UNIVERSITÉ DU QUÉBEC

EFFETS DE L'HYBRIDATION INTER-SOUCHES SUR LES PERFORMANCES DES PREMIERS STADES DE DÉVELOPPEMENT CHEZ L'OMBLE DE FONTAINE (*SALVELINUS FONTINALIS*)

MÉMOIRE PRÉSENTÉ A
L'UNIVERSITÉ DU QUÉBEC À RIMOUSKI
Comme exigence partielle de la Maîtrise ès Sciences en Océanographie

PAR
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Décembre 2007

REMERCIEMENTS

Tout d'abord, je tiens à remercier ma directrice Céline Audet pour m'avoir fait découvrir le domaine de la recherche et des salmonidés, ainsi que pour sa disponibilité, son écoute et sa patience durant tout le temps qu'a duré ma maîtrise. Je la remercie aussi pour son exigence et sa rigueur, qui sont indispensables dans un tel domaine. Son dynamisme et sa passion pour ses recherches ont été un exemple pour moi. J'aimerais également remercier mon co-directeur Louis Bernatchez pour son aide indispensable lors de l'interprétation des résultats, ainsi que pour ses commentaires lors des différentes périodes de rédaction.

Je voudrais aussi remercier tout le personnel du Laboratoire Régional des Sciences Aquatiques (LARSA), à l'Université Laval, qui s'est occupé de l'élevage des nombreux poissons utilisés pour cette étude et plus particulièrement Serge Higgins, responsable du LARSA, et Jean-Christophe Therrien pour avoir toujours été disponibles quand j'avais besoin de leur aide. J'aimerais également remercier Bérénice Bougas et Dominique Lavallée pour leur aide précieuse durant mes nombreux échantillonnages, ainsi que pour les bons moments passés toutes les trois dans les profondeurs et le froid du LARSA…

Finalement, un merci tout particulier à ma famille qui m'a toujours soutenue dans mes choix et m'a permis de quitter la Suisse pour le Québec. Je sais qu'il n'a pas été facile pour eux d'accepter que je veuille faire de l'océanographie, à des milliers de kilomètres, alors que je viens d'un pays plutôt montagnard ! Je terminerais en remerciant mon chum, Erwann, qui m'a soutenue et encouragée durant la majeure partie de ma maîtrise.

RÉSUMÉ

L'hétérosis est un phénomène très étudié chez les plantes, mais les mécanismes sous-jacents chez les vertébrés, et plus particulièrement chez les poissons, demeurent un sujet controversé. Nous avons donc voulu mettre en évidence la présence ou non de vigueur hybride inter-souches chez les jeunes stades d'omble de fontaine (*Salvelinus fontinalis* Mitchill). Cette espèce a été choisie, car sa production dans l'Est du Canada est très importante et également parce que des souches sauvages commencent à être utilisées par certains producteurs en complément de la souche domestique, afin d'améliorer cette dernière.

Pour étudier le phénomène d'hétérosis, nous avons donc réalisé des croisements entre deux souches sauvages génétiquement distinctes (Laval et Rupert) et une souche domestique d'omble de fontaine. Huit types de croisements ont été réalisés (3 purs et 5 hybrides) et pour chaque croisement 10 familles plein-frère ont été produites. La présence d'hétérosis a été mise en évidence dans plusieurs croisements. Le croisement ♀L x ♂D est celui qui présente le pourcentage d'hétérosis le plus élevé, avec 80 % d'accroissement en masse de plus comparativement aux souches pures. De la dépression de croisement a aussi été observée, mais moins souvent et moins intensément. Ces deux phénomènes vont varier tout d'abord en fonction des souches étudiées. La souche Laval est plus souvent en cause que les deux autres souches dans la présence d'hétérosis, mais la direction du croisement est également un facteur à considérer. Par exemple, nous avons observé de l'hétérosis pour le croisement ♀L x ♂D, mais pas pour le croisement inverse (♀D x ♂L). Finalement, des résultats différents ont été obtenus en fonction du stade de développement. Ainsi, de l'hétérosis a été mis en évidence chez le croisement ♀L x ♂D pour les trois premiers stades, mais non au dernier. L'expression de l'hétérosis chez l'omble de fontaine paraît donc être un phénomène complexe et largement dépendant de l'architecture génétique des génomes qui interagissent.

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INTRODUCTION GÉNÉRALE

1.1 Biologie de l'espèce

L'omble de fontaine, *Salvelinus fontinalis*, fait partie de la grande famille des Salmonidés, qui est largement répartie dans tout l'Hémisphère Nord. D'une manière générale, c'est une espèce que l'on va retrouver dans des rivières aux eaux froides et bien oxygénées ; certaines populations dites anadromes sont également présentes dans les estuaires et les eaux marines côtières (Bernatchez & Giroux 1991).

De par son omniprésence dans la quasi-totalité des rivières du Québec, l'omble de fontaine est donc l'espèce la plus pêchée dans son milieu naturel. Dans certaines régions, des hybrides inter-souches sont même utilisés afin d'y régénérer la pêche. En effet, ces hybrides sont utilisés, car ils possèdent une croissance plus rapide que les poissons domestiques, ainsi qu'une meilleure survie lorsqu'ils sont relâchés après une mauvaise prise (Karas 1997).

1.2 Mise en contexte

Dans le domaine de l'aquaculture, l'omble de fontaine est d'une très grande importance au Québec, car à lui seul, il représente jusqu'à 50% de la production aquicole ;

il serait donc intéressant de pouvoir en améliorer la production. En Amérique du Nord, la production d'omble de fontaine a débuté dès le milieu du 19ème siècle et dès lors, cette espèce n'a pas cessé d'être élevée en pisciculture (Balon 1980). Au Québec, le gros de la production vise principalement l'ensemencement en milieu naturel et non le marché de la table.

1.3 Problématique

En Amérique du Nord, on produit principalement des salmonidés et les recherches en génétique quantitative portent donc essentiellement sur ces espèces. En effet, de nombreuses études sont réalisées afin d'acquérir une meilleure compréhension des schémas de croissance, de développement et de reproduction pour la sélection de souches permettant d'optimiser ce type d'élevage (Fjalestad *et al.* 2003: Kause *et al.* 2004). Pour que cela soit possible, il est tout d'abord nécessaire de bien connaître les bases de la vigueur hybride (ou hétérosis), ainsi que les différents effets parentaux obtenus chez ces espèces.

1.3.1 *L'hétérosis*

Le mot hétérosis fait référence au fait que la progéniture de différentes variétés ou souches va présenter une biomasse plus importante, ainsi qu'un développement et un pourcentage de survie plus élevé que la meilleure des souches parentales (Birchler *et al.* 2003). C'est un phénomène qui est étudié depuis de nombreuses années, principalement chez les plantes, les mammifères et les mollusques (see Hedgecock *et al.* 2007). Les connaissances chez les poissons sont beaucoup plus restreintes et il n'y a que peu d'espèces

qui sont étudiées. Celles-ci incluent la carpe (*Cyprinus carpio*), le guppy (*Poecilia reticulata*), le tilapia (*Oreochromis niloticus*) et le poisson chat (*Clarias* spp.). Chez la carpe et le guppy des croisements entre souches de différentes origines ont révélé, respectivement, la présence d'hétérosis pour le taux de croissance (Wohlfarth 1993) et la tolérance à la salinité (Shikano *et al.* 2000). Chez le tilapia, ce sont des croisements entre souches sauvages et domestiquées qui ont révélé la présence d'hétérosis pour le poids (Bentsen *et al.* 1998), alors que chez le poisson chat, de l'hétérosis a été obtenu pour la survie et la croissance lors de croisements entre les espèces *Clarias batrachus* et *Clarias gariepinus* (Rahman *et al.* 1995). Chez les salmonidés, la présence d'hétérosis est plus controversée. Malgré la présence du phénomène pour plusieurs traits, tels que le taux de survie chez la truite arc-en-ciel (Ayles and Baker 1983) ou la croissance chez des hybrides de souche sauvage et domestique d'ombles de fontaine (e.g. Chevassus 1980), une généralisation ne peut pas être tirée. En effet, dépendamment de l'espèce ou du trait considéré, la présence d'hétérosis ne sera pas la même, ce phénomène étant dépendant du caractère observé, mais également des populations parentales.

