Heterosis and outbreeding depression between strains of young-of-the-year brook trout (*Salvelinus fontinalis*)

S. Granier, C. Audet, and L. Bernatchez

Abstract: Brook trout (*Salvelinus fontinalis* (Mitchill, 1814)) supports a lucrative fish aquaculture industry in Quebec and production of this species is mainly oriented to stock enhancement supporting sport fisheries. The aim of this study was to verify the expression of interstrain heterosis, i.e., increased performance of first generation hybrid progeny, during the first stages of development in brook trout. Two wild populations that were recently introduced to fish production in Quebec, the Laval (L) and the Rupert (R) strains, and a domestic strain (D) that is present in most Quebec fish farms were used in this study. The growth of 72 full-sibling families, representing three pure (♀D × ♂D, ♀L × ♂L, ♀R × ♂R) and five hybrid (♀D × ♂L, ♀D × ♂R, ♀L × ♂D, ♀L × ♂R, ♀R × ♂L) cross types, were surveyed from hatching to 2136 degree-days. Both heterosis and outbreeding depression were observed, depending on the hybrid cross type. The occurrence of heterosis was dependent on the developmental stage, and growth advantage at a very early developmental stage did not necessarily translate into bigger size later on. Outbreeding depression in growth (mass or length) was much less common than heterosis, and when occurring, it varied from 9.2% to 33.3% compared with 9.0% to 88.2% improvement in growth traits for heterosis. The results indicate that in early development, there was higher occurrence of heterosis relative to fish mass than to fish length and that, overall, the occurrence of heterosis was unpredictable.

Résumé : L'omble de fontaine (*Salvelinus fontinalis* (Mitchill, 1814)) est une espèce très importante au Québec, aussi bien dans le domaine de la pêche que dans celui de l'aquaculture et la production aquacole est principalement axée vers l'ensemencement. L'objectif de notre étude était de vérifier la présence d'hétérosis, soit une augmentation de performance durant les premiers stades du développement chez les hybrides de première génération, lors de croisements inter-souche d'ombles de fontaine. Trois souches ont été utilisées, soit une souche domestique (D), largement utilisée dans les piscicultures québécoises et deux populations sauvages récemment introduites dans le cheptel aquacole, soit la Laval (L) et la Rupert (R). Nous avons étudié la croissance de 72 familles de type plein-frère, représentant 3 croisements purs (♀D × ♂D, ♀L × ♂L, ♀R × ♂R) et 5 croisements hybrides (♀D × ♂L, ♀D × ♂R, ♀L × ♂D, ♀L × ♂R, ♀R × ♂L), de l'éclosion jusqu'à 2136 degrés-jours. De l'hétérosis et de la dépression de croisement ont été observées chez différents croisements hybrides. La présence d'hétérosis était dépendante du stade de développement et une bonne croissance à un jeune stade de développement ne se traduisait pas nécessairement par une taille plus importante lors des stades suivants. Lorsque présente, la dépression de croisement se traduisait par des baisses de croissance (masse ou longueur) entre 9,2 % et 33,3 %, alors que dans le cas d'hétérosis, des améliorations des traits de croissance variant de 9,0 % à 88,2 % ont été observées. Ces résultats montrent une présence accrue d'hétérosis durant les premiers stades du développement en fonction de la masse plutôt que de la longueur des poissons et ils illustrent dans leur ensemble l'imprévisibilité de l'occurrence de l'hétérosis chez cette espèce.

Introduction

Brook trout (*Salvelinus fontinalis* (Mitchill, 1814)) is a salmonid species that is widely present in eastern North America's rivers where it supports an important sport fishing industry. In Quebec, production of brook trout represents 50% of freshwater aquaculture and most of this production is used for stock enhancement to support fishing activities (Ministère des Ressources Naturelles de la Faune du Québec 2008). Heterosis refers to the phenomenon that first generation progeny of diverse species or populations exhibit greater trait performance, either in terms of biomass, development, or fertility, than the better of the two parents (Gjedrem 2005). In the agri-food industry, heterosis is largely used to improve performance traits. In fishes, evidence for heterosis has been found for neonatal survival in the guppy (*Poecilia reticulata* Peters, 1859) (Shikano and Taniguchi 2002) and growth rate in carp (*Cyprinus carpio* L., 1758) (Wohlfarth 1993; Vandeputte 2003; Nielsen et al. 2010), Nile tilapia (*Oreochromis niloticus* (L., 1758)), walking catfish (genus *Clarias* Scopoli, 1777) (see Bryden et al. 2004), and silver perch (*Bidyanus bidyanus* (Mitchell, 1838)) (Guy et al. 2009). Because of the high heritability of growth traits, most of the work on salmonids has concentrated on family selection and little is known about crossbreeding. A more extensive utilization of heterosis in the selective breeding of

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fish species can be another effective way to improve fish quality and increase production even though heterosis is a one time event. However, the general belief is that heterosis is rare in salmonids (Bryden et al. 2004).

