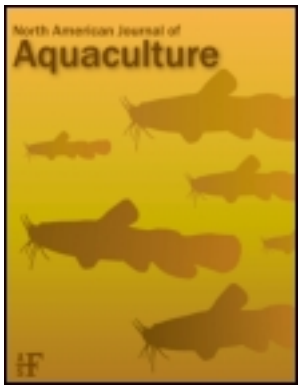


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# Effects of Rearing Environment and Strain Combination on Heterosis in Brook Trout

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ARTICLE

# Effects of Rearing Environment and Strain Combination on Heterosis in Brook Trout

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***Abstract***

**Three strains of brook trout *Salvelinus fontinalis* (domestic [D], Laval [L], and Rupert [R]) and their reciprocal hybrids were reared from 7 to 21 months of age in three different environments (indoor, constant temperature conditions; indoor, seasonal temperature variations; and outdoor, seasonal temperature variations) to test for the occurrence of heterosis in important life history traits of interest for production (body mass, length, condition factor, the absence of early sexual maturation, and survival). For each cross, body mass, length, and mortality were measured at regular intervals and sexual maturity was assessed in age-1+ fish (21 months of age). We found evidence for heterosis in mass and length that varied according to strain, cross direction in reciprocal hybrids, developmental stage, or environment; no significant outbreeding depression was detected for these traits. Heterosis expression for weight varied from 4.9% to 23.8% depending on the hybrids and environments. We found that one out of five reciprocal hybrids tested ($L_{[female]}R_{[male]}$) expressed heterosis at each age stage throughout the experiment in the three environments while the other four had mixed results. No evidence for heterosis was observed for sexual maturity and survival. These results not only provide one of the first clear pieces of evidence for the occurrence of heterosis in salmonids but also illustrate the complex nature and the unpredictability of this phenomenon.**

Heterosis, or hybrid vigor, refers to the increased performance and fitness of first generation progeny when compared with parental lines (Falconer and Mackay 1996; Birchler et al. 2003). The main explanation supporting the occurrence of heterosis is based on nonadditive genetic components: the dominance effect seen in hybrids, which is based on the replacement or complementation of deleterious alleles accumulated in one parental line by superior alleles from the other parent; overdominance, which suggests that heterozygotes perform better than homozygotes; and epistasis, which refers to allelic position and interactions in the hybrid (Birchler et al. 2003; Hochholdinger and Hoecker 2007; Lippman and Zamir 2007). The relative contribution of each of these processes in the expression of heterosis is still a matter of debate (Lippman and Zamir 2007).

The intensity of heterosis is usually higher when parental lines are highly inbred or genetically distant from each other (Shikano et al. 2000; Wang and Xia 2002; Hochholdinger and Hoecker 2007). However, the opposite phenomenon that results from genome admixture—outbreeding depression—could also affect crosses involving genetically distant strains.

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Outbreeding depression may arise from a disruption of the linkage arrangement of co-adapted gene complexes in the presence of a divergence in the genetic architecture of populations (based on epistasis components and referred to as intrinsic outbreeding depression) or from a loss of favorable allelic interactions (based on additive and dominance components and referred to as extrinsic outbreeding depression) (Edmands 2007; McClelland and Naish 2007; Tymchuk et al. 2007; Wang et al. 2007). When a cross is made, it is difficult to predict which phenomenon might appear since both heterosis and outbreeding depression result from outbreeding crosses between distant parental lines and are controlled, at least in part, by similar nonadditive effects.

Breeding programs in plants and animals commonly use heterosis to improve traits of interest for production as an alternative to the use of additive genetic components (Falconer and Mackay 1996; Comings and MacMurray 2000; Hochholdinger and Hoecker 2007). While such practice has been more limited in fish production, it has been used to improve aquaculture in common carp *Cyprinus carpio* (Wohlfarth 1993; Hulata 1995; Nielsen et al. 2010) and Nile tilapia *Oreochromis niloticus* (Marengoni et al. 1998), and has also been experimentally explored in guppy *Poecilia reticulata* (Shikano and Taniguchi 2002a). Previous studies have also investigated heterosis for various traits, including growth, survival, salinity, and temperature tolerance (Moav and Wohlfarth 1976; Bentsen et al. 1998; Nakadate et al. 2003), and more recently for patterns of gene expression (Bougas et al. 2010).

In salmonids, it is still unclear whether heterosis occurs. Heterosis for growth and survival in intraspecific hybrid crosses have been reported (Ayles and Baker 1983; Gjerde and Refstie 1984; Bryden et al. 2004) while other investigators only observed additive interactions for these same traits (Cheng et al. 1987; Einum and Fleming 1997; Glover et al. 2006) and even outbreeding depression (Gharrett et al. 1999). From these studies, it has been hypothesized that heterosis may be generally rare in salmonids (Gjerde and Refstie 1984; Gharrett et al. 1999; Bryden et al. 2004). More specifically, Tymchuk et al. (2007) suggested that salmonid populations may be too genetically distant and locally adapted to produce heterosis. However, in brook trout *Salvelinus fontinalis* in particular, previous studies on hybrid crosses between wild and domestic populations have suggested a potential for heterosis expression for growth and survival (Fraser 1981; Webster and Flick 1981) although it has not been investigated in detail.

The choice of the strain used as dam or sire in the cross may also be determinant on heterosis expression (Bentsen et al. 1998). A strain can perform better when used as dam or sire, improving specific capacities in hybrids (Bentsen et al. 1998; Perry et al. 2004; X. X. Wang et al. 2006). The environment may also modify genetic expression and influence the additive and nonadditive genetic components. A decrease in the additive variance and an increase in the epistasis variance are usually expected under unfavorable environmental conditions (Wohlfarth 1993; Hoffmann and Merilä 1999). In addition, heterosis seems to be more sensitive to environmental variations than to additive components (Bentsen et al. 1998). Different strains could also express different sensitivities to environmental variations involving possible genotype–environment interactions relative to heterosis expression (Falconer and Mackay 1996; Bentsen et al. 1998).

In this context, the aim of this study was to investigate the effects of rearing environment and strain combination on the occurrence of heterosis for growth in the brook trout. In teleost fishes, body mass and size at the juvenile stage can be considered as fitness-related traits since they are correlated with different components of fitness such as survival, life history tactic, or reproductive success (Sogard 1997; Wilson et al. 2003; Garcia de Leaniz et al. 2007; Thériault et al. 2007). Our specific objectives were therefore to evaluate (1) the occurrence of intraspecific heterosis on important life history traits that are also of interest for production (body mass, length, condition factor, absence of early sexual maturation, survival), (2) the presence of dam or sire effects on the hybrid performance and heterosis for the traits considered, and (3) the effects of environment on heterosis expression.

## METHODS

*Brook trout strains*.—Three strains of brook trout were used as parental stock. The Laval strain originates from a wild population of anadromous brook trout from the Laval River (48°44′N, 69°05′W) on the north shore of the St. Lawrence estuary, Quebec. The fish used as breeders were third generation individuals produced in captivity at the aquaculture laboratory of the Institut des Sciences de la Mer de Rimouski (ISMER), Université du Québec à Rimouski. The Rupert strain originates from a freshwater resident wild population inhabiting the Rupert River system (51°05′N, 73°41′W), which drains Mistassini Lake, Quebec. The breeders were again third generation fish produced in captivity at the Laboratoire régional en sciences aquatiques (LARSA), Université Laval, Quebec. The domestic strain is widely used by the Quebec fish farming industry. It originates from two strains (Nashua and Baldwin), and breeders were obtained from the Pisciculture de la Jacques Cartier, Cap-Santé, Quebec. The two strains recently domesticated from wild populations were selected for breed improvement because adults exhibit late sexual maturation and large adult size in the wild. The Laval and Rupert strains were shown to be genetically distant from the domestic strain. Thus 76.2% of the alleles from the wild strains were not found in the domestic strain, resulting in high $F_{ST}$ between the domestic versus Rupert and Laval strains (mean $\pm$ SD $F_{ST} = 0.187 \pm 0.009$). The Laval and Rupert strains were even more genetically differentiated than the domestic versus Laval or domestic versus Rupert strains (mean $F_{ST} = 0.427 \pm 0.020$; Martin et al. 1997). Finally, Martin et al. (1997) found no evidence for pronounced inbreeding in any of these three strains that had inbreeding coefficient ($F$) values varying between 0.18 and 0.35.