Les mécanismes sous-jacents à l'hétérosis sont encore peu connus (Hedgecock *et al.* 2007). Cependant, certaines études ont démontré que la différence génétique entre les souches pures est un élément dont il faut tenir compte. En effet, deux souches génétiquement distantes l'une de l'autre auraient plus de chance d'avoir une progéniture démontrant de l'hétérosis (Shamsuddin 1985; Bentsen *et al.* 1998; Wang & Xia 2002). Ce dernier point doit être considéré avec beaucoup d'attention, car il peut aussi engendrer

l'inverse de l'hétérosis, qui est la dépression de croisement. Ce phénomène résulte donc en une diminution du fitness de la progéniture par rapport aux souches parentales (Templeton 1986).

1.3.2 *Les effets parentaux*

Les effets parentaux sont divisés en effet maternel et paternel. Ces deux effets sont importants durant le développement des jeunes stades de poissons, mais à des moments différents. En effet, l'effet maternel est plus marqué durant les premiers stades, lorsque le sac vitellin est présent (truite brune, *Salmo trutta*, Vandeputte *et al.* 2002). Les premiers stades de développement sont donc fortement influencés par le génome maternel, via la qualité du vitellus (Hebert 1998) et l'effet maternel est donc très important jusqu'à la résorption du sac vitellin (Perry *et al.* 2004). Une fois celui-ci résorbé, il n'y a plus d'évidence de la présence de l'effet maternel (Nakajima & Taniguchi 2002), la contribution génétique de l'individu remplaçant ce dernier (Perry *et al.* 2004). Cependant, il a été démontré que les effets maternels peuvent durer plus longtemps (Fishback *et al.* 2002). Différentes études ont montré que l'effet maternel agit sur la survie de l'individu (guppy, Shikano & Taniguchi 2005), mais aussi sur la taille (guppy, Shikano *et al.* 1997) et le développement (saumon keta, *Oncorhynchus keta*, Smoker 1986). L'effet maternel peut donc être non génétique dans les premiers stades de développement, lorsqu'il résulte de la composition du vitellus (Perry *et al.* 2005), ou génétique (Pakkasmaa 2002; Bang *et al.* 2006) dans des stades plus avancés, lorsque le vitellus n'est plus présent. A l'inverse, l'effet paternel est principalement génétique, car le géniteur ne fournit pas de réserves à sa

descendance. D'une manière générale, l'effet paternel est beaucoup moins étudié que l'effet maternel chez les jeunes stades. Cela est principalement dû au fait que l'effet paternel est beaucoup plus difficilement identifiable lorsque l'effet maternel est présent. Cependant, des études sur des jeunes stades ont montré que l'effet paternel va influencer le taux de croissance, le développement (truite brune, Vøllestad & Lillehamer 2000) et des traits liés au taux métabolique, comme la taille des otolithes et le ratio ARN/ADN (hareng, *Clupea harengus*, Bang *et al.* 2006).

1.4 Objectifs

Ce projet de maîtrise fait partie d'une étude plus globale dont l'objectif général est d'essayer de mieux comprendre les bases physiologiques et génomiques fonctionnelles de l'hétérosis afin, éventuellement, de pouvoir améliorer la production aquacole de l'omble de fontaine au Québec. Plus précisément pour mon projet, il s'agissait de vérifier la présence ou non d'hétérosis lors de croisements inter-souches au cours des premiers stades de développement.

Mes objectifs spécifiques étaient de :

1) vérifier si l'hétérosis s'exprime chez les différents croisements effectués entre trois souches pures (domestique, Laval et Rupert) et leurs hybrides réciproques ;
2) déterminer si l'hétérosis s'exprime différemment en fonction des différents stades de développement.

CHAPITRE 2

EVIDENCE FOR BOTH HETEROSIS AND OUTBREEDING DEPRESSION RESULTING FROM INTER-POPULATION HYBRIDIZATION IN YOUNG OF THE YEAR BROOK CHARR (*SALVELINUS FONTINALIS*)

Granier, S.

ABSTRACT

Inter and intra-species hybridizations have been used with success to improve growth or disease resistance in different fish species. However, in salmonids it is still unclear if heterosis can be expressed and to what extent it can be used in fish production. Our objective was to underline the presence or the absence of inter-strain heterosis during the first stages of development in brook charr (*Salvelinus fontinalis* Mitchill). Two wild populations recently introduced in fish production in Québec (Laval and Rupert; L and R respectively) and the domestic type (D) largely present in the fish farms in Québec were used. We surveyed the growth of 72 full-sib families, representing eight cross-types (♀D x ♂D, ♀D x ♂L, ♀D x ♂R, ♀L x ♂D, ♀L x ♂L, ♀L x ♂R, ♀R x ♂L and ♀R x ♂R), from

hatching to 2136 degree-days (dd). Both, heterosis and outbreeding depression were observed. The Laval strain was the most often involved in heterosis expression, especially when Laval females were used as dams: we observed heterosis in the ♀L x ♂D hybrid (at yolk sac resorption stage and after 15 weeks of exogenous feeding) but not in the reciprocal hybrid (♀D x ♂L). The results were strongly dependent of the developmental stage, and an advantage at a very early stage of development did not necessarily lead to a higher growth rate later on. For example, the ♀L x ♂D hybrid, which showed the highest percentage of heterosis (an 80% increase compared to the mean of the two parental strains) at the yolk sac resorption stage, was no longer, larger, and heavier than the ♀D x ♂D siblings at the end of the first summer of growth. Outbreeding depression was also observed, but more rarely and less intensely; the highest percentage (36%) was observed in the ♀R x ♂L cross type at hatching. It is noteworthy that heterosis was not powered by crosses between the two most genetically distinct strains (Laval and Rupert), but mostly occurred with the presence of domestic males. While this study provides one of the most detailed evidence for the occurrence of heterosis in salmonids, it also illustrates that studies on the gene architecture is essential towards understand the mechanisms underlying the expression of heterosis in brook charr so that predictable results can be obtained when crossing different strain types.

2.1 Introduction

Heterosis is a phenomenon that has been studied for almost a century, particularly in plants (Zhang et al. 2007), mammals (Gama *et al.* 1991) and molluscs (Hedgecock *et al.* 2007). In fish, it was suggested that crossing inbred strains allows the formation of a new synthetic population by mixing the best strains (Gjedrem 1983), which can show superiority compared to pure ones (Hulata 2001; Dong & Yuan 2002; Doupé *et al.* 2003). The word heterosis was introduced for the first time in 1914 by Harrison Shull (Shull 1914), but exploitation of hybrid vigour in plant breeding began in 1908 (Crow 1980). 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 (Hotz *et al.* 1999; Burke & Arnold 2001; Dong & Yuan 2002; Birchler *et al.* 2003). Alternatively, crosses between genetically distinct populations and species can result in outbreeding depression whereby hybrid performance is reduced relatively to that of parental forms (Templeton 1986). Genetically distant strains could also be expected to express heterosis, more than genetically closer ones, and several authors suggest that there is a positive relationship between the genetic divergence between parents and performance of their hybrids (Shamsuddin 1985; Wang & Xia 2002). Heterosis also exists in the natural environment, where hybrids demonstrate fitness equivalent to the two parental taxa or higher levels of fitness than at least one of the parents (Arnold & Hodges 1995). When heterosis results from crosses between strains or between different

races or varieties it is theoretically known as the reverse of inbreeding depression and forms an important means for genetic improvements (Falconer & Mackay 1996).