Within species, crosses between genetically distant populations have generally been expected to enhance heterosis more than genetically closer ones, and several authors have suggested that there is a positive relationship between the genetic divergence between parents and the performance of their hybrid offspring (Shamsuddin 1985; Wang and Xia 2002). Additive and nonadditive (dominance or epistasis) genetic effects are also important in the study of heterosis because they influence the choice of the paternal and (or) maternal strain to be used in a crossbreeding program (Maluwa and Gjerde 2006). The different performances between strains thus may depend on the origin of the breeders. A given strain can perform better as sire or conversely as dam, and a specific crossing scheme may improve an intended trait (Eknath et al. 2007).

For this study, we used three different strains: a domestic one and two strains recently introduced in the Quebec livestock. The three strains are genetically distinct based on neutral microsatellite marker and on gene expression measured in controlled conditions, with the two wild strains being the most genetically distinct and the domestic strain being about equal genetic distance between them (Martin et al. 1997; Bougas et al. 2010). We then hypothesized that crossing the two most genetically distant strains (Laval × Rupert) would increase the potential of a positive heterotic outcome. To our knowledge, no other study focussing on salmonids has looked at interstrain heterosis using a multi-strain design through different developmental stages.

Our objectives were (*i*) to investigate the presence of heterosis using reciprocal intraspecific crosses between three genetically different strains, (*ii*) to verify the presence of cross-type effects on the occurrence of heterosis, and (*iii*) to estimate heterosis at different developmental stages.

Materials and methods

Origin and maintenance of brood stock

Brook trout from three distinct genetic strains were used (Martin et al. 1997). The first is a domestic strain (D) that has been largely used by fish farmers in Quebec for more than 100 years and that originates from two strains (Nashua and Baldwin) that were intercrossed for many generations. The other two strains, Laval (L) and Rupert (R), have shorter domestication histories (Martin et al. 1997), and breeders used in the present study were F_3 animals. The Laval is a wild anadromous strain that originates from the Laval River near Forestville (north shore of the St. Lawrence River, Quebec), whereas the Rupert is a wild freshwater strain that originates from the Rupert River in James Bay (northwestern Quebec).

All animal procedures were approved by the University Animal Care Committee. The domestic breeders were obtained from Pisciculture de la Jacques Cartier (Cap Santé, Quebec), the Laval breeders from the Institut des sciences de la mer de Rimouski (ISMER), and the Rupert breeders from the Laboratoire de recherche en sciences aquatiques (LARSA, Université Laval, Quebec). They were all fed the same feed (Corey, Aqua-brood, 7.5 mm) at a daily ration of 1% wet mass except that fish stopped eating close to the reproduction period. The mass and total length of breeders (n = 160) used for the different crosses are presented in Table 1.

Mating design

During the autumn of 2005 (October–December), egg fertilization was done at LARSA using milt and eggs obtained from the three different strains. Eight cross types with 10 full-sibling families per cross type were done: domestic dams with domestic sires (♀D × ♂D), domestic dams with Laval sires (♀D × ♂L), domestic dams with Rupert sires (♀D × ♂R), Laval dams with domestic sires (♀L × ♂D), Laval dams with Laval sires (♀L × ♂L), Laval dams with Rupert sires (♀L × ♂R), Rupert dams with Laval sires (♀R × ♂L), and Rupert dams with Rupert sires (♀R × ♂R) (Table 1). The cross between Rupert dams and domestic sires (♀R × ♂D) was not possible because of asynchronicity in their sexual maturation period (October for domesticated sires and December for Rupert dams).