*Breeding design*.—Hybrid and purebred crosses were made from mid-November 2005 until the end of December 2005 at LARSA with eggs and milt obtained from the different fish-rearing locations. Three purebred brook trout strains were produced: [female] domestic × [male] domestic ($D_{[female]}D_{[male]}$), [female] Laval × [male] Laval ($L_{[female]}L_{[male]}$), and [female] Rupert × [male] Rupert ($R_{[female]}R_{[male]}$). Five reciprocal hybrids were produced: $D_{[female]}R_{[male]}$, $D_{[female]}L_{[male]}$, $L_{[female]}D_{[male]}$, $L_{[female]}R_{[male]}$, and $R_{[female]}L_{[male]}$. It was not possible to obtain the $R_{[female]}D_{[male]}$ 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 matings, but 8 of these 80 families were eliminated (because of low hatching success for some due to poor egg or milt quality, and random elimination of two families with high hatching success rate to get similar numbers of families in each rearing tank). The final numbers of families were 10 $D_{[female]}D_{[male]}$, 10 $L_{[female]}L_{[male]}$, 9 $R_{[female]}R_{[male]}$, 9 $D_{[female]}R_{[male]}$, 7 $D_{[female]}L_{[male]}$, 9 $L_{[female]}D_{[male]}$, 10 $L_{[female]}R_{[male]}$, and 8 $R_{[female]}L_{[male]}$.

*Family rearing*.—During the first 6 months, i.e., from egg incubation (January) to exogenous feeding (June), families were kept separate in recirculating freshwater and reared in seven troughs, each of which was divided into 12 units. Water temperature was maintained at 6°C during egg incubation and at 8°C after hatching. In June, families were marked and later identified by different combinations of adipose and pelvic fin clippings and transferred to nine 3-$m^3$ tanks, each of which contained eight families. All families were reared to the same fry stage by the end of the summer and maintained at 10°C in recirculating freshwater. The photoperiod followed the natural seasonal cycle, and fish were fed rations according to the feed manufacturer's guidelines.

In September, fish from each family were randomly divided among three rearing environments. At ISMER, 230 fish per family were reared in ten 0.5-$m^3$ indoor tanks, with six to eight families per tank according to the initial pool conditions set up at LARSA, under natural temperature and photoperiod conditions in flow-through, dechlorinated freshwater. To maintain sustainable rearing densities, the number of fish per family was gradually reduced to 60 by the end of the experiment (Table 1), and all reductions in number were done randomly. Fish were fed daily (1% ration, w/w) with commercial dry pellets. At LARSA, 150 fish per family were reared in nine 3-$m^3$ indoor tanks under natural photoperiod conditions at 10°C in recirculating freshwater. Fish numbers were gradually decreased to 50 fish per family by the end of the experiment (Table 1). Fish were fed daily (1% ration, w/w) with commercial dry pellets. At the fish farm (Pisciculture de la Jacques Cartier facility), it was not possible to follow individual families, and only cross type comparisons were done. Two hundred fish per cross type were reared in one outdoor pond under natural temperature and photoperiod conditions. The experiment lasted from September 2006 (7-month-old fish) to November 2007 (21-month-old fish).

*Performance traits*.—Every 8 weeks at ISMER and LARSA, 25 fish per family ($n$ = 1,800 for each location: 250 fish [25 fish × 10 families] for $D_{[female]}D_{[male]}$, $L_{[female]}L_{[male]}$, and $L_{[female]}R_{[male]}$ cross types; 225 fish [25 fish × 9 families] for the $R_{[female]}R_{[male]}$, $D_{[female]}R_{[male]}$, and $L_{[female]}D_{[male]}$ cross types; 200 fish [25 fish × 8 families] for the $R_{[female]}L_{[male]}$ cross type; and 175 fish [25 fish × 7 families] for the $D_{[female]}L_{[male]}$ cross type) were anesthetized in MS-222 (3-aminobenzoic acid ethyl ester; 0.16 g/L) and their body mass (to nearest 0.1 g) and fork length (FL, to nearest 0.1 cm) were measured. At the fish farm, mass and length were measured only twice: on 25 fish per cross type in July ($n$ = 200) and on every remaining fish in November ($n$ = 710). In the two other environments, mass and length were also recorded for every remaining fish at the final sampling in November ([1] LARSA, $n$ = 3,500: $D_{[female]}D_{[male]}$ and $L_{[female]}R_{[male]}$: 500 fish [50 fish × 10 families]; $L_{[female]}L_{[male]}$: 477 fish [~48 fish × 10 families]; $R_{[female]}R_{[male]}$ and $D_{[female]}R_{[male]}$: 450 fish [50 × 9 families]; $R_{[female]}L_{[male]}$: 400 fish [50 × 8 families]; $L_{[female]}D_{[male]}$: 373 fish [~42 fish × 9 families]; and $D_{[female]}L_{[male]}$: 350 fish [50 × 7 families]; [2] ISMER, $n$ = 4,115: $D_{[female]}D_{[male]}$, $L_{[female]}L_{[male]}$, and $L_{[female]}R_{[male]}$: 600 fish [60 × 10 families];, $D_{[female]}R_{[male]}$ and $L_{[female]}D_{[male]}$: 540 fish [60 × 9 families]; $R_{[female]}R_{[male]}$: 39 fish [~49 fish × 9 families]; $D_{[female]}L_{[male]}$: 420 fish [60 × 7 families]; and $R_{[female]}L_{[male]}$: 376 fish [~47 fish × 8 families]). Condition factor was calculated according to the formula: (mass/length$^3$) × 100.

In November 2007, the presence or absence of sexual maturation was determined at the three rearing environments. For

TABLE 1. Number of brook trout per family in different rearing environments at each age stage. The environments were as follows: ISMER (Institut des Sciences de la Mer de Rimouski, Université du Québec à Rimouski): indoor, running freshwater, seasonal temperature variations; LARSA (Laboratoire régional en sciences aquatiques, Université Laval): indoor, recirculating water, constant 10°C temperature conditions. Percentages refer to the reduction in fish number relative to the initial number.

| | Age stage (months) | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Environment | 7 | 9 | 11 | 13 | 15 | 17 | 18 | 21 |
| ISMER | 230 | 230 | 190 (−17%) | 120 (−48%) | 120 (−48%) | 110 (−52%) | 60 (−74%) | 60 (−74%) |
| LARSA | 150 | 150 | 150 | 150 | 100 (−33%) | 100 (−33%) | 50 (−67%) | 50 (−67%) |

25 fish per family at ISMER and LARSA, and 25 fish per cross type at Pisciculture de la Jacques Cartier, gonads were excised and weighed and the gonadosomatic index was determined as: (gonad mass/total mass) × 100.

A daily record of mortalities was made at ISMER and LARSA. The relative mortality was determined for each family in these two environments. At Pisciculture de la Jacques Cartier, all fish were captured and counted at the end of the experiment and the relative mortality determined for each cross type.

*Statistical analysis*.—Data normality and homogeneity of variance were tested with the Kolmogorov–Smirnov and the Brown–Forsythe tests, respectively. Mass data ($\log_{10}$), condition factor (rank), and all percentage indexes (arcsin) were transformed to obtain normality and account for heteroscedasticity. Since body mass and length were highly correlated ($r = 0.98$, $P < 0.05$), we only tested models by using body mass.