To explain heterosis, three major mechanisms have been proposed: i) the overdominance is based on the principle that an heterozygote will be superior to the best homozygote; ii) the dominance explains heterosis by the acquisition of dominant alleles inherited from one or the two parents that would mask deleterious recessive mutations; and iii) the epistasis according to which heterosis would result from interactions of alleles at different loci (Hedgecock *et al.* 2007). Until now, however, the general mechanisms involved in the phenomenon of heterosis in aquatic animals are not well understood (see Hedgecock *et al.* 2007 for Pacific oyster, *Crassostrea gigas*).

Since traits are affected by both genetic and environmental factors, heterosis should be examined under controlled conditions where environmental variation can be minimized (Nakadate *et al.* 2003). Additive (allelic variation) and non-additive (dominance or epistasis) genetic effects are also important in the study of heterosis because they influence the choice of paternal and/or maternal strain to be used in a crossbreeding program (Maluwa & Gjerde 2006). The different performances between strains thus depend on the breeders' origin. 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.* 1998).

Occurrence of heterosis is unclear in fishes and only a few studies have been conducted on this subject (Nakadate *et al.* 2003). However, some heterosis has been found for neonatal survival on the guppy (*Poecilia reticulate*, Shikano & Taniguchi 2002), growth rate of carp (*Cyprinus carpio*, Wohlfarth 1993), tilapia (*Oreochromis niloticus*), and catfish (*Clarias* spp.) (see Bryden *et al.* 2004). A more extended utilization of heterosis in selective breeding of fish species can be an effective way to improve fish quality and increase production (Dong & Yuan 2002). In salmonids, the presence of heterosis is unclear; the general belief is that heterosis is rare in this family (Bryden *et al.* 2004). Indeed, in Atlantic salmon (*Salmo salar*) (Chevassus 1980; Kinghorn 1983) and Arctic charr (*Salvelinus alpinus*) (Nilsson 1993), little heterosis has been observed (length, weight and condition factor). In rainbow trout (*Oncorhynchus mykiss*), it was not possible to predict the proportion of hybrids that will show evidence of heterosis in terms of growth rate (Hulata 2001). However in natural environment, different studies were performed on brook charr and their hybrids. A research by Gunther *et al.* (2005) on growth rate and body mass in brook charr, lake charr, and their hybrids (splake) revealed that the hybrids had the highest growth rate and body mass compared to the pure strains. A very short report in Chevassus (1980) also suggested a potential presence of heterosis resulting from crosses done between a wild and a domestic strains of brook charr (*Salvelinus fontinalis*) for growth and biomass but very few details were provided.

In the present study, we examine the complexity of the genetic interaction in hybrid crosses of brook charr. Our objectives are to investigate the presence of heterosis in brook

charr, using reciprocal intraspecific crosses between three genetically different strains, to verify the presence of cross direction effects on the occurrence of heterosis, and how stable is heterosis through development stages in young of the year.

2.2 Materials and methods

2.2.1 *Strains*

Breeders from three different strains were used: a domestic strain largely used by fish farmers in Québec for more than a hundred years and that originates from two strains (the Nashua and Baldwin) that were inter-crossed many times, and two strains with short domestication histories, the Laval and the Rupert strains (Martin *et al.* 1997). The Laval is a wild anadromous strain that originates from the Laval River near Forestville (north shore of the St. Lawrence River) and the Rupert is a wild freshwater strain that originates from the Rupert River in James Bay (northern Québec). The three strains are genetically distinct, with the two wild strains being the most genetically distinct (Martin *et al.* 1997). In terms of heterozygosity, Martin *et al.* (1997) showed that the two wild strains (Laval and Rupert) were outbreed, and presented a heterozygosity of 65% and that they were distinct from domestic fish used in Québec (76% of the alleles from the wild strains are not found in domestic fish).

2.2.2 *Breeders*

The domestic breeders came from Pisciculture de la Jacques Cartier (Cap Santé, Québec), the Laval breeders from the Institut des Sciences de la Mer à Rimouski (ISMER),

and the Rupert breeders from the Laboratoire Régional des Sciences Aquatiques (LARSA, Université Laval, Québec). The mass and length of breeders (n = 80) used for the different crosses are presented in Table 1. During the fall of 2005 (October to December), egg fertilization was done at LARSA using milt and eggs obtained from the three different sites. The following crosses were done: domestic dams with domestic sires (♀D x ♂D), domestic dams with Laval sires (♀D x ♂L), domestic dams with Rupert sires (♀D x ♂R), Laval dams with domestic sires (♀L x ♂D), Laval dams with Laval sires (♀L x ♂L), Laval dams with Rupert sires (♀L x ♂R), Rupert dams with Laval sires (♀R x ♂L), and Rupert dams with Rupert sires (♀R x ♂R). The cross between Rupert dams and domestic sires (♀R x ♂D) was not possible because of incompatibility in their sexual maturation period (October for domesticated sires and December for Rupert dams). A total of three pure crosses and five hybrid crosses were thus made, with ten full-sib families per cross. During the experiment, high mortality rates occurred in three families (two from ♀D x ♂L and one from ♀D x ♂R), families that had been eliminated after the first or the second sampling when numbers of individuals became too low.

Table 1. Mean masses and lengths of breeders used for each cross type. Means with different superscript letters indicate significant difference between crosses ($p < 0.05$).

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

The 77 families were reared separately in seven troughs divided into twelve units; water flow came from the same recirculation system. Fertilized eggs were incubated at 6°C. After hatching, the photoperiod was set at 12L:12D and temperature maintained at 8°C. From June to August, we reduced the number of families from 77 to 72 because of limited rearing capacities: five small (<200 individuals) families were eliminated from the study (one from ♀D x ♂L, one from ♀L x ♂D, two from ♀R x ♂L, and one from ♀R x ♂R). Twenty-two weeks after hatching all juveniles were fin-marked and then transferred to nine 3000-L tanks. The photoperiod was then adjusted to follow natural conditions. Feeding frequency was adjusted according to the age of fish, average weight, and temperature conditions, and temperature was set so that all experimental families had experienced the same number of degree days (2136 dd) at the end of the summer (September).

2.2.3 *Samplings*

The first sampling was done at 100% hatching. Twenty 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). A second sampling was done at the time of complete resorption of the yolk sac. Twenty individuals per family were sampled (n = 1540) for fry length and mass. For the last two samplings, 50 individuals per family were sampled, measured and weighted. 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 dd) (Table 2).

Specific growth rates (SGR) based on fork length (FL) measurements were calculated for three specific periods: from hatching to yolk sac resorption, from yolk sac resorption to 15 weeks of exogenous feeding, and from 15 weeks of exogenous feeding to 2136 dd. We used the following formula:

$$SGR = \ln FL_2 - \ln FL_1 / t_2 - t_1$$

where FL_2 represents fork length at time 2 (t_2) and FL_1 represents fork length at time 1 (t_1) and time is expressed in days (Ricker 1979). As fish marks allowed to recognize the families and not the individuals, specific growth rates were calculated on a family basis and n = 8 to 10 per cross type.

Table 2. Different periods of the experiment and months of sampling.