Hatching and yolk-sac resorption

At hatch, the number of fry was randomly standardized to 1000 per family, then to 700 and 600 as fry grew. During the experiment, high mortality rates (poor egg or milt quality) occurred in three families (two from ♀D × ♂L and one from ♀D × ♂R); these families were eliminated from the study after the first or second sampling, when numbers became too low. The remaining 77 families were reared separately in seven troughs divided into 12 units with water flow coming from the same recirculation system. Fertilized eggs were incubated at 6 °C. The first sampling was done at 100% hatching: 20 individuals per family were sampled (n = 1540), and measurements of embryonic length, yolk-sac length (YSL), and yolk-sac diameter (mm) were made using a calliper. The standard cylindrical relationship of yolk-sac volume (YSV = $\pi \times$ YSL $\times r^2$) was used as an estimate of yolk-sac volume (mm^3), where r represents the yolk-sac radius (Perry et al. 2004).

After hatching, the photoperiod was set at 12 h light : 12 h dark and temperature maintained at 8 °C. The second sampling was done at the time of complete resorption of the yolk sac, when 20 individuals per family were sampled (n = 1540) for fry length and mass. Condition factor (K) was calculated using $K = (M \times 1000)/L^3$, where M represents the mass in grams and L represents the length in millimetres.

Exogenous feeding and end of the summer (2136 degree-days)

From June to August, the number of families was reduced from 77 to 72 because of limited rearing capacity: five small (<200 individuals) families were eliminated from the study (one ♀D × ♂L, one ♀L × ♂D, two ♀R × ♂L, and one ♀R × ♂R). Twenty-two weeks after hatching, all juveniles were fin-marked (clipping of pelvic and (or) adipose fins) and then transferred to nine 3000 L tanks (eight families per tank). The photoperiod was then adjusted to follow natural conditions. Feeding frequency was adjusted according to fish age, mean mass, and temperature conditions, and the temperature was set so that all experimental families would

Table 1. Mass and lengths (mean ± SD) of brook trout (*Salvelinus fontinalis*) breeders used for each cross type.

	Females		Males	
Cross	Mass (kg)	Length (cm)	Mass (kg)	Length (cm)
♀D × ♂D	0.70±0.06c	36.75±1.13a	0.81±0.10a	38.42±2.21a
♀D × ♂L	0.78±0.21bcd	38.05±4.10ab	1.03±0.37ab	43.95±2.09bc
♀D × ♂R	0.59±0.07ab	35.72±1.27a	0.63±0.12a	37.72±3.23a
♀L × ♂D	0.97±0.31cd	41.25±2.30b	0.71±0.11a	37.68±1.33a
♀L × ♂L	1.07±0.24d	42.60±2.74b	1.25±0.18bc	44.83±1.98bc
♀L × ♂R	1.16±0.44c	42.21±2.35b	0.85±0.30ab	40.26±4.03ab
♀R × ♂L	1.39±0.66bcd	45.46±6.37b	1.46±0.54c	46.34±1.95a
♀R × ♂R	0.47±0.13a	35.71±3.19a	0.77±0.34a	40.33±5.52abc

Note: Mean values (n = 8) with different letters indicate a significant difference between crosses ($p < 0.05$). For cross types, the first letter represents the dam and the second one the sire, with D for the domestic strain, L for the Laval strain, and R for the Rupert strain. The cross between Rupert dams and domestic sires (♀R × ♂D) was not possible because of asynchronicity in their sexual maturation period (October for domesticated sires and December for Rupert dams).

experience the same number of degree-days (2136 degree-days) by the end of the summer (September). Degree-days were calculated using degree-days = $\Delta t \times T$, where Δt is development time in days and T is the temperature in degrees Celsius (Grodzinski et al. 1975). For the last two samplings, 50 individuals per family were sampled, measured, weighed, and condition factor was calculated. The third sampling (n = 3801) was done after 15 weeks of exogenous feeding, and the fourth sampling (n = 3600) was done in September 2006, when all families had been brought to the same number of degree-days (2136 degree-days) (Table 2).

The thermal growth coefficient (TGC), based on mass measurements, was calculated for two specific periods: from yolk-sac resorption to 15 weeks of exogenous feeding, and from 15 weeks of exogenous feeding to 2136 degree-days. We used TGC = $(M_2 - M_1)^{1/3} \times \Sigma(\text{temperature} \times \text{days})^{-1}$, where M_2 represents final body mass, M_1 represents initial body mass, and temperature is expressed in degrees Celsius (Cho 1992). Because fish markings allowed us to recognize families but not individuals, TGCs were calculated on a family basis, with n = 8–10 per cross type.

