UNIVERSITÉ DU QUÉBEC À RIMOUSKI

ÉVALUATION DES COMPOSANTES GÉNÉTIQUE ET ENVIRONNEMENTALE SUR DIFFÉRENTS TRAITS DE PERFORMANCE D'INTÉRÊT AQUACOLE CHEZ L'OMBLE DE FONTAINE (*SALVELINUS FONTINALIS*)

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PAR

AMÉLIE CRESPEL

Composition du jury :

Jocelyne Pellerin, présidente du jury, Université du Québec à Rimouski

Céline Audet, directeure de recherche, Université du Québec à Rimouski

Louis Bernatchez, codirecteur de recherche, Université Laval

Dany Garant, codirecteur de recherche, Université de Sherbrooke

Christophe Herbinger, examinateur externe, Dalhousie University

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À mes parents,

"Le commencement de toutes les sciences, c'est l'étonnement de ce que les choses sont ce qu'elles sont."
(Aristote / 384-322 av. J.-C.)

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RÉSUMÉ

L'évaluation des composantes génétique et environnementale contrôlant l'expression d'un phénotype est essentielle pour mieux comprendre comment celui-ci peut évoluer. Les principales composantes génétiques intervenant dans le contrôle de cette expression sont les composantes additives, qui se transmettent au cours des générations, et les composantes non-additives plus facilement observables chez des croisements hybrides. L'hétérosis est une composante non-additive particulièrement intéressante car elle représente une capacité supérieure des hybrides face aux lignées parentales. Chez les salmonidés, les composantes génétiques additives commencent à être bien documentées. Par contre, la présence d'hétérosis reste très controversée. Chez les ombles, il existe encore moins d'information sur ces différentes composantes. Le potentiel évolutif de ces espèces est donc encore à explorer. L'objectif général de cette thèse était de documenter le potentiel évolutif de l'omble de fontaine (*Salvelinus fontinalis*) en étudiant les composantes génétiques additives et non-additives, ainsi que les interactions gène x environnement, sur différents traits de performance.

Un premier objectif était de vérifier la présence d'un effet hétérosis chez l'omble de fontaine. Des croisements purs et hybrides, entre trois souches divergentes (domestique [D], Laval [L] et Rupert [R]), élevées dans plusieurs environnements (environnement intérieur à température variable ; environnement intérieur à température constante, environnement extérieur à température variable) de 7 à 21 mois ont été utilisés pour déterminer l'expression d'hétérosis sur la croissance, la survie et l'absence de maturation sexuelle précoce. Les résultats ont pu mettre en évidence l'existence d'un effet hétérosis chez cette espèce mais uniquement pour la croissance. Cet effet hétérosis dépendait cependant des souches, de l'orientation du croisement (souche utilisée en tant que maternelle ou paternelle) et du stade de développement (ontogenèse). Un effet hétérosis intéressant a néanmoins été observé chez l'hybride $L_{♀}R_{♂}$ (environ 12% d'accroissement de la masse comparé aux souches parentales) quel que soit l'âge des individus ou l'environnement. L'hybride $L_{♀}D_{♂}$ présentait également un intérêt dans l'expression d'hétérosis, sa croissance étant de 10% supérieure à celle des souches parentales, mais seulement dans l'environnement à température constante.

Un autre objectif était de distinguer la part des composantes génétiques additives, environnementales et de leur interaction dans l'expression de la masse chez cette espèce. La variance génétique additive de la masse a été mesurée dans les trois croisements purs dans chaque environnement. Les résultats ont montré que l'héritabilité de la masse était différente selon le croisement et qu'elle variait entre les différents environnements de manière spécifique à chaque croisement. Nous avons donc mis en évidence que les trois

souches étaient très divergentes et que l'interaction gène x environnement tenait une place importante dans l'expression de la masse.

Un troisième objectif était de comprendre les bases génétiques de la mobilisation d'énergie durant le premier hiver des ombles de fontaine. Le niveau de réserves énergétiques accumulées pendant l'automne ainsi que leur utilisation pendant l'hiver ont été mesurés dans tous les croisements purs et hybrides. Les résultats ont mis en évidence que chaque souche avait sa propre stratégie d'accumulation/utilisation d'énergie, contrôlée par une architecture génétique spécifique, révélant une grande divergence entre les souches. L'analyse des hybrides a montré peu d'effets non-additifs mais par contre, elle a révélé un contrôle génétique plus important lors de l'accumulation des réserves que lors de leur mobilisation.

Enfin, notre dernier objectif était d'évaluer l'importance des effets génétiques additifs et non-additifs dans la résistance au stress. La résistance au stress a été évaluée à l'aide d'indicateurs primaires (cortisol) et secondaires (glucose, osmolalité, hématocrite) de réponse au stress dans chacun des croisements, suite à un stress de transport. Des héritabilités significatives ($h^2 > 0.60$) ont été obtenues pour les deux niveaux de réponse. La souche Rupert s'est avérée être la moins sensible au stress. Peu d'effets non-additifs ont été observés. Ces résultats ont ainsi montré la possibilité d'améliorer cette performance principalement par l'utilisation des effets additifs.

L'ensemble de cette thèse a permis de montrer la complexité du contrôle de l'expression phénotypique chez l'omble de fontaine. Dépendamment du trait, le phénotype peut être contrôlé par des interactions gènes x environnement, par une base génétique additive importante mais aussi par des effets non-additifs, l'importance relative de chacune de ces composantes étant spécifique à chaque population. Cette étude a ainsi mis en évidence que le potentiel évolutif de l'omble de fontaine est propre à chaque population et donc imprévisible.

Mots clés :

Bases génétiques ; héritabilité ; hétérosis ; interaction gène x environnement ; potentiel évolutif ; omble de fontaine ; croissance ; stress ; réserves énergétiques hivernales

ABSTRACT

The evaluation of genetic and environmental components controlling phenotypic expression is essential to understand how phenotypes can evolve. The main genetic components underlying phenotypic expression are additive genetic components, which are heritable trough generations, and non-additive genetic components, easily observed in hybrids crosses. Heterosis is a non-additive genetic component that presents particular interest as it refers to the increased performance of hybrids compared to parental lines. In salmonids, additive genetic components are well documented. However, the occurrence of heterosis is still not clear. In charrs, there is even less information on the different components. Therefore, the evolutionary potential of such species needs further investigations. The general objective of this thesis was to document the evolutionary potential of brook charr (*Salvelinus fontinalis*) by evaluating the additive and non-additive genetic components as well as gene x environment interaction, on several performance traits.

A first objective was to test for the occurrence of heterosis in brook charr. Purebred and hybrids crosses between three divergent strains (domestic [D], Laval [L] and Rupert [R]) of brook charr were reared in different environments (indoor, variable temperature environment; indoor, constant temperature environment; outdoor, variable temperature environment) from 7 to 21 months of age in order to determine heterosis expression for growth, survival and absence of precocious sexual maturity. Results highlight the presence of heterosis in this species but only for variables related to growth. Heterosis varied according to strains, cross direction (strain used as dam or sire in the cross), and developmental stage (ontogeny). An interesting occurrence of heterosis was found in the $L_{♀}R_{♂}$ hybrid (about 12% body mass increase compared to parental lines) independently of age or environments. The $L_{♀}D_{♂}$ hybrid was also interesting for heterosis expression, its growth being 10% higher than parental lines, but only at the constant temperature environment.

A second objective was to assess the relative importance of additive genetic and environmental components, as well as their interaction on the phenotypic expression of mass in this species. Additive genetic variance of body mass at the different time periods was estimated in the three purebred strains in each environment. Results showed that heritability of mass differed among the strains and environments, each strain having its own variation according to the different environmental conditions. We thus showed that the three strains were highly divergent and that gene x environment interaction was mainly important in mass phenotypic expression.

A third objective was to understand the genetic basis of first winter energy mobilization of brook charr. The amount of energy reserves accumulated during fall and their use during winter was measured in all purebred and hybrid crosses. Results indicated

that each strain had its own energy strategy in the accumulation/use of reserves, controlled by specific genetic architecture, thus revealing important divergence among strains. Hybrid showed limited occurrence of non-additive effects but these results also revealed a tighter genetic control in energy accumulation than in energy mobilization.

A last objective was to evaluate the importance of additive and non-additive genetic effects on stress resistance. Stress resistance was measured on the primary (cortisol) and secondary (glucose, osmolality, haematocrit) stress response in each crosses, after transport-induced stress. Significant heritabilities ($h^2 > 0.60$) were obtained for both levels of stress response. The Rupert strain appears to be the least sensitive to stress. Only little non-additive effects were observed. Results thus revealed possibility for genetic improvement in the stress response principally by the use of additive effects.

This thesis allowed highlighting the complexity of the underlying control of phenotypic expression in brook charr. Depending on the traits, phenotypes may be controlled by gene x environment interaction, by important additive genetic basis or by non-additive effects. However, the relative importance of each component is particular to each population and the evolutionary potential of brook charr seems to be population specific and thus unpredictable.

Keywords :

Genetic basis; heritability; heterosis; gene x environment interaction; evolutionary potential; brook charr; growth; stress; winter energy reserves

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INTRODUCTION GÉNÉRALE

Afin de mieux comprendre comment une espèce peut s'adapter à un changement ou répondre à une sélection, que la sélection soit naturelle ou artificielle, il est important de documenter les composantes génétique et environnementale servant à contrôler son phénotype, ainsi que leur interaction (Fig. 1). Les principales composantes génétiques pouvant intervenir dans l'expression d'un phénotype sont les effets additifs, héritables au cours des générations, et les effets non-additifs (effets de dominance ou d'interaction entre gènes) qui s'expriment majoritairement lors de croisement hybrides (Falconer & Mackay, 1996). L'environnement peut lui aussi avoir un impact direct sur l'expression d'un phénotype, c'est la plasticité phénotypique, quand le même génotype exprime différents phénotypes sous différents environnements (Falconer & Mackay, 1996). L'environnement peut aussi modifier l'ampleur des effets additifs et non-additifs. Le potentiel évolutif d'une espèce dépend alors de l'environnement dans lequel elle se trouve (Hoffmann & Merilä, 1999; Charmantier & Garant, 2005). Cependant, cet effet de l'environnement dépend aussi des espèces et populations étudiées (Visscher *et al.*, 2008). Différents génotypes auront alors différentes réponses aux variations de l'environnement (Falconer & Mackay, 1996). Il est alors essentiel de distinguer l'importance relative de chacune de ces composantes dans le contrôle de l'expression phénotypique pour évaluer les capacités d'évolution des populations.

LES EFFETS ADDITIFS

Les effets génétiques additifs correspondent à la base génétique d'un phénotype, qui se transmet d'une génération à la suivante et qui s'exprime de manière égale. Ils s'expriment généralement au sein d'une même population ou entre populations proches au niveau génétique. La part de la variance phénotypique totale d'une population contrôlée par ces effets est la variance génétique additive. La plupart des traits possèdent une variance

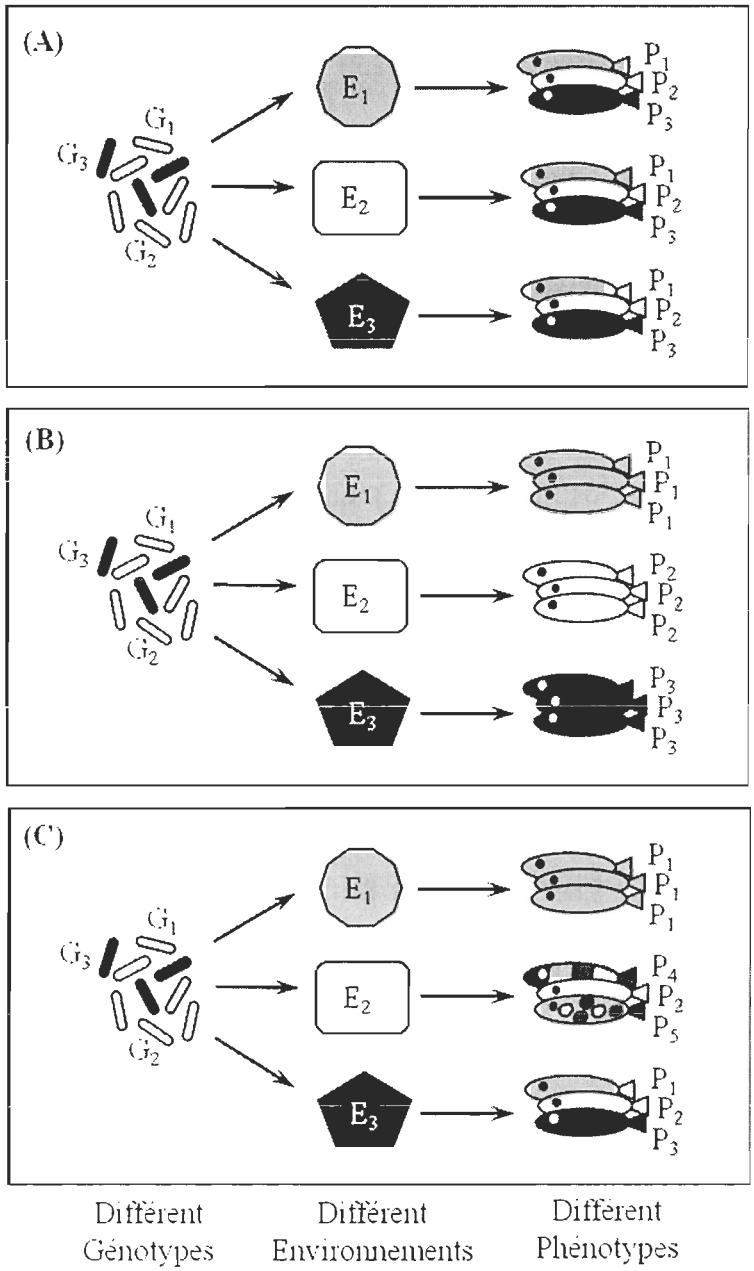


Figure 1 : Les principaux processus pouvant contrôler l'expression phénotypique de populations. (A) Les effets génétiques : les variations phénotypiques sont le résultat uniquement des variations génétiques (chaque génotype donnant un phénotype précis) ; (B) les effets environnementaux : l'hétérogénéité des habitats entraine l'apparition de phénotypes adaptés ; (C) l'interaction génotype x environnement : les génotypes interagissent de manières différentes avec l'environnement pour donner une large gamme de phénotypes différents. D'après Garcia de Leaniz *et al.* (2007).

additive car ils sont tous contrôlés par des gènes (Houle, 1992) mais l'ampleur de celle-ci est propre à chaque trait. Cette variance permet d'estimer le potentiel évolutif d'un trait (Houle, 1992; Wilson & Réale, 2006). Lors d'un croisement entre deux lignées, pour un trait contrôlé par des effets additifs, un hybride présentera alors une performance égale à la moyenne des performances de ses lignées parentales (Fig. 2A). À l'aide de cette variance additive, il est aussi possible de calculer un indice d'héritabilité au sens strict, h^2, qui correspond au ratio de la variance génétique additive sur la variance phénotypique totale d'un trait ($h^2 = V_A/V_P$; Falconer & Mackay, 1996).

L'indice d'héritabilité est très important pour comprendre le potentiel évolutif d'une espèce car il permet de prédire les capacités de l'espèce à répondre à la sélection (R), celle-ci se définit par l'équation $R = h^2 S$ où h^2 représente l'indice d'héritabilité et S la pression de sélection exercée. L'héritabilité exprime également l'importance relative des gènes et de l'environnement dans la variation d'un trait phénotypique (Visscher *et al.*, 2008) et donc nous informe de l'ampleur de la base génétique sur laquelle une sélection peut agir. Plus un estimé sera proche de 1, plus le trait sera contrôlé de manière génétique et sera transmissible, donc plus il pourra avoir une forte réponse à la sélection. À l'inverse, plus l'estimé sera proche de 0, plus le trait sera contrôlé par d'autres processus comme l'environnement ou des effets génétiques non-additifs et sera donc peu héritable. Dans ce cas, la réponse à la sélection sera très faible. Les mesures d'héritabilité sont théoriquement spécifiques à une population pour un trait donné à un moment particulier mais il est possible que ces mesures soient relativement similaires entre populations ou espèces proches génétiquement (Visscher *et al.*, 2008).

Les effets génétiques ne sont souvent pas constants au cours du temps. Sur le court terme, des groupes de gènes spécifiques aux différents stades de développement peuvent être exprimés différentiellement pendant l'ontogenèse (Atchley & Zhu, 1997; Wilson & Réale, 2006; Darias *et al.*, 2008). Comme ces gènes peuvent interagir entre eux et avec d'autres gènes, les interactions et expressions de nombreux gènes peuvent alors changer

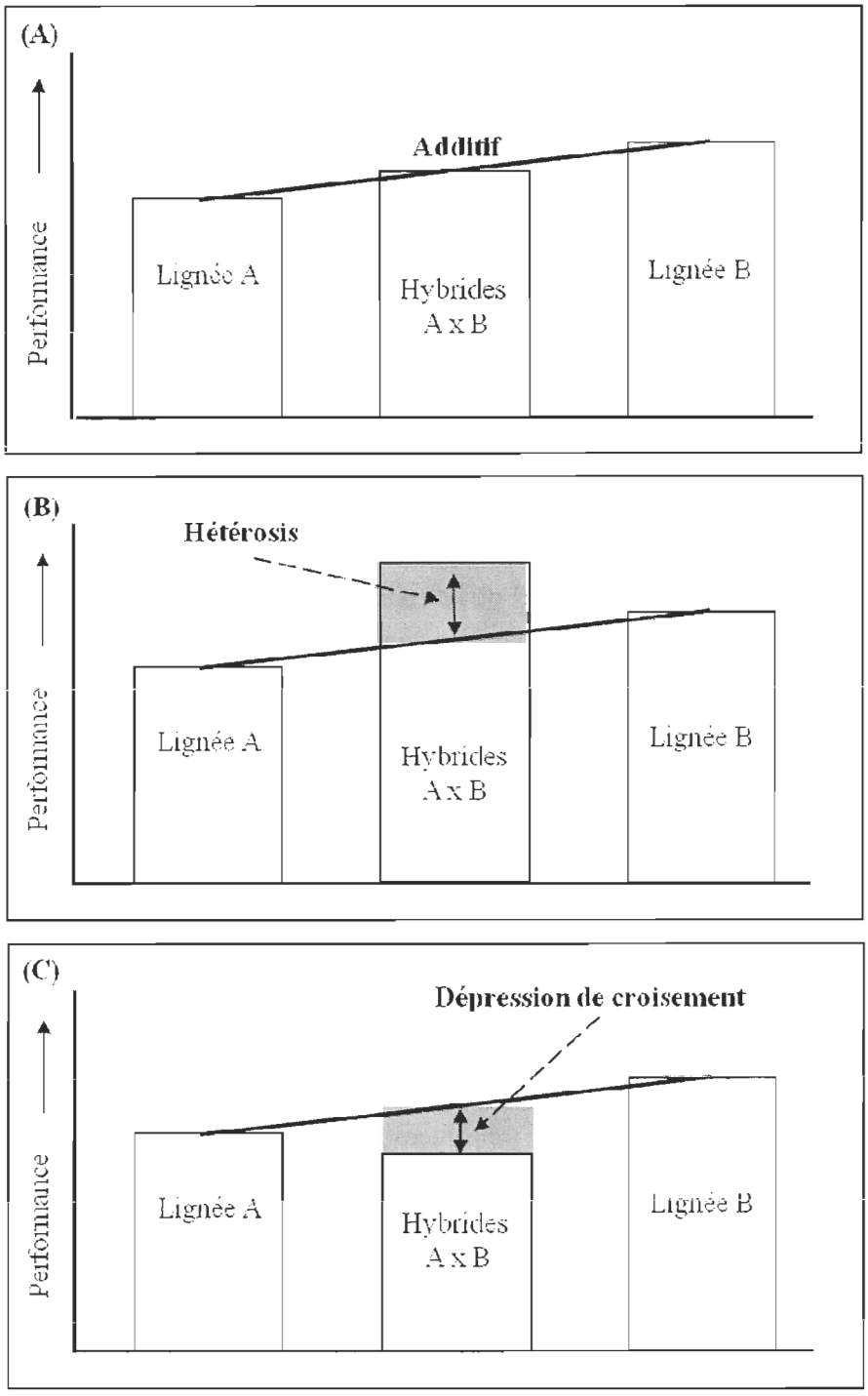


Figure 2 : Représentation graphique des principaux effets génétiques visibles sur la mesure d'une performance lors d'un croisement hybride entre deux lignées. (A) les effets additifs ; (B) et (C) les effets non-additifs (inspiré de Comings & MacMurray, 2000).

pendant le développement (Atchley & Zhu, 1997; Perry *et al.*, 2005a; Wang *et al.*, 2006a; Darias *et al.*, 2008; Nolte *et al.*, 2009). Ces changements d'expression peuvent faire varier la part des composantes génétiques dans l'expression phénotypique. Ils modifient alors la variance additive et l'héritabilité d'un trait pendant l'ontogenèse (Atchley & Zhu, 1997; Wang *et al.*, 2006a; Wilson & Réale, 2006; Wilson *et al.*, 2007; Kruuk *et al.*, 2008). Le potentiel de réponse à la sélection dépend donc de l'âge des individus. Sur le long terme, la variance génétique additive peut aussi changer avec l'apparition de nouveaux allèles dans la population suite à des mutations ou migrations, mais aussi si la fréquence des allèles est modifiée avec les pressions de sélection ou la consanguinité (Hoffmann & Merilä, 1999; Roff, 2000; Visscher *et al.*, 2008). Cette évolution des bases génétiques d'un trait au cours des générations modifie donc aussi son potentiel de réponse à la sélection.