To test for the presence of heterosis (objective 1), hybrid performance was compared with the performance of parental strains using analyses of variance (ANOVA) and posthoc tests. We used a conservative approach and considered that heterosis was present only when hybrids significantly outperformed both parental strains. Mass and condition factor were analyzed with two linear mixed models:

$$y_{ijkl} = \mu + AS_i + E_j + C_k + (AS \times E)_{ij} + (AS \times C)_{ik} + (E \times C)_{jk} + (AS \times E \times C)_{ijk} + F_{kl} + e_{ijkl} (\text{model A})$$

and

$$y_{ijkl} = m + AS_i + E_j + C_k + (AS \times E)_{ij} + (AS \times C)_{ik} + (E \times C)_{jk} + (AS \times E \times C)_{ijk} + e_{ijkl} (\text{model B}),$$

where $y_{ijkl}$ is the phenotypic observation, $\mu$ is the sample mean, $AS_i$ is the effect of the $i$th age stage, $E_j$ is the effect of the $j$th environment, and $C_k$ is the effect of the $k$th cross type, all of which were fitted as fixed effects as well as their interactions; $F_{kl}$ is the effect of the $l$th full-sib families nested in $k$th cross types fitted as a random effect, and $e_{ijkl}$ is the random residual effect. Model A includes the two environments, ISMER and LARSA, at each age stage, while model B includes the three environments at two age stages (17 and 21 months). The a posteriori Tukey's honestly significant difference (HSD) tests applied on least-squares means were used to detail significant factor or interaction effects. Sexual maturity and survival were analyzed with two-way ANOVA that used environment and cross type as factors. The a posteriori Tukey's test was used for mean comparisons when possible or replaced by the Games and Howell test when variances were not homogenous (Sokal and Rohlf 1981).

When the presence of significant heterosis or outbreeding depression was found, the intensity was expressed in percentage according to Shikano and Taniguchi (2002):

$$[(f_1/m) - 1] \times 100,$$

where $f_1$ is the mean performance of the $F_1$ hybrids and $m$ the mean performance of parental strains. To test for the effects of cross direction (objective 2) and environment (objective 3) on the intensity of heterosis, we took into account either the presence or absence of significant heterosis, or when heterosis was present in both reciprocal hybrids or for a same hybrid in different environments, the intensity was compared with ANOVA.

The relative importance of additive, dominant, and epistatic genetic interactions in determining the performance of hybrids were calculated according to Wu and Li (2002) and based on the partitioning of the phenotypic variance of the full-sibs$F_1$ into each component of the variance ($V$) as follows:

$$V_{A(f_1)} = (1/2)(V_{f1} + V_m - V_H),$$
$$V_{NA(f_1)} = (1/2)(V_{f1} + V_H - V_m),$$
$$d/a = 2(f_1 - m)/(P_i - P_j),$$
$$V_{D(f_1)} = [(d/a)^2 \times V_{A(f_1)}]/2,$$

and

$$V_{I(f1)} = V_{NA(f1)} - V_{D(f1)},$$

where $V_{A(f1)}$ is the additive variance and $V_{NA(f1)}$ the nonadditive variance of the $F_1$ hybrids; $V_{f1}$, $V_m$, and $V_H$ are the variance of the performance of the $F_1$ hybrids, the variance of the mean performance of the parental strains, and of the variance of heterosis, respectively; $d/a$ is the dominance ratio; $f_1$ is the mean performance of the $F_1$ hybrids; $m$ is the mean performance of parental strains; $P_i$ and $P_j$ are the mean performance of each $i$ and $j$ parental strains; and $V_{D(f1)}$ is the dominance variance and $V_{I(f1)}$ the epistasis variance of the $F_1$ hybrids.

Mixed-model analyses were performed with JMP 7 (SAS Institute, Cary, North Carolina); other statistical analyses were conducted with Statistica version 6.0 for Windows (StatSoft, Tulsa, Oklahoma). The statistical analyses were not corrected for multiple tests. A significance level of $\alpha = 0.05$ was used in all statistical tests.

## RESULTS

Fish body mass differed among environments, age stages, and cross types (significant interaction, $P < 0.001$; Table 2). The mixed models explained a large proportion of the total variance with an adjusted $R^2$ of 0.82 (model A) and 0.64 (model B) for body mass (Table 2). All cross types were significantly heavier when raised in the constant temperature environment (LARSA), except for domestic fish, which showed similar weights in the three different environments at the end of the experiment (Table 3). When the three pure cross types were compared, domestic brook trout were always significantly bigger than the two other strains in all three environments ($P < 0.05$; Table 3). In the constant temperature environment at LARSA, the Rupert strain was significantly heavier than the

TABLE 2. Summary of statistical analyses for the body mass of brook trout. Model A includes two environments (ISMER and LARSA [see Table 1]) at each age stage; Model B includes three environments (ISMER, LARSA, and Farm [outdoor, seasonal temperature variations, fish farm pond) at the two age stages (17 and 21 months) measured at the farm.

| | Model A | | | | Model B | | | |
|---|---|---|---|---|---|---|---|---|
| Variable or statistic | df | Mean squares | $F$ | $P$-value | df | Mean squares | $F$ | $P$-value |
| Age stage | 6 | 444.18 | 12,635.9 | $<0.001$ | 1 | 135.91 | 3,320.5 | $<0.001$ |
| Environment | 1 | 591.98 | 16,840.5 | $<0.001$ | 2 | 102.24 | 2,497.9 | $<0.001$ |
| Cross type | 7 | 92.20 | 34.4 | $<0.001$ | 7 | 14.29 | 349.2 | $<0.001$ |
| Age stage × environment | 6 | 21.28 | 605.4 | $<0.001$ | 2 | 16.74 | 409.0 | $<0.001$ |
| Age stage × cross type | 42 | 0.49 | 13.9 | $<0.001$ | 7 | 0.05 | 1.2 | 0.28 |
| Environment × cross type | 7 | 6.48 | 184.4 | $<0.001$ | 14 | 2.21 | 54.0 | $<0.001$ |
| Age stage × environment × cross type | 42 | 0.33 | 9.5 | $<0.001$ | 14 | 0.18 | 4.3 | $<0.001$ |
| Family (nested in cross type), random | 64 | 2.93 | 83.3 | $<0.001$ | | | | |
| Error | 28,022 | 0.04 | | | 11,587 | 0.04 | | |
| Model $R^2$ | 0.82 | | | | 0.64 | | | |
| $R^2$ adjusted | 0.82 | | | | 0.64 | | | |



Laval strain ($P < 0.05$; Table 3). At ISMER, such a difference was only observed at 17 months of age (Table 3).