Data analysis

Data normality was tested using the Kolmogorov–Smirnov test and homoscedasticity was checked with the Brown and Forsythe test (Quinn and Keough 2005). The different crosses were compared with a mixed model of the form Y = developmental stage + cross + developmental stage × cross + family(cross) + e, with developmental stage and cross type as the fixed effects and family nested within cross type as the random effect. ANOVAs were followed by a posteriori analysis when relevant. Because a preliminary statistical test indicated that there was no significant tank effect, we did not include rearing tank in the final model. To verify the occurrence of heterosis or outbreeding depression, parental strains were compared with their two reciprocal hybrid crosses (one-way ANOVA: cross type). For mean comparisons, we used Tukey's tests, or Games and Howell tests when transformations failed to provide homoscedasticity. Mixed models were performed using ASReml version 2 for Windows (VSN International, Hemel Hempstead, UK), ANOVAs using Statistica version 6.0 for Windows (StatSoft, Tulsa, Oklahoma, USA), and Games and Howell using SPSS version 13.0 for Windows (SPSS Inc., Chicago, Illinois, USA). When heterosis or outbreeding depression was found, the intensity was expressed in percentage as $[(f_1m^{-1}) - 1] \times 100$ for heterosis and as $[1 - (f_1m^{-1})] \times 100$ for outbreeding depression (Shikano and Taniguchi 2002), where f_1 represents the mean value in the F_1 hybrids and m represents the mean pure-strain value. To validate our results, the percentages of heterosis and outbreeding depression were also calculated using the least-square means according to Gjerde et al. (2002). Both methods gave similar results and then ontly the results obtained based on mean calculations are presented. When statistical analyses indicated similar results for length, mass, and condition factor data, we only showed the results for the mass data except for the first sampling (100% hatching), where the fork length data are presented.

Results

Heterosis and outbreeding depression

During the experiment, we observed 10 instances of heterosis and 2 instances of outbreeding depression. However, because there were differences with respect to developmental stage (crosses × developmental stages, $p < 0.001$ for all variables; Table 3), we present the results according to specific developmental stage. Because the results obtained on condition factors were similar, although less pronounced than those for mass and length, they are described only when different from the mass and length results. Family effects were always present, but we do not present them in detail because our main objective was to assess the net effect of heterosis or outbreeding depression among types of crosses.

At hatching, we observed two cases of heterosis but no outbreeding depression. The ♀D × ♂R fry were 7.4% longer than those from the parental strains (Fig. 1A). The ♀L × ♂R fry also exhibited heterosis and were 9.0% longer than their parental lines (Fig. 1B). At yolk-sac resorption, three cases of heterosis and two cases of outbreeding depression were observed. The ♀L × ♂D fry were 88.2% heavier and 19.6%

Table 2. Different periods of the experiment and months of sampling (October–December 2005 and January–September 2006) of brook trout (*Salvelinus fontinalis*).

		Samplings			
Cross	Egg fertilization	Hatching	Yolk-sac resorption (degree-days)	After 15-weeks of exogenous feeding (degree-days)	2136 degree-days
♀D × ♂D	October	January	February (253.0)	May (1254.4)	September
♀D × ♂L	October	January	February (283.4)	June (1297.4)	September
♀D × ♂R	October	January	February (279.7)	June (1276.9)	September
♀L × ♂D	November	January	March (378.7)	June (1492.3)	September
♀L × ♂L	November	February	March (407.6)	July (1532.4)	September
♀L × ♂R	November	February	March (354.9)	July (1493.5)	September
♀R × ♂L	December	February–March	April–May (434.4)	July (1603.7)	September
♀R × ♂R	December	March	May (514.0)	August (1720.6)	September

Note: For cross types, the first letter represents the dam and the second one the sire, with D for the domestic strain, L for the Laval strain, and R for the Rupert strain.

Table 3. Results of the mixed models (developmental stage, cross type) for individual mass and length of brook trout (*Salvelinus fontinalis*).

Variable	Effect	df	*F*	*p*
Individual length	Developmental stage	3	67 898.5	<0.001
	Cross type	7	25.3	<0.001
	Developmental stage × cross type	21	243.1	<0.001
Individual mass	Developmental stage	3	78 457.7	<0.001
	Cross type	7	27.5	<0.001
	Developmental stage × cross type	14	291.7	<0.001

longer than fry from parental strains (Fig. 1C) and had a condition factor 13.1% higher (Table 4), whereas the reciprocal hybrids displayed intermediate growth compared with parental strains. The ♀R × ♂L fry were 33.3% lighter and 9.2% shorter than the parental crosses (Fig. 1D), but outbreeding depression was not observed in the reciprocal hybrid.