En milieu naturel

Dans les populations naturelles, de nombreuses études ont mis en évidence une héritabilité significative pour de nombreux traits intervenant dans la morphologie, le comportement, la physiologie ou la valeur adaptative (« fitness ») chez des populations variées d'oiseaux, de poissons, d'amphibiens, de reptiles et de mammifères (Brodie, 1993; Wilson *et al.*, 2003; Charmantier *et al.*, 2004; Merila *et al.*, 2004; Laugen *et al.*, 2005; Nespolo *et al.*, 2005). Ces différents traits peuvent cependant présenter des héritabilités différentes au sein d'une même population. En effet, les traits liés à la valeur adaptative ont une héritabilité souvent plus faible que les traits morphométriques (Houle, 1992; Charmantier & Garant, 2005; Kruuk *et al.*, 2008; Visscher *et al.*, 2008; Teplitsky *et al.*, 2009). Ces différences sont souvent liées à d'importantes pressions de sélection. En général, quand un trait reste sous une pression de sélection forte et stable pendant un certain temps, celle-ci réduit la variabilité génétique par la fixation d'allèles bénéfiques et donc diminue l'héritabilité du trait (Stearns, 1984; Uller *et al.*, 2002; Danielson-Francois *et al.*, 2009; Teplitsky *et al.*, 2009). Les traits liés à la valeur adaptative subissent généralement des pressions de sélection très fortes (Stearns, 1984; Pakkasmaa *et al.*, 2003) et leur

héritabilité est donc inversement proportionnelle à leur importance pour celle-ci (Falconer & Mackay, 1996).

Des différences d'héritabilité peuvent aussi être observées pour des mêmes traits entre populations différentes (Snyder, 1991; Charmantier *et al.*, 2004; Laugen *et al.*, 2005). Ces différences sont généralement attribuées à des divergences génétiques entre populations. Suite à une séparation, les populations isolées peuvent subir une adaptation locale de leurs bases génétiques par des pressions de sélection ou encore diverger sous l'effet de la dérive génétique (Roff & Mousseau, 1999; Roff, 2000; Charmantier & Garant, 2005; Marcil *et al.*, 2006; Jetz *et al.*, 2009). Un faible échange de gènes entre les populations peut alors conduire à de la divergence génétique (Edmands, 1999; Harder & Johnson, 2009; Jetz *et al.*, 2009) et influencer l'architecture génétique des populations, soit les différentes bases et relations génétiques présentes dans leur génome (Roff & Mousseau, 1999; Roff, 2000; Uller *et al.*, 2002; de Brito *et al.*, 2005; Brenneman *et al.*, 2009). Les différences d'héritabilité entre populations reflètent alors des capacités de réponse à la sélection différentes.

En milieu contrôlé

Généralement, les programmes de sélection artificielle sont basés sur l'exploitation des effets additifs pour améliorer certaines performances des lignées afin d'obtenir un meilleur rendement. Dans ce contexte, l'indice d'héritabilité est le paramètre le plus important à prendre en compte. En général, l'héritabilité de la taille est très importante ($h^2 > 0.3$) chez un grand nombre d'espèces animales (oiseaux, poissons, mammifères), il est donc possible de mettre en place des programmes de sélection génétique pour améliorer ce trait (Aziz *et al.*, 2005; Visscher *et al.*, 2008). De tels programmes ont déjà été mis en place chez diverses espèces. Chez le poulet, ils ont permis d'augmenter la masse par des facteurs variant entre 3 et 5 depuis les années 50 (Havenstein *et al.*, 2003; Navarro *et al.*, 2006). Chez la dinde, ils ont permis d'augmenter la masse corporelle de 75 à 93% en 30 ans (Nestor *et al.*, 2000). Des héritabilités intéressantes ont été mesurées pour d'autres traits d'intérêt pour la production comme la qualité de la chair chez les poulets (h^2 de 0,20 à 0,40)

(Navarro *et al.*, 2006) ou de la carcasse chez les vaches (h^2 de 0,11 à 0,60) (Hoque *et al.*, 2009) et on pourrait donc également sélectionner pour ces traits. La connaissance des bases génétiques héritables d'une population permet aussi de prédire les valeurs reproductives des individus, soit la performance moyenne de la descendance, et donc de déterminer des plans de croisement (Gjedrem, 2000; Wang *et al.*, 2006b; Wang & Li, 2007; Visscher *et al.*, 2008; Wang, 2009).

En aquaculture, les effets additifs ont été étudiés chez de nombreuses espèces de poissons pour être exploités par des programmes de sélection (Tableau 1). Chez la carpe, *Cyprinus carpio*, les mesures d'héritabilité pour la masse sont très variables (Tableau 1) et les programmes de sélection pour ce caractère ne se sont pas révélés efficaces au bout de plusieurs générations de sélection (Moav & Wohlfarth, 1976; Vandeputte *et al.*, 2008). Par contre, chez le tilapia, *Oreochromis niloticus*, (gains de 7 à 35% par générations) ou le poisson chat, *Ictalurus punctatus*, (avec gains de 21 à 29% par générations), la masse a pu être significativement améliorée (Rezk *et al.*, 2003; Charo-Karisa *et al.*, 2006; Rezk *et al.*, 2009). D'autres trais d'intérêt pour la production, comme la survie, la résistance au stress ou aux maladies, la maturité sexuelle, la qualité de la chair ou de la carcasse, présentent aussi des héritabilités intéressantes chez des espèces variées (Tableau 1). Cependant, chez les poissons, les estimations d'héritabilités sont généralement plus faibles que les estimations rapportées pour des mammifères ou des oiseaux, possiblement en raison d'une plus grande plasticité phénotypique. Les effets additifs présentent aussi souvent une grande variabilité due aux méthodes et lignées utilisées pour effectuer les estimations (Vandeputte, 2003; Wang, 2009). Ainsi avec une sélection artificielle bien orientée vers certaines performances (essentiellement croissance et résistance aux maladies), les éleveurs ont pu obtenir des résultats intéressant en seulement quelques générations (Rezk *et al.*, 2003; Vandeputte, 2003; Rezk *et al.*, 2009).

Une sélection artificielle importante peut cependant avoir un effet négatif sur la variance génétique d'une population. Plusieurs auteurs ont observé une diminution de l'héritabilité d'un trait au cours des générations suite à la forte pression de sélection qui

Tableau 1 : Estmations d'héritabilité (h^2) chez plusieurs espèces de poissons et pour différents traits d'intérêt pour l'aquaculture.

Espèce	Trait	h^2	Références
Carpe (*Cyprinus carpio*)	Masse	0 - 0,71	Vandeputte, 2003
			Wang *et al.*, 2006a
			Vandeputte *et al.*, 2008
			Wang, 2009
			Nielsen *et al.*, 2010
	Survie	0,20	Nielsen *et al.*, 2010
	résistance au stress	0,37 - 0,90	Vandeputte, 2003
	résistance aux maladies	0,15 - 0,20	Vandeputte, 2003
Tilapia (*Oreochromis niloticus*)	Masse	0,26 - 0,60	Charo-Karisa *et al.*, 2006
			Rezk *et al.*, 2009
	Survie	0,03 - 0,14	Charo-Karisa *et al.*, 2006
	maturité sexuelle	0,13	Charo-Karisa *et al.*, 2007
	qualité de la chair	0,12 - 0,24	Rutten *et al.*, 2005
Poisson-chat (*Ictalurus punctatus*)	Masse	0,16 - 0,23	Rezk *et al.*, 2003
Daurade (*Sparus aurata*)	résistance aux maladies	0,12 - 0,45	Antonello *et al.*, 2009
Morue (*Gadus morhua*)	résistance aux maladies	0,08 - 0,43	Kettunen *et al.*, 2007
			Odegard *et al.*, 2010
Bar (*Dicentrarchus labrax*)	qualité de la carcasse	0,48 - 0,87	Saillant *et al.*, 2009

réduit la variance additive (Falconer & Mackay, 1996; Nestor *et al.*, 2000; Neira *et al.*, 2004; Postma *et al.*, 2007). Ainsi, quelques générations de domestication suffisent aussi pour changer de manière héritable les profils de transcription donc d'expression génique (Roberge *et al.*, 2006; Sauvage *et al.*, 2010). Ces modifications révèlent un changement dans l'architecture génétique et peuvent alors affecter l'héritabilité des traits. De plus, l'utilisation d'un stock limité de géniteurs dans les programmes de sélection peut conduire à une augmentation de la proportion d'homozygotes dans la population, réduisant la variance génétique de celle-ci (Falconer & Mackay, 1996). Cette augmentation d'homozygotes peut alors entrainer une diminution des performances par l'expression d'allèles récessifs ce que l'on appelle de la dépression de consanguinité (Martin *et al.*, 1997; Wang *et al.*, 2001; Shikano & Taniguchi, 2002a; Nakadate *et al.*, 2003). Le potentiel d'amélioration par sélection artificielle peut donc diminuer au fur et à mesure des générations, cette sélection pouvant même aller jusqu'à entrainer une diminution des performances. Cependant, il arrive parfois que la pression de sélection artificielle n'ait pas d'effet sur la variance génétique d'un trait (Navarro *et al.*, 2006). Cette absence de modification semble être due à des mutations ou des interactions entre gènes, une pression de sélection trop légère ou encore à des croisements bien choisis qui maintiendraient la variance génétique (Navarro *et al.*, 2006).

LES EFFETS NON-ADDITIFS

D'autres effets génétiques peuvent intervenir dans l'expression d'une performance, ce sont les effets non-additifs qui apparaissent généralement lors de croisements hybrides entre parents ayant une grande divergence génétique. Les principaux effets non-additifs sont l'hétérosis et la dépression de croisement. L'effet hétérosis, aussi appelé vigueur hybride, correspond à la supériorité des performances d'un hybride F1 pour un trait donné comparé à la moyenne des performances pour ce trait chez les deux lignées ou les deux espèces parentales (Fig. 2B). Cet effet est très intéressant car il permet d'améliorer les performances de la nouvelle génération (Falconer & Mackay, 1996; Lippman & Zamir, 2007). L'effet hétérosis est généralement plus important si les lignées parentales sont

chacune homozygotes ou génétiquement très différentes (Shikano *et al.*, 2000; Wang & Xia, 2002; Hochholdinger & Hoecker, 2007). Cependant, une trop grande distance génétique entre les parents peut aussi entrainer de la dépression de croisement qui est l'effet opposé de l'hétérosis (Emlen, 1991; Edmands, 1999; Parisod *et al.*, 2005). Cet effet correspond alors à une diminution des performances des hybrides (Fig. 2C). Ce phénomène est généralement rencontré à partir d'une deuxième génération de croisement mais il peut aussi apparaitre dès la F1 s'il existe des adaptations locales importantes chez les lignées parentales (Edmands, 1999; Gharrett *et al.*, 1999; Parisod *et al.*, 2005; Becker *et al.*, 2006; Tymchuk *et al.*, 2007). Comme l'hétérosis et la dépression de croisement résultent d'un éloignement génétique entre les lignées parentales, il est difficile de prédire si les hybrides exprimeront l'un ou l'autre.

Les effets non-additifs reposent sur les mêmes types de processus génétiques (Gharrett *et al.*, 1999). Trois hypothèses génétiques sont généralement utilisées pour les expliquer : la dominance, la sur-dominance et l'épistasie (Birchler *et al.*, 2003; Hochholdinger & Hoecker, 2007; Lippman & Zamir, 2007). Elles participeraient toutes les trois à la formation des effets non-additifs mais la part relative de chacune reste encore mal connue (Lippman & Zamir, 2007). Les différentes hypothèses sont décrites dans un cas d'hétérosis.

- La dominance (Fig. 3A) : cette hypothèse est basée sur la présence d'allèles récessifs accumulés dans les lignées parentales au cours des générations. Avec le croisement de deux lignées, les allèles dominants vont masquer les allèles récessifs et se compléter permettant aux hybrides d'exprimer une supériorité phénotypique.

- La sur-dominance (Fig. 3B) : cette hypothèse propose que les interactions entre les allèles d'un même locus combinés lors du croisement de deux lignées provoquent un effet de synergie sans qu'il y ait une relation de dominance/récessivité entre les allèles.

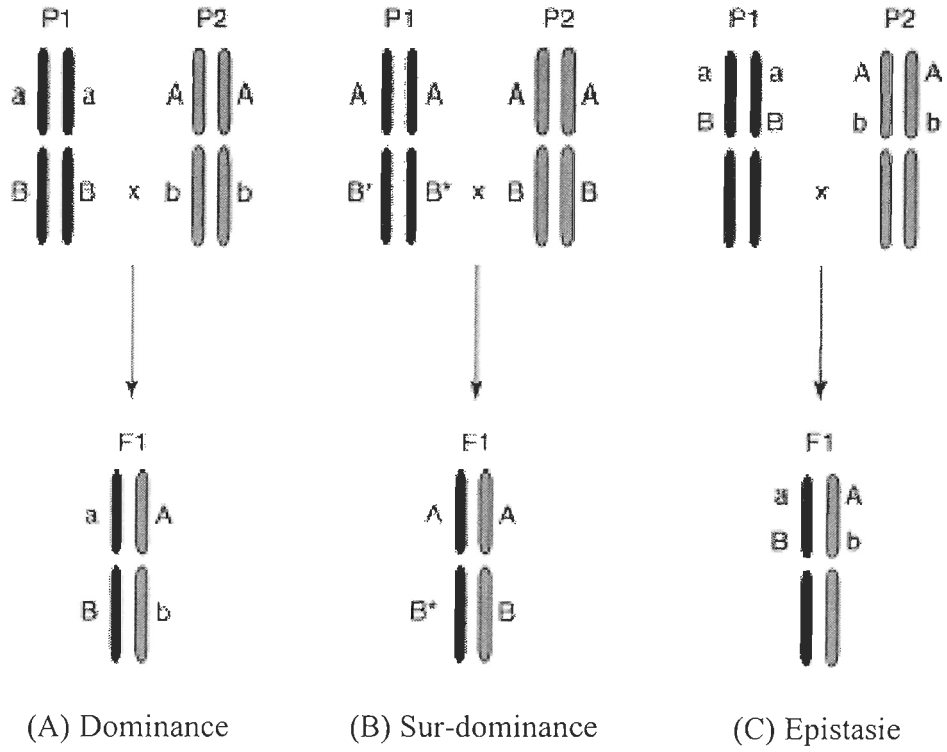


Figure 3 : Les différentes hypothèses génétiques expliquant la formation d'effets non-additifs. (A) l'hypothèse de dominance ; (B) l'hypothèse de sur-dominance ; (C) l'hypothèse d'épistasie. P1 et P2 représentent deux populations parentales éloignées au niveau génétique et F1 leurs hybrides. Sur les gènes, A et B représentent les allèles dominants, a et b les allèles récessifs et B* un autre allèle aussi dominant que B (d'après Lippman & Zamir, 2007).

- L'épistasie (Fig. 3C) : cette hypothèse indique que c'est la disposition suite aux croisements des allèles et des gènes à plusieurs loci, ainsi que leurs interactions, qui donnent aux hybrides des capacités supérieures aux lignées parentales.

Certains chercheurs se sont intéressés à distinguer ces trois composantes à l'aide d'outils moléculaires comme les puces à ADN ou les cartes de QTLs (« quantitative trait locus »). Ainsi, des observations sur des cultures de maïs, *Zea mays*, suggèrent que l'hétérosis serait lié à un autre phénomène que la simple dominance car l'amélioration de lignées pures depuis plusieurs générations n'a pas fait diminuer l'effet hétérosis mais au contraire, l'a accru (Birchler *et al.*, 2003). Si l'hétérosis était lié à un simple phénomène de dominance, les allèles récessifs auraient été éliminés des lignées au fur et à mesure des générations et l'effet hétérosis aurait fini par s'atténuer. Birchler *et al.* (2003) suggèrent que l'hétérosis résulte de la sélection d'allèles au bon endroit pour faire des combinaisons plus performantes, donc d'un effet d'épistasie en combinaison avec de la sur-dominance. L'analyse de cartes de QTLs et de puces à ADN permettent généralement d'arriver aux mêmes conclusions (Stuber *et al.*, 1992; Uzarowska *et al.*, 2007). Cependant, ce n'est pas le cas pour d'autres études. La comparaison de lignées pures de maïs (analyse de colinéarité) montrent des disparitions de gènes chez certaines lignées (Hochholdinger & Hoecker, 2007). Lors d'hybridations, les gènes se complètent et donnent une performance accrue aux hybrides, ce qui correspond à l'hypothèse de dominance (Rodrigues *et al.*, 2006; Hochholdinger & Hoecker, 2007). Dans les cultures de riz, *Oryza sativa*, certaines études montrent également un effet d'épistasie et de sur-dominance (Alam et al., 2004) alors que d'autres montrent une plus grande importance des effets de dominance pour les mêmes traits (Grillo *et al.*, 2009). Ces contradictions montrent la complexité du processus.

Au niveau physiologique, l'apparition d'hétérosis résulte le plus souvent d'un meilleur équilibre dans le potentiel de l'hybride pour la croissance ou le rendement plutôt que d'hétérosis pour certaines fonctions (Griffing, 1990; Ahmadzadeh *et al.*, 2004). Par exemple, chez le maïs, le rendement supérieur des hybrides semble plus lié à leur

possibilité de maintenir un taux d'échange en CO_2 tard dans la saison que d'un potentiel d'échange supérieur (Ahmadzadeh *et al.*, 2004). Ce rendement est aussi lié à la taille des feuilles : les feuilles plus grandes des hybrides pourront absorber plus de lumière donc faire plus de photosynthèse et accumuler de la matière pour augmenter le rendement en grain (Tollenaar *et al.*, 2004). Cependant, il existe encore peu d'études sur les bases physiologiques fonctionnelles des effets non-additifs.

En milieu naturel

Dans les populations naturelles, il est possible de rencontrer des effets non-additifs car malgré les barrières empêchant les flux de gènes ou la dispersion, plusieurs espèces de plantes et d'animaux sont impliquées dans des hybridations (Rieserberg *et al.*, 1999). Dans une population, les croisements entre individus très proches génétiquement, souvent en raison d'isolement géographique avec d'autres populations, peuvent conduire à des dépressions de consanguinité (augmentation de l'homozygotie, accumulation d'allèles récessifs et diminution de la variabilité génétique) et des risques d'extinction (Wang *et al.*, 2001; Parisod *et al.*, 2005; Becker *et al.*, 2006). Les hybridations sont alors importantes car elles peuvent contrer ces risques en apportant de nouveaux allèles ou en masquant les allèles récessifs présents dans la population lui permettant d'avoir une plus grande diversité génétique et donc d'avoir une plus grande capacité d'adaptation. Ces hybridations peuvent alors améliorer les performances des descendants par rapport aux lignées parentales (hétérosis) pour la croissance, la survie ou autres traits liés à la valeur adaptative chez de nombreuses espèces, surtout lors de la première génération (Emlen, 1991; Hotz *et al.*, 1999; Rieserberg *et al.*, 1999; Becker *et al.*, 2006; Stelkens *et al.*, 2009).

Cependant, la dépression de croisement est l'effet non-additif le plus souvent rencontré en milieu naturel. En effet, l'hybridation entre populations très divergentes et très adaptées à leurs conditions locales entraine généralement la rupture des liens des complexes génétiques coadaptés provoquant la stérilité ou une valeur d'adaptation réduite chez les hybrides (Edmands, 1999; Cooke *et al.*, 2001; Parisod *et al.*, 2005; Becker *et al.*, 2006; Tymchuk *et al.*, 2007).