When hybrid body mass was compared with those of their respective parental lines, heterosis was present but varied according to the type of hybrid cross; no outbreeding depression was observed (Tables 3 and 4). The $D_{[female]}R_{[male]}$ hybrid was intermediate to the values measured for the two parental strains in all three environments (Table 3) and never expressed heterosis. $L_{[female]}R_{[male]}$ hybrids were significantly heavier than their two parental lines ($P < 0.01$; Table 3). These hybrids also expressed heterosis at each age stage and in all three environments (Table 4). Globally, the intensity of heterosis expressed by $L_{[female]}R_{[male]}$ hybrids was higher at ISMER than at LARSA ($14.6 \pm 1.5$ versus $10.2 \pm 1.0$; $F = 6.6294$, df $= 1$, $P = 0.011$) and decreased over time, i.e., the intensities in 18- and 21-month-old fish were significantly lower than in 9-, 11-, 13-, and 15-month-old fish ($F = 4.0388$, df $= 6$, $P < 0.001$; interaction of site × age stage: $P > 0.05$). In contrast, $R_{[female]}L_{[male]}$ hybrids were usually intermediate to their parental lines, except for 17- and 21-month-old trout, which were significantly heavier than their two parental lines in the two environments with less controlled rearing conditions, i.e., ISMER (17-month-old fish only) and the fish farm (Table 3). The intensity of heterosis expressed by the $R_{[female]}L_{[male]}$ hybrids was similar in both LARSA and ISMER environments for 17-month-old fish, similar between 17-month-old and 21-month-old fish at the fish farm, and similar to the heterosis intensity expressed by the $L_{[female]}R_{[male]}$ hybrids when they occurred simultaneously at the farm and at ISMER ($P < 0.05$ for all statistical comparisons). The $D_{[female]}L_{[male]}$ and $L_{[female]}D_{[male]}$ hybrids both had intermediate mass compared with the parental lines in the varying temperature environments (ISMER and the fish farm) and presented no heterosis (Table 3). However, under constant temperature at LARSA, $L_{[female]}D_{[male]}$ hybrids were significantly heavier than fish from the two parental lines ($P < 0.05$; Table 3) and expressed heterosis, but only starting at 15 months of age. The intensity of heterosis did not vary over time ($F = 0.2544$, df $= 3$, $P > 0.05$; Table 4). In contrast, the reciprocal hybrid $D_{[female]}L_{[male]}$, remained intermediate to its parental lines and never expressed heterosis (Table 3).

The calculated dominance ratio ($d/a$) revealed that hybrids expressing heterosis also had a high dominance ratio and seemed therefore to be more susceptible to nonadditive than to additive effects (Table 5). The dominance variance ($V_D$) was also greater in hybrids that expressed heterosis than in hybrids that did not, while no clear pattern emerged from the additive variance ($V_A$) values. On the other hand, the epistasis variance component was null in all hybrid crosses with the exception of the $D_{[female]}R_{[male]}$ cross type at LARSA.

## Condition Factor, Sexual Maturity, and Survival

Even though some hybrid crosses differed from parental lines at certain ages or locations, the effects of hybridization on condition factor were less consistent and marked than those for mass; thus, we only present results for mass. The occurrence of sexual maturity varied among cross types ($P < 0.05$; Figure 1) and was also greater in males than in females ($P < 0.001$). However, there was no significant effect of rearing environment, and no significant interaction between environment, sex, and cross type on the expression of early sexual maturation ($F = 0.65$, df $=$ 14, $P = 0.82$). The percentage of early sexual maturation was significantly higher in the domestic strain (more than 25%) than in the other two pure crosses (less than 10% in both Laval and Rupert strains) ($P < 0.001$; Figure 1). In hybrids, the percentage of fish reaching early sexual maturation was intermediate ($L_{[female]}D_{[male]}$) or similar (all other hybrid cross types) to the percentage observed in the parental line expressing the lowest percentage of sexual maturation. Thus, no heterosis or outbreeding depression was observed for the occurrence of early sexual maturity. Finally, trout survival differed among environments,

TABLE 3. Growth performance of brook trout measured as body mass (g) in the purebred strains (bold italics) and their hybrids in three different environments at each age stage. Statistical analyses were done on log-transformed data and post hoc analyses on least-squares means, but the results are presented as arithmetic means ± SEs ($n$ [number of families] = 10 for $D_♀D_♂$, $L_♀L_♂$, and $L_♀R_♂$; 9 for $R_♀R_♂$, $D_♀R_♂$, and $L_♀D_♂$; 8 for $R_♀L_♂$; and 7 for $D_♀L_♂$, where D = domestic, L = Laval, and R = Rupert strains). Within age stages and environments, different letters indicate significant differences among cross types ($P < 0.05$). Grey shading indicates hybrids that had significantly higher growth rates than both of their parental lines (indicating heterosis).

| | Age stage (months) | | | | | | |
|---|---|---|---|---|---|---|---|
| Cross | 9 | 11 | 13 | 15 | 17 | 18 | 21 |
| | | | | **ISMER** | | | |
| $D_♀R_♂$ | 18.4 ± 1.2 w | 25.1 ± 1.7 w | 25.8 ± 2.2 w | 34.2 ± 3.0 x | 42.5 ± 4.2 v | 58.7 ± 4.3 x | 121.7 ± 6.7 x |
| ***$D_♀D_♂$*** | ***23.6 ± 2.2 v*** | ***39.7 ± 3.7 v*** | ***34.6 ± 3.6 v*** | ***45.2 ± 4.6 w*** | ***65.1 ± 6.7 u*** | ***100.5 ± 8.2 w*** | ***197.6 ± 11.9 w*** |
| $D_♀L_♂$ | 16.7 ± 1.0 w | 24.5 ± 1.4 w | 25.3 ± 1.7 w | 29.6 ± 2.2 x | 41.0 ± 1.9 v | 60.6 ± 3.5 x | 124.3 ± 6.4 x |
| $L_♀D_♂$ | 16.4 ± 1.1 w | 25.6 ± 1.9 w | 25.2 ± 1.8 w | 32.3± 2.6 x | 46.2 ± 3.5 v | 66.9 ± 4.5 x | 128.8 ± 5.2 x |
| ***$L_♀L_♂$*** | ***6.8 ± 0.2 z*** | ***9.1 ± 0.4 z*** | ***7.9 ± 0.3 z*** | ***8.4 ± 0.3 z*** | ***16.2 ± 0.5 z*** | ***35.3 ± 1.4 z*** | ***68.8 ± 2.1 z*** |
| $L_♀R_♂$ | 11.9 ± 0.9 x | 16.7 ± 1.7 x | 16.2 ± 1.8 x | 19.2 ± 2.2 x | 29.2 ± 2.3 w | 41.6 ± 2.7 y | 83.2 ± 4.2 y |
| $R_♀L_♂$ | 9.3 ± 0.6 y | 15.0 ± 0.9 yx | 14.2 ± 1.2 y | 16.1 ± 1.4 y | 23.9 ± 2.1 x | 36.8 ± 3.7 zy | 71.8 ± 6.0 z |
| ***$R_♀R_♂$*** | ***9.5 ± 0.6 y*** | ***12.6 ± 0.8 y*** | ***12.6 ± 0.8 y*** | ***14.8 ± 0.8 y*** | ***20.1 ± 1.3 y*** | ***31.5 ± 2.0 z*** | ***66.9 ± 4.5 z*** |
| | | | | **LARSA** | | | |
| $D_♀R_♂$ | 23.5 ± 1.8 wv | 43.0 ± 4.0 wv | 69.0 ± 7.2 v | 88.9 ± 11.0 w | 103.7 ± 11.9 x | 123.4 ± 13.5 x | 183.8 ± 20.1 w |
| ***$D_♀D_♂$*** | ***29.0 ± 3.0 v*** | ***50.1 ± 4.7 v*** | ***82.4 ± 6.4 vu*** | ***109.6 ± 10.8 v*** | ***121.5 ± 10.2 w*** | ***148.0 ± 12.5 w*** | ***217.6 ± 15.5 v*** |
| $D_♀L_♂$ | 20.7 ± 1.4 w | 33.4 ± 2.2 x | 47.5 ± 3.4 xw | 62.6 ± 4.1 yx | 68.7 ± 3.3 y | 83.3 ± 4.0 y | 134.1 ± 7.4 y |
| $L_♀D_♂$ | 24.3 ± 1.9 wv | 50.3 ± 4.9 v | 86.0 ± 9.9 u | 114.9 ± 14.3 u | 133.6 ± 16.1 v | 165.1 ± 21.4 v | 241.1 ± 27.3 u |
| ***$L_♀L_♂$*** | ***9.4 ± 0.5 z*** | ***18.8 ± 1.4 z*** | ***30.4 ± 2.7 z*** | ***43.1 ± 3.0 z*** | ***54.8 ± 4.1 z*** | ***67.1 ± 4.6 z*** | ***106.3 ± 6.4 z*** |
| $L_♀R_♂$ | 15.3 ± 0.9 x | 30.5 ± 2.6 x | 56.2 ± 5.4 w | 70.5 ± 4.6 x | 85.5 ± 7.8 x | 107.1 ± 9.2 x | 155.7 ± 9.7 x |
| $R_♀L_♂$ | 13.2 ± 0.9 yx | 23.0 ± 2.1 y | 39.1 ± 4.3 y | 56.6 ± 5.8 y | 73.5 ± 7.6 yx | 79.9 ± 7.5 zy | 129.7 ± 12.9 y |
| ***$R_♀R_♂$*** | ***11.8 ± 0.8 y*** | ***23.6 ± 1.3 y*** | ***41.9 ± 2.2 yx*** | ***54.7 ± 2.0 y*** | ***72.1 ± 3.2 y*** | ***82.3 ± 4.5 y*** | ***126.9 ± 7.7 y*** |
| | | | | **Farm** | | | |
| $D_♀R_♂$ | | | | | 46.0 ± 3.0 w | | 125.6 ± 4.8 v |
| ***$D_♀D_♂$*** | | | | | ***87.4 ± 7.4 v*** | | ***199.8 ± 13.1 wv*** |
| $D_♀L_♂$ | | | | | 43.7 ± 1.8 xw | | 117.9 ± 3.9 xw |
| $L_♀D_♂$ | | | | | 35.8 ± 2.3 xw | | 97.8 ± 2.6 w |
| ***$L_♀L_♂$*** | | | | | ***16.6 ± 0.8 z*** | | ***39.4 ± 2.2 z*** |
| $L_♀R_♂$ | | | | | 29.8 ± 3.4 y | | 67.6 ± 4.7 y |
| $R_♀L_♂$ | | | | | 36.6 ± 5.3 yx | | 97.8 ± 4.4 yx |
| ***$R_♀R_♂$*** | | | | | ***16.0 ± 1.4 z*** | | ***35.1 ± 8.6 z*** |