After 15 weeks of exogenous feeding, heterosis was detected in two cases, but no outbreeding depression was observed. The ♀L × ♂D fry exhibited heterosis and were 48.3% heavier and 13.4% longer than both parental strains (Fig. 1E), whereas the reciprocal hybrids were similar to pure domestic fry. At the end of the summer (2136 degree-days), only two cases of heterosis were detected. The ♀L × ♂R fry were 44.9% heavier and 13.2% longer compared with their parental strains (Fig. 1F). The ♀D × ♂R fry exhibited intermediate growth performance compared with the two parental lines (Fig. 1G).

Pure strain and hybrid cross comparisons

The ♀L × ♂L fry had the biggest yolk-sac volume at hatching and the highest mass at yolk-sac resorption compared with the other strain crosses. After 15 weeks of exogenous feeding, the ♀D × ♂D and ♀R × ♂R fry were bigger compared with the other pure-strain cross (♀L × ♂L), whereas at the last sampling (at the end of the summer), the ♀D × ♂D fry exhibited the highest increase in mass and length compared with the other strains (Table 5).

From yolk-sac resorption to 15 weeks of exogenous feeding, ♀D × ♂D and ♀D × ♂R fry had the highest TGC (Table 6). At this stage, cross types were clearly divided into two groups, with the three cross types with domestic dams showing significantly higher TGC than the other cross types. From 15 weeks of exogenous feeding to 2136 degree-days, the three cross types with domestic dams also presented a higher TGC compared with the other crosses. It is notable, however, that L × R fry exhibited heterosis and had 60.8% higher TGC than both parental strains.