En milieu contrôlé

Dans les programmes de sélection artificielle, c'est surtout l'effet hétérosis qui est intéressant car il permet d'améliorer les performances des descendants tout en contrant le déclin de la production lié à la consanguinité et en maintenant une grande variabilité génétique dans les lignées (Nakadate *et al.*, 2003; Tollenaar *et al.*, 2004; Vandeputte & Launey, 2004; Garcia de Leaniz *et al.*, 2007). La notion d'hétérosis a été mise évidence par Charles Darwin il y a plus d'un siècle en observant des croisements hybrides de maïs qui étaient 25% plus grands que les croisement issus des lignées pures (Duvick, 2001; Hochholdinger & Hoecker, 2007). Depuis, ce phénomène est surtout utilisé à des fins commerciales. Il a été retrouvé et utilisé chez de nombreuses espèces d'intérêt car il représente une bonne alternative à la culture de lignées pures (Birchler *et al.*, 2003; Hochholdinger & Hoecker, 2007; Lippman & Zamir, 2007). Chez le maïs, l'hétérosis a ainsi permis l'amélioration de nombreuses performances d'intérêt commercial comme la croissance, le rendement de productivité (2 à 167%), la reproduction (1 à 62%), la résistance aux maladies ou aux insectes nuisibles (0,2 à 27%) (Soengas *et al.*, 2003; Moreno-Gonzalez *et al.*, 2004; Soengas *et al.*, 2004; Tollenaar *et al.*, 2004; Rodrigues *et al.*, 2006). Depuis, la production de maïs est composée à 65% d'hybrides au niveau mondial (Hochholdinger & Hoecker, 2007). Chez d'autres espèces végétales, cet effet a été utilisé pour améliorer le rendement de production du riz (1 à 200%) (Alam *et al.*, 2004), du soya, *Glycine max*, (19%) (Dinkins *et al.*, 2002), de la pomme de terre, *Solanum tuberosum* (15 à 76%) (Gopal *et al.*, 2000), de la luzerne, *Medicago sativa* (7 à 12%) (Riday & Brummer, 2002), du millet, *Setaria italica* (68%) (Siles *et al.*, 2004), ou du coton, *Gossypium hirsutum* (de 16 à 30%) (Wu *et al.*, 2004; Dong *et al.*, 2006). L'effet hétérosis est cependant très variable dépendamment du trait et des lignées parentales.

Chez les animaux, l'effet hétérosis est moins bien connu et utilisé que chez les végétaux mais il commence à être exploité (Comings & MacMurray, 2000). Chez les poulets, on retrouve un effet hétérosis pour la croissance (4 à 28%) (Yang & Siegel, 1998). Chez les porcs, la croissance (10 à 20%) mais aussi la qualité de la carcasse (1,5 à 11,5%)

et de la reproduction (2 à 4%) présentent un effet hétérosis (Baas *et al.*, 1992; Muller *et al.*, 2000; Cassady *et al.*, 2002a, 2002b). Chez les vaches, l'utilisation d'hybrides est déjà plus commune avec une réduction de la mortalité et des maladies (15 à 16%), une amélioration générale de la santé (37%), de la masse et de la taille (2 à 11%), de la production et la qualité du lait (environ 7 à 15%) (Ahlbornbreier & Hohenboken, 1991; Nunezdominguez *et al.*, 1991; Gregory *et al.*, 1992a, 1992b; Arthur *et al.*, 1999).

En aquaculture, l'hétérosis commence aussi à être utilisé pour améliorer les productions de certaines espèces de poissons mais il reste beaucoup moins reconnu qu'en agriculture (Gjedrem, 2000; Wang & Xia, 2002; Nakadate *et al.*, 2003). Les effets hétérosis sont étudiés depuis plus de 30 ans chez la carpe tant pour la croissance (10 à 29%) que la survie (8 à 37%), la tolérance aux températures froides (30 à 77%) et la résistance aux maladies (Moav & Wohlfarth, 1976; Wohlfarth, 1993; Hulata, 1995; Vandeputte, 2003; Nielsen *et al.*, 2010). Chez cette espèce, les effets hétérosis sont plus utilisés que les effets additifs dans les programmes d'amélioration génétique (Wang, 2009). Chez le guppy, *Poecilia reticulata,* la présence d'hétérosis a été observée pour de nombreux traits liés au développement et à la croissance (1 à 46%) mais aussi à la tolérance à la salinité (0 à 80%) (Shikano *et al.*, 2000; Shikano & Taniguchi, 2002a, 2002b; Nakadate *et al.*, 2003). Chez le tilapia, un effet hétérosis a aussi été observé pour la croissance (4 à 39%) et la tolérance à la salinité (Bentsen *et al.*, 1998; Marengoni *et al.*, 1998; Hena *et al.*, 2005; Maluwa & Gjerde, 2006b). Cependant il existe souvent une grande variabilité de l'effet hétérosis suivant les combinaisons de lignées; le choix des parents est alors un des principaux processus influençant l'expression d'hétérosis (Wohlfarth, 1993; Hulata, 1995; Bentsen *et al.*, 1998; Shikano *et al.*, 2000; Shikano & Taniguchi, 2002b). Dans ces espèces, certains croisements hybrides ont cependant montré leur utilité pour l'améliorer des performances. D'autres espèces de poissons d'intérêt aquacole présentent aussi un effet hétérosis pour la croissance comme le bar, *D. labrax* (10%) (Gorshkov *et al.*, 2004) ou la perche, *Bidyanus bidyanus* (21%) (Guy *et al.*, 2009) mais l'utilisation de programmes de sélection basé sur ces effets reste encore à mettre au point.

Prédiction des effets non-additifs

Quelques études ont cherché à prédire l'apparition et l'amplitude des effets non-additifs lors de croisements en utilisant des techniques variées comme des modèles mathématiques complexes de génétique (Emlen, 1991; Xu & Zhu, 1999) ou encore des marqueurs de polymorphisme génétique (microsatellites ; RAPD, « Random Amplified Polymorphic DNA » ; empreinte génétique, « DNA fingerprinting »), (Shikano & Taniguchi, 2002b; Wang & Xia, 2002; Parisod *et al.*, 2005). Les modèles mathématiques intègrent de nombreux paramètres comme les effets additifs, les effets de dominance, de l'environnement et des interactions entre les effets. Ils peuvent fournir des formules de prédiction intéressantes (Emlen, 1991; Xu & Zhu, 1999). En général, quand ces modèles intègrent un effet d'épistasie en plus des effets de dominance, ils sont encore plus précis (Emlen, 1991; Arthur *et al.*, 1999; Xu & Zhu, 1999). Cependant, ces modèles sont complexes et basés sur des suppositions au niveau des populations (essentiellement peu de divergence génétique). Ils restent donc peu pratiques à utiliser. Concernant les marqueurs génétiques, la distance et la diversité génétique entre populations représentent une bonne base dans la prédiction d'un effet hétérosis (Shikano & Taniguchi, 2002b; Wang & Xia, 2002).

LES EFFETS PARENTAUX

Les bases phénotypiques et génétiques des parents peuvent également influencer les caractéristiques d'une descendance. Les effets maternels s'expriment généralement au début de la vie quand le phénotype et l'environnement de la mère (soins maternels, alimentation, qualité des œufs) ont une influence sur le développement des descendants que ce soit chez les mammifères, les oiseaux ou les poissons (Atchley & Zhu, 1997; Heath *et al.*, 1999; Perry *et al.*, 2005a; Wilson & Réale, 2006; Kruuk *et al.*, 2008). Ces effets ont alors un impact sur les paramètres génétiques des descendants pouvant modifier l'héritabilité d'un trait (Falconer & Mackay, 1996; Charmantier & Garant, 2005; Visscher *et al.*, 2008). Des effets paternels ont aussi parfois été observés mais leur fonctionnement reste mal connu (Cheng *et al.*, 1987; Perry *et al.*, 2005a; Wang *et al.*, 2006c). Ces effets

parentaux dépendent généralement des populations étudiées (Bentsen *et al.*, 1998; Perry *et al.*, 2005a). L'orientation des lignées dans un croisement est alors importante car les capacités des descendants peuvent varier si une lignée est utilisée en tant que mâle ou femelle pendant la reproduction. Un impact de l'orientation des croisements a aussi été observé dans la formation d'hétérosis, certaines souches entraînant de meilleures performances chez les hybrides quand elles sont utilisées en tant que mâle ou femelle (Bentsen *et al.*, 1998; Gjerde *et al.*, 2002; Wang *et al.*, 2006c).

L'ENVIRONNEMENT

L'environnement tient aussi un rôle important dans l'expression des paramètres génétiques additifs et non-additifs. Les conditions environnementales peuvent modifier l'expression des gènes avec certains allèles qui ne s'expriment parfois que sous certaines conditions (Hoffmann & Merilä, 1999; Côté *et al.*, 2007; Visscher *et al.*, 2008). Ces modifications peuvent alors faire varier les interactions entre gènes et la part des composantes génétiques dans l'expression phénotypique d'un trait (Hoffmann & Merilä, 1999; Charmantier & Garant, 2005). Cependant, les populations ne réagissent pas toutes de la même manière aux variations de l'environnement (Falconer & Mackay, 1996; Côté *et al.*, 2007; Visscher *et al.*, 2008), ce qui entraine des interactions gènes x environnement. Ces interactions sont importantes à considérer quand on cherche à connaitre le potentiel d'adaptation d'une population car elles modifient l'expression des phénotypes et les bases génétiques sur lesquelles la sélection peut agir (Charmantier & Garant, 2005; Côté *et al.*, 2007; Kruuk *et al.*, 2008). Différents génotypes peuvent donc produire leurs phénotypes optimums sous différentes conditions environnementales.

Interaction avec les effets additifs

Les interactions entre l'environnement et la variance additive modifient souvent les mesures d'héritabilité. Dans les milieux naturels ou artificiels, l'héritabilité des traits morphométriques est généralement plus grande sous des conditions favorables chez de nombreuses espèces d'oiseaux, de poissons, d'amphibiens ou de mammifères (Hoffmann &

Merilä, 1999; Olsson & Uller, 2002; Charmantier & Garant, 2005; Wilson *et al.*, 2006; Jetz *et al.*, 2009; Robinson *et al.*, 2009). La présence de contraintes importantes dans les environnements difficiles augmenterait les pressions de sélection sur certains traits ce qui diminuerait leur variance génétique additive. L'inverse est cependant observé pour les traits en rapport avec la valeur adaptative car ceux-ci sont favorisés sous des conditions stressantes (Hoffmann & Merilä, 1999; Charmantier & Garant, 2005). Les modifications d'héritabilité entre environnements ne sont pourtant pas toujours liées à un changement de la variance génétique et peuvent aussi dépendre d'un changement dans la variance environnementale (Hoffmann & Merilä, 1999; Uller *et al.*, 2002; Charmantier & Garant, 2005). En général, la variance environnementale augmente dans les environnements variables et plus difficiles ce qui diminue l'héritabilité (Hoffmann & Merilä, 1999; Charmantier & Garant, 2005).

La sensibilité des génotypes aux variations environnementales dépend cependant des populations (Falconer & Mackay, 1996; Visscher *et al.*, 2008). Bien qu'elles soient très importantes pour le potentiel évolutif d'une espèce, ces interactions génotype x environnement ont pourtant été assez peu documentées dans les populations naturelles. Certains auteurs soutiennent que ces interactions permettent un maintien d'une variance additive ce qui serait favorable pour le potentiel d'adaptation d'une population (Charmantier & Garant, 2005; Laugen *et al.*, 2005; Kruuk *et al.*, 2008; Danielson-Francois *et al.*, 2009) alors que d'autres expliquent que ces interactions diminuent le potentiel évolutif en diminuant la vitesse de réponse à la sélection (Wilson *et al.*, 2006). Dans le cadre de sélection artificielle, l'étude de ces interactions est par contre répandue afin de savoir comment exploiter au mieux les génotypes (Fishback *et al.*, 2002; Kause *et al.*, 2004; Maluwa *et al.*, 2006; Saillant *et al.*, 2006; Dupont-Nivet *et al.*, 2008). S'il n'y a pas d'interaction, le meilleur génotype le sera dans tous les environnements ce qui facilitera la production alors que s'il y a des interactions, il sera nécessaire de connaitre les capacités particulières des génotypes dans les différents environnements (Gjedrem, 1992; Falconer & Mackay, 1996).

Interaction avec les effets non-additifs

L'environnement peut aussi interagir avec les effets non-additifs en modifiant les interactions entre gènes et alors influencer l'expression d'hétérosis. Généralement, les composantes non-additives (la dominance, la sur-dominance ou l'épistasie) sont plus sensibles au variations de l'environnement que les composantes additives (Bentsen *et al.*, 1998; Gjerde *et al.*, 2002), avec une augmentation des effets d'épistasie et donc d'hétérosis sous des conditions moins favorables (Wohlfarth, 1993; Bentsen *et al.*, 1998; Hoffmann & Merilä, 1999; Bryant *et al.*, 2007). L'expression des effets non-additifs dépend alors beaucoup des conditions environnementales et c'est ce qui a été observé chez de nombreuses espèces végétales et animales (Ayles & Baker, 1983; Brown *et al.*, 2001; Bryant *et al.*, 2007; Lippman & Zamir, 2007; Qi *et al.*, 2009). Cependant, l'impact de l'environnement dépend aussi des populations étudiées suggérant une interaction entre l'environnement et le génome dans l'expression d'hétérosis (Ayles & Baker, 1983; Bentsen *et al.*, 1998). Lors de programmes de sélection artificielle, il sera donc nécessaire de tester l'expression d'hétérosis dans les différents environnements d'intérêt et de bien définir les caractéristiques de celui dans lequel l'expression d'hétérosis a été intéressante (Bentsen *et al.*, 1998).

CHEZ LES SALMONIDÉS

Chez les salmonidés, il existe encore assez peu d'informations sur les bases génétiques et environnementales des populations naturelles (seulement 2% des estimations de la littérature se rapportent aux populations naturelles dans leurs milieux naturels, Carlson & Seamons, 2008). Des héritabilités significatives pour la taille (0,04 à 0,36) et l'âge à maturité (0,65) ont cependant été observées chez le saumon atlantique, *Salmo salar* (Garant *et al.*, 2003; Garcia de Leaniz *et al.*, 2007). Par contre, en milieu d'élevage, ces différentes composantes sont souvent étudiées, avec un intérêt surtout pour deux espèces : la saumon atlantique et la truite arc-en-ciel, *Oncorhynchus mykiss* (Carlson & Seamons, 2008). La présence d'effets additifs a d'abord été recherchée pour la croissance afin de savoir s'il était possible d'améliorer ce trait par sélection artificielle (Gjedrem, 2000;

Weber *et al.*, 2008). Avec une héritabilité intéressante (0,20 à 0,40), la croissance a alors pu être améliorée de 10 à 15% par génération chez le saumon atlantique et la truite arc-en-ciel (Gjedrem, 1992, 2000; Garcia de Leaniz *et al.*, 2007). D'autres traits utiles pour la production ont été étudiés. Les héritabilités pour l'âge de maturation sexuelle (0,05 à 0,21), la résistance au stress (0,41 à 0,56) et aux maladies (0 à 0,69), la survie (0,09 à 0,29), la tolérance aux températures chaudes (0,41) et la qualité de la chair (0,06 à 0,47 dépendamment du trait) pour le saumon atlantique et la truite arc-en-ciel ont été estimées pour connaitre les potentiels de sélection (Fevolden *et al.*, 1991; Gjedrem, 2000; Fevolden *et al.*, 2002; Perry *et al.*, 2005b; Quinton *et al.*, 2005; Tobin *et al.*, 2006; Garcia de Leaniz *et al.*, 2007; Kjoglum *et al.*, 2008). En général, chez les salmonidés, la plupart des traits liés à l'histoire de vie, la morphologie ou la physiologie ont une héritabilité moyenne comprise entre 0,20 et 0,30 (Carlson & Seamons, 2008). Suite à la mise en place de programmes de sélection appropriés, un gain de 22% par génération a été obtenu pour la diminution de la maturation sexuelle précoce chez le saumon atlantique (Gjedrem, 2000). Pour la résistance au stress, la sélection a été efficace et deux lignées de truite arc-en-ciel et de saumon atlantique ont été obtenues selon leur degré de réponse au stress (Fevolden *et al.*, 1991; Pottinger & Carrick, 1999; Fevolden *et al.*, 2002). L'estimation des interactions entre ces effets additifs et l'environnement n'a pas montré d'influence significative (Fishback *et al.*, 2002; Kause *et al.*, 2004).

Au niveau des effets non-additifs, la présence d'hétérosis chez les hybrides de salmonidés n'est pas encore claire. Certains auteurs ont observé un effet hétérosis pour la croissance (1 à 60%) et la survie (1 à 150%) chez certains croisements de truites arc-en-ciel (Ayles & Baker, 1983; Wangila & Dick, 1996) ou entre souches domestiques et sauvages de saumon atlantique (croissance : 2,5 à 8,6% ; survie : 1 à 18%) et chinook, *Oncorhynchus tshawytscha*, (croissance : 1 à 15%) mais la performance des hybrides ne dépassait pas la plus forte des deux lignées (Gjerde & Refstie, 1984; Einum & Fleming, 1997; Bryden *et al.*, 2004). D'autres études entre populations sauvages et domestiques de saumon atlantique, de saumon chinook et de truite arc-en-ciel ont plutôt mis en évidence la présence d'effet additifs pour les mêmes traits chez les hybrides (Cheng *et al.*, 1987; Tymchuk *et al.*,

2007; Glover *et al.*, 2009) et certains travaux ont même montré un effet de dépression de croisement (Gharrett *et al.*, 1999). D'autres traits comme la résistance aux maladies ou au stress, la tolérance à l'eau salée et la fécondité ont montré majoritairement un contrôle de nature additive chez les hybrides (Gjerde & Refstie, 1984; Bryden *et al.*, 2004; Glover *et al.*, 2006b; Glover *et al.*, 2009). Il en a donc été déduit que l'hétérosis est un phénomène assez rare chez les salmonidés et peu efficace, donc une méthode risquée pour l'amélioration des productions (Gharrett *et al.*, 1999; Gjedrem, 2000; Bryden *et al.*, 2004). Ce serait la trop grande distance génétique et les adaptations locales qui empêcheraient la formation d'hétérosis chez les salmonidés (Tymchuk *et al.*, 2007).

Chez les ombles (genre *Salvelinus*), il existe encore peu d'information sur les effets additifs et non-additifs, ainsi que sur les effets et interactions de l'environnement. Cependant, des effets additifs significatifs ont été observés pour la taille d'omble de fontaine, *Salvelinus fontinalis*, en nature (h^2 de 0,15 à 0,50) et en milieu contrôlé (0,14 à 0,57), ainsi que pour la résistance aux maladies (0,51) révélant que ces traits peuvent répondre à une sélection (Wilson *et al.*, 2003; Perry *et al.*, 2004a, 2004b; Thériault *et al.*, 2007b). Pour les effets non-additifs, des croisements entre différentes espèces ont montré un potentiel dans l'expression d'hétérosis (Chevassus, 1979). L'hybridation entre l'omble de fontaine et l'omble chevalier, *S. alpinus*, a montré que certains descendants pourraient présenter de l'hétérosis pour la croissance, la survie, l'acclimatation à l'eau de mer et la maturation sexuelle (Chevassus, 1979; Dumas *et al.*, 1995, 1996). Des croisements entre l'omble de fontaine et le touladi, *S. namaycush*, ont montré des capacités de croissance supérieures pour l'hybride comparé aux lignées parentales (Chevassus, 1979; Gunther *et al.*, 2005). D'autres études, sur des croisements intraspécifiques entre des souches sauvages et domestiques, ont montré la présence d'un effet hétérosis significatif au niveau de la survie et du rendement des hybrides (Fraser, 1981; Webster & Flick, 1981). Il semblerait donc qu'en croisant des lignées de la même espèce mais éloignées génétiquement, il serait possible d'obtenir une distance génétique favorable à l'expression d'hétérosis.