Cross	Egg fertilization	Hatching	Samplings		
			Yolk sac resorption	After 15 weeks of exogenous feeding	2136 degree-days
♀D x ♂D	October 2005	January	February (253.0 dd)	May (1254.4 dd)	September
♀D x ♂L	October 2005	January	February (283.4 dd)	June (1297.4 dd)	September
♀D x ♂R	October 2005	January	February (279.7 dd)	June (1276.9 dd)	September
♀L x ♂D	November 2005	January	March (378.7 dd)	June (1492.3 dd)	September
♀L x ♂L	November 2005	February	March (407.6 dd)	July (1532.4 dd)	September
♀L x ♂R	November 2005	February	March (354.9 dd)	July (1493.5 dd)	September
♀R x ♂L	December 2005	Feb.-March	April-May (434.4 dd)	July (1603.7 dd)	September
♀R x ♂R	December 2005	March	May (514.0 dd)	August (1720.6 dd)	September

2.2.4 *Data analysis*

Data normality was tested using the Kolmogorov-Smirnov (K-S) test and homoscedasticity was checked with the Brown and Forsythe test (Quinn & Keough 2005). The different crosses were compared with a three-way ANOVA (sampling time, cross type, family nested in cross) followed by a posteriori analysis when relevant. To verify the presence 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 tests or Games and Howell tests when transformations failed to provide homoscedasticity. All analyses were made using Statistica version 6.0 for Windows

(StatSoft, Tulsa, OK, USA) and SPSS version 13.0 for Windows. When heterosis or outbreeding depression were found, their intensity was expressed in percent as $[(f_1 m^{-1})-1]$ 100 for heterosis and as $[1-(f_1 m^{-1})]$ 100 for outbreeding depression (Shikano & Taniguchi 2002), where f_1 represents the mean value in the F_1 hybrids and m represents the mid-pure strain value. When statistical analysis indicated similar results for length and mass data, we only showed results for the mass data. If different statistical results were obtained for condition factors, these are presented.

2.3 Results

In many instances, hybrids exhibited growth characteristic significantly greater (heterosis) or lower (outbreeding depression) than the ones present in parental lines. However, the relationship among crosses and families differed according to the developmental stage; crosses x developmental stages, $p < 0.001$ for all variables (Table 3). Results will then be presented in function of stage of development. As the results obtained on condition factors were quite similar, although less pronounced than the ones on mass and length, these are described only when different from those obtained with the other variables. Familial effects (nested ANOVAs) were always present but are not detailed as our main objective was to assess the net effect of heterosis or outbreeding depression among crosses.

At hatching, the ♀L x ♂L fry were the largest and had the biggest yolk sac volume compared to the other pure strain crosses (♀L x ♂L > ♀R x ♂R > ♀D x ♂D) (Table 4). The ♀D x ♂R fry had 22.3 % heavier yolk sac volume (Fig 1A) and were 7.4 % longer than fry issued from parental strains. The ♀L x ♂R fry also exhibited heterosis and were 9.0 % longer than their parental lines (Fig. 1B), while the reciprocal hybrids, ♀R x ♂L fry, were 4.3 % shorter (Fig. 1B) and had 36.1 % smaller yolk sac volume (Fig. 1C). Despite, smaller size, condition factor was similar (Table 5). Neither heterosis nor outbreeding depression was seen at that stage in hybrids between the Laval and Domestic strains.

Table 3. Results of three-ways ANOVA (sampling, cross-type, family) for mass and fork length.

Variable	Effect	df	F	p
Fork length	Sampling	2	57264.0	< 0.000
	Cross	7	343.5	< 0.000
	Sampling * Cross	14	310.2	< 0.000
	Family (Cross)	69	12.2	< 0.000
	Sampling * Family (Cross)	133	8.9	< 0.000
Individual mass	Sampling	2	14458.9	< 0.000
	Cross	7	366.6	< 0.000
	Sampling * Cross	14	378.7	< 0.000
	Family (Cross)	69	10.8	< 0.000
	Sampling * Family (Cross)	133	12.5	< 0.000

Table 4. Yolk sac volume (YSV), fry length (TL: total length, FL: fork length), and fry mass (W) for pure strains (boldface) and their hybrids measured at hatching, at yolk sac resorption, after 15 weeks of exogenous feeding, and at 2136 degree-days. Means with different superscript letters indicate significant difference between crosses for a same trait at a same sampling period ($p < 0.05$).

	Hatching		Yolk sac resorption		15 weeks of exogenous feeding		2136 dd	
Cross	YSV (mm^3) ± sd	TL (mm) ± sd	FL (mm) ± sd	W (g) ± sd	FL (mm) ± sd	W (g) ± sd	FL (mm) ± sd	W (g) ± sd
♀Dx♂D	**189.1 ± 65.4** ^{a}	**14.9 ± 1.2** ^{a}	**22.3 ± 0.9** ^{a}	**0.08 ± 0.01** ^{a}	**60.3 ± 5.1** ^{c}	**2.3 ± 0.7** ^{d}	**101.6 ± 12.2** ^{f}	**11.9 ± 4.6** ^{f}
♀Dx♂L	242.4 ± 112.1 ^{bc}	15.8 ± 1.3 ^{bc}	23.0 ± 1.4 ^{b}	0.09 ± 0.02 ^{b}	60.2 ± 4.8 ^{c}	2.2 ± 0.6 ^{cd}	92.8 ± 10.3 ^{d}	8.2 ± 2.8 ^{d}
♀Dx♂R	245.5 ± 71.6 ^{c}	16.4 ± 0.9 ^{e}	23.1 ± 1.2 ^{b}	0.09 ± 0.02 ^{b}	59.7 ± 4.0 ^{c}	2.2 ± 0.4 ^{c}	96.6 ± 9.5 ^{e}	9.6 ± 3.1 ^{e}
♀Lx♂D	359.0 ± 66.2 ^{e}	16.2 ± 1.4 ^{de}	28.7 ± 1.7 ^{f}	0.19 ± 0.03 ^{e}	67.0 ± 5.9 ^{e}	3.0 ± 0.9 ^{f}	95.3 ± 11.3 ^{e}	8.8 ± 3.4 ^{d}
♀Lx♂L	**342.0 ± 75.5** ^{e}	**15.9 ± 1.1** ^{cd}	**25.7 ± 1.0** ^{e}	**0.12 ± 0.02** ^{d}	**57.9 ± 4.0** ^{a}	**1.7 ± 0.4** ^{a}	**77.6 ± 6.8** ^{ab}	**4.1 ± 1.2** ^{a}
♀Lx♂R	300.5 ± 64.9 ^{d}	17.2 ± 1.2 ^{f}	25.3 ± 1.2 ^{d}	0.12 ± 0.02 ^{d}	58.5 ± 4.4 ^{ab}	1.8 ± 0.5 ^{b}	87.6 ± 8.6 ^{c}	6.5 ± 2.2 ^{c}
♀Rx♂L	177.0 ± 60.2 ^{a}	15.1 ± 1.2 ^{a}	22.5 ± 1.4 ^{a}	0.08 ± 0.02 ^{a}	59.3 ± 5.3 ^{bc}	1.9 ± 0.6 ^{b}	79.1 ± 8.5 ^{b}	4.8 ± 1.6 ^{b}
♀Rx♂R	**212.3 ± 71.4** ^{b}	**15.6 ± 0.7** ^{b}	**23.9 ± 1.4** ^{c}	**0.11 ± 0.03** ^{c}	**62.3 ± 7.3** ^{d}	**2.5 ± 1.0** ^{e}	**77.1 ± 9.1** ^{a}	**4.9 ± 1.7** ^{b}