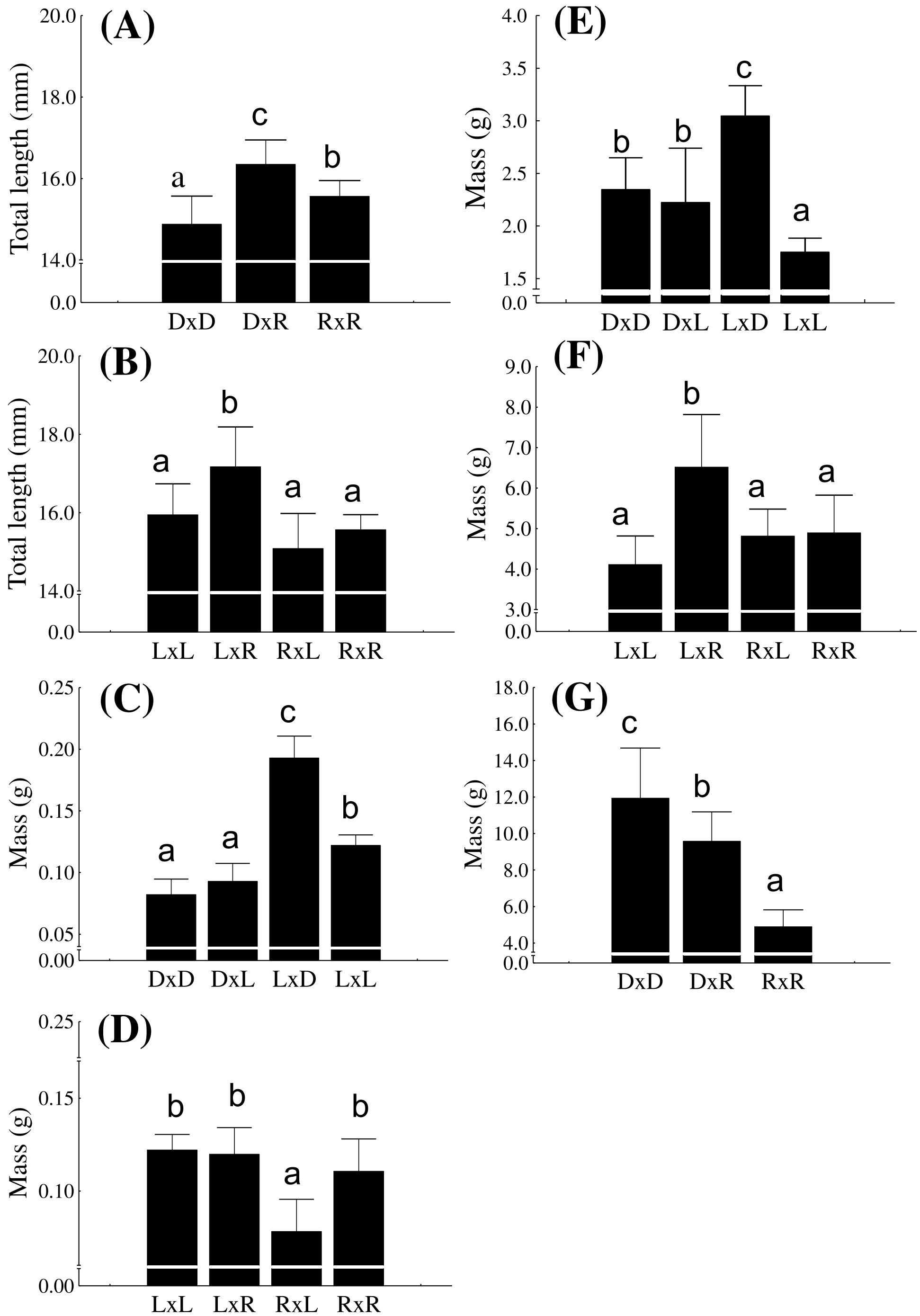
Discussion

Heterosis and outbreeding depression

This study revealed a complex pattern for both heterosis and outbreeding depression in interstrain hybrids of brook trout that varied according to developmental stage. In contrast to previous studies in fish, and particularly in salmonids where the presence of heterosis in hybrids of the first generation does not seem to be a general feature (Nilsson 1993; Hulata 2001; Bryden et al. 2004; Gunther et al. 2005), we observed 10 occurrences of heterosis for different growth traits and cross types. The heterosis expression levels observed in hybrids were variable depending on the trait or the period considered, but these levels are quite high when compared with other studies dealing with heterosis in fishes. For instance, the percentage of heterosis in guppy ranged from –1.3% for body length to 42.2% for salinity tolerance (Shikano et al. 1997; Nakadate et al. 2003), whereas we found a mass advantage of 88.2% at the yolk-sac resorption stage and 48.3% after 15 weeks of exogenous feeding in hybrids between Laval dams and domestic sires compared with the mean values of pure strains.

In the present study, outbreeding depression was less frequent than heterosis (2 occurrences compared with 10 occurrences) and, when present, its intensity varied from 9.2% to 33.3% compared with intensities of 9.0% to 88.2% for heterosis. Only a few studies have focussed on outbreeding de-

Fig. 1. Comparisons among strains and crosses of brook trout (*Salvelinus fontinalis*) are presented according to the presence of significant heterosis for length or for mass. (A, B) Hatching, length; (C, D) yolk-sac resorption, mass; (E) 15 weeks after exogenous feeding, mass; and (F, G) 2136 degree-days, mass. Values are means ± SD. Hatching and yolk-sac resorption: 20 individuals per family were sampled; 15 weeks of exogenous feeding and 2136 degree-days: 50 individuals per family were sampled. Strains are domestic (D), Laval River (L), and Rupert River (R), with the first letter indicating the strain of the dam and the second the strain of the sire. Different letters indicate significantly different mean values ($p < 0.05$).



pression in fishes. No outbreeding depression was found for growth in walleye (*Sander vitreus* (Mitchill, 1818)) (Cena et al. 2006), but altered physiological performance were observed in interstock hybrids of four genetically distinct wild stocks of largemouth bass (*Micropterus salmoides* (Lacepède, 1802)). Two other studies on pink salmon (*Oncorhynchus gorbuscha* (Walbaum, 1792)) showed outbreeding depression—lower survival at sea—in the F_2 generation hybrids compared with both parental forms and the F_1 hybrids (Gharrett et al. 1999; Gilk et al. 2004).

Laval dams tended to be more often associated with heterosis, whereas Laval sires were mostly associated with outbreeding depression when present. This suggests that the use of a strain either as dam or as sire may lead to very different

Table 4. Condition factors for pure strains (values in boldface type) of brook trout (*Salvelinus fontinalis*) and their hybrids measured at yolk-sac resorption, after 15 weeks of exogenous feeding and at 2136 degree-days.