NOTRE MODÈLE : L'OMBLE DE FONTAINE

L'omble de fontaine est une espèce indigène du Nord-est de l'Amérique du nord. Sa colonisation dans le fleuve Saint Laurent est estimée à environ 10 000 ans après le retrait de la couverture de glace de cette région (Castric & Bernatchez, 2003; Thériault *et al.*, 2007a). Cette espèce est adaptée à de nombreux environnements, elle peut être lacustre, résidente ou anadrome et peut donc vivre en eau douce ou saumâtre. Cette espèce est aussi une des principales espèces d'intérêt pour l'aquaculture au Québec (60% des parts de marché de la production d'eau douce, MAPAQ, 2007), elle est donc aussi adaptée aux environnements contrôlés et à la sélection artificielle. Chez l'omble de fontaine utilisée pour aquaculture au Québec, il existe trois souches génétiquement distinctes : la souche Laval, la souche Rupert et la domestique. Elles présentent de fortes différenciations génétiques au niveau des marqueurs moléculaires neutres (F_{ST}) et une grande distance génétique (Martin *et al.*, 1997), mais diffèrent également au niveau de l'expression de gènes (Bougas *et al.*, 2010) et au niveau allélique (76% des allèles des souches sauvages n'existent pas chez la domestique).

La souche Laval est issue d'une population anadrome de la rivière Laval (48°44'N; 69°05'W) sur la côte nord du Saint Laurent. Cette population effectue des migrations annuelles de 22 km entre l'eau douce en hiver pour la reproduction et l'eau saumâtre en été pour la nourriture (Boula *et al.*, 2002; Curry *et al.*, 2006). Elle peut donc supporter une large gamme d'environnements avec une salinité allant de 1 à 34 ppm, des températures de 5 à 18°C et des courants de faibles à importants (Curry *et al.*, 2006) et présente des adaptations physiologiques spécifiques (Boula *et al.*, 2002). La souche Rupert est issue d'une population nordique résidente de la rivière Rupert (51°05'N; 73°41'W) près du lac Mistassini. Cette population occupe des aires d'alimentation et de reproduction de 22 à 15 km respectivement, toujours en eau douce, et se reproduit tardivement dans la saison (Fraser & Bernatchez, 2005). La souche domestique est issue de nombreux croisements entre deux populations utilisées pour maintenir une variabilité génétique et éviter la

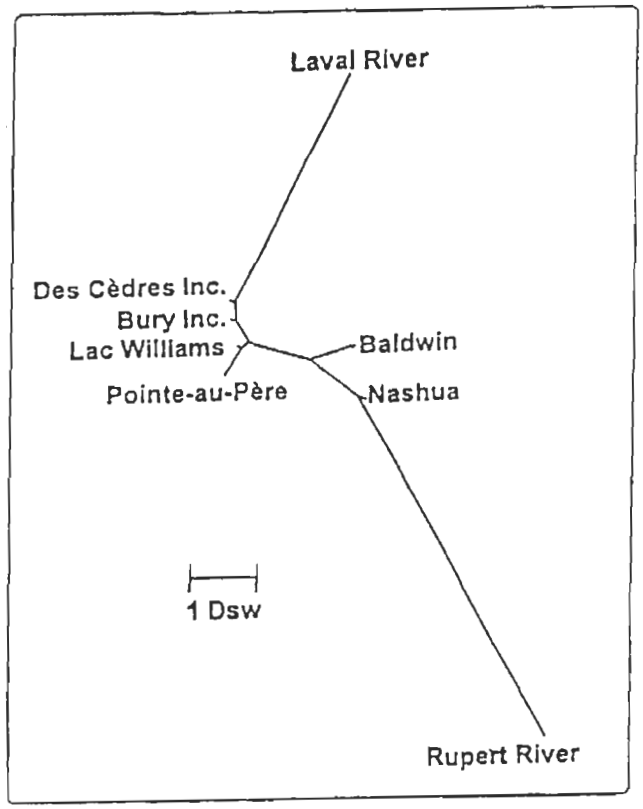


Figure 4 : Phénogramme des distances génétiques de différents stocks d'omble de fontaine au Québec (méthode de Neighbor Joining) (d'après Martin *et al.*, 1997).

consanguinité : la Nashua et la Baldwin. Cette souche est maintenant en usage depuis plus de 100 ans dans les productions québécoises.

Ces souches présentent aussi des potentiels d'expression phénotypique différents. Les souches d'origine sauvage ont été sélectionnées à la base car elles montraient des caractéristiques intéressantes pour la production, soit une maturation sexuelle tardive accompagnée d'un potentiel de croissance important (Martin *et al.*, 1997). Leurs capacités seraient alors différentes de celles de la souche domestique qui présente une maturation sexuelle précoce. Une étude de la croissance durant les premiers stades de vie a effectivement montré des capacités phénotypiques différentes entre les trois souches (Granier, 2007). Ces souches étant donc très différentes au niveau génétique, phénotypique et dans leurs adaptations locales, elles sont alors de très bons modèles pour explorer la divergence des effets additifs et l'apparition d'effet non-additifs entre populations intra-spécifiques éloignées génétiquement. L'éloignement génétique étant plus important entre les souches Laval et Rupert, on peut s'attendre à un effet hétérosis plus marqué chez leurs hybrides par rapport à ceux issus de la lignée domestique.

OBJECTIF GÉNÉRAL DU PROJET

Cette étude s'inscrit dans un projet vaste et multidisciplinaire cherchant à élucider les bases physiologiques et génomiques fonctionnelles de l'hétérosis afin d'exploiter ce phénomène pour améliorer les productions d'omble de fontaine au Québec. Ce projet regroupe donc de nombreuses disciplines comme la physiologie, la génétique quantitative mais aussi la génomique et l'endocrinologie qui sont étudiées en collaboration entre différents laboratoires. Le but de ce projet est de pouvoir améliorer rapidement la production d'omble de fontaine en identifiant des croisements et des environnements permettant de maximiser l'effet hétérosis et à plus long terme, de mieux prédire l'apparition de ce processus afin de pouvoir s'en servir dans diverses systèmes de production.

A l'intérieur de ce vaste projet, l'objectif de mon doctorat est de documenter les composantes génétique et environnementale qui interviennent dans l'expression de caractères phénotypiques d'intérêt pour la production aquacole. Mon travail est donc d'évaluer les composantes génétiques additives (héritables) et non-additives (surtout l'hétérosis) dans plusieurs environnements d'élevage chez trois souches d'ombles de fontaine pour distinguer l'importance relative de ces composantes et voir comment l'environnement et les croisements peuvent interagir dans l'expression de phénotypes. Les résultats de ces travaux aident à mieux comprendre les capacités d'évolution de l'omble de fontaine vers certains phénotypes.

OBJECTIFS SPÉCIFIQUES

Premier objectif de recherche

Mon premier objectif est de vérifier la présence d'un effet hétérosis chez l'omble de fontaine selon les croisements entre trois souches génétiquement distinctes (domestique, Laval et Rupert) et de voir s'il existe un effet de l'environnement sur cet effet principalement dans la croissance mais aussi pour l'absence de maturation sexuelle précoce

et la survie. Je cherche également à savoir si la distance génétique entre les souches, la nature des croisements ainsi que l'ontogenèse peuvent modifier l'expression d'hétérosis.

Deuxième objectif de recherche

Le deuxième objectif de cette étude est d'évaluer et de distinguer la part des composantes génétiques additives, environnementales et de l'interaction entre les deux dans l'expression de la masse chez l'omble de fontaine. Mon but est d'abord de documenter les divergences génétiques du contrôle de la masse chez les trois souches puis de voir si l'environnement peut influencer ce contrôle génétique. Je cherche aussi à savoir si cette influence est identique pour toutes les souches ou dépendante de celles-ci afin de déterminer l'importance de l'interaction gène x environnement.

Troisième objectif de recherche

Mon troisième objectif est de comprendre les bases génétiques de la mobilisation des réserves énergétiques durant le premier hiver chez les juvéniles d'omble de fontaine. Je vise d'abord à estimer l'héritabilité des réserves énergétiques dans chacune des trois souches élevées dans un environnement commun afin de documenter les bases génétiques additives des réserves et les divergences entre les souches. Je vérifie ensuite la présence d'effets non-additifs chez les hybrides qui pourraient également participer au contrôle génétique de la mobilisation d'énergie.

Quatrième objectif de recherche

Mon quatrième objectif est de tester l'importance des effets génétiques additifs et non-additifs dans la réponse au stress chez l'omble de fontaine afin de savoir si cette performance peut évoluer au cours des générations. Mon but est de voir s'il est possible d'utiliser les bases génétiques afin d'améliorer la résistance au stress chez l'omble de fontaine à l'aide de programmes basés soit sur de la sélection génétique additive soit sur l'utilisation d'hybrides.

CHAPITRE 1
ÉVALUATION DES EFFETS DES ENVIRONNEMENTS D'ÉLEVAGE ET DES COMBINAISONS DE CROISEMENTS SUR L'EXPRESSION D'HÉTÉROSIS CHEZ L'OMBLE DE FONTAINE

RÉSUMÉ

Dans cette étude, trois souches d'omble de fontaine (domestique [D], Laval [L] et Rupert [R]), ainsi que leurs hybrides réciproques, ont été élevés dans trois environnements différents (environnement intérieur à température constante ; environnement intérieur à température variable ; environnement extérieur à température variable), de 7 à 21 mois, pour quantifier l'expression d'hétérosis. La masse, la longueur, la survie et la présence de maturité sexuelle à 1+ ont été mesurés dans chacun des croisements. Nous avons alors mis en évidence la présence d'hétérosis pour la masse et la longueur mais nous n'avons pas observé de dépression de croisement. L'effet hétérosis dépendait cependant des souches, de l'orientation des croisements dans les hybrides réciproques, du stade de développement, et de l'environnement. L'expression d'hétérosis pour la masse variait de 4% à 24% selon l'hybride et l'environnement. Un des cinq hybrides réciproques testés (l'hybride $L_{♀}R_{♂}$) s'est par contre démarqué en exprimant un effet hétérosis à chaque stade de développement dans les trois environnements. Une interaction hétérosis x environnement a aussi été observée chez un autre hybride (l'hybride $L_{♀}D_{♂}$), qui a exprimé de l'hétérosis seulement dans l'environnement à température constante. Les autres croisements n'ont pas montré de profils d'hétérosis clairs. Il n'a pas non plus été observé d'effet hétérosis pour la maturité sexuelle et la survie. Ces résultats mettent clairement en évidence la présence d'effet hétérosis chez les salmonidés mais ils révèlent aussi la nature complexe et imprévisible de ce phénomène.

Ce premier article, intitulé « *Investigating the effects of rearing environment and strain combination on heterosis in brook charr* », a été corédigé par moi-même ainsi que par ma directrice Céline Audet, et mes codirecteurs Louis Bernatchez et Dany Garant. Il a été soumis récemment dans *North American Journal of Aquaculture* et est en cours d'évaluation. Ma contribution à ce travail a été l'essentiel des échantillonnages et des analyses statistiques ainsi que l'interprétation des résultats et la rédaction de l'article. Céline Audet a fourni l'idée et conçu le plan de l'étude, et a aussi aidé à la coordination de la recherche et à l'écriture du manuscrit. Louis Bernatchez a également fourni l'idée originale et a participé à la conception du plan de l'étude et à la révision de l'article. Dany Garant a aidé pour la révision de l'article. Tous les auteurs ont lu et approuvé le manuscrit final. Une version abrégée de cet article a été présenté au *11ème colloque annuel du CIRSA* à Québec et à la conférence *Canadian Society of Zoologists annual meeting* à Halifax au printemps 2008.

INVESTIGATING THE EFFECTS OF REARING ENVIRONMENT AND STRAIN COMBINATION ON HETEROSIS IN BROOK CHARR

ABSTRACT

In this study, three strains (domestic [D], Laval [L] and Rupert [R]) of brook charr (*Salvelinus fontinalis*) 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; outdoor, seasonal temperature variations) to quantify heterosis expression. Body mass, length, survival, and occurrence of sexual maturity in the first year were measured for each cross. We found evidence for heterosis in mass and length that varied according to strain, cross direction in reciprocal hybrids, developmental stage, or environment, but no significant outbreeding depression was detected for those traits. Heterosis expression for weight varied from 4% to 24% depending on hybrids and environments. We found that one out of five reciprocal hybrids tested ($L_{♀}R_{♂}$) expressed heterosis at each age stage throughout the experiment in the three environments. Heterosis by environment interaction was also observed in another hybrid cross ($L_{♀}D_{♂}$), which expressed heterosis only in the constant temperature environment. Other crosses did not show any clear pattern of heterosis. No evidence for heterosis was observed for sexual maturity and survival. These results provide one of the first clear evidence for the occurrence of heterosis in salmonids but also illustrate the complex nature and the unpredictability of this phenomenon.

KEYWORDS:

Heterosis; environment; performance; hybrids; brook charr, *Salvelinus fontinalis*

INTRODUCTION

Heterosis, or hybrid vigor, refers to the increased performance of first generation progeny when compared to parental lines (Falconer & Mackay, 1996; Birchler *et al.*, 2003). The main explanation supporting the occurrence of heterosis is based on non-additive 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; over-dominance, which suggests that heterozygotes perform better than homozygotes; and epistasis, which refers to allelic position and interactions in the hybrid (Birchler *et al.*, 2003; Lippman & Zamir, 2007). The relative contribution of each of these processes in the expression of heterosis is still a matter of debate (Lippman & Zamir, 2007).

The intensity of heterosis is usually higher when parental lines are genetically distant from each other (Shikano *et al.*, 2000; Wang & Xia, 2002). However, the opposite phenomenon that results from genome admixture—outbreeding depression—could also affect crosses involving genetically distant strains. Outbreeding depression may arise from a disruption of the linkage arrangement of co-adapted gene complexes when the genetic composition of populations diverges from local adaptation (Cooke *et al.*, 2001; Tymchuk *et al.*, 2007; Wang *et al.*, 2007). When a cross is made, it is difficult to predict which phenomenon might appear since both are controlled by the same underlying genetic processes (Gharrett *et al.*, 1999).

Breeding programs in plants and animals already use heterosis and additive genetic components to improve traits of interest for production (Falconer & Mackay, 1996). Heterosis application has been more limited in fish production. Yet, it has been used to improve aquaculture in carp (*Cyprinus carpio*; Wohlfarth, 1993; Hulata, 1995), tilapia (*Oreochromis niloticus*; Marengoni *et al.*, 1998), and also investigated in guppy (*Poecilia reticulate*; Shikano & Taniguchi, 2002a). Previous studies have also investigated heterosis for various traits, including growth, survival, salinity and temperature tolerance (Moav & Wohlfarth, 1976; Bentsen *et al.*, 1998; Nakadate *et al.*, 2003).

In salmonids, it is still unclear if heterosis occurs in inter- and intra-specific crosses. Inter-specific hybridization between several species gave no evidence for hybrid superiority (Chevassus, 1979; Blanc & Chevassus, 1982, 1986). Heterosis for growth and survival in intra-specific hybrid crosses have been reported (Ayles & Baker, 1983; Gjerde & Refstie, 1984; Bryden *et al.*, 2004) while other authors only observed additive interactions for these same traits (Einum & Fleming, 1997; Glover *et al.*, 2006a), and even outbreeding depression (Gharrett *et al.*, 1999). From these studies, it has been hypothesized that heterosis may be generally rare in salmonids (Gjerde & Refstie, 1984; Gharrett *et al.*, 1999; Bryden *et al.*, 2004). More specifically, Tymchuk et al. (2007) suggested that salmonid species may be too genetically distant and locally adapted to produce heterosis. However, in charrs (genus *Salvelinus*) in particular, studies on hybrid crosses between different species suggested a potential for heterosis expression for growth and survival (Dumas *et al.*, 1992, 1996; Gunther *et al.*, 2005). We hypothesized that the use of different strains of the same species could result in a genetic distance that could be favorable for heterosis.

The choice of the strain used as dam or sire in the cross may also have an important impact 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; Wang *et al.*, 2006c). The environment may also influence the additive and non-additive genetic components in different ways, with heterosis being more sensitive to environmental variations (Bentsen *et al.*, 1998). Hence, genotype (strain combination) by environment interactions can have important effect on heterosis expression (Bentsen *et al.*, 1998).

In this context, the aim of this study was to investigate the occurrence of heterosis in the brook charr (*Salvelinus fontinalis*). Our specific objectives were to evaluate (i) the occurrence of intra-specific heterosis on different traits of interest, i.e., body mass, length, growth, absence of early sexual maturation, survival; (ii) the presence of dam or sire effects on the hybrid performance for the traits considered; and (iii) the effects of environment on heterosis expression.

MATERIALS AND METHODS

Brook charr strains

Three strains of brook charr were used as parental stock. The Laval strain originates from a wild population of anadromous brook charr from the Laval River (48°44'N; 69°05'W) on the north shore of the St. Lawrence estuary (QC, Canada). The fish used as breeders were third generation individuals produced in captivity at the Station aquicole of ISMER/UQAR (Rimouski, QC, Canada). The Rupert strain originates from a freshwater resident wild population inhabiting the Rupert River system (51°05'N; 73°41'W) draining Mistassini Lake (QC, Canada). The breeders were again third generation fish produced in captivity at the Laboratoire régional en sciences aquatiques (LARSA, Université Laval, Québec, QC, Canada). The domestic strain is widely used by the Québec fish farming industry. It originates from two strains (Nashua and Baldwin), and breeders were obtained from the Pisciculture de la Jacques Cartier (Cap-Santé, QC, Canada). The two wild strains were selected for breed improvement because adults of these populations exhibit late sexual maturation and large size. They were shown to be genetically distant from the domestic strain as well as from each other (Martin *et al.*, 1997).

Breeding design

Hybrid and purebred crosses were made from mid-November 2005 until the end of December 2005 at LARSA using eggs and milt obtained from the different fish rearing locations. Three purebred strains were produced: ♀ domestic X ♂ domestic ($D_{♀}D_{♂}$), ♀ Laval X ♂ Laval ($L_{♀}L_{♂}$), and ♀ Rupert X ♂ Rupert ($R_{♀}R_{♂}$). Five reciprocal hybrids were produced: $D_{♀}R_{♂}$, $D_{♀}L_{♂}$, $L_{♀}D_{♂}$, $L_{♀}R_{♂}$, and $R_{♀}L_{♂}$. It was not possible to obtain the $R_{♀}D_{♂}$ cross because of the temporal differences in sexual maturation between these two strains (October for domestic males and December for Rupert females). All breeders were used only once due. For each cross, 10 full-sib families were obtained through single-pair mating, but 8 of these 80 families were eliminated due to the limited number of individuals

that could be pooled in each tank. The final numbers of families were 10 D♀D♂, 10 L♀L♂, 9 R♀R♂, 9 D♀R♂, 7 D♀L♂, 9 L♀D♂, 10 L♀R♂ and 8 R♀L♂.

Family rearing

During the first six months, i.e., from egg incubation (January) to exogenous feeding (June), families were kept separate in recirculating fresh water and reared in seven troughs, each of which was divided into twelve units. Water temperature was maintained at 6°C during egg incubation and at 8°C after hatching. In June, families were identified by different combinations of adipose and pelvic fin clippings and transferred to nine 3 m^3 tanks, with eight families per tank. All families were brought to 2136 degree-days by the end of the summer and maintained at 10°C in recirculating fresh water. The photoperiod followed the natural seasonal cycle and fish were fed according to commercial charts.

In September, fish were 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 the LARSA, under natural temperature and photoperiod conditions in running dechlorinated fresh water. To maintain sustainable rearing densities, the number of fish per family was gradually reduced to 60 by the end of the experiment, with all reductions in number being done randomly. Fish were fed daily (1% w/w ration) with commercial dry pellets. At LARSA, 150 fish per family were reared in the same nine $3m^3$ tanks than before September under natural photoperiod conditions at 10°C in recirculating indoor freshwater tanks. Fish numbers were gradually decreased to 50 fish per family by the end of the experiment. Fish were fed daily (1% w/w ration) with commercial dry pellets. At the 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-months-old).

Performance traits

Every eight weeks at ISMER and LARSA, 25 fish per family ($n = 1800$ for each location) were anaesthetized in MS 222 (0.16 g L^{-1} [3-aminobenzoic acid ethyl ester]) and their body mass (0.1 g) and fork length (0.1 cm) were measured. At Pisciculture de la Jacques Cartier, mass and length were measured only twice: on 25 fish per cross-type in July, and on every remaining fish in November. In the two others environments, mass and length were also recorded for every remaining fish at the final sampling in November. Condition factor was estimated according to the equation (weight $length^{-3}$) X 100.

In November 2007, the presence or absence of sexual maturation was determined at the three rearing environments. For 25 fish per family at ISMER and LARSA and 25 fish per cross-type at the Pisciculture de la Jacques Cartier, gonads were excised and weighted and the gonadosomatic index was calculated as (gonad mass / total mass) X 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.