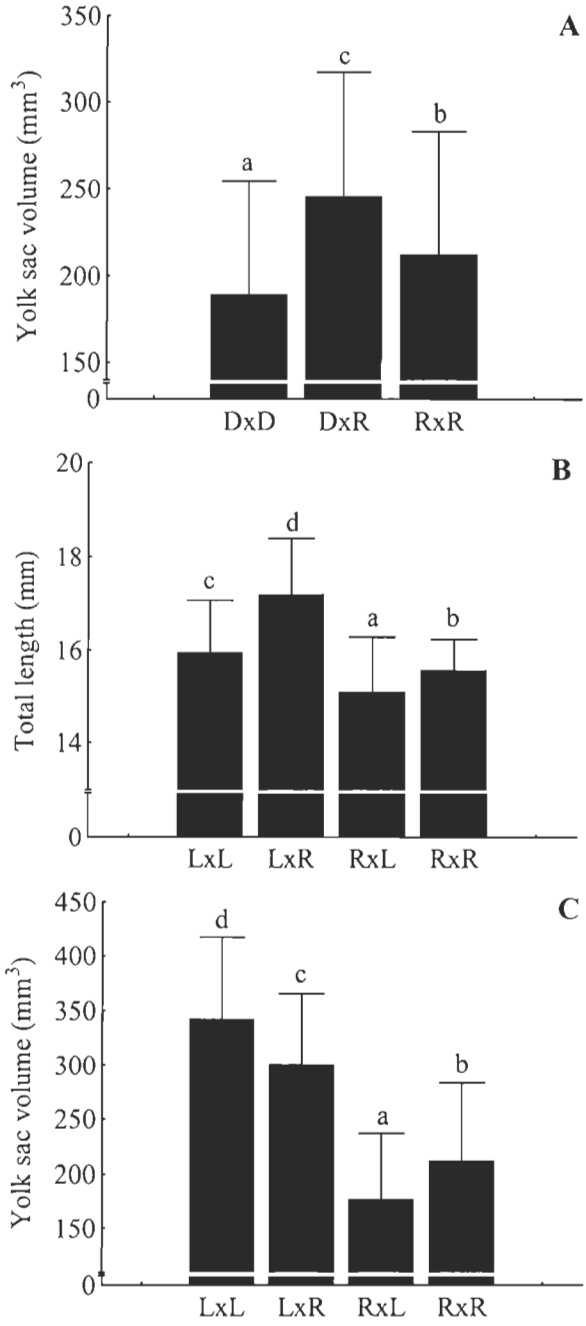

Figure 1. Comparisons between domestic and Rupert strains and their reciprocal hybrids for yolk sac volume (A), between Laval and Rupert for total length (B), and yolk sac volume (C) at hatching. Means ± sd. Different letters indicate significantly different means ($p < 0.05$). In crosses identification, the first letter indicates the strain of dam and the second one, the strain of sire.

Table 5. Condition factors for pure strains (bold characters) and their hybrids measured at yolk sac resorption, after 15 weeks of exogenous feeding, and at 2136 degree-days. Means with different superscript letters indicate significant difference between crosses for the same trait at a same sampling time ($p < 0.05$).

Cross	Yolk sac resorption (g/mm^3) ± sd	15 weeks of exogenous feeding (g/mm^3) ± sd	2136 dd (g/mm^3) ± sd
♀Dx♂D	**0.73 ± 0.07** ^{bc}	**1.04 ± 0.08** ^{e}	**1.09 ± 0.12** ^{f}
♀Dx♂L	0.75 ± 0.06 ^{c}	0.99 ± 0.08 ^{cd}	0.99 ± 0.09 ^{d}
♀Dx♂R	0.71 ± 0.08 ^{b}	1.01 ± 0.07 ^{d}	1.03 ± 0.06 ^{e}
♀Lx♂D	0.82 ± 0.22 ^{d}	0.98 ± 0.10 ^{c}	0.97 ± 0.07 ^{c}
♀Lx♂L	**0.72 ± 0.05** ^{b}	**0.88 ± 0.05** ^{a}	**0.86 ± 0.06** ^{a}
♀Lx♂R	0.74 ± 0.07 ^{bc}	0.90 ± 0.07 ^{b}	0.93 ± 0.06 ^{b}
♀Rx♂L	0.67 ± 0.08 ^{a}	0.90 ± 0.06 ^{b}	0.94 ± 0.08 ^{b}
♀Rx♂R	**0.80 ± 0.15** ^{d}	**1.00 ± 0.08** ^{cd}	**1.03 ± 0.07** ^{e}

At the yolk sac resorption stage, the ♀L x ♂L fry were the most performant in terms of mass and length compared to the other pure strain crosses (♀L x ♂L > ♀R x ♂R > ♀D x ♂D) (Table 4). The ♀L x ♂D fry were 88.2 % heavier and 19.6 % longer than fry issued from parental strains (Fig. 2A), while the reciprocal hybrids displayed intermediate growth compared to these. The ♀R x ♂L fry were 33.3 % lighter and 9.2 % shorter, compared to their parental lines (Fig. 2B), but outbreeding depression was not observed in the reciprocal hybrid. At this specific stage, hybrids between Rupert and Domestic strains did not exhibit heterosis or outbreeding depression.

After 15 weeks of exogenous feeding, the ♀R x ♂R fry were the biggest and largest compared to the other pure strain crosses (♀R x ♂R > ♀D x ♂D > ♀L x ♂L) (Table 4). The ♀L x ♂D fry exhibited heterosis and were 48.3 % heavier and 13.4 % longer than both parental strains (Fig. 3A), while reciprocal hybrids did not exhibit any and were very similar to pure domestic fry. The ♀D x ♂R fry were 10.7 % lighter and 2.5 % shorter than the two parental crosses (Fig. 3B). Hybrids between Rupert and Laval were non significantly different from both parental lines at this stage of development.

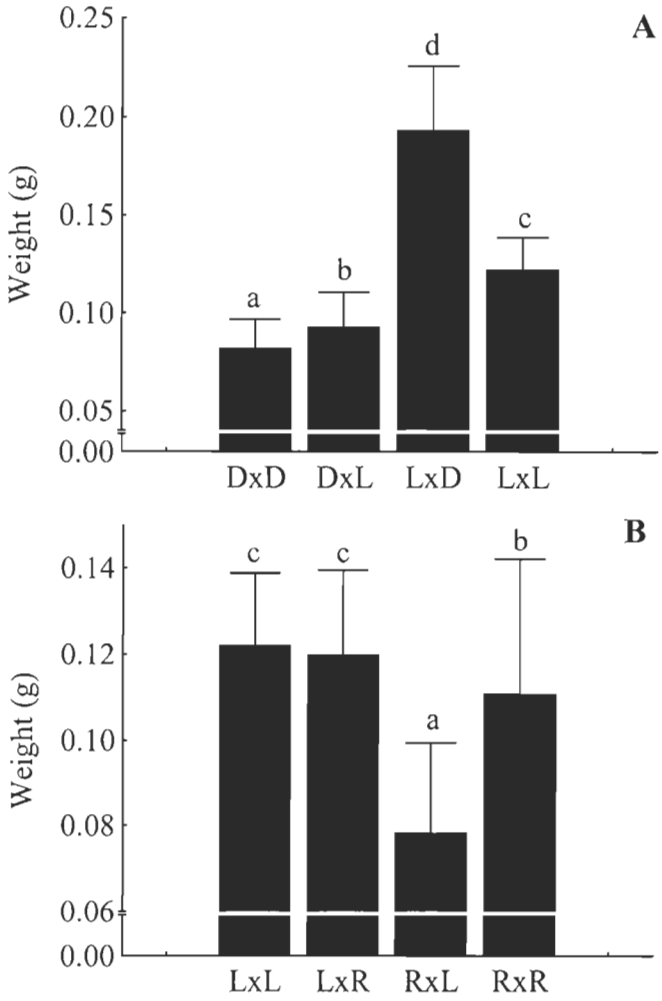

Figure 2. Comparisons for masses between Laval and domestic strains and their reciprocal hybrids (A) and between Laval and Rupert strains (B) at the yolk sac resorption. Means ± sd. Different letters indicate significantly different means ($p < 0.05$). In crosses identification, the first letter indicates the strain of dam and the second one, the strain of sire.