TABLE 4. Heterosis intensity for each brook trout cross having a trait performance significantly higher than that of its two parental lines in the three environments and for each age stage. Heterosis intensity was calculated as $[(f_1/m) - 1] \times 100$, where $f_1$ is the mean performance of the $F_1$ hybrids and $m$ the mean performance of the parental strains. Values are presented as means ± SEs.

| | | Age stage (months) | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Environment | Cross | 9 | 11 | 13 | 15 | 17 | 18 | 21 |
| ISMER | $L_♀R_♂$ | 18.5 ± 3.9 | 17.0 ± 4.5 | 19.0 ± 5.3 | 20.3 ± 5.0 | 16.1 ± 2.7 | 6.1 ± 1.8 | 4.9 ± 1.1 |
| | $R_♀L_♂$ | | | | | 9.2 ± 3.0 | | |
| LARSA | $L_♀D_♂$ | | | | 11.7 ± 2.7 | 10.7 ± 2.6 | 10.3 ± 2.7 | 8.7 ± 2.1 |
| | $L_♀R_♂$ | 16.4 ± 2.5 | 11.8 ± 3.0 | 12.3 ± 3.1 | 9.6 ± 1.8 | 7.0 ± 2.4 | 8.2 ± 2.1 | 6.2 ± 1.4 |
| Farm | $L_♀R_♂$ | | | | | 18.1 ± 3.7 | | 16.5 ± 1.8 |
| | $R_♀L_♂$ | | | | | 23.8 ± 4.2 | | 22.8 ± 1.2 |

TABLE 5. Dominance ratio (*d*/*a*) at each age stage and contributions of the different genetic components ($V_A$ = additive variance; $V_D$ = dominance variance; and $V_I$ = epistasis variance) to the phenotypic variance (Wu et al. 2002) expressed in each cross type and in two different environments. Negative values were defined as zero.

| | Age stage (months) | | | | | | | Pooled sampling times | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Cross | 9 | 11 | 13 | 15 | 17 | 18 | 21 | *d*/*a* | $V_A$ | $V_D$ | $V_I$ |
| | | | | | **ISMER** | | | | | | |
| $D_♀R_♂$ | 0.26 | 0.08 | 0.21 | 0.27 | 0.01 | 0.22 | 0.18 | 0.07 | 1248.8 | 3.2 | 0 |
| $D_♀L_♂$ | 0.18 | 0.00 | 0.31 | 0.15 | 0.01 | 0.22 | 0.13 | 0.04 | 1338.3 | 1.0 | 0 |
| $L_♀D_♂$ | 0.15 | 0.08 | 0.30 | 0.30 | 0.23 | 0.03 | 0.07 | 0.07 | 1388.3 | 3.1 | 0 |
| $L_♀R_♂$ | 2.81 | 3.36 | 2.58 | 2.36 | 5.61 | 4.56 | 28.92 | 6.04 | 472.0 | 8611.6 | 0 |
| $R_♀L_♂$ | 0.97 | 2.40 | 1.70 | 1.40 | 2.90 | 1.79 | 4.86 | 2.70 | 409.6 | 1494.7 | 0 |
| | | | | | **LARSA** | | | | | | |
| $D_♀R_♂$ | 0.36 | 0.46 | 0.34 | 0.25 | 0.28 | 0.25 | 0.51 | 0.36 | 2466.1 | 155.5 | 129.0 |
| $D_♀L_♂$ | 0.15 | 0.07 | 0.34 | 0.42 | 0.59 | 0.60 | 0.47 | 0.43 | 1520.0 | 140.2 | 0 |
| $L_♀D_♂$ | 0.52 | 1.01 | 1.14 | 1.16 | 1.36 | 1.45 | 1.56 | 1.31 | 3055.4 | 2606.7 | 0 |
| $L_♀R_♂$ | 3.83 | 3.81 | 3.51 | 3.91 | 2.56 | 4.28 | 3.62 | 3.56 | 1448.2 | 9188.0 | 0 |
| $R_♀L_♂$ | 2.08 | 0.74 | 0.52 | 1.41 | 1.16 | 0.69 | 1.62 | 1.15 | 1243.4 | 817.1 | 0 |



and mortalities were more numerous in the variable temperature environments ($P < 0.05$; fish farm, 58 ± 32%; ISMER, 7.25 ± 8.7%; LARSA, 1 ± 1.3%), but there was no cross type effect. It is noteworthy that, at the fish farm, predation played an important role in mortalities that occurred in the outdoor pond. Overall, no heterosis or outbreeding depression was observed in the three environments.

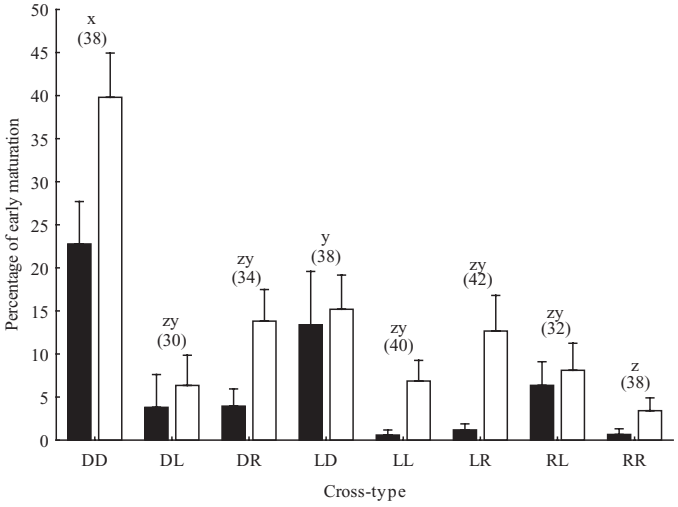


FIGURE 1. Early maturation in the three purebred strains of brook trout and their hybrids. No environment effect was observed, so data from the three study sites were pooled. The first letter of the cross type indicates the dam and the second letter the sire. Solid bars are for females and open bars for males. Statistical analyses were done on arcsine-transformed data, but results are presented as arithmetical means ± SE. Number of families (*n*) is indicated in parentheses. Cross types with different letters are significantly different ($P < 0.05$).