Estimation of heterosis

In the present study, we considered that heterosis was present when the performance of hybrids significantly outperformed the performance of both parental strains which is the most extreme case of heterosis. It was then expressed as [(f1 m^{-1})-1] X 100, where f_1 is the mean performance of the F_1 hybrids and m the mean performance of parental strains based on least square means according to Maluwa and gjerde (2006a). Due to the complication in calculating standard error, the differences between these percentages were not statistically tested.

Statistical analysis

Data normality and homogeneity of variance were tested with the Kolmogorov-Smirnov and the Brown-Forsythe tests respectively. Mass data (log), condition factor (rank) and all percentage indexes (arcsin) were transformed to account for heteroscedasticity. Mass, length and condition factor were analyzed using mixed models with environment, age stage, cross-type and their interactions fitted as fixed effects and full-sib families fitted as the random effect. Two models were used: model A which includes the two environments ISMER and LARSA at each age stage; and model B which includes the three environments at two age stages (17 and 21 months). The a posteriori Tukey test applied on least square means was used for comparisons. Sexual maturity and survival were analyzed using two-way ANOVAs with environment and cross-type as factors. The a posteriori Tukey test was used for mean comparisons when possible or replaced by the Games and Howell test when variances were not homogenous. Mixed model analyses were performed using JMP 7 (SAS Institute, NC, USA) and ASReml 2.0 softwares (VSN International, UK). A significance level of $\alpha = 0.05$ was used in all statistical tests.

RESULTS

Body mass

Significant environment – age stage – cross-type interactions ($P < 0.001$) were present for both mass and length. The mixed models explained a large proportion of the total variance with an R^2 adjusted of 0.815 (Model A) and 0.687 (Model B) for body mass (Table I.1), and of 0.805 (Model A) and 0.661 (Model B) for length. Since analysis of both traits gave similar results, we only present the mass comparisons. When the three pure cross-types were compared, domestic fish were always significantly bigger than the two other strains in all three environments ($P < 0.05$; Table I.2). In the constant temperature environment at LARSA, the Rupert strain was always heavier than the Laval strain, while at ISMER, it was just the case until fish reached 17 months ($P < 0.05$; Table I.2).

Heterosis was present but varied according to the type of hybrid crosses as well as on the strain used as dam or sire. No outbreeding depression was observed for mass in any of the hybrid crosses (Table I.3). The $D♀R♂$ hybrid was usually intermediate to the values measured for the two parental strains in all three environments (Table I.2). $L♀R♂$ hybrids were significantly heavier than its two parental lines ($P < 0.01$; Table I.2). It also expressed heterosis averaging 12% at each age stage and in all three environments (Table I.2). In contrast, heterosis was not always observed and seemed to be less pronounced in $R♀L♂$ than in $L♀R♂$ hybrids, except at the farm that $R♀L♂$ had a tendency to express strong heterosis (from 21% to 24% for weight) (Table I.2, Table I.3).

$D♀L♂$ and $L♀D♂$ hybrids both had intermediate mass compared to the parental lines and presented no heterosis in the varying temperature environments (ISMER and the fish farm) (Table I.2). However, under constant temperature at LARSA, $L♀D♂$ hybrids were significantly heavier than the two parental lines ($P < 0.05$; Table I.2) and expressed heterosis (about 12%), but only starting at 15 months of age (Table I.3). In contrast, the reciprocal hybrid $D♀L♂$, remained similar to the smallest parental line ($L♀L♂$) and never expressed heterosis (Table I.2).

Table I. 1 : Summary of statistical analyses for body mass. Model A includes two environments (indoor, running freshwater, seasonal temperature variations [ISMER]; indoor, recirculating water, constant 10°C temperature conditions [LARSA]) at each age stage; Model B includes the three environments (ISMER; LARSA; outdoor, seasonal temperature variations, fish farm pond [Farm]) at the two age stages (17 and 21 months) measured at the Farm.

	Model A				Model B			
	df	mean squares	F	*P*-values	df	mean squares	F	*P*-values
Age stage	6	444.18	12635.87	< 0.001	1	135.91	3320.5	< 0.001
Environment	1	591.98	16840.46	< 0.001	2	102.24	2497.9	< 0.001
Cross-type	7	92.20	34.40	< 0.001	7	14.29	349.2	< 0.001
Age stage x Environment	6	21.28	605.38	< 0.001	2	16.74	409.0	< 0.001
Age stage x Cross-type	42	0.49	13.91	< 0.001	7	0.05	1.2	0.28
Environment x Cross-type	7	6.48	184.43	< 0.001	14	2.21	54.0	< 0.001
Age stage x Environment x Cross-type	42	0.33	9.51	< 0.001	14	0.18	4.3	< 0.001
Family (nested in Cross-type), random	64	2.93	83.30	< 0.001				
Error	28022	0.04			11587	0.04		
Model R^2	0.816				0.640			
R^2 adjusted	0.815				0.639			

Table I. 2 : Growth performance measured as body mass (g) in the purebred strains (bold) and their hybrids in the three different environments (indoor, running freshwater, seasonal temperature variations [ISMER]; indoor, recirculating water, constant 10°C temperature conditions [LARSA]; outdoor, seasonal temperature variations, fish farm pond [Farm]) for each age stage. Statistical analyses were done on log-transformed data, and post-hoc analyses on least square means, but results are presented as arithmetical means ± SEM (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♂ cross-type). Different letters indicate significant differences among cross-types for one environment and one age stage ($P < 0.05$). Grey highlights indicate hybrids that are significantly higher than both of their parental lines (heterosis).

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

Table I. 3 : Percentage of heterosis and outbreeding depression (negative values) based on least square means in the different hybrid cross-types for performance traits (W: weight; L: length; CF: condition factor) in the three environments (indoor, running freshwater, seasonal temperature variations [ISMER]; indoor, recirculating water, constant 10°C temperature conditions [LARSA]; outdoor, seasonal temperature variations, fish farm pond [Farm]) for each age stage. Cells in bold characters refer to cross X age stage combinations for which weight, length, or condition factor were found to be statistically higher or lower than both parental lines.

	9 months		11 months		13 months		15 months		17 months		18 months			21 months		
Cross	W	L	W	L	W	L	W	L	W	L	W	L	CF	W	L	CF
ISMER																
D♀R♂	8.5	6.5	4.6	3.4	5.2	3.2	6.8	4.9	2.9	1.8	-0.3	-1.6	-3.2	0.1	-0.9	-1.4
D♀L♂	11.3	7.1	8.0	5.1	12.2	7.6	11.8	6.8	5.3	3.9	-0.9	-1.1	-6.5	0.0	-0.7	-0.3
L♀D♂	10.1	6.9	9.0	7.1	12.5	8.2	13.8	9.7	8.7	9.0	1.3	2.6	-7.3	0.9	1.8	-3.9
L♀R♂	**18.9**	**13.4**	**16.8**	**13.2**	**18.5**	**13.6**	**18.9**	**14.9**	**16.0**	**16.9**	**5.2**	**8.8**	**-7.9**	**4.4**	**6.7**	-1.2
R♀L♂	5.8	3.4	9.6	5.7	10.0	4.8	9.4	5.4	**5.0**	**5.9**	-1.0	0.6	**-5.9**	-2.0	-0.1	**-5.4**
LARSA																
D♀R♂	9.5	8.6	7.0	7.4	4.5	4.6	3.1	3.3	1.5	2.5	1.7	2.1	1.6	2.0	2.8	2.1
D♀L♂	8.7	5.5	3.3	2.7	-1.7	-2.4	-1.5	-2.7	-4.1	-5.7	-4.1	-6.9	1.2	-3.3	-5.0	-1.0
L♀D♂	14.4	11.9	15.2	16.6	14.5	17.1	**12.8**	16.9	**11.1**	**16.7**	**11.0**	**16.8**	1.4	**10.0**	**16.0**	2.2
L♀R♂	**16.7**	**13.2**	**12.2**	**13.8**	**12.5**	**15.1**	**10.0**	**12.9**	**7.2**	**10.3**	**7.9**	**11.5**	1.1	**6.0**	**10.0**	0.2
R♀L♂	9.2	7.1	2.2	4.1	1.9	2.9	4.1	4.3	3.2	3.7	1.1	1.2	1.5	1.3	2.8	0.5
Farm																
D♀R♂									16.2	20.5				19.5	24.4	6.4
D♀L♂									5.3	5.5				7.4	9.6	1.2
L♀D♂									4.6	9.7				7.5	11.3	-1.2
L♀R♂									**11.8**	**6.5**				**14.2**	**11.6**	10.4
R♀L♂									**21.3**	**20.3**				**23.8**	**27.4**	**12.0**

Condition factor

The analysis of the condition factor data indicated a significant environment – age stage – cross-type interaction ($P < 0.001$; adjusted R^2 of 0.534). In all environments, the domestic strain had the largest condition factor (Table I.4) and the Laval strain the smallest ($P < 0.01$). However, the Rupert strains had similar condition factors as the Laval strain at the fish farm. The condition factor (Table I.4) in hybrids with one domestic parent was always intermediate to parental lines, so no expression of strong heterosis or outbreeding depression was observed. In hybrids between the Laval and Rupert strains, condition factor was intermediate until 18 months old ($P < 0.01$). After this, differences occurred according to the rearing environments: at LARSA, the condition factor remained intermediate; at ISMER, the condition factor was significantly smaller than those of parental lines; at the farm, $R_{♀}L_{♂}$ had a higher condition factor than the parental lines (measured at 21 months of age) (Table I.4). This translated into outbreeding depression for condition factor which was observed in $R_{♀}L_{♂}$ and $L_{♀}R_{♂}$ hybrids at ISMER once they reached 18 months of age (about – 6%) whereas $R_{♀}L_{♂}$ expressed heterosis at the farm (about 12% at 21 months of age) (Table I.3); neither heterosis nor outbreeding depression was observed at LARSA.

Sexual maturity and survival

No heterosis or outbreeding depression was observed for occurrence of early sexual maturity. Thus, early sexual maturation in hybrids was intermediate ($L_{♀}D_{♂}$) or similar (all others) to average of the parental lines expressing the lower percentage of sexual maturation. Occurrence of early sexual maturation was greater in males than in females ($P < 0.001$), and there was also a significant effect of cross-type (Fig. I.1). 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 ($df = 14$; $F = 0.65$; $P = 0.82$). 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) ($P < 0.001$). Finally, no heterosis or outbreeding depression related to survival was observed in the three environments. Mortality was greater in the variable

Table I. 4 : Condition factor in the three purebred strains (bold) and their hybrids in the three different environments (indoor, running freshwater, seasonal temperature variations [ISMER]; indoor, recirculating water, constant 10°C temperature conditions [LARSA]; outdoor, seasonal temperature variations, fish farm pond [Farm]) for each age stage. Statistical analyses were done on rank-transformed data, and post-hoc analyses on least square means, but results are presented as arithmetical means ± SEM (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 $D_{♀}L_{♂}$ cross-type). Different letters indicate significant differences among cross-types for one environment and one age stage ($P < 0.05$). Grey highlights indicate hybrids with significantly higher or lower condition factor than both of their parental lines (heterosis or outbreeding depression).

Cross	9 months	11 months	13 months	15 months	17 months	18 months	21 months
ISMER							
D R	1.05 ± 0.01^{d}	1.05 ± 0.01^{c}	0.99 ± 0.03^{c}	1.05 ± 0.02^{e}	1.05 ± 0.01^{d}	1.08 ± 0.01^{d}	1.09 ± 0.02^{e}
D D	**1.09 ± 0.01^{e}**	**1.15 ± 0.01^{f}**	**1.07 ± 0.01^{f}**	**1.16 ± 0.01^{f}**	**1.16 ± 0.01^{e}**	**1.20 ± 0.03^{e}**	**1.22 ± 0.01^{f}**
D L	1.03 ± 0.02^{cd}	1.02 ± 0.02^{de}	0.94 ± 0.01^{de}	1.01 ± 0.01^{d}	1.03 ± 0.02^{cd}	1.06 ± 0.01^{cd}	1.08 ± 0.02^{e}
L D	1.01 ± 0.01^{c}	1.00 ± 0.01^{d}	0.92 ± 0.01^{cd}	1.00 ± 0.01^{d}	1.01 ± 0.01^{bc}	1.05 ± 0.01^{cd}	1.04 ± 0.01^{d}
L L	**0.93 ± 0.01^{a}**	**0.88 ± 0.01^{a}**	**0.74 ± 0.01^{a}**	**0.79 ± 0.01^{a}**	**0.94 ± 0.01^{a}**	**1.07 ± 0.03^{bc}**	**0.95 ± 0.02^{b}**
L R	0.97 ± 0.01^{b}	0.93 ± 0.01^{b}	0.83 ± 0.02^{ab}	0.88 ± 0.01^{b}	0.94 ± 0.01^{a}	0.96 ± 0.02^{a}	0.96 ± 0.01^{b}
R L	0.97 ± 0.01^{b}	0.94 ± 0.02^{bc}	0.86 ± 0.02^{ab}	0.89 ± 0.02^{b}	0.93 ± 0.01^{a}	0.99 ± 0.02^{a}	0.92 ± 0.02^{a}
R R	**1.01 ± 0.02^{c}**	**0.96 ± 0.01^{c}**	**0.89 ± 0.02^{bc}**	**0.93 ± 0.01^{c}**	**0.99 ± 0.02^{b}**	**1.02 ± 0.02^{b}**	**0.99 ± 0.02^{c}**
LARSA							
D R	1.09 ± 0.02^{d}	1.08 ± 0.02^{c}	1.07 ± 0.01^{d}	1.06 ± 0.01^{e}	1.09 ± 0.02^{d}	1.13 ± 0.02^{d}	1.13 ± 0.03^{e}
D D	**1.18 ± 0.01^{e}**	**1.14 ± 0.01^{d}**	**1.11 ± 0.03^{d}**	**1.09 ± 0.02^{e}**	**1.13 ± 0.02^{d}**	**1.15 ± 0.01^{d}**	**1.16 ± 0.02^{e}**
D L	1.11 ± 0.01^{d}	1.04 ± 0.02^{b}	0.98 ± 0.01^{b}	0.98 ± 0.01^{b}	1.00 ± 0.02^{b}	1.07 ± 0.02^{c}	1.03 ± 0.02^{c}
L D	1.09 ± 0.01^{d}	1.06 ± 0.01^{bc}	1.04 ± 0.01^{cd}	1.01 ± 0.02^{d}	1.03 ± 0.02^{c}	1.07 ± 0.02^{c}	1.06 ± 0.02^{d}
L L	**0.97 ± 0.02^{a}**	**0.98 ± 0.02^{a}**	**0.92 ± 0.01^{a}**	**0.90 ± 0.01^{a}**	**0.93 ± 0.01^{a}**	**0.95 ± 0.02^{a}**	**0.94 ± 0.01^{a}**
L R	1.00 ± 0.01^{b}	0.98 ± 0.01^{a}	0.98 ± 0.02^{a}	0.96 ± 0.01^{b}	1.01 ± 0.02^{b}	1.02 ± 0.02^{b}	0.98 ± 0.01^{b}
R L	1.00 ± 0.01^{bc}	0.96 ± 0.01^{a}	0.95 ± 0.01^{ab}	0.98 ± 0.02^{bc}	1.03 ± 0.02^{bc}	1.02 ± 0.01^{b}	0.99 ± 0.01^{b}
R R	**1.03 ± 0.01^{c}**	**1.03 ± 0.01^{b}**	**1.01 ± 0.01^{c}**	**1.00 ± 0.01^{cd}**	**1.08 ± 0.01^{d}**	**1.07 ± 0.02^{c}**	**1.03 ± 0.01^{c}**
Farm							
D R					0.99 ± 0.02^{a}		0.97 ± 0.01^{d}
$D_{♀}D_{♂}$					**1.12 ± 0.02^{b}**		**1.11 ± 0.02^{e}**
D L					0.99 ± 0.01^{a}		0.97 ± 0.01^{c}
L D					0.96 ± 0.01^{a}		0.94 ± 0.01^{c}
$L_{♀}L_{♂}$					**0.97 ± 0.02^{a}**		**0.81 ± 0.01^{a}**
$L_{♀}R_{♂}$					0.96 ± 0.01^{a}		0.86 ± 0.02^{ab}
$R_{♀}L_{♂}$					0.99 ± 0.02^{a}		0.89 ± 0.01^{b}
$R_{♀}R_{♂}$					**0.95 ± 0.02^{a}**		**0.79 ± 0.03^{a}**

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.

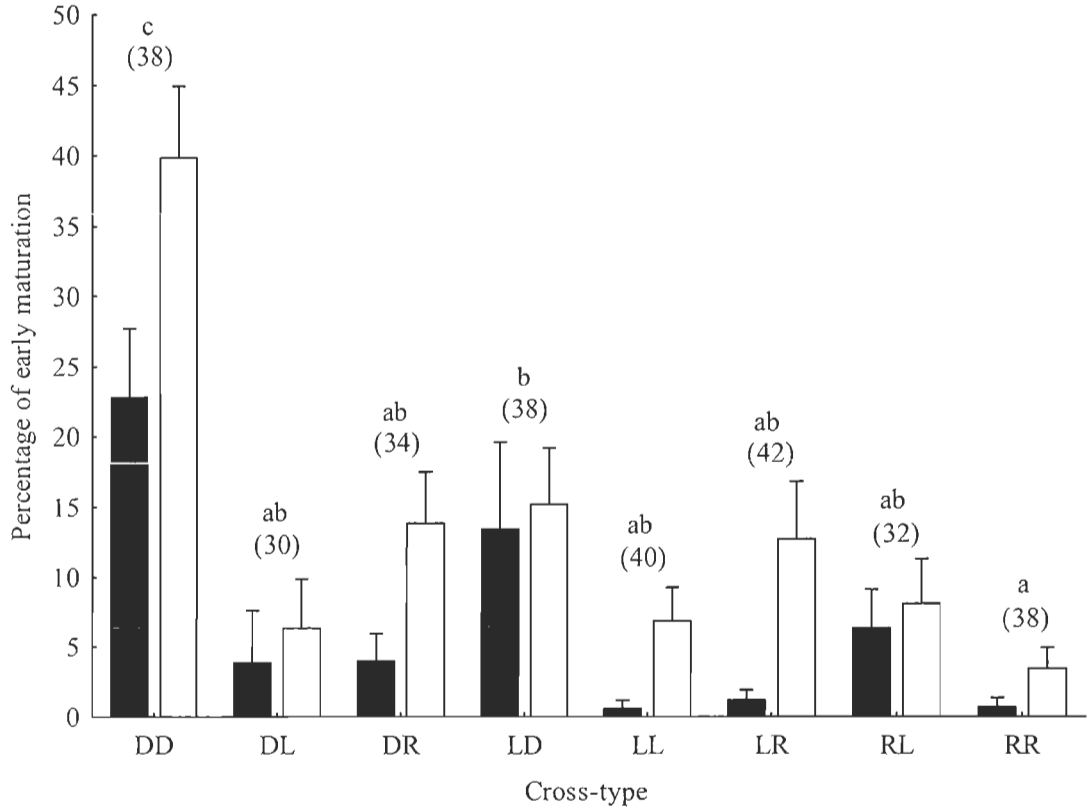


Figure I. 1 : Early maturation in the three purebred strains and their hybrids. No environment effect was observed, so data from the three study sites were pooled. The first letter of the cross-type indicates the dam and the second letter the sire. Solid bars are for females and open bars for males. Statistical analyses were done on arcsin-transformed data but results are presented as arithmetical means ± SEM. Number of families (n) is indicated in parenthesis. 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 and length in brook charr using inter-strain crosses but provided limited evidence for outbreeding depression. Strong heterosis expression was observed in a few cases: as high as 24% for mass in some crosses. However, in general, heterosis expression levels were similar to those reported for the same traits in tilapia (12% to 17%; Bentsen *et al.*, 1998; Maluwa & Gjerde, 2006b), guppy (4.5%; Nakadate *et al.*, 2003), and carp (10%; Gjerde *et al.*, 2002). In general, 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 and survival.

Genetic distance

The genetic distance between the strains may partly explain the variable patterns of heterosis being expressed among different strains (Shikano *et al.*, 2000; Linhart *et al.*, 2002; Wang & Xia, 2002; Nakadate *et al.*, 2003). Heterosis is known to be linked to the genetic distance between the parental strains owing to local adaptations that can fix different alleles in the strains. Yet, some authors found no correlation between genetic distance and heterosis (Bentsen *et al.*, 1998) and argued that the genetic diversity and dissimilarity among individuals in strains would be a more important factor for the expression of heterosis (Shikano & Taniguchi, 2002b). Interestingly, we observed the highest percentage of heterosis in intra-specific crosses involving the highest genetic distance, i.e., between the two strains from wild origins (Martin *et al.*, 1997).