Cross	Yolk-sac resorption (g/mm^3)	After 15 weeks of exogenous feeding (g/mm^3)	2136 degree-days (g/mm^3)
♀D × ♂D	**0.73±0.07abc**	**1.04±0.08c**	**1.09±0.12d**
♀D × ♂L	0.75±0.06bcd	0.99±0.08bc	0.99±0.09bc
♀D × ♂R	0.71±0.08ab	1.01±0.07bc	1.03±0.06c
♀L × ♂D	0.82±0.22d	0.98±0.10	0.97±0.07b
♀L × ♂L	**0.72±0.05ab**	**0.88±0.05a**	**0.86±0.06a**
♀L × ♂R	0.74±0.07abc	0.90±0.07a	0.93±0.06b
♀R × ♂L	0.67±0.08a	0.90±0.06a	0.94±0.08b
♀R × ♂R	**0.80±0.15cd**	**1.00±0.08bc**	**1.03±0.07c**

Note: Values are means ± SD. Mean values with different letters indicate a significant difference between crosses for the same trait at a same sampling time ($p < 0.05$). For cross types, the first letter represents the dam and the second one the sire, with D for the domestic strain, L for the Laval strain, and R for the Rupert strain. Yolk-resorption stage: 20 fish per family were sampled; 15 weeks and 2136 degree-days: 50 fish per family were sampled.

Table 5. Yolk-sac volume (YSV), fry length (TL, total length; FL, fork length), and fry mass (*M*) for pure strains of brook trout (*Salvelinus fontinalis*) measured at hatching, at yolk-sac resorption, after 15 weeks of exogenous feeding, and at 2136 degree-days.

	Hatching		Yolk-sac resorption		After 15 weeks of exogenous feeding		2136 degree-days	
Cross	YSV (mm^3)	TL (mm)	FL (mm)	*M* (g)	FL (mm)	*M* (g)	FL (mm)	*M* (g)
♀D × ♂D	189.1±65.4a	14.9±1.2a	22.3±0.9a	0.08±0.01a	60.3±5.1a	2.3±0.7b	101.6±12.2b	11.9±4.6b
♀L × ♂L	342.0±75.5b	15.9±1.1b	25.7±1.0c	0.12±0.02b	57.9±4.0b	1.7±0.4a	77.6±6.8a	4.1±1.2a
♀R × ♂R	212.3±71.4a	15.6±0.7ab	23.9±1.4b	0.11±0.03b	62.3±7.3a	2.5±1.0b	77.1±9.1a	4.9±1.7a

Note: Values are means ± SD. Means with different letters indicate a significant difference between crosses for a same trait at a same sampling period ($p < 0.05$). For cross types, the first letter represents the dam and the second one the sire, with D for the domestic strain, L for the Laval strain, and R for the Rupert strain. Hatching and yolk-sac resorption: 20 fish per family were sampled; 15 weeks and 2136 degree-days: 50 fish per family were sampled.

Table 6. Thermal growth coefficient (g/degree-days) for all cross types of brook trout (*Salvelinus fontinalis*) from yolk-sac resorption to 15 weeks of exogenous feeding and from 15 weeks of exogenous feeding to 2136 degree-days.

Cross	From yolk-sac resorption to 15 weeks of exogenous feeding	From 15 weeks of exogenous feeding to 2136 degree-days
♀D × ♂D	0.00071d	0.00045e
♀D × ♂L	0.00063c	0.00036de
♀D × ♂R	0.00067cd	0.00039e
♀L × ♂D	0.00058b	0.00029bc
♀L × ♂L	0.00046a	0.00019a
♀L × ♂R	0.00049a	0.00028bc
♀R × ♂L	0.00050a	0.00021ab
♀R × ♂R	0.00051ab	0.00017a

Note: Mean values with different letters indicate a significant difference between crosses for the same sampling period ($p < 0.05$). For cross types, the first letter represents the dam and the second one the sire, with D for the domestic strain, L for the Laval strain, and R for the Rupert strain.

results and that some strains will perform better as sires and others as dams, as found by Eknath et al. (2007) for the Nile tilapia. Similar results have been found in walking catfishes (Rahman et al. 1995) and salmonid hybrids, particularly sockeye salmon and kokanee salmon (*Oncorhynchus nerka* (Walbaum in Artedi, 1792)) (Wood and Foote 1990). This could be due to the occurrence of sex-biased gene expression, as previously reported in other species (Ellegren and Parsch 2007), including salmonids (Derome et al. 2008). Based on our results, the use of Laval dams to improve performance of some traits of importance may therefore represent particular interest in aquaculture.

Prefeeding stages (hatching and yolk-sac resorption)

During these early stages of development, we found that at hatch progeny from the Laval dams were longer than the others, and that at yolk-sac resorption the cross between the Laval dam and the domestic sire (♀L × ♂D) presented the highest performance in terms of mass, length, and condition factor. At these stages, growth performance could be greatly influenced by maternal effects. Early development is preprogrammed by the maternal genome through gene products contained in the yolk (Hebert et al. 1998; Nakajima and Taniguchi 2002; Pakkasmaa and Jones 2002), thus we can presume that the maternal effect will be more important at hatching than in the other developmental stages. In brook trout, and especially in the Laval strain, Perry et al. (2004) demonstrated the importance of maternal genetic effects until yolk-sac resorption is completed. Perry et al. (2005) also showed that maternal effect is strongly correlated with the size of the female, and that larger females will produce larger eggs and thus larger progeny. In the present study, the Laval dams were notably longer than the domestic or Rupert dams, which could explain the results that we found for the progeny of Laval dams. Yolk-sac reserves play an important role in the early development of fishes (Vandeputte et al. 2002), and maternal strain may have a strong influence on the offspring's body size (Shikano and Taniguchi 2005). Some factors such as physiological condition or the diet of breeders will have major effects on egg quality and progeny performance (Washburn et al. 1990; Campbell et al. 1994). Based on our results, the Laval strain and especially the Laval dams would be the best strain to improve the performance of fry at prefeeding stages.

Postfeeding stage

Contrary to previous finding, from yolk-sac resorption to 15 weeks of exogenous feeding, the TGC in cross types having the Laval strain as dam (♀L × ♂D, ♀L × ♂L, ♀L × ♂R) were among the lowest compared with the other cross types, perhaps because of the transition from maternal to individual genotype effects as previously suggested by Perry et al. (2004). The maternal influence of the domestic dams was less important at hatching than it was for dams from the short-term domesticated strains (Laval and Rupert). However, the influence of the mother's origin could also be modulated by environmental conditions as found by Fishback et al. (2002).

At the end of the summer (2136 degree-days), the domestic strain was undoubtedly the most performant for all growth traits. These results corroborate those obtained by Mason et al. (1967) who showed that a domesticated strain of brook trout grew rapidly in the hatchery. This could be explained by the fact that wild strains and their hybrids could have different requirements than domestic fry, which are more adapted to the "artificial" environment of the laboratory. However, the ♀D × ♂D fry also hatched earliest in the season, and despite the equivalent degree-day exposure, they were almost 8 weeks older than crosses between Rupert and Laval strains at the end of the experiment, a factor that cannot be ruled out when explaining their performance. Differences in degree-days must be taken into account at each specific sampling time. At 15 weeks after the beginning of exogenous feeding, ♀D × ♂D and ♀R × ♂R (which is the most distant cross types with respect to degree-day exposure) showed similar growth at the same age, indicating either differences in food utilization related to temperature conditions or an absence of temperature effect at this temperature range. It should also be noted that the ♀L × ♂R fry exhibited heterosis at different developmental stages in presence of fewer degree-days than their two parental strains at yolk-sac resorption and end of exogenous feeding. Mason et al. (1967) showed that fingerling hybrids between wild dams and domestic sires grow nearly as well in the hatchery as the domestic strain, whereas the hybrids between domestic dams and wild sires were shorter. This corroborates our observations with the ♀L × ♂D and ♀D × ♂L hybrids. Although the Rupert and Laval strains were from an F_3 generation produced in captivity, they are still closer to a feral state than the domestic strain, as several generations of domestication are required to suppress all feral characteristics (e.g., Osure and Phelps 2006).

Conclusions

In summary, the results indicate higher levels of heterosis for mass than for length, but in general, heterosis occurrence remains unpredictable. Because of this, specific interstrain cross could not be suggested to increase performance through heterosis. However, strain differences in association with heterosis occurrence or with parental effects indicate the need to better understand parental genomic interactions. Future work could also include a better understanding of the influence of rearing environments on growth performance between pure and hybrid strains.

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