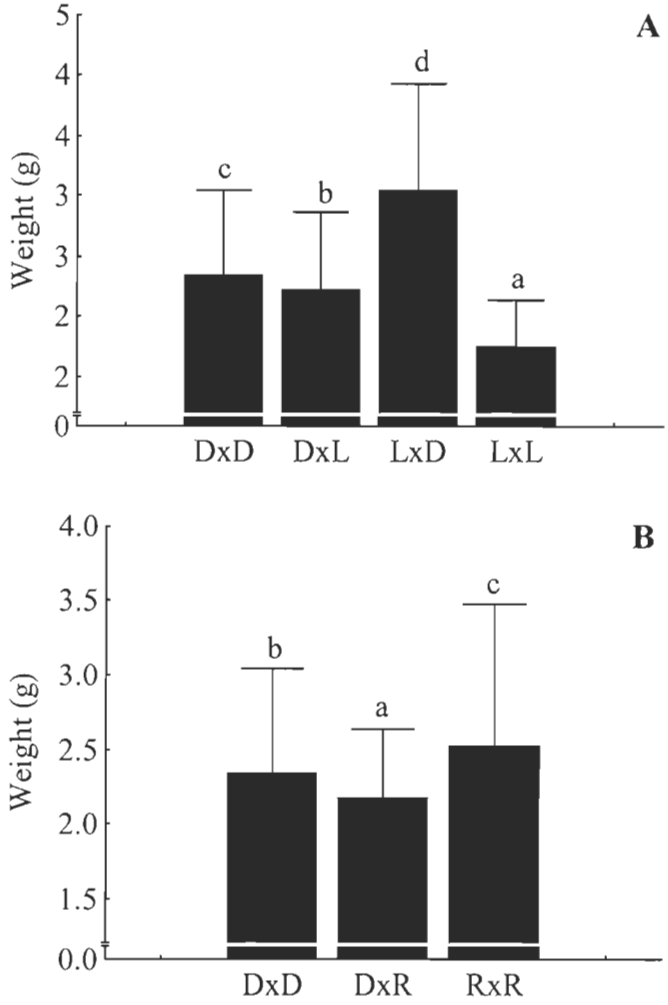

Figure 3. Comparisons for masses between Laval and domestic strains and their reciprocal hybrids (A) and between domestic and Rupert strains (B) after 15 weeks of exogenous feeding. Means ± sd. Different letters indicate significantly different means ($p < 0.05$). In crosses identification, the first letter indicates the strain of dam and the second one, the strain of sire.

At the end of the summer (2136 dd), the ♀D x ♂D fry exhibited the highest increase in weight compared to the others strains (♀D x ♂D > ♀R x ♂R ≥♀L x ♂L) (Table 4). The ♀L x ♂R fry were 44.9 % heavier and 13.2 % longer compared to the parental strains (Fig. 4A), with similar condition factor while the reciprocal hybrid was very similar to the Rupert fry (Table 5). The ♀D x ♂R fry exhibited intermediate growth performance compared to the two parental lines (Fig. 4B), while the hybrids issued from crosses between the Laval and Domestic strains exhibited intermediate performance compared to the parental lines.

From hatching to yolk sac resorption, the ♀L x ♂D and ♀D x ♂D fry had the highest SGR. From yolk sac resorption to 15 weeks of exogenous feeding, cross-types were clearly divided into two groups; the three cross-types with Laval dams showed significantly lower SGR than the other cross-types. From 15 weeks of exogenous feeding to 2136 dd, the ♀L x ♂R, the ♀R x ♂L, and the ♀R x ♂R had significantly higher SGR compared to the others.

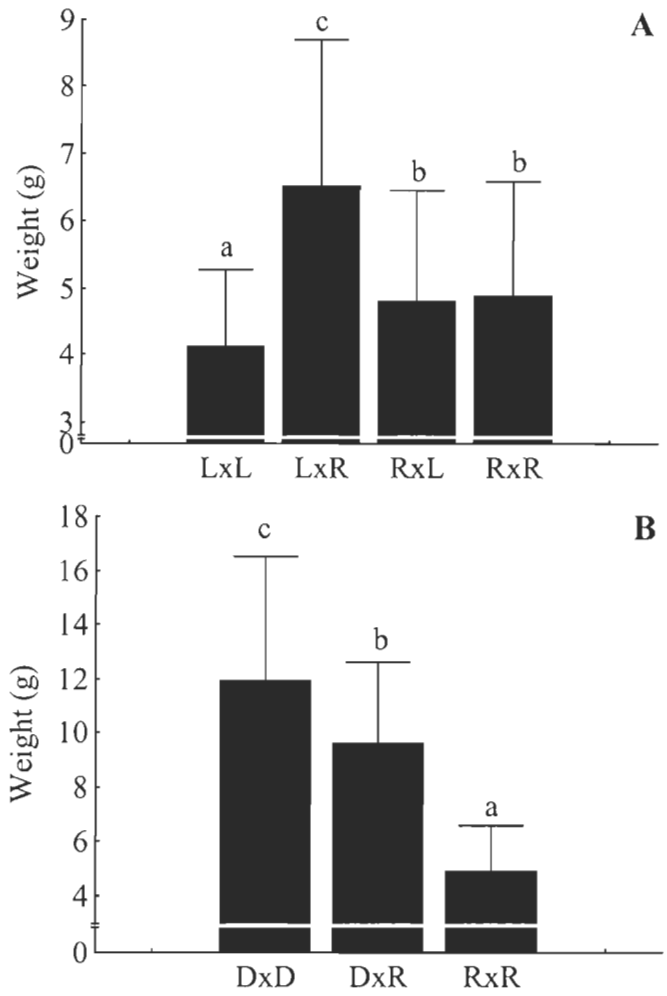

Figure 4. Comparisons for masses between Laval and Rupert strains and their reciprocal hybrids (A) and between domestic and Rupert strains (B) at 2136 degree-days. Means ± sd. Different letters indicate significantly different means ($p < 0.05$). In crosses identification, the first letter indicates the strain of dam and the second one, the strain of sire.

Table 6. Specific growth rates for all cross-types, from hatching to yolk sac resorption (1), from yolk sac resorption to 15 weeks of exogenous feeding (2), and from 15 weeks of exogenous feeding to 2136 degree-days (3). Means with different superscript letters indicate significant difference between crosses for a same trait at a same sampling period ($p < 0.05$).

Periods	Crosses							
	♀Dx♂D	♀Dx♂L	♀Dx♂R	♀Lx♂D	♀Lx♂L	♀Lx♂R	♀Rx♂L	♀Rx♂R
1	1.041 ^{cd}	0.910 ^{abc}	0.840 ^{ab}	1.132 ^{d}	0.966 ^{bc}	0.903 ^{abc}	0.839 ^{ab}	0.793 ^{a}
2	0.915 ^{b}	0.888 ^{b}	0.892 ^{b}	0.778 ^{a}	0.746 ^{a}	0.763 ^{a}	0.880 ^{b}	0.861 ^{b}
3	0.455 ^{abc}	0.415 ^{ab}	0.442 ^{abc}	0.393 ^{a}	0.380 ^{a}	0.521 ^{bcd}	0.542 ^{cd}	0.586 ^{d}

2.4. Discussion

Our study clearly indicates the presence of both heterosis and outbreeding depression in inter-strain brook charr hybrids at different development stages. In salmonids, the presence of heterosis in hybrids of the first generation does not seem to be a general feature. Indeed, Gjerde (1981) found no evidence of heterosis in inter-strain Atlantic salmon hybrid. Nilsson (1993) used three different strains of Arctic charr in their first generation of rearing to produce hybrids and found no evidence for heterosis for mass in 1+, 2, and 2+ year-old animals. However, Fraser (1981), using inter-strain crosses between wild and domestic brook charr, found higher survival in wild X domestic brook charr hybrids in fish older than 1+ year-old. In the present study, we took into account both heterosis and outbreeding depression, while most of the studies did not look at both effects. Indeed, only few studies have focused on outbreeding depression (walleye, *Sander vitreus*, Cena *et al.* 2006; largemouth bass, *Micropterus salmoides*, Cooke *et al.* 2001; pink salmon, *Oncorhynchus gorbuscha,* Gharrett *et al.* 1999 and Gilk *et al.* 2004). No outbreeding depression was found for growth in the walleye (Cena *et al.* 2006), while Cooke *et al.* (2001) found altered physiological performance and efficiencies in inter-stocks hybrids of four genetically distinct wild stocks of largemouth bass. However these two studies were carried out in different environments and environmental variables may influence fish performances. Indeed, the first study was carried out in natural environment while the second one was done in laboratory conditions. Inversely, other studies revealed some outbreeding depression in fishes and especially in pink salmon. Thus, Gharrett *et al.* (1999)

and Gilk *et al.* 2004) showed lower survival in the second generation of genetically divergent pink salmon hybrids. Overall the divergence in results obtained in different fish species could be caused by the use of different environmental conditions, by the traits considered, presence of genetic divergence and so on. In the present study, outbreeding depression was less frequent than heterosis and, when present, occurred with lower intensity.