Cross direction

The cross direction also seemed to also have played a role in the intensity of heterosis expression for growth. This was particularly evident in hybrid crosses between the Rupert and the Laval strains. More generally also, the extent of heterosis was more pronounced when the Laval strain was used as dam than when it was used as sire. 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 & Price, 1994; growth in tilapias, Bentsen *et al.*, 1998; swimming performance in largemouth bass, Cooke *et al.*, 2001). Different factors may explain such reciprocal effects: 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 development of fry (Klupp, 1979; Wangila & Dick, 1996; Bentsen *et al.*, 1998; Heath *et al.*, 1999; Perry *et al.*, 2004a; Wang *et al.*, 2006c). 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; Wang *et al.*, 2006c). 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 & Parsch, 2007; Derome *et al.*, 2008).

Environment interaction

Genomic influence on performance and heterosis expression is also dependent on environmental conditions. The environment may modify gene expression that is already known in the physiological pathway for growth (Côté *et al.*, 2007). Here, such heterosis by environment interaction was more important in the $L_{♀}D_{♂}$ hybrid, which expressed heterosis only in the constant temperature environment. Other studies have reported the occurrence of heterosis by environment interactions in rainbow trout (Ayles & Baker, 1983), tilapia (Bentsen *et al.*, 1998) and carp (Wohlfarth, 1993). Such interactions on heterosis expression could be explained by non-additive genetic components since these are more sensitive to environmental variations than the additive ones (Bentsen *et al.*, 1998; Gjerde *et al.*, 2002). However, in our study, environmental interactions were not observed for all hybrid crosses, suggesting that different genomes are not influenced the same way by environmental variability. Because of genotype by environment interactions, the phenotypes of laboratory-reared animals 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 additive genetic effect and

environment, a given breeding program can combine the best strains into a synthetic population (Eknath *et al.*, 1993; Maluwa & Gjerde, 2006b; Maluwa *et al.*, 2006). An analogous approach could potentially be used in breeding programs related to heterosis expression using hybrids that express heterosis in all environments tested. For example, the $L_{♀}R_{♂}$ hybrid could be a good candidate for the application of such an approach in brook charr 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 reduced; it may then be desirable to develop strains for crossbreeding that are specific to each particular environment (Gjedrem, 1992). Such approach could also be adjusted in the presence of heterosis by environment interactions to take full advantage of heterosis expression in aquaculture production. In our study, heterosis expression observed for the $L_{♀}D_{♂}$ hybrid was sensitive to environmental conditions, and the use of such hybrids in production may require that the test and the farm environments be very similar (Bentsen *et al.*, 1998).

Variation with ontogeny

We observed that in some hybrid crosses, heterosis expression 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.*, 2005a; Wang *et al.*, 2006a; Darias *et al.*, 2008; Nolte *et al.*, 2009) that would affect heterosis expression. Late heterosis expression in the course of development may also result from a larger differentiation among strains with increasing age (Klupp, 1979; Wang *et al.*, 2006a; Nolte *et al.*, 2009).

CONCLUSION

Intra-specific heterosis is present in brook charr. However, its expression seems complex and difficult to predict, being influenced by a variety of biotic and abiotic factors, including genetic distance between parental lines, strain combination, cross direction,

developmental stage as well as rearing environment. However, one hybrid cross, $L_{♀}R_{♂}$, stood out as the best candidate for using heterosis in enhancing brook charr production in various types of environments. Studies on gene expression in hybrids expressing heterosis and in backcrosses should provide a better understanding of the molecular mechanisms underlying heterosis. We are currently completing such investigations.

CHAPITRE 2
POTENTIEL ÉVOLUTIF DE LA CROISSANCE CHEZ DES POPULATIONS D'OMBLE DE FONTAINE (*SALVELINUS FONTINALIS*)

RÉSUMÉ

Pour comprendre le potentiel évolutif de différentes populations, il est essentiel de distinguer les variations génétiques des variations environnementales qui déterminent l'expression des phénotypes. Cependant, l'ampleur à laquelle les variations génétiques peuvent varier entre les populations et les environnements pendant l'ontogénèse a rarement été analysée. Dans cette étude, la variance génétique additive de la masse corporelle de trois populations divergentes d'omble de fontaine (*Salvelinus fontinalis*) issues de trois origines différentes (lacustre [souche Rupert], anadrome [souche Laval] et domestique) a été mesurée sous deux conditions environnementales (environnement à température constante ou variable) à différents moments. Les résultats ont indiqué que la masse corporelle était un trait héritable dans toutes les populations mais que le niveau d'héritabilité variait beaucoup entre populations (h^2 de $0,61 \pm 0,07$, $0,37 \pm 0,06$ et $0,30 \pm 0,08$ pour les populations domestique, Laval et Rupert, respectivement). De plus, les estimations d'héritabilité de chaque population étaient aussi influencées par les conditions environnementales mais de manière différente (pas de changement d'héritabilité pour la population domestique, une diminution pour la population Laval et une augmentation pour la population Rupert, quand estimée dans l'environnement à température constante ou celui à température variable), révélant une interaction gène x environnement spécifique à chaque population. Les estimations d'héritabilité ont également été modifiées pendant l'ontogenèse, avec une diminution de moitié des estimations à partir de la résorption du sac vitellin jusqu'à l'âge de 21 mois. Cette étude met en évidence la divergence d'architecture génétique et du

potentiel évolutif de ces populations. Elle révèle aussi comment chacune de ces populations peut avoir sa propre réponse à la sélection selon les variations environnementales.

Ce deuxième article, intitulé « *Differential evolutionary potential for growth among brook charr populations (Salvelinus fontinalis)* », a été corédigé par moi-même ainsi que par ma directrice Céline Audet, et mes codirecteurs Louis Bernatchez et Dany Garant. Nous envisageons de le soumettre dans *Genetics*. Ma contribution à ce travail a été la recherche sur l'état de l'art, l'essentiel des échantillonnages, et l'ensemble des analyses de génétique quantitative ainsi que l'interprétation des résultats et la rédaction de l'article. Céline Audet a participé à la conception du plan de l'étude, et a aussi aidé à la coordination de la recherche et à l'écriture du manuscrit. Louis Bernatchez a fourni l'idée et a participé à la conception du plan de l'étude, à la réflexion et à l'écriture de l'article. Dany Garant a aidé au développement et à la mise au point de la méthode d'analyse ainsi qu'à la révision du manuscrit. Une version abrégée de cet article a été présenté au *12ème colloque annuel du CIRSA* à Québec et à la conférence *Canadian Society of Zoologists annual meeting* à Toronto au printemps 2009.

DIFFERENTIAL EVOLUTIONARY POTENTIAL FOR GROWTH AMONG BROOK CHARR POPULATIONS (*SALVELINUS FONTINALIS*)

ABSTRACT

Discriminating between genetic and environmental variations that shape phenotypes is an essential requirement for understanding the evolutionary potential of different populations. However, the extent to which genetic variation differs among conspecific populations and environments during ontogeny has rarely been investigated. In this study, the additive genetic variance of body mass was measured in three divergent populations of brook charr (*Salvelinus fontinalis*) from three different origins (lacustrine [Rupert strain], anadromous [Laval strain], and domestic) in two different environmental conditions (constant and seasonal fluctuating temperatures), and at different time periods. The results indicate that body mass was a heritable trait in all populations but that the level of heritability greatly differed among populations (h^2 of 0.61 ± 0.07, 0.37 ± 0.06, and 0.30 ± 0.08 for the domestic, Laval, and Rupert populations, respectively). Moreover, heritability estimates of each population varied differently according to environmental rearing conditions (no change for the domestic population, a decrease for the Laval population, and an increase for the Rupert population from the constant to the varying temperature environment), indicating population specific pattern of genotype–environment interactions. Heritability estimates also varied throughout ontogeny and decreased by half from yolk sac resorption to 21 months of age. This study highlights the divergence in genetic architecture and evolutionary potential among these populations, and how, each of these may have their own response to selection according to environmental variation.

KEYWORDS:

Heritability, environment, genetic architecture, populations, evolutionary potential, gene x environment interactions

INTRODUCTION

In the current context of increasing anthropogenic selection pressures, such as climate change, pollution or artificial selection, it is essential to document the evolutionary potential of populations which can be rapidly submitted to new environmental conditions (Smith & Bernatchez, 2008). The evolutionary potential is principally dependent on the genetic basis underlying phenotypic variation on which selection may act. To understand this potential, it is then necessary to discriminate the genetics and the direct effect of environmental components of variation, as well as the possible interaction between the two. The main genetic parameter used to predict the capacity of population to respond to selection is the heritability of a trait (Falconer & Mackay, 1996), that represents the additive component of genetic variation. The amount of additive genetic variance can be modified through local adaptations to native environmental conditions (Charmantier & Garant, 2005; Laugen *et al.*, 2005; Visscher *et al.*, 2008; Jetz *et al.*, 2009), thus resulting in population divergence in genetic architecture and potential to respond to selection (Roff, 2000; Uller *et al.*, 2002; de Brito *et al.*, 2005).

The expression of additive genetic variance may also change in response to environmental conditions (Hoffmann & Merilä, 1999; Charmantier & Garant, 2005). Most evidences gathered so far suggest that habitat quality can increase heritability of traits, under favorable conditions (Olsson & Uller, 2002; Charmantier & Garant, 2005; Jetz *et al.*, 2009; Robinson *et al.*, 2009). Moreover, different genotypes can express different sensitivity to environments, resulting in genotype-environment interactions (Falconer & Mackay, 1996; Visscher *et al.*, 2008). This in turn may modify the genetic basis on which selection pressure can act (Charmantier & Garant, 2005; Kruuk *et al.*, 2008). Considering genotype-environment interactions is therefore fundamental towards understanding the evolutionary potential of populations.

Generally speaking, the ability of organisms to express different genes under different environmental conditions allows maintaining additive variance which is favorable for the capacity of response of populations (Charmantier & Garant, 2005; Laugen *et al.*, 2005;

Kruuk *et al.*, 2008). On the other hand, this interaction may also reduce the evolutionary potential by reducing the speed of evolutionary changes especially in heterogeneous environments (Charmantier & Garant, 2005; Wilson *et al.*, 2006). On the opposite, in production, genotype-environment interactions are frequently investigated as such interaction can limit the diffusion of genetic progress, they are thus undesired (Fishback *et al.*, 2002; Kause *et al.*, 2004; Maluwa *et al.*, 2006; Saillant *et al.*, 2006; Dupont-Nivet *et al.*, 2008). The relative role of these opposite effects of genotype-environment interactions is still poorly understood.

Parental effect is another factor that can influence the offspring genetic and phenotypic expression (Charmantier & Garant, 2005; Visscher *et al.*, 2008). Maternal effects are generally involved during early life when maternal phenotype (like maternal care, maternal feeding or yolk sac quality) still influences offspring development (Falconer & Mackay, 1996; Heath *et al.*, 1999; Perry *et al.*, 2004a; Visscher *et al.*, 2008). Paternal effects can also modify offspring expression but their influence is still unclear (Cheng *et al.*, 1987; Wang *et al.*, 2006c). However, these effects may vary among populations and can have an impact on their evolutionary potential divergence (Perry *et al.*, 2005a; Kruuk *et al.*, 2008).

An additional factor that can potentially affect evolutionary potential is the developmental time which can also modify heritability of traits. During ontogeny, phenotypic traits and their underlying genetic control can vary due to the differential age-specific expression of genes (Atchley & Zhu, 1997; Wilson & Réale, 2006). It is therefore important to examine heritability variations at more than one age towards a better understanding of response to selection of organisms through their lifetime (Atchley & Zhu, 1997; Obedzinski & Letcher, 2004; Wilson & Réale, 2006; Wilson *et al.*, 2007; Robinson *et al.*, 2009).

The main objective of this study is to investigate ontogenic change in genetic, environmental and genotype-environment components influencing growth in mass among conspecific populations of brook charr (*Salvelinus fontinalis*) to assess their evolutionary

potential. Brook charr is an endemic fish of northeastern North America. Its last colonization in eastern Canada is believed to have occurred 10 000 years ago, following the last glacier retreat (Castric & Bernatchez, 2003; Thériault *et al.*, 2007a). This species can occupy various environments: it can be lacustrine, river-resident, or anadromous, inhabiting fresh or brackish water. It can also adapt to artificial environments and is an economically important farming species that represents 60% of Québec's freshwater aquaculture production (MAPAQ, 2007). Understanding the evolutionary potential of this fish has thus fundamental interest as it can be sensitive to various conditions and applied interest for its management in aquaculture. More specifically, ours objectives were (i) to investigate differences in the genetic basis of growth in mass among the three populations by comparing the relative importance of additive genetic effects in a common environment, (ii) to evaluate the environmental effects on heritability in each population in order to estimate the importance of genotype-environment interaction in the genetic control of growth and, (iii) to assess the parental and ontogenic effects on the observed patterns.

MATERIALS AND METHODS

Brook charr populations

The Laval population (L) originates from a wild anadromous population from the Laval River (48°44'N; 69°05'W) on the north shore of the St. Lawrence estuary (QC, Canada). The fish used were from third-generation breeders reared in captivity at the Station aquicole ISMER/UQAR (Rimouski, QC, Canada). The Rupert population (R) originates from a northern lacustrine freshwater-resident wild population inhabiting the Rupert River system (51°05'N; 73°41'W) (QC, Canada). The fish used as breeders were also from the third generation produced in captivity at the Laboratoire régional en sciences aquatiques (LARSA, Laval University, Québec, QC, Canada). The domestic population (D) has been widely used by Québec's fish farming industry for more than a hundred years and originates from many crosses between two freshwater strains (Nashua and Baldwin). Breeders of the domestic population were obtained from the Pisciculture de la Jacques Cartier (Cap-Santé, QC, Canada).

Family crosses and rearing

Three purebred cross-types ($D_{♀}D_{♂}$, $L_{♀}L_{♂}$, and $R_{♀}R_{♂}$) were made from mid-November 2005 until the end of December 2005 at LARSA between 10 sires and 10 dams of each population. All breeders were used only once and 10 full-sib families were obtained from each cross. During the first six months, i.e., from egg incubation (January) until exogenous feeding (June), families were kept separately in recirculating freshwater tanks at LARSA. Water temperature was maintained at 6°C during egg incubation and at 8°C after hatching. In June, families were identified and transferred to 3 m^3 tanks, with eight families per tank. All families were brought to 2136 degree-days by the end of the summer and maintained at 10°C. The photoperiod followed the natural seasonal cycle and fish were fed according to commercial charts.

Rearing environments

In September, fish were divided among two rearing environments that differ according to tank rearing system, water source, and water temperature conditions. At ISMER, 230 fish per family were reared in 0.5 m^3 indoor tanks under natural temperature and photoperiod conditions in running dechlorinated fresh water (density of about 35 kg m^3). To maintain sustainable rearing densities, the number of fish per family was gradually reduced to 60 by the end of the experiment, with all reductions in number being done randomly. Fish were fed daily (1% w/w ration) with commercial dry pellets. At LARSA, 150 fish per family were reared in 3 m^3 indoor tanks under natural photoperiod conditions at constant temperature of 10°C in recirculating fresh water (density of about 20 kg m^3). Fish numbers were gradually decreased to 50 fish per family by the end of the experiment. Fish were fed daily (1% w/w ration) with commercial dry pellets. This experiment ended in November 2007 (21-months-old). The first three samplings were made at LARSA: 20 fish par family were randomly sampled (n = 600) at complete resorption of the yolk sac (about 2-months-old), 50 fish per family were randomly sampled (n = 1500) at 15 weeks after exogenous feeding (about 4-months-old), and 50 fish per family were randomly sampled (n = 1500) at 2136 degree-days in September 2006 (about 7-months-old). Following transfer at the two rearing locations, 25 fish per family (n = 750 for each location) were randomly sampled every eight weeks. For each sampling, fish were anaesthetized in MS 222 (0.16 g L^{-1} [3-aminobenzoic acid ethyl ester]) and their body mass (to the nearest 0.1 g) was measured. Mass was recorded for every remaining fish at the final sampling in November.

Data analysis

Data normality and homogeneity of variance were tested with Kolmogorov-Smirnov and the Brown-Forsythe tests respectively. Mass data were log-transformed before analysis to obtain homoscedasticity. Variance components were analyzed separately in each population and environment for each sampling time (ontogeny) and were estimated by

Restricted Maximum Likelihood (REML) implemented in ASReml (V2.0;Gilmour *et al.*, 2006) using the following model:

$$y = \mu + A + e$$

where y is the phenotypic observation; μ is the overall mean; A is the additive genetic effect; and e is the residual. Total phenotypic variance (V_P) of each trait was decomposed into additive genetic variance (V_A) and residual variance (V_R). The narrow-sense heritability (h^2) for each trait was estimated as the ratio of the additive genetic variance to the total phenotypic variance: $h^2 = V_A/V_P$. Genetic correlation was also estimated for each population between the two environments on data from 9 to 21 months of age, as $r_G = COV_{Ai,j}/(V_{Ai} V_{Aj})$. Standard errors for variance and covariance components as well as for heritabilities and genetic correlations were also estimated using ASReml. The statistical significance of the additive genetic variance and covariance were tested by comparing the full model with a restricted model, where the additive variance (or covariance) was set to be equal to zero, using a likelihood ratio test (against the chi-square distribution, where χ^2 = -2*difference in log likelihood).The relative influence of maternal versus paternal effect on progeny mass in each population, and at each time sampling, was estimated as described by Heath *et al.* (1999) which is a regression of mean offspring size against the size of each of their parents. The difference between the two regression slopes indicates the relative influence of maternal or paternal effects. Maternal effects were considered to be present when the relative influence was significantly positive while a negative relative influence indicated that variations in the progeny were more related to sire effects (Heath *et al.*, 1999).

The statistical analysis on the complete interaction (population x environment x ontogeny) was not possible because only one measure of heritability for each data was obtained. Therefore, we analyzed the effects of populations on heritability estimates and parental effects with randomized block ANOVAs and the significance of differences among heritability estimates according to environments was analyzed using two-way ANOVAs including population, rearing environment, and population × rearing

environment interaction as factors. The change in heritability estimates through time was then analyzed using Spearman correlations. A posteriori Tukey tests were used for mean comparisons. Statistical analyses were conducted using Statistica version 6.0 for Windows (StatSoft, USA).

RESULTS

Additive effects

For the constant temperature environment, heritability estimates were generally medium to high (principally between 0.20 and 0.80) and differed among populations (Table II.1, ANOVA 1; Fig. II.1). Heritability was significantly higher in the domestic population (0.61 ± 0.07) than in the two others, which were not different from one another (0.37 ± 0.06 and 0.30 ± 0.08 for the Laval and the Rupert populations, respectively).

Genotype-environment interactions

A significant interaction was observed between populations and environments on heritability estimates (Table II.1, ANOVA 2). No significant environmental effect was detected in the domestic population (P = 0.14; Fig. II.2), whereas we observed a significant genetic covariance and a high correlation between the additive components measured in the two environments ($r_G = 0.87 \pm 0.09$; Table II.2). The heritability estimates for the Rupert population were always lower than those of the domestic population. However, h^2 was significantly higher for fish reared in the varying temperature environment ($P < 0.01$) (Fig. II.2). From 9 to 21 months, the genetic covariance of body mass between the two environments was significant and genetic correlation was high ($r_G = 0.88 \pm 0.11$; Table II.2). For the Laval population the h^2 estimates significantly decreased ($P = 0.01$) in the varying temperature environment relative to the constant temperature environment (Fig. II.2). They also became lower than those for the Rupert population in the varying temperature environment. For the Laval population, the genetic covariance and the genetic correlation of body mass between the two environments were not significant (Table II.2).