## DISCUSSION

This experiment highlights the presence of heterosis for variables related to growth—i.e. mass—in brook trout using interstrain crosses and provides no evidence for outbreeding depression. Strong heterosis expression was observed in a few cases that were as high as 24% for mass in some crosses. In general, however, heterosis expression levels were slightly higher or similar to those reported for the same traits in Chinook salmon *Oncorhynchus tshawytscha* (up to 10%; Bryden et al. 2004), Nile tilapia (Bentsen et al. 1998) and Mphende tilapia *Oreochromis shiranus* (Maluwa and Gjerde 2006; 12% to 17%), guppy (4.5%, Nakadate et al. 2003), and Rohu carp *Labeo rohita* (10%, Gjerde et al. 2002). Also, the expression of heterosis for growth variables varied according to rearing environments and to the strains involved in the cross. No evidence for heterosis was observed for sexual maturity or survival.

### Genetic Distance

The genetic distance between strains involved in hybridization may partly explain the variable patterns of heterosis that were expressed (Shikano et al. 2000; Linhart et al. 2002; Wang and Xia 2002; Stelkens et al. 2009). Heterosis is known to be linked to the extent of genetic differentiation between the parental strains owing to local adaptations that can fix different alleles in populations (Falconer and Mackay 1996). Yet, some investigators found no correlation between genetic distance and heterosis (Bentsen et al. 1998), and it was argued that the genetic diversity and dissimilarity among individuals in strains (Shikano and Taniguchi 2002b) or the degree of inbreeding (Nakadate et al. 2003) would be more important factors for the expression of heterosis. Here, it is noteworthy that we observed the highest occurrence of heterosis in intraspecific crosses involving parental populations with the highest level of genetic

differentiation, that is, between the Rupert and Laval strains with $F_{ST} = 0.427$ (Martin et al. 1997). As mentioned in the Introduction, the three brook trout strains used in this study previously showed no sign of inbreeding, which suggests that genetic divergence more than inbreeding may have been responsible in explaining variable patterns of heterosis observed between the different crosses.

### Cross Direction

The cross direction also played a role in the intensity of heterosis expression for growth. This was particularly evident in hybrid crosses between the Rupert and Laval brook trout strains. More generally, the extent of heterosis was more pronounced when the Laval strain was used as dam than when it was used as sire in hybrid crosses involving either the Rupert or the domestic strains. The importance of cross direction in heterosis expression has been reported in other species for different performance traits (resistance to infections in poeciliid fish, Clayton and Price 1994; growth in tilapias, Bentsen et al. 1998; swimming performance in largemouth bass *Micropterus salmoides*, Cooke et al. 2001). Different factors may explain such reciprocal effects: namely, maternal effects, paternal effects, and genetic linkage between sex genes and performance genes. Maternal effects are generally involved in cross direction, but are more often observed during the early fry development (Klupp 1979; Wangila and Dick 1996; Bentsen et al. 1998; Heath et al. 1999; Perry et al. 2004; X. X. Wang et al. 2006). Paternal effects have also been reported, but their underlying genetic mechanisms are still unclear (Cheng et al. 1987; Bentsen et al. 1998; Gjerde et al. 2002; X. X. Wang et al. 2006). The genetic linkage between sex genes and genes associated with specific traits of performance can result in sex-biased gene expression that may influence the predominance of a specific strain as dam or sire (Nilsson 1993; Bentsen et al. 1998; Ellegren and Parsch 2007; Derome et al. 2008). Further investigations are needed to discriminate the influence of each of these factors on heterosis expression.

### Family Effects

Within cross types, significant family effects were present; some families expressed strong and significant heterosis, while others did not (data not shown). Such differences among families have also been observed in common carp (Moav and Wohlfarth 1976), rainbow trout *Oncorhynchus mykiss* (Klupp 1979), and guppy (Shikano et al. 2000). However, familial variability was lowest in the $L_{[female]}R_{[male]}$ hybrid, which constantly expressed significant heterosis, while in most other crosses, even though some families expressed heterosis, there was no significant outperformance when the cross type was considered as a whole. Shikano et al. (2000) explained that such family differences could result from differences in the degree of genetic differentiation among parental strains. As already demonstrated by Martin et al. (1997), the Rupert and Laval strains were the most genetically distant.

### Environment Interaction

Genomic influence on performance and heterosis expression is also dependent on environmental conditions. The environment may modify gene expression as previously shown for the physiological pathway of growth in brook trout (Côté et al. 2007). In the present study, such a modification by the environment was more important in the $L_{[female]}D_{[male]}$ hybrid, which expressed heterosis only in the constant temperature environment. Therefore, heterosis expression in this hybrid seemed to be phenotypically plastic. Other studies have reported the occurrence of heterosis modified by environment in rainbow trout (Ayles and Baker 1983), Nile tilapia (Bentsen et al. 1998), and common carp (Wohlfarth 1993). It should be emphasized that the three environments used in this study differed in many other ways, including temperature regime, indoor versus outdoor environment, flow-through versus recirculation, and tank size and type. Moreover, the limited number of samplings at the fish farm may have limited our capacity to obtain detailed information about hybrid performances at this site, although highly significant heterosis was also detected at this site. Also, it is difficult to identify the specific rearing factors that most influence fish performance. Nevertheless, our primary objective was to assess different rearing conditions (rather than decipher the precise role of specific environmental factors) to test whether some hybrids would always outperform parental strains independently of the conditions.

In our study, environmental interactions were not observed for all hybrid crosses, suggesting that different genomes are influenced in different ways by environmental variability and thus that environmental interactions can reveal genotypes (strain combinations). Because of such interactions, the phenotypes of laboratory-reared fish may not reflect the phenotypes that would develop heterosis in other rearing or natural environments (Wohlfarth 1993; Fishback et al. 2002; Sundstrom et al. 2007; Tymchuk et al. 2007). In the absence of an interaction between an additive genetic effect and environment, a given breeding program can combine the best strains into a synthetic population (Eknath et al. 1993; Maluwa and Gjerde 2006; Maluwa et al. 2006). An analogous approach could potentially be used in breeding programs related to heterosis expression by using hybrids that express heterosis in all environments tested. For example, the $L_{[female]}R_{[male]}$ hybrid could be a good candidate for the application of such an approach in brook trout as it expressed heterosis in the three tested rearing environments. On the other hand, in the presence of genotype–environment interactions, the response to selection will be less predictable; it may then be desirable to develop strains for crossbreeding that are specific to each particular environment (Gjedrem 1992). Such an approach could also be adjusted by environment interactions in the presence of heterosis to take full advantage of heterosis expression in aquaculture production. In our study, heterosis expression observed for the $L_{[female]}D_{[male]}$ hybrid was sensitive to environmental conditions, and the use of such hybrids in

production may require that the experimental and farm environments be very similar (Bentsen et al. 1998).

### Variation with Ontogeny

We observed that heterosis expression in some hybrid crosses varied over time and was influenced by age or developmental stage in addition to genomic and environmental components. During ontogeny, genes associated with different biological processes can be expressed differentially, and gene expression can also be modified by interactions with other genes (Perry et al. 2005; C. H. Wang et al. 2006; Darias et al. 2008; Nolte et al. 2009) that would affect heterosis expression. Heterosis expression later in development may also result from a larger differentiation among strains with increasing age (Klupp 1979; C. H. Wang et al. 2006; Nolte et al. 2009).