The three strains we used showed different growth characteristics during the first months of development. In the very early stages (hatching and yolk sac resorption), the Laval strain was the most performant but at the end of the summer (2136 dd), the Domestic strain was undoubtedly the most performant. The levels of heterosis expression observed, in hybrids between Laval dams and domestic sires at the yolk resorption stage and after 15 weeks of exogenous feeding, are quite high when compared to other studies dealing with heterosis in fishes. For instance, in guppy, percentage of heterosis ranged from -1.3 % for body length to 42.2 % for salinity tolerance (Shikano *et al.* 1997; Nakadate *et al.* 2003). In this species and others, heterosis has been proposed to be related to the degree of divergence between strains (Rainbow trout, Klupp 1979; Brook charr, Webster & Flick 1981), to maternal effect, to the general level of heterozygosity, to epistatic gene interactions (Pacific oyster, Hedgecock *et al.* 2007), or to other mechanisms yet to be identified (fishes, Wang & Xia 2002). In the present study, if genetic distance is in cause, it can not be the sole factor as genetic distance between wild and domestic strains was lower than the one that exists between the Laval and Rupert strains (Martin *et al.* 1997). In terms

of heterozygosity, these authors showed that the two wild strains presented a heterozygosity of 65 % and that they were distinct from domestic fish used in Quebec (76 % of wild strains alleles are not found in domestic fish). The inbreeding effect is also important in the expression of heterosis and the occurrence of this phenomenon is greater when inbred populations are used (Nakadate *et al.* 2003). These authors suggest that salinity tolerance and survival in inbred lines of guppies are correlated with the inbreeding coefficient that is important in the expression of heterosis. In our study, the three different strains used were genetically distinct one from another (Martin *et al.* 1997); thus limiting biases related to inbreeding effect.

Differences in the expression of heterosis or outbreeding depression through early development raise several questions. Of course, at the beginning of the development, maternal effects should be taken into consideration. Early development is pre-programmed by the maternal genome through gene products contained in the yolk (Hebert 1998; Nakajima & Taniguchi 2002; Pakkasmaa 2002), thus we can presume that at hatching the maternal effect will be more important than in the other developmental stages. In brook charr, and especially in the Laval strain, Perry *et al.* (2004) demonstrated the importance of maternal genetic effects until the resorption of the yolk sac is completed. They also showed that after this point, the genetic contribution of individual progeny replaces the genetic contribution from the mother. Perry *et al.* (2005) also showed that maternal effect is strongly correlated with the size of the female, and that longer females will produce longer eggs and thus longer progeny. Yolk sac reserves, in quantity and quality, 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 & Taniguchi 2005). In the present study, the Laval dams were notably longer than the domestic or Rupert dams. At hatch, the progeny from the Laval dams were also longer than the others which support the hypothesis of a possible maternal effect. However, during the period of yolk utilization, it is interesting to note that we observed the highest SGR in the ♀L x ♂D and ♀D x ♂D, but that dam origin did not insure a similar growth rate in all cross types. However, from yolk sac resorption to 15 weeks of exogenous feeding, the SGR in cross-types having the Laval strain as dam (♀L x ♂D, ♀L x ♂L, ♀L x ♂R) decreased suddenly underlying the transition from maternal to individual genotype effects as previously suggested by Perry *et al.* (2004).

The influence of the mother's origin could also be related to the environment. A study on rainbow trout found that the influence of maternal effects on growth of progeny may be greater in more favourable rearing environments (Fishback *et al.* 2002). Studies on brook charr reveal that a high maternal genetic differentiation of embryonic phenotype might be necessary for local adaptation to early rearing habitat (Perry *et al.* 2005) and that the maternal genetic control reflects greater energetic investment for early traits (Perry *et al.* 2004). Our results thus suggest that the maternal influence of the domestic dams was less important at hatching than it was for dams from short-term domesticated strains (Laval and Rupert). Those two strains are recognized has having a lower occurrence of early sexual maturation in 1+ females and energy investment in gonad production should differ

between these three strains. The follow-up of the present individuals until they reach 22 months old (study in progress) should provide some highlights on these specific aspects.

The most pronounced outbreeding depression we observed was in the ♀R x ♂L hybrid (36.1 % for yolk sac volume). In the ♀D x ♂R hybrid, heterosis was present at hatching and outbreeding depression was observed in a later stage of development (15 weeks after exogenous feeding). This difference between the two hybrids could be related to a different mother origin. Indeed, as discussed earlier, the results at hatching could be the consequences of maternal effects rather than heterosis, so outbreeding depression observed later on would be more indicative of the effect on the progeny for this cross. It will be interesting to see how this evolves later on in progenies and to check if outbreeding depression is maintained in the ♀D x ♂R cross-type.

In addition to maternal effect and genetic distance, the use of a strain either as dam or as sire may lead to very different results. Thus Laval dams tended to be more often associated with heterosis while Laval sires were mostly associated with outbreeding depression. Thus some strains will perform better as sires and others as dams, as found by Eknath *et al.* (1998) for the Nile tilapia. Similar results have been found in catfishes (Rahman *et al.* 1995) and salmonid hybrids, particularly sockeye and kokanee salmon, where the cross type (male-type and female-type) influences growth (Wood & Foote 1990).

Rearing conditions may also influence the expression of heterosis (gene x environment interaction). Indeed, wild strains and their hybrids could have different requirements than domestic fry which are more adapted to the "artificial and safe" environment of the laboratory. Mason *et al.* (1967) have shown that a brook charr strain domesticated for more than 30 years, and originating from the Wisconsin, grew rapidly in the hatchery as a result of artificial selection. In the present study, the ♀D x ♂D fry were clearly the most performant in terms of growth when all the fry have been brought to 2136 dd. On the other hand, this cross is the one that occurs the earlier in season and despite same degree-days exposure, they were almost 8 weeks older than crosses between Rupert and Laval strains for instance. Mason *et al.* (1967) have shown that fingerling hybrids between wild dams and domestic sires grow nearly as well in the hatchery as the domestic strain while the hybrids between domestic dams and wild sires are shorter which corresponds to our observations with the ♀L x ♂D and ♀D x ♂L hybrids. Although the Rupert and Laval strains were from an F3 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 & Phelps 2006). If we consider the data at 2136 dd, when maternal effect is replaced by the expression of the offspring genome, we did not obtain results that would allow us to conclude that domestic breeders would always give an advantage for the expression of heterosis when used in a cross type. Indeed at this last sampling, heterosis was no more present in cross-types involving domestic breeders (♀D x ♂L, ♀D x ♂R, ♀L x ♂D). The higher specific growth observed in the ♀L x ♂R, ♀R x ♂L, and ♀R x ♂R cross-types in the period covering the interval

between 15 weeks of exogenous feeding to 2136 dd undoubtedly reflects the increase in temperature rearing conditions that was applied to reach similar degree-days (2136 dd) for all crosses at the end of the experimentation.

Overall, our results indicate that mass seems to be a better indicator of heterosis than length. In general, results obtained with mass, length and condition factor all presented similar trends, but the percentage of heterosis or outbreeding depression was always greater when mass was considered. In summary, results from our study show the presence of both heterosis and outbreeding depression but the occurrence of these phenomenons is very complex and depends on many factors including cross direction and developmental stages. Maternal effect was also present and its importance was greater before the the yolk sac resorption stage than later on. Thus performance measurements would have to be done only after maternal effects have disappeared. It would certainly be of interest to verify how growth performance is maintained over time and how it is influenced by the rearing environments. Such a study is now in progress at our laboratory. Inter-strain heterosis is thus a mechanism by which brook charr production could be improved.