Parental effects and ontogenic changes

Parental effects on progeny mass varied significantly among populations (Table II.1, ANOVA 3; Fig. II.3). Averaged over the experiment, relative maternal versus paternal effect were significantly lower in the Rupert population (-0.75 ± 0.15) than in the two

Table II. 1 : Summary of ANOVAs with ANOVA 1 being the randomized block ANOVA of population effect on heritability, ANOVA 2 the two-way ANOVA of population and environmental effects on heritability and ANOVA 3 the randomized block ANOVA of population effect on parental effects. Df is the degrees of freedom; F is the F-ratio and P is the P-values.

	df	mean squares	F	P
ANOVA 1				
Ontogeny	9	0.08	2.16	0.08
Populations	2	0.26	6.92	0.01
Error	18	0.04		
ANOVA 2				
Environment	1	0.01	0.23	0.63
Populations	2	0.64	33.62	< 0.001
environment x populations	2	0.18	9.40	< 0.001
Error	36	0.02		
ANOVA 3				
Ontogeny	9	0.65	3.11	0.02
Populations	2	1.20	5.78	0.01
Error	18	0.21		

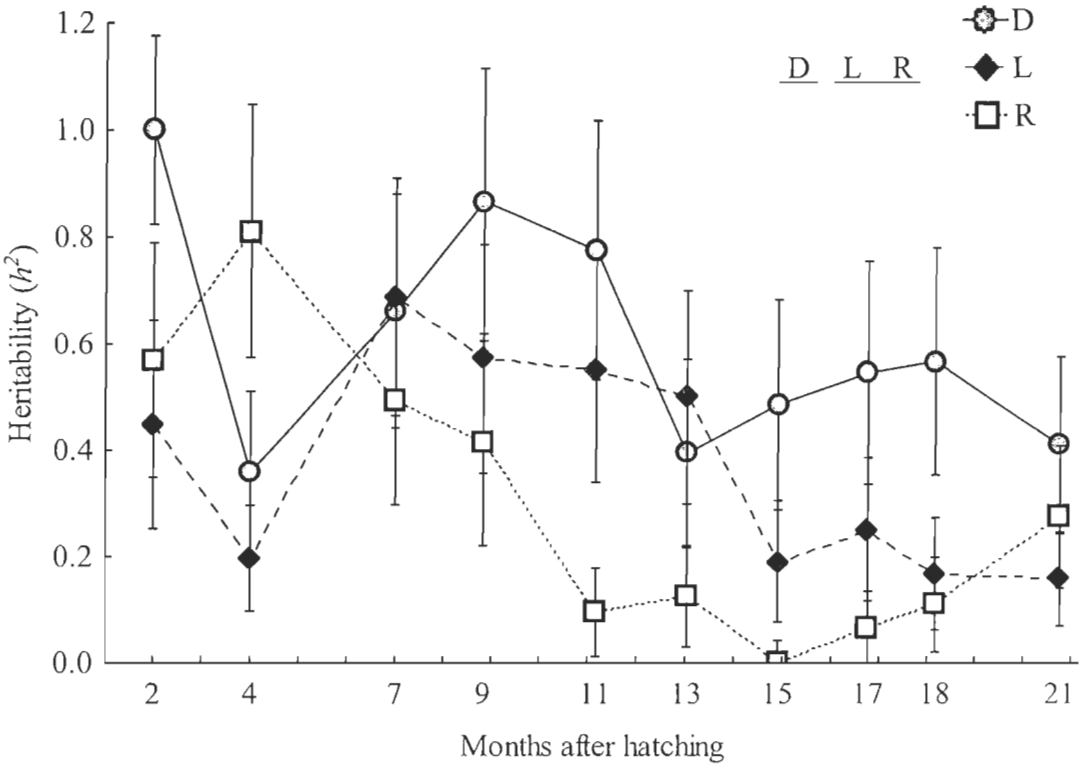


Figure II. 1 : Temporal variation in heritability estimates (h^2 ± SE) for body mass, from yolk sac resorption to 21 months of age, among the three brook charr populations (domestic [D], Laval [L], Rupert [R]) reared in the constant temperature environment (LARSA).

Table II. 2 : Estimates of additive genetic correlations, phenotypic correlations and genetic covariance for the three populations for body mass at age between environments (running freshwater, seasonal temperature variations [ISMER]; recirculating water, constant 10°C temperature conditions [LARSA]). Means ± SE. *P* values < 0.05 indicates that genetic covariance is significantly different from zero (likelihood ratio test).

Population	Genetic correlation	Phenotypic correlation	Genetic covariance	*P values*
domestic	0.87 ± 0.09	0.21 ± 0.11	0.013 ± 0.006	< 0.001
Laval	0.50 ± 0.31	- 0.16 ± 0.03	0.001 ± 0.001	0.209
Rupert	0.88 ± 0.11	- 0.08 ± 0.05	0.003 ± 0.002	0.003

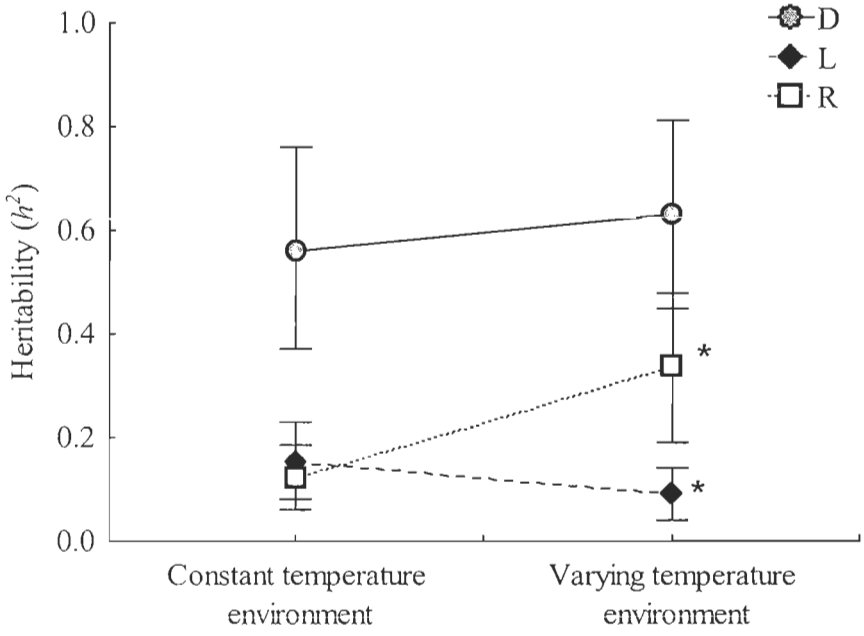


Figure II. 2 : Comparison of the heritability (h^2 ± SE) for body mass of juvenile stages (data on samplings done from 9 to 21 months of age) of the three populations (domestic [D], Laval [L], Rupert [R]) in the constant temperature environment (LARSA) and in the varying temperature environment (ISMER). Asterisks indicate significantly different means between environments ($P < 0.05$).

others that were not different (-0.13 ± 0.21 and -0.17 ± 0.18 for the domestic and the Laval population, respectively). There was no positive estimate, indicating the absence of maternal effects. However, sire effects were present in the Rupert population based on significant negative estimates. Finally, during ontogeny, heritability estimates decreased over time ($P < 0.05$), with a Spearman correlation of -0.70 for both the Laval and the Rupert populations and -0.52 for the domestic population. The paternal effect on the Rupert population also decreased from 7 to 22 months, changing from being significant to near 0 ($P < 0.05$).

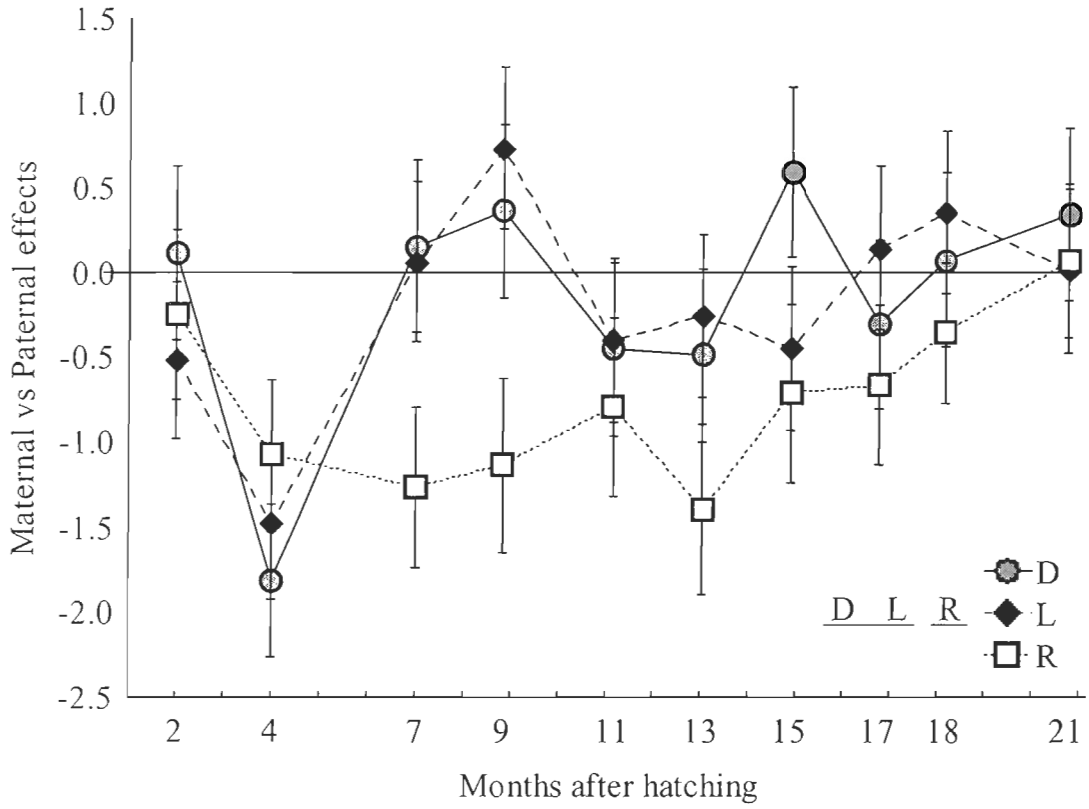


Figure II. 3 : Estimated maternal effects (± SE) on body mass for early development (months 2 to 7) and juvenile (months 9 to 21) stages of the three populations (domestic [D], Laval [L], Rupert [R]) in the constant temperature environment (LARSA).

DISCUSSION

The main objective of this study was to investigate ontogenic change in genetic, environmental and genotype-environment components influencing growth in mass among conspecific populations of brook charr to assess their evolutionary potential. Heritability estimates for body mass were significant in the three populations indicating potential for evolutionary response. However, these estimates differed according to the population with higher heritability in the domestic population, and medium similar heritability in the two others. Moreover, the rearing environment modified heritability estimates differently according to populations revealing important genotype-environment interactions in the genetic control of mass (9 to 21-months-old fish). Our results thus strongly suggest that these three brook charr populations differ in terms of their evolutionary potential to respond to selection. Moreover, heritability also decreased throughout the ontogeny suggesting that the potential to respond to selection may be higher at early life stages.

Inter-population variations

Mass at age was twice as much heritable in domestic fish (0.61 ± 0.07) than in Laval and Rupert fish (0.37 ± 0.06 and 0.30 ± 0.08 respectively). These estimates are of the same order of magnitude than previous estimations reported in natural populations of brook charr (Thériault *et al.*, 2007b) or other salmonids reared in artificial conditions, such as coho salmon (*Oncorhynchus kisutch*, Myers *et al.*, 2001), Atlantic salmon (*Salmo salar*, Garcia de Leaniz *et al.*, 2007), and masu salmon (*Oncorhynchus masou*, Choe & Yamazaki, 1998). Few studies have also revealed similar level of differences in heritability among natural populations, namely between two brook charr populations (*S. fontinalis*) in Cape Race (Wilson *et al.*, 2003). However, these results were obtained under different environmental conditions for each population, such that the observed differences could be biased by environmental effects (Roff *et al.*, 2004). In the present study, the differences in heritability estimates were obtained in a common environment. The differences observed are thus directly linked to divergent genetic basis. Common environment experiment had previously allowed documenting the divergent genetic basis between populations of common frog

(*Rana temporaria*, Laurila *et al.*, 2002; Uller *et al.*, 2002), brook charr (Perry *et al.*, 2005a) and brown trout (*Salmo trutta*, Jensen *et al.*, 2008) on early life history traits including length, mass, growth rate or yolk sac volume.

Heritability differences among populations indicate divergent genetic architecture and therefore different potentials for selective response, i.e., these populations may respond differentially to a same selection pressure. In our study, the lower heritability in the Laval and Rupert populations suggested slower responses to selection than was found for the domestic population. Genetic divergence among these populations was previously demonstrated using microsatellite (Martin *et al.*, 1997) and transcriptome analyses (Bougas *et al.*, 2010). In particular, the transcriptomic analysis also revealed that the domestic population was the most differentiated and differential patterns of gene expression in hybrid crosses between these three populations suggested that they have a unique genetic architecture. Differences in genetic architecture can be explained by the adaptive response to distinct environments (i.e., artificial, lacustrine, or fluctuating in relation to anadromy). In vertebrates, local adaptation to a specific habitat is often linked to divergence in gene expression which could also affect the expression of additive genetic variance and therefore heritability (Olsson & Uller, 2002; Sommer & Pearman, 2003; Wilson *et al.*, 2003; Cano *et al.*, 2004; Charmantier *et al.*, 2004; Jensen *et al.*, 2008). However, heritability differences can also be due to differences in additive genetic variance among populations (Table II.3), the additive genetic variance resulting from genetic variation that exists within populations. This is in accordance with previous studies on genetic diversity among domestic and wild populations of brook charr that also reported higher genetic variation in domestic fish (Martin *et al.*, 1997; Marie *et al.*, 2010). In the wild, populations of brook charr are generally small and isolated one from the other which could limit the occurrence of new genetic variation. On the opposite, domestic fish may be considered as part of a metapopulation, breeder's management allowing interconnection among the different, maintaining a high genetic diversity.

Table II. 3 : Genetic components of body mass at age for the three populations at each age and in both environments (running freshwater, seasonal temperature variations [ISMER]; recirculating water, constant 10°C temperature conditions [LARSA]). Estimates of total phenotypic (V_P), residual (V_R), and additive (V_A) variance components; means ± SE.

Age in	Domestic			Laval			Rupert		
months	V_P	V_R	V_A	V_P	V_R	V_A	V_P	V_R	V_A
LARSA									
2	0.004 ± 0.001	0.000 ± 0.000	0.004 ± 0.001	0.003 ± 0.001	0.002 ± 0.001	0.002 ± 0.001	0.014 ± 0.002	0.006 ± 0.002	0.008 ± 0.004
4	0.016 ± 0.002	0.010 ± 0.002	0.006 ± 0.003	0.010 ± 0.001	0.008 ± 0.001	0.002 ± 0.001	0.031 ± 0.006	0.006 ± 0.006	0.025 ± 0.012
7	0.029 ± 0.005	0.010 ± 0.005	0.019 ± 0.009	0.017 ± 0.003	0.005 ± 0.003	0.012 ± 0.006	0.026 ± 0.004	0.013 ± 0.004	0.013 ± 0.007
9	0.045 ± 0.010	0.006 ± 0.010	0.039 ± 0.019	0.026 ± 0.004	0.011 ± 0.004	0.015 ± 0.008	0.033 ± 0.005	0.019 ± 0.005	0.014 ± 0.008
11	0.050 ± 0.010	0.011 ± 0.010	0.039 ± 0.019	0.043 ± 0.007	0.019 ± 0.007	0.023 ± 0.012	0.040 ± 0.004	0.036 ± 0.004	0.004 ± 0.003
13	0.056 ± 0.007	0.034 ± 0.007	0.022 ± 0.012	0.055 ± 0.008	0.028 ± 0.008	0.027 ± 0.014	0.050 ± 0.005	0.044 ± 0.005	0.006 ± 0.005
15	0.063 ± 0.009	0.032 ± 0.009	0.030 ± 0.016	0.058 ± 0.006	0.047 ± 0.006	0.011 ± 0.007	0.049 ± 0.005	0.049 ± 0.005	0.001 ± 0.002
17	0.052 ± 0.008	0.024 ± 0.008	0.028 ± 0.015	0.043 ± 0.005	0.033 ± 0.005	0.011 ± 0.007	0.049 ± 0.005	0.045 ± 0.005	0.003 ± 0.003
19	0.048 ± 0.008	0.021 ± 0.008	0.027 ± 0.014	0.049 ± 0.005	0.040 ± 0.005	0.008 ± 0.005	0.046 ± 0.005	0.041 ± 0.005	0.005 ± 0.004
21	0.045 ± 0.005	0.027 ± 0.005	0.018 ± 0.009	0.045 ± 0.003	0.038 ± 0.004	0.007 ± 0.004	0.043 ± 0.004	0.031 ± 0.004	0.012 ± 0.007
ISMER									
9	0.037 ± 0.008	0.008 ± 0.008	0.029 ± 0.014	0.021 ± 0.002	0.017 ± 0.002	0.003 ± 0.002	0.026 ± 0.004	0.012 ± 0.004	0.013 ± 0.007
11	0.050 ± 0.008	0.021 ± 0.008	0.030 ± 0.015	0.027 ± 0.003	0.022 ± 0.003	0.005 ± 0.003	0.036 ± 0.004	0.026 ± 0.004	0.010 ± 0.006
13	0.041 ± 0.009	0.012 ± 0.009	0.029 ± 0.017	0.028 ± 0.003	0.025 ± 0.003	0.003 ± 0.003	0.041 ± 0.005	0.027 ± 0.005	0.014 ± 0.009
15	0.050 ± 0.011	0.014 ± 0.011	0.035 ± 0.020	0.026 ± 0.003	0.023 ± 0.003	0.004 ± 0.003	0.036 ± 0.004	0.027 ± 0.004	0.009 ± 0.006
17	0.050 ± 0.010	0.018 ± 0.010	0.033 ± 0.019	0.038 ± 0.004	0.038 ± 0.004	0.001 ± 0.002	0.036 ± 0.004	0.027 ± 0.004	0.009 ± 0.006
19	0.033 ± 0.006	0.013 ± 0.006	0.020 ± 0.012	0.034 ± 0.003	0.030 ± 0.004	0.003 ± 0.003	0.028 ± 0.004	0.016 ± 0.004	0.012 ± 0.007
21	0.024 ± 0.003	0.012 ± 0.004	0.012 ± 0.007	0.025 ± 0.002	0.022 ± 0.002	0.003 ± 0.002	0.032 ± 0.005	0.016 ± 0.005	0.016 ± 0.009

Genotype–environment interactions

Significant genotype–environment interactions were observed on heritability estimates, which indicate population-specific potential for adaptation to environmental modifications and selection pressure. In natural conditions, the environment influences heritability by decreasing its estimates under unfavorable conditions (i.e., restricted food abundance or harsh habitat quality) (Hoffmann & Merilä, 1999; Laugen *et al.*, 2005; Kruuk *et al.*, 2008). Such environmental influence has been reported for size-related traits (e.g., mass and length of the head, tarsus, tail, or the whole body of individuals) in various vertebrates such as birds, amphibians, mammals, and fish (Charmantier *et al.*, 2004; Charmantier & Garant, 2005; Laugen *et al.*, 2005). This decrease is generally the result of a decrease in additive components and/or an increase in environmental variance (Hoffmann & Merilä, 1999; Uller *et al.*, 2002; Charmantier & Garant, 2005). In the present study, none of the controlled environments could be qualified as unfavorable. However, environment can modify gene expression in brook charr (Côté *et al.*, 2007) and such environmental impact could be different among populations according to their distinct genetic architecture, thus causing genotype-environment interactions. This interaction is then generally favorable for evolutionary potential as it modifies the genetic basis on which selection pressure will act depending on environments (Charmantier & Garant, 2005; Kruuk *et al.*, 2008). According to environments, the three populations will then have their own evolutionary response.

Parental and ontogeny variations

Parental effects, especially maternal effects, can influence offspring genetic variance (Kruuk *et al.*, 2008; Visscher *et al.*, 2008). However, in the present study, no significant maternal effect was detected and paternal effects were observed only in the Rupert population during the first months. Stronger evidence for paternal effects was somewhat unexpected since dam effects on offspring early development are reported more commonly in salmonid fishes (Heath *et al.*, 1999; Perry *et al.*, 2004a). Therefore, its influence is still unclear. On the other hand, ontogeny seemed to have an important influence on heritability

estimates as they were significant throughout development, but decreased with fish growth. This temporal decrease thus suggests a higher potential to respond to selection response at early ages. In fish, decrease in heritability through the ontogeny was previously observed in size-related traits (e.g. body weight and length) in carp (*Carassius langsdorfii*, Koedprang *et al.*, 2000), Atlantic salmon (*Salmo salar*, Gjerde *et al.*, 1994), and masu salmon (*Oncorhynchus masou*, Choe & Yamazaki, 1998). During development, many genes can act and interact differently with other genes or environments which can modify the global pattern of genetic expression (Atchley & Zhu, 1997; Perry *et al.*, 2005a; Darias *et al.*, 2008). Such modifications can modify the genetic control of a complex trait like body mass along with stage of development (ontogeny), and therefore its heritability, creating age-specific responses to selection (Atchley & Zhu, 1997; Wilson & Réale, 2006; Robinson *et al.*, 2009).

Phenotypic plasticity

It is noteworthy that no genetic correlation was found between the two rearing environments for the Laval population. This suggests that this brook charr population expressed different sets of genes when found in different environments, therefore translating pronounced phenotypic plasticity that could be adaptive (Falconer & Mackay, 1996; Charmantier & Garant, 2005; Laugen *et al.*, 2005). In the wild, fish from the Laval population undergo an annual migration from freshwater in summer and fall to an estuarine habitat in spring–summer. Variable environments favor phenotypic plasticity (Charmantier & Garant, 2005; Wilson *et al.*, 2006; Lind & Johansson, 2007; Lardies & Bozinovic, 2008), and wild Laval River fish are known to be exposed to strong variations in salinity (from 1 to 34), temperature (from 5 to 18°C), and water velocity (Curry *et al.*, 2006).

Potential limitations

The full-sib effect could have inflated heritability estimates obtained in this study because the purely additive genetic variance cannot be separated from the other variance components related to non-additive, common environment, or maternal effects (Falconer &

Mackay, 1996; Merila *et al.*, 2001; Perry *et al.*, 2004a). However, as we did not observe maternal effects, this variable could be excluded. Even though other factors could have influenced heritability estimates, we may suppose that, considering the experimental design, their effects were similar among populations and so comparisons among populations and environments are realistic.

Conclusion

In summary, this study revealed that these brook charr populations differed importantly in their evolutionary potential to respond to selective pressures, as revealed by distinct patterns of additive genetic variance, heritability and genotype-environment interactions. As such, our results reinforce the importance of documenting quantitative genetic parameters through time and in different environments in order to better understand such population-specific differences in evolutionary potential. They also stress that any given change in environmental conditions may have unpredictable response among conspecific populations. In future studies, it will also be essential to document genetic correlations among traits, through pleiotropy or genetic linkage that can also have an important impact on the evolutionary capacity of a phenotypic trait by indirect selection (Falconer & Mackay, 1996; Roff, 2000).

CHAPITRE 3
BASES GÉNÉTIQUES DE LA MOBILISATION D'ÉNERGIE PENDANT L'HIVER D'OMBLE DE FONTAINE 0+ (*SALVELINUS FONTINALIS*)

RÉSUMÉ

L'hiver est une saison critique pour les poissons, spécialement pour les juvéniles, car ils ont besoin de compenser le faible apport d'énergie externe par la mobilisation de leurs réserves d'énergie. Dans les zones tempérées, les poissons d'eau douce mobilisent généralement leurs réserves de glycogène hépatique et de gras péri-viscéral. Cependant, les bases phénotypiques et génétiques de l'accumulation et de la mobilisation de ces réserves ont rarement été analysées. Dans cette étude, les réserves énergétiques accumulées à l'automne et leur utilisation hivernale ont été mesurées chez des juvéniles d'omble de fontaine (*Salvelinus fontinalis*) de trois souches divergentes (domestique [D], Laval [L], and Rupert [R]) et chez leurs hybrides réciproques, lors de leur premier hiver. Les résultats ont révélé que les stratégies de préparation et de mobilisation des réserves d'énergie pendant l'hiver étaient propres à chaque souche, et que chaque souche avait une base génétique spécifique pour ces traits : 1) les poissons domestiques ont accumulé une importante quantité de réserves énergétique avant l'hiver et ont continué d'accumuler du glycogène hépatique pendant l'hiver bien qu'ils soient moins nourris ; 2) les poissons de la souche Laval ont utilisé leurs glycogène et lipides hépatiques pendant l'hiver et ont eu une importante diminution de leur facteur de condition ; 3) les poissons de la souche Rupert avaient peu d'énergies accumulées à la fin de l'automne et ont préférentiellement mobilisé leur gras péri-viscéral pendant l'hiver. Cependant, des héritablilités significatives ont été obtenues seulement chez les stratégies des souches domestiques (h^2 de 0,56 pour le gras péri-viscéral, 0,29 pour le contenu en eau du muscle, 0,20 pour le HSI et 0,90 pour le contenu energétique du foie) et Laval (h^2 de 0,32 pour le facteur de condition, 0,31 pour le

gras péri-viscéral, 0,26 pour le HSI et 0,42 pour la concentration hépatique en glycogène). Les résultats ont alors montré la présence de divergence d'architecture génétique entre les souches pour ces traits. Chez les hybrides, il n'y avait pas beaucoup d'expression d'effets non-additifs, effets généralement présents lors de croisements entre souches divergentes, suggérant des complexes génétiques relativement proches entre les souches pour le contrôle de l'accumulation et de l'utilisation des réserves. Par contre, les résultats ont montré que les bases génétiques héritables étaient plus souvent exprimées dans les performances de la fin de l'automne, révélant un contrôle génétique plus important lors de l'accumulation des réserves que lors de leur mobilisation.

Ce troisième article, intitulé « *Genetic basis of energy mobilization during winter in 0-year brook charr (Salvelinus fontinalis)* », a été corédigé par moi-même ainsi que par ma directrice Céline Audet, et mes codirecteurs Louis Bernatchez et Dany Garant. Ma contribution à ce travail a été l'essentiel de la recherche sur l'état de l'art, la mise au point et l'exécution du plan d'expérience, l'ensemble des analyses en laboratoires, des analyses statistiques et de génétique quantitative, ainsi que l'interprétation des résultats et la rédaction de l'article. Céline Audet a aidé à la mise au point des expériences, à la coordination de la recherche, à l'interprétation des résultats et à l'écriture du manuscrit. Louis Bernatchez a participé à la conception du plan d'analyse. Dany Garant a aidé à la réalisation des analyses de génétique quantitative et à la révision de l'article. Une version abrégée de cet article a été présenté au *13ème colloque annuel du CIRSA* à Québec au printemps 2010 et au congrès *9th International congress of the Biology of Fish* à Barcelone, en Espagne, à l'été 2010.

KEYWORDS:

Heritability, genetic basis, non-additive effects, energy strategy

GENETIC BASIS OF ENERGY MOBILIZATION DURING WINTER IN 0-YEAR BROOK CHARR (*SALVELINUS FONTINALIS*)

ABSTRACT

Winter is a critical season for fishes, especially for juveniles, as they need to compensate for the low external energy intake by mobilizing their energy reserves. Freshwater fish from temperate areas generally mobilized energy reserves as liver glycogen and visceral fat. However, the phenotypic and genetic bases of such energy reserve accumulation and mobilization have rarely been investigated. In the present study, energy reserves accumulated during fall and their use during winter was measured during the first winter of life in three divergent strains (domestic [D], Laval [L], and Rupert [R]) of brook charr (*Salvelinus fontinalis*) and their reciprocal hybrids. The results indicate that the strategy of winter energy preparation and mobilization was specific to each strain, and each strain had its own genetic basis underlying its strategy: 1) domestic fish accumulated a high amount of energy reserves before winter and kept accumulating liver glycogen during winter despite lower feeding; 2) the Laval fish used liver glycogen and lipids during winter and experienced a significant decrease in condition factor; 3) the Rupert fish had relatively fewer energy reserves accumulated at the end of autumn and preferentially mobilized visceral fat during winter. However, heritability for traits related to accumulation and use of energy reserves was only found in the domestic (h^2 of 0.56 for visceral fat, 0.29 for muscle water content, 0.20 for HIS, and 0.90 for liver total energy) and Laval strains (h^2 of 0.32 for the condition factor, 0.31 for visceral fat, 0.26 for HSI, and 0.42 for the relative liver glycogen). The results then revealed the presence of differences in genetic architecture among the strains related to the use of energy reserves. In hybrids, there was a very limited occurrence of non-additive effects which generally occur in crosses between genetically distant strains. This would suggest relatively closed genetic associations related to the accumulation and use of energy among the strains. Finally, heritable genetic traits were mostly expressed at the end of autumn, indicating a tighter genetic control in energy accumulation than in energy mobilization.

INTRODUCTION

In temperate climates, the annual fluctuations in temperature and food productivity create cycles in energy availability. These cycles induce periods of accumulation and depletion of energy reserves in fishes (Hutchings *et al.*, 1999; Schultz & Conover, 1999; Finstad *et al.*, 2004; Huss *et al.*, 2008; Heermann *et al.*, 2009). Because of the low temperatures, short days, and limited food access, winter is a critical period for survival. During their first winter, juvenile fish are particularly susceptible to these winter conditions that could result in mortality risk altering population recruitment (Sogard, 1997; Garvey *et al.*, 1998; Huss *et al.*, 2008). To compensate the low energy intake and limit mortality risk, fish thus need to mobilize energy reserves stored during the fall (Schultz & Conover, 1999; Heermann *et al.*, 2009). The general pattern of energy reserve mobilization in freshwater fish is characterized by depletion of glycogen (inducing reduction of liver mass), followed by the use of perivisceral fat and hepatic lipids, and finally by depletion of tissue proteins (Collins & Anderson, 1995; Rios *et al.*, 2006). Important total body energy depletion may then increase the incidence of disease (Eckmann, 2004; Martin *et al.*, 2010) and extreme protein mobilization may severely affect fish metabolism (Rios *et al.*, 2006). A reduction in energy reserves accumulated before winter combined with long winter conditions can thus induce critical energy depletion and lead to death (Post & Evans, 1989; Schultz *et al.*, 1998; Biro *et al.*, 2004; Eckmann, 2004; Finstad *et al.*, 2004; Pangle *et al.*, 2004; Huss *et al.*, 2008; Heermann *et al.*, 2009).

Within populations, variation in energy mobilization has been extensively documented in several fish species such as perch (*Perca fluviatilis*, Post & Evans, 1989; Heermann *et al.*, 2009), largemouth bass (*Micropterus salmoides*, Miranda & Hubbard, 1994), Atlantic silverside (*Menidia menidia*, Schultz *et al.*, 1998), rainbow trout (*Oncorhynchus mykiss*, Biro *et al.*, 2004), Atlantic salmon (*Salmo salar*, Finstad *et al.*, 2004), and lake herring (*Coregonus artedi*, Pangle *et al.*, 2004). Differences among individuals were often related to body size due to the allometry of energy metabolism: larger individuals had larger energy accumulation with higher lipid reserves and lower

depletion rates than smaller individuals (Post & Evans, 1989; Miranda & Hubbard, 1994; Cargnelli & Gross, 1997; Schultz & Conover, 1999; Biro *et al.*, 2004; Eckmann, 2004; Hurst, 2007; Huss *et al.*, 2008). Therefore, the facility to deal with winter constraints seems highly size-dependent, with smaller fish experiencing higher overwinter mortality and larger fish emerging from winter in better energetic condition.

Among populations, differences in the ability to cope with winter related to energetic strategies have also been reported in Atlantic silverside (*M. menidia,* Schultz & Conover, 1997), and Atlantic salmon (*S. salar*, Finstad *et al.*, 2010). These studies showed that differences in energy storage and depletion were generally linked to local adaptations to latitudinal clines with northern populations being more tolerant to winter temperatures and more efficient with regard to energy processes (Post & Evans, 1989; Schultz *et al.*, 1998; Billerbeck *et al.*, 2001; Hurst, 2007; Finstad *et al.*, 2010). Energy accumulation and mobilization could thus not only be related to size but also result from local adaptation and genetic control (Schultz & Conover, 1997; Schultz *et al.*, 1998; Billerbeck *et al.*, 2001; Finstad *et al.*, 2010). Yet, such comparisons were generally made in the field, making the separation of the genetic basis from environmental effects more difficult (Stelkens *et al.*, 2009). In the few cases where common-environment comparisons were performed, they indeed suggest the presence of a genetic basis for rates of energy accumulation (Schultz & Conover, 1997).

The genetic basis of energy reserve accumulation and mobilization has however rarely been investigated. The few studies that were done focused on farmed fish and aimed to determine the heritability of carcass composition traits to improve flesh quality (Neira *et al.*, 2004; Tobin *et al.*, 2006; Navarro *et al.*, 2009). Their results indicate a large range of heritability and genetic correlations depending on traits and species. But until now, the genetic basis of energy reserve strategies during periods of high energy demands has never been explored.

Inter-strains hybridization can also give interesting information on the genetic basis of performance. When populations are genetically closer and display significant

heritabilities for traits of interest, hybrids can express additive effects and show performance intermediate to parental lines. Conversely, when populations are genetically divergent, hybrids can express non-additive effects due to genetic associations which can be positive (heterosis) or negative (outbreeding depression) on performance (Falconer & Mackay, 1996; Tymchuk *et al.*, 2007; Stelkens *et al.*, 2009). Non-additive effects have been observed for many fish performance traits such as growth rate, survival, and salinity tolerance revealing evolutionary divergence among populations (Bentsen *et al.*, 1998; Shikano & Taniguchi, 2002a; Bryden *et al.*, 2004; Hena *et al.*, 2005; Tymchuk *et al.*, 2007). However, the occurrence of non-additive effects in energy processes has never been investigated.

The aim of the present study was to investigate intraspecific strategies of energy mobilization in three strains of brook charr (*Salvelinus fontinalis*) and their reciprocal hybrids by documenting the phenotypic and genetic basis of traits related to energy reserves accumulation in fall and their use during the first winter of life. More specifically, the objectives were (i) to compare energy reserve accumulation and mobilization among strains during winter in order to determine the different energy strategies of strains, (ii) to estimate heritability and genetic correlations in energy reserves related-traits in the three strains in a common environment, and (iii) to evaluate the importance of non-additive effects in energy strategies of hybrids.

MATERIALS AND METHODS

Brook charr strains

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

Breeding design

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

Family rearing

During the first six months, i.e., from egg incubation (January) to exogenous feeding (June), families were kept separately in recirculating fresh water at LARSA. Water temperature was maintained at 6°C during egg incubation and at 8°C after hatching. All families were brought to 2136 degree-days by the end of the summer and maintained at 10°C in recirculating fresh water. The photoperiod followed the natural seasonal cycle, and fish were fed according to commercial charts. In September, fish were transferred to the Station aquicole ISMER/UQAR, where they were reared indoors under natural temperature and photoperiod conditions in running dechlorinated fresh water. Fish were fed daily (1% w/w ration) with commercial dry pellets until water temperature decreased to 4°C (in January), then fish were fed twice a week. Due to the limited number of fish in some families, the number of families used for this experiment was: 10 for L♀R♂, 9 for L♀D♂ and L♀L♂, 8 for D♀D♂, 7 for D♀L♂ and D♀R♂, 6 for R♀L♂, and 5 for R♀R♂. A daily record of mortalities was made throughout the winter and the relative mortality was determined for each family.

Sampling

Two samplings were performed during the first winter of life to evaluate energy mobilization among the different crosses. The first sampling was accomplished in December (water temperature at 7°C) and the second in March (water temperature at 3°C). The winter temperature profile is presented in Fig. III.1. For each sampling, ten fish per family were sacrificed (total number of fish sampled = 1220). Fish were anaesthetized in MS 222 (0.16 g L^{-1} [3-aminobenzoic acid ethyl ester]) and their body mass (to the nearest 0.1 g) and fork length (0.1 cm) were measured. The condition factor was estimated according to the equation (weight $length^{-3}$) X 100. Liver was excised, weighed to determine the hepato-somatic index (HSI: liver weigh / body weight X 100), rapidly frozen in liquid nitrogen, and stored at -80°C until further analysis. Visceral fat deposits were collected, weighed, and were expressed in percentage of body weight. One piece of epaxial dorsal muscle was excised, weighed and dried for 72h at 70°C for the determination of water

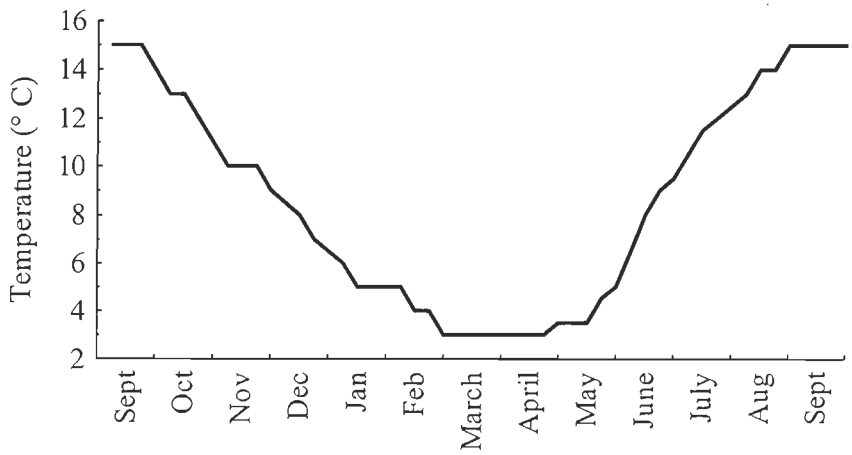


Figure III. 1 : Annual temperature profile of freshwater at the Station aquicole of ISMER/UQAR at Rimouski (Qc, Canada).

content. Liver glycogen concentration was measured on fresh liver using the amyloglucosidase digestion method (Carr & Neff, 1984) followed by glucose concentration determination (QuantiChrom^{TM} Glucose Assay kit, BioAssay Systems, USA); total liver lipid concentration was evaluated on fresh liver using the phospho-vanillin method (Frings *et al.*, 1972); and liver protein concentration was determined on fresh liver using a protein dye binding method (Protein Assay kit, Biorad, USA) according to Bradford (1976). Total liver energy content was estimated after conversion of protein, total lipid, and glycogen cconcentrations to energy using conversion factors of 24 kJ g^{-1}, 38 kJ g^{-1}, and 17 kJ g^{-1} for proteins, lipids, and carbohydrates, respectively (Jobling, 1993).

Statistical analyses

Data normality and homogeneity of variance were verified with Kolmogorov-Smirnov and Brown-Forsythe tests, respectively. Muscle water content (rank), liver total energy content (log), and survival index (arcsin) data had to be transformed to obtain normality. The different response variables were analyzed using mixed models with cross-type, sampling time, and their interaction fitted as fixed effects and full-sib families fitted as a random effect. The percentage of fish that died during winter was analyzed using one-way ANOVA with cross-type as factor (n = 61 families). The presence of non-additive

effects was determined by the presence of significant differences between the mean trait values of hybrids compared to the mean traits of both parental strains (Bryden *et al.*, 2004). The a posteriori Tukey test was used for mean comparisons when possible or replaced by the Games and Howell test when variances were not homogenous. Analyses were made using Statistica 7.0 version for Windows (StatSoft, USA). A significance level of $\alpha = 0.05$ was used in all statistical tests.

Quantitative genetic analysis

Our breeding design was used to fit animal models (Lynch & Walsh, 1998) with the software ASReml (V 2.0; Gilmour *et al.*, 2006). Variance components for all traits in each population were estimated by Restricted Maximum Likelihood (REML) using the following linear model:

$$y = \mu + \text{Months} + A + e$$

where y is the phenotypic observation for each population in December and March, μ is the overall mean, Months is the fixed effect of the sampling time, A is the random additive genetic effect, and e is the random residual effect. The total phenotypic variance (V_P) of each trait was decomposed into additive genetic variance (V_A) and residual variance (V_R). The narrow-sense heritability (h^2) for each trait was estimated as the ratio of the additive genetic variance to the total phenotypic variance: $h^2 = V_A/V_P$. Genetic and phenotypic correlations were also estimated for each strain between traits for which heritability was significant using the relationship $r_G = COV_{Ai,j}/(V_{Ai}\ V_{Aj})$ and $r_P = COV_{Pi,j}/(V_{Pi}\ V_{Pj})$ respectively. Standard errors for variance and covariance components as well as for heritabilities and genetic correlations were also estimated using the ASReml software. The statistical significance of the additive genetic variance and of the genetic covariances were tested by comparing the full model with a constrained model in which the (co)variance was set to be equal to zero using a likelihood ratio test (against the chi-square distribution, where χ^2 = -2*difference in log likelihood).

RESULTS

Overwinter mortalities were generally low (mean of 2.4% with a range from 0.32 ± 0.12 in $D_{♀}L_{♂}$ to 5.60 ± 3.60 in $D_{♀}R_{♂}$) and similar among crosses ($df = 7$, $F = 1.61$, $P = 0.14$). However, the difference in the use of energy reserve during winter varied among cross-types (significant interactions between sampling time and cross-types for all variables measured). Tables III.1 and III.2 summarize the statistical results of all energy reserves and the percentage of total variance explained by the models varied from 5% (liver protein concentration) to 53% (total liver energy content).

Condition factor

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

Body reserves

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

Table III. 1 : Summary the mixed model statistics on sampling time x cross-types interactions for the condition factor and body energy reserves traits (visceral fat, muscle water