### The Genetic Basis of Heterosis

Even though only estimates of the different components of genetic variance were used in a qualitative manner, they still provided a potential explanation of the genetic mechanisms that underlie the expression of heterosis. For instance, these estimates pointed to the importance of dominance effects in the expression of heterosis rather than additive or epistasis effects. This is in accordance with the dominance hypothesis of heterosis expression (Hochholdinger and Hoecker 2007). A previous study of gene expression during early growth, which used the same hybrid crosses as in this study, revealed that gene expression in hybrid crosses was highly dependent on the specific genetic architecture of parental lines with a prevalence of dominance in heterosis expression. Thus, Bougas et al. (2010) compared transcription profiles among the same three populations of brook trout and their hybrids by using microarrays to assess the influence of hybrid origin on modes of transcription regulation inheritance and on the mechanisms underlying growth. Those investigators found that hybrids exhibited strikingly different patterns of mode of transcription regulation, which were mostly additive (94%) for domestic and nonadditive for the Laval (45.7%) and Rupert–Laval hybrids (37.5%). Their results also indicated that prevalence of dominance in transcription regulation was related to growth heterosis. In fact, the study of Bougas et al. (2010) clearly showed, for the first time in vertebrates, that the consequences of hybridization on both the transcriptome level and the phenotype are highly dependent on the specific genetic architectures of crossed populations and therefore hardly predictable. As such, the parallelism in patterns of heterosis observed in the present study for growth and in Bougas et al. (2010) at the transcriptome level is quite striking.

## CONCLUSION

Intraspecific heterosis is present in brook trout. However, its expression seems complex and difficult to predict as it is influenced by a variety of biotic and abiotic factors, including genetic distance between parental lines, strain combination, cross direction, and developmental stage, as well as rearing environment. However, one hybrid cross, $L_{[female]}R_{[male]}$, stood out as the best candidate for using heterosis to enhance brook trout production in various types of environments. Further studies combining the analysis of gene expression and quantitative genetics performed in both $F_1$ hybrids and backcrosses should provide a better understanding of the mechanisms underlying heterosis in fish.

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## REFERENCES

Ayles, G. B., and R. F. Baker. 1983. Genetic differences in growth and survival between strains and hybrids of rainbow trout (*Salmo gairdneri*) stocked in aquaculture lakes in the Canadian prairies. Aquaculture 33:269–280.

Bentsen, H. B., A. E. Eknath, M. S. Palada-de Vera, J. C. Danting, H. L. Bolivar, R. A. Reyes, E. E. Dionisio, F. M. Longalong, A. V. Circa, M. M. Tayamen, and B. Gjerde. 1998. Genetic improvement of farmed tilapias: growth performance in a complete diallel cross experiment with eight strains of *Oreochromis niloticus*. Aquaculture 160:145–173.

Birchler, J. A., D. L. Auger, and N. C. Riddle. 2003. In search of the molecular basis of heterosis. Plant Cell 15:2236–2239.

Bougas, B., S. Granier, C. Audet, and L. Bernatchez. 2010. The transcriptional landscape of cross-specific hybrids and its possible link with growth in brook charr (*Salvelinus fontinalis* Mitchill). Genetics 186:97–107.

Bryden, C. A., J. W. Heath, and D. D. Heath. 2004. Performance and heterosis in farmed and wild Chinook salmon (*Oncorhynchus tshawytscha*) hybrid and purebred crosses. Aquaculture 235:249–261.

Cheng, K. M., I. M. McCallum, R. I. McKay, and B. E. March. 1987. A comparison of survival and growth of two strains of Chinook salmon (*Oncorhynchus tshawytscha*) and their crosses reared in confinement. Aquaculture 67:301–311.

Clayton, G. M., and D. J. Price. 1994. Heterosis in resistance to *Ichthyophthirius multifiliis* infections in poeciliid fish. Journal of Fish Biology 44: 59–66.

Comings, D. E., and J. P. MacMurray. 2000. Molecular heterosis: a review. Molecular Genetics and Metabolism 71:19–31.

Cooke, S. J., T. W. Kassler, and D. P. Philipp. 2001. Physiological performance of largemouth bass related to local adaptation and interstock hybridization: implications for conservation and management. Journal of Fish Biology 59(Supplement A):248–268.

Côté, G., G. Perry, P. Blier, and L. Bernatchez. 2007. The influence of gene-environment interactions on GHR and IGF-1 expression and their association with growth in brook charr, *Salvelinus fontinalis* (Mitchill). BMC Genetics 8:87.

Darias, M. J., J. L. Zambonino-Infante, K. Hugot, C. L. Cahu, and D. Mazurais. 2008. Gene expression patterns during the larval development of European sea bass (*Dicentrarchus labrax*) by microarray analysis. Marine Biotechnology (New York) 10:416–428.

Derome, N., B. Bougas, S. M. Rogers, A. R. Whiteley, A. Labbe, J. Laroche, and L. Bernatchez. 2008. Pervasive sex-linked effects on transcription regulation as revealed by expression quantitative trait loci mapping in

lake whitefish species pairs (*Coregonus* sp., Salmonidae). Genetics 179: 1903–1917.

Edmands, S. 2007. Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. Molecular Ecology 16:463–475.

Einum, S., and I. A. Fleming. 1997. Genetic divergence and interactions in the wild among native, farmed and hybrid Atlantic salmon. Journal of Fish Biology 50:634–651.

Eknath, A. E., M. M. Tayamen, M. S. Palada-de Vera, J. C. Danting, R. A. Reyes, E. E. Dionisio, J. B. Capili, H. L. Bolivar, T. A. Abella, A. V. Circa, H. B. Bentsen, B. Gjerde, T. Gjedrem, and R. S. V. Pullin. 1993. Genetic improvement of farmed tilapias: the growth performance of eight strains of *Oreochromis niloticus* tested in different farm environments. Aquaculture 111:171–188.

Ellegren, H., and J. Parsch. 2007. The evolution of sex-biased genes and sex-biased gene expression. Nature Reviews Genetics 8:689–698.

Falconer, D. S., and T. F. C. Mackay. 1996. Introduction to quantitative genetics, 4th edition. Longman Group, Essex, UK.

Fishback, A. G., R. G. Danzmann, M. M. Ferguson, and J. P. Gibson. 2002. Estimates of genetic parameters and genotype by environment interactions for growth traits of rainbow trout (*Oncorhynchus mykiss*) as inferred using molecular pedigrees. Aquaculture 206:137–150.

Fraser, J. M. 1981. Comparative survival and growth of planted wild, hybrid, and domestic strains of brook trout (*Salvelinus fontinalis*) in Ontario lakes. Canadian Journal of Fisheries and Aquatic Sciences 38: 1672–1684.

Garcia de Leaniz, C., I. A. Fleming, S. Einum, E. Verspoor, W. C. Jordan, S. Consuegra, N. Aubin-Horth, D. Lajus, B. H. Letcher, A. F. Youngson, J. H. Webb, L. A. Vollestad, B. Villanueva, A. Ferguson, and T. P. Quinn. 2007. A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. Biological Reviews 82:173–211.

Gharrett, A. J., W. W. Smoker, R. R. Reisenbichler, and S. G. Taylor. 1999. Outbreeding depression in hybrids between odd- and even-broodyear pink salmon. Aquaculture 173:117–129.

Gjedrem, T. 1992. Breeding plans for rainbow trout. Aquaculture 100:73–83.

Gjerde, B., P. V. G. K. Reddy, K. D. Mahapatra, J. N. Saha, R. K. Jana, P. K. Meher, M. Sahoo, S. Lenka, P. Govindassamy, and M. Rye. 2002. Growth and survival in two complete diallele crosses with five stocks of Rohu carp (*Labeo rohita*). Aquaculture 209:103–115.

Gjerde, B., and T. Refstie. 1984. Complete diallel cross between five strains of Atlantic salmon. Livestock Production Science 11:207–226.

Glover, K. A., O. Bergh, H. Rudra, and O. Skaala. 2006. Juvenile growth and susceptibility to *Aeromonas salmonicida* subsp *salmonicida* in Atlantic salmon (*Salmo salar* L.) of farmed, hybrid and wild parentage. Aquaculture 254:72–81.

Heath, D. D., C. W. Fox, and J. W. Heath. 1999. Maternal effects on offspring size: variation through early development of Chinook salmon. Evolution 53:1605–1611.

Hochholdinger, F., and N. Hoecker. 2007. Towards the molecular basis of heterosis. Trends in Plant Science 12:427–432.

Hoffmann, A. A., and J. Merilä. 1999. Heritable variation and evolution under favourable and unfavourable conditions. Trends in Ecology and Evolution 14:96–101.

Hulata, G. 1995. A review of genetic improvement of the common carp (*Cyprinus carpio* L.) and other cyprinids by crossbreeding, hybridization and selection. Aquaculture 129:143–155.

Klupp, R. 1979. Genetic variance for growth in rainbow trout (*Salmo gairdneri*). Aquaculture 18:123–134.

Linhart, O., D. Gela, M. Rodina, V. Slechtova, and V. Slechta. 2002. Top-crossing with paternal inheritance testing of common carp (*Cyprinus carpio* L.) progeny under two altitude conditions. Aquaculture 204: 481–491.

Lippman, Z. B., and D. Zamir. 2007. Heterosis: revisiting the magic. Trends in Genetics 23:60–66.

Maluwa, A. O., and B. Gjerde. 2006. Genetic evaluation of four strains of *Oreochromis shiranus* for harvest body weight in a diallel cross. Aquaculture 259:28–37.

Maluwa, A. O., B. Gjerde, and R. W. Ponzoni. 2006. Genetic parameters and genotype by environment interaction for body weight of *Oreochromis shiranus*. Aquaculture 259:47–55.

Marengoni, N. G., Y. Onoue, and T. Oyama. 1998. Offspring growth in a diallel crossbreeding with three strains of Nile tilapia *Oreochromis niloticus*. Journal of the World Aquaculture Society 29:114–119.

Martin, S., J. Y. Savaria, C. Audet, and L. Bernatchez. 1997. Microsatellites reveal no evidence for inbreeding effects but low inter-stock genetic diversity among brook charr stocks used for production in Quebec. Bulletin of Aquaculture Association of Canada 97:21–23.

McClelland, E. K., and K. A. Naish. 2007. What is the fitness outcome of crossing unrelated fish populations? a meta-analysis and an evaluation of future research directions. Conservation Genetics 8:397–416.

Moav, R., and G. W. Wohlfarth. 1976. Two-way selection for growth rate in the common carp (*Cyprinus carpio* L.). Genetics 82:83–101.

Nakadate, M., T. Shikano, and N. Taniguchi. 2003. Inbreeding depression and heterosis in various quantitative traits of the guppy, *Poecilia reticulata*. Aquaculture 220:219–226.

Nielsen, H. M., J. Ødegård, I. Olesen, B. Gjerde, L. Ardo, G. Jeney, and Z. Jeney. 2010. Genetic analysis of common carp (*Cyprinus carpio*) strains. I: genetic parameters and heterosis for growth traits and survival. Aquaculture 304:14–21.

Nilsson, J. 1993. Arctic charr strain crosses: effects on growth and sexual maturity. Journal of Fish Biology 43:163–171.

Nolte, A. W., S. Renaut, and L. Bernatchez. 2009. Divergence in gene regulation at young life history stages of whitefish (*Coregonus* sp.) and the emergence of genomic isolation. BMC Evolutionary Biology 9:59.

Perry, G. M. L., C. Audet, and L. Bernatchez. 2005. Maternal genetic effects on adaptive divergence between anadromous and resident brook charr during early life history. Journal of Evolutionary Biology 18:1348–1361.

Perry, G. M. L., C. Audet, B. Laplatte, and L. Bernatchez. 2004. Shifting patterns in genetic control at the embryo-alevin boundary in brook charr. Evolution 58:2002–2012.

Shikano, T., M. Nakadate, and Y. Fujio. 2000. An experimental study on strain combinations in heterosis in salinity tolerance of the guppy *Poecilia reticulata*. Fisheries Science 66:625–632.

Shikano, T., and N. Taniguchi. 2002a. Heterosis for neonatal survival in the guppy. Journal of Fish Biology 60:715–725.

Shikano, T., and N. Taniguchi. 2002b. Using microsatellite and RAPD markers to estimate the amount of heterosis in various strain combinations in the guppy (*Poecilia reticulata*) as a fish model. Aquaculture 204:271–281.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60:1129–1157.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research, 2nd edition. Freeman, San Francisco.

Stelkens, R. B., C. Schmid, O. Selz, and O. Seehausen. 2009. Phenotypic novelty in experimental hybrids is predicted by the genetic distance between species of cichlid fish. BMC Evolutionary Biology 9:283.

Sundstrom, L. F., M. Lohmuis, W. E. Tymchuk, and R. H. Devlin. 2007. Gene-environment interactions influence ecological consequences of transgenic animals. Proceedings of the National Academy of Sciences of the USA 104:3889–3894.

Thériault, V., D. Garant, L. Bernatchez, and J. J. Dodson. 2007. Heritability of life-history tactics and genetic correlation with body size in a natural population of brook charr (*Salvelinus fontinalis*). Journal of Evolutionary Biology 20:2266–2277.

Tymchuk, W. E., L. F. Sundstrom, and R. H. Devlin. 2007. Growth and survival trade-offs and outbreeding depression in rainbow trout (*Oncorhynchus mykiss*). Evolution 61:1225–1237.

Wang, C. H., S. F. Li, Z. G. Liu, S. P. Xiang, J. Wang, Z. Y. Pang, and J. P. Duan. 2006. Developmental quantitative genetic analysis of body weight and

morphological traits in red common carp, *Cyprinus carpio* L. Aquaculture 251:219–230.

Wang, I. A., S. E. Gilk, W. W. Smoker, and A. J. Gharrett. 2007. Outbreeding effect on embryo development in hybrids of allopatric pink salmon (*Oncorhynchus gorbuscha*) populations, a potential consequence of stock translocation. Aquaculture 272(Supplement 1):S152– S160.

Wang, J., and D. Xia. 2002. Studies on fish heterosis with DNA fingerprinting. Aquaculture Research 33:941–947.

Wang, X. X., K. E. Ross, E. Saillant, D. M. Gatlin, and J. R. Gold. 2006. Quantitative genetics and heritability of growth-related traits in hybrid striped bass (*Morone chrysops* female × *Morone saxatilis* male). Aquaculture 261:535–545.

Wangila, B. C. C., and T. A. Dick. 1996. Genetic effects and growth performance in pure and hybrid strains of rainbow trout, *Oncorhynchus mykiss* (Walbaum) (Order: Salmoniformes, Family: Salmonidae). Aquaculture Research 27:35–41.

Webster, D. A., and W. A. Flick. 1981. Performance of indigenous, exotic, and hybrid strains of brook trout (*Salvelinus fontinalis*) in waters of the Adirondack Mountains, New York. Canadian Journal of Fisheries and Aquatic Sciences 38:1701–1707.

Wilson, A. J., J. A. Hutchings, and M. M. Ferguson. 2003. Selective and genetic constraints on the evolution of body size in a stream-dwelling salmonid fish. Journal of Evolutionary Biology 16:584–594.

Wohlfarth, G. W. 1993. Heterosis for growth rate in common carp. Aquaculture 113:31–46.

Wu, Z. X., and M. D. Li. 2002. Analysis of heterosis by a direct method using the concept of heritability. Genetica 114:163–170.