DISCUSSION GÉNÉRALE

Cette discussion générale est plus un complément à celle du manuscrit dont je ne vais pas reprendre les éléments déjà discutés précédemment; je vais plutôt développer les points non mentionnés, ainsi que ce qui aurait pu être amélioré.

L'étude globale dont fait partie mon projet de maîtrise avait pour objectif général de déterminer les bases physiologiques et génomiques fonctionnelles de la vigueur hybride et ensuite de pouvoir exploiter ce phénomène afin d'essayer d'améliorer la production aquacole de l'omble de fontaine au Québec. Une première étape était de comparer des croisements hybrides et témoins (souches pures) afin de mettre en évidence (ou non) et de caractériser la présence d'hétérosis inter-souches chez les jeunes stades d'omble de fontaine.

Tel que démontré dans le chapitre II, nous avons observé la présence d'hétérosis, mais également de dépression de croisement durant les premières étapes de développement chez l'omble de fontaine. Ces phénomènes paraissent dépendants du stade de développement des individus, mais aussi du type de croisement et du trait considéré, ce qui ne nous permet donc pas de tirer de généralités. Cependant, la variable masse parait être la meilleure mesure pour quantifier l'hétérosis, car c'est elle qui présentait toujours le pourcentage d'hétérosis le plus élevé. Une étude chez le hareng de l'Atlantique a également démontré que cette même variable était la meilleure mesure pour quantifier

l'investissement maternel (Bang *et al.* 2006). Cette variable masse n'a pas pu être quantifiée à l'éclosion, simplement pour des raisons de précision des mesures.

Un des problèmes majeurs rencontré lors de ce projet est la différence de période de maturité sexuelle entre les différentes souches. En effet, les périodes se sont échelonnées d'octobre pour la souche domestique, jusqu'à décembre pour la souche Rupert; la souche Laval frayant aux environs du mois de novembre. Ce grand décalage dans le temps ne nous a donc pas permis de réaliser le croisement entre la femelle Rupert et le mâle domestique, supprimant ainsi une des possibilités de croisement prévue dans notre plan expérimental.

Ce décalage de frai s'est également répercuté tout au long du projet, échelonnant ainsi les éclosions sur deux mois et provoquant un retard identique à l'éclosion. Cela a empêché la réalisation d'échantillonnages à une période identique et précise pour chaque croisement. Pour essayer de pallier à cela, nous avons décidé de ramener tous les croisements à un même degré jour (2136 dd) à la fin de l'été, afin qu'à défaut d'être au même âge, les différents individus aient atteint le même stade de développement, exprimé en degrés jours.

De l'incubation, jusqu'à la quinzième semaine d'alimentation exogène, toutes les familles des différents croisements étaient élevées séparément dans des clayettes alimentées par une source d'eau commune. La répartition des familles dans les auges ne s'est pas faite au hasard, mais selon l'ordre du frai; les différentes familles d'un même croisement se

trouvant les unes à la suite des autres, induisant certainement un effet amont-aval par rapport à l'arrivée d'eau. Les familles se trouvant proches de l'arrivée d'eau recevaient potentiellement une eau de meilleure qualité que celles se trouvant en bout d'auge. La température de l'eau augmentait aussi graduellement le long des clayettes, provoquant ainsi une différence de 1°C entre l'arrivée et la sortie d'eau. Cependant, les temps de développement, exprimés en jours, sont similaires pour des familles ayant été produites en même temps et se trouvant dans une même auge. Des études sur la morue (*Gadus morhua*) et le saumon rose (*Oncorhynchus gorbuscha*) ont montré que les conditions environnementales pendant l'incubation et le régime de température auquel est soumis l'embryon peuvent influencer son métabolisme et par la suite la taille de l'alevin (Murray & Beacham 1986; Miller *et al.* 1995). Dans notre système d'élevage, il est vrai que la température est passée de 6 à 8°C entre les premières (croisement pur domestique) et les dernières éclosions (croisement pur Rupert), mais les temps d'incubation, exprimés en degré jour ne présentaient pas de différence.

Jusqu'à la quinzième semaine d'alimentation exogène, tel que mentionné précédemment, les familles étaient élevées chacune séparément, mais après cela elles ont été rassemblées dans des bassins de 3 m^3, à raison de huit familles par bassin. Après ce changement de milieu, de la prédation (cannibalisme) a été observée dans les différents bassins à chaque fois que nous faisions des échantillonnages. En effet, plusieurs individus de grande taille ont été observés se nourrissant d'individus plus petits, laissant penser que les familles ayant accumulé plus de degrés jours sont plus grosses et ainsi plus voraces.

Cependant ces observations n'étaient que ponctuelles, puisque aucun suivi comportemental n'a été effectué de façon régulière. De plus, lors du dernier échantillonnage (en septembre), un dénombrement a été effectué et le nombre total d'individus restant pour chaque famille était dans la majorité des cas inférieur à celui présumé d'après les relevés de mortalités. Finalement, nos résultats montrent très clairement, lors du dernier échantillonnage, à 2136 dd, qui a donc été effectué dans ces bassins, que la souche domestique est la plus performante et cela va dans le même sens qu'une autre étude sur différents souches d'omble de fontaine, où la souche domestique grandissait plus rapidement en milieu d'élevage que les souches sauvages (Mason *et al.* 1967). Cette dernière observation est possiblement due au fait que les conditions d'élevage (incluant le type de bassin, la densité, la ration alimentaire ou le mode d'alimentation) de cette étude devaient probablement mieux correspondre aux exigences de la souche domestique, qui est élevée depuis de nombreuses générations, ce qui n'est pas le cas des deux souches sauvages.

Dans le domaine de l'aquaculture, l'utilisation de l'hétérosis n'est pas encore très répandue. Cependant ce phénomène pourrait être très utile pour l'amélioration des performances des souches utilisées pour l'élevage. Ainsi, chez le saumon atlantique, il a été montré que l'élevage artificiel entraîne une diminution de la variabilité génétique (Cross & King 1983). L'utilisation de souches nouvelles dans les élevages permettrait d'apporter de nouveaux allèles, responsables par exemple d'une maturation sexuelle tardive et d'une bonne croissance (Morin 2003), et avec cela peut-être de l'hétérosis, dépendamment, entre autres, de la distance génétique existant entre les différentes souches. La présence

d'hétérosis chez des souches hybrides est très certainement quelque chose de positif du point de vue production, car cela est souvent lié à une amélioration des performances et de la croissance.

Un des objectifs général du projet était de déterminer s'il est possible d'améliorer les performances de la souche domestique au Québec, à l'aide de deux souches sauvages. Cette étude ne nous permet pas vraiment de faire ressortir un hybride comme étant le plus performant tout au long des premiers stades de développement, car comme vu précédemment, nous n'avons pas observé une constance de la présence d'hétérosis chez un même hybride. Cependant, si on ne considérait que les résultats obtenus jusqu'à 15 semaines d'alimentation exogène, on pourrait dire que le croisement entre la femelle Laval et le mâle domestique serait le meilleur, car à la résorption du sac vitellin il présente plus de 80 % d'hétérosis pour la masse, ce qui représente la quantité d'hétérosis la plus élevée rencontrée durant toute l'étude. Cet hybride permettrait ainsi l'amélioration de la souche domestique. Mais à la fin de l'été, celui-ci ne présente plus d'hétérosis et ses performances en termes de taille et de masse sont inférieures à celles de la souche pure domestique. La poursuite de cette étude est donc indispensable afin de voir si cette tendance se confirme, ne permettant donc pas l'amélioration de cette souche avec une des deux souches sauvages choisies.

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