					
HSI	−0.91 ± 0.56	0.52 ± 0.36	**0.88 ± 0.16**		–	**0.39 ± 0.08**	
	(*−0.05 ± 0.04*)	(*0.01 ± 0.01*)	(***0.04 ± 0.02***)				
Liver glycogen	−0.78 ± 0.58	**0.96 ± 0.15**	**0.94 ± 0.14**		**0.83 ± 0.23**	–	
	(*−3.41 ± 3.28*)	(***0.37 ± 0.24***)	(***3.44 ± 2.04***)		(***0.66 ± 0.48***)		
Rupert							
Mass	–	−0.04 ± 0.14					
Condition factor	–0.10 ± 0.62	–					
	(*−0.01 ± 0.06*)						

Significant genetic covariances (from the likelihood ratio test) are in bold and asterisks indicate marginally non-significant covariances



$D_♀D_♂$	Strategy	H^2
Condition factor	+	
Visceral fat	+	0.56
Muscle energy	+	0.29
HSI	+↑	0.20
Liver glycogen	+↑	
Liver protein	=	
Liver lipid	+	
Liver energy	+	0.90

$D_♀R_♂$	Genetic effect
Condition factor	Dominance
Visceral fat	Dominance
Muscle energy	Additive
HSI	Additive
Liver glycogen	Non-Additive
Liver protein	Non-Additive
Liver lipid	Additive
Liver energy	Additive

$R_♀R_♂$	Strategy	H^2
Condition factor	-↓	0.50
Visceral fat	-↓	
Muscle energy	=	
HSI	-	
Liver Glycogen	=	
Liver Protein	=	
Liver Lipid	-	
Liver energy	-	

$D_♀L_♂$	Genetic effect
Condition factor	Additive
Visceral fat	Additive
Muscle energy	Additive
HSI	Additive
Liver glycogen	Additive
Liver protein	Additive
Liver lipid	Additive
Liver energy	Additive

$R_♀L_♂$	Genetic effect
Condition factor	Additive
Visceral fat	Non-Additive
Muscle energy	Additive
HSI	Additive
Liver glycogen	Dominance
Liver protein	Additive
Liver lipid	Additive
Liver energy	Dominance

$L_♀D_♂$	Genetic effect
Condition factor	Additive
Visceral fat	Additive
Muscle energy	Additive
HSI	Additive
Liver glycogen	Dominance
Liver protein	Non-Additive
Liver lipid	Additive
Liver energy	Additive

$L_♀R_♂$	Genetic effect
Condition factor	Additive
Visceral fat	Dominance
Muscle energy	Non-Additive
HSI	Additive
Liver glycogen	Dominance
Liver protein	Additive
Liver lipid	Dominance
Liver energy	Dominance

$L_♀L_♂$	Strategy	H^2
Condition factor	-↓	0.32
Visceral fat	-	0.31
Muscle energy	-	
HSI	+↓	0.26
Liver Glycogen	-↓	0.42
Liver Protein	=	
Liver Lipid	-↓	
Liver energy	-↓	

Fig. 2 Schematic summary of energy reserve mobilization strategies, broad-sense heritabilities (H^2) in the three purebred strains (*bold*), and the genetic effects observed in their hybrids. In purebred strains, *plus* indicates significantly more energy than in the other strains in December, *minus* indicates significantly less, *Equal* indicates similar or intermediate energy compared to the other strains in December, and arrows indicate the energy reserve that significantly changed during winter (the strain with *up arrow* indicates significantly more energy in March than in December and *down arrow* significantly less). For heritability (H^2), only significant heritabilities are mentioned. In hybrids, "Additive" indicates intermediate energy compared to parental lines (i.e., additive genetic effects), "Dominance" indicates energy similar of one of the parental lines, and *grey* highlight indicates non-additive genetic effects when hybrids had or used significantly more or less energy reserves than both parental lines

strong directional selection pressure over a long time are predicted to show eroded genetic variance due to fixation of beneficial alleles (Uller et al. 2002; Teplitsky et al. 2009). In the Rupert strain, traits related to energy reserves may thus have been shaped by strong local selection that drastically reduced heritability. Similar results of low heritable variation have been observed for physiological traits related to energy in mice (Nespolo et al. 2003) and birds (Polo et al. 2007).

Divergences observed here in genetic architecture and strategies in energy accumulation and mobilization could hypothetically be attributed to the adaptive response to distinct natural environments (Collins and Anderson 1995; Roff and Mousseau 1999; Charmantier et al. 2004; Hurst 2007). Although this remains to be more rigorously investigated, some ecological differences among the three strains are worth mentioning. Namely, the Laval strain is anadromous and originates from a population that migrates from freshwater for reproduction and overwintering to saltwater in summer for feeding. The Rupert strain originates from a northern lacustrine population subjected to harsh and long winter conditions. In contrast, the domestic strain has been reared under artificial environments for about 100 years. Differences in fluctuations of food abundance and winter conditions in these environments could thus have influenced the strategies of energy storage and metabolism among strains. Clearly, a possible causal link between differences among populations with different ecological conditions and genetically based strategies of energy mobilization deserves further investigation.

Overall, we observed a limited occurrence of non-additive effects in hybrids. Non-additive effects previously reported in hybrids mostly occurred when parental lines were divergent and adapted to their own environments (Edmands 1999; Stelkens et al. 2009). In the present study, we used purebred strains that are genetically very distinct both from a neutral (Martin et al. 1997) and a functional (Bougas et al. 2010) standpoint. Therefore, the occurrence of non-additive effects was expected, especially negative

ones that would translate into outbreeding depression (Bieri and Kawecki 2003). Although mainly expected to occur in later hybrid generations, outbreeding depression may occur in the first generation, when the genetic composition of populations is sufficiently divergent (Edmands 1999; Cooke et al. 2001; Tymchuk et al. 2007). Moreover, non-additive effects on growth and gene expression have been reported for these same three brook charr strains (Bougas et al. 2010; Granier et al. 2011). Bieri and Kawecki (2003) indicated that small non-additive effects among genetically divergent populations may suggest the absence of divergent evolution in coadapted gene complexes. This, and other possible effects related to genetic architecture (e.g., pleitropy or other genetic linkage) deserve further rigorous investigation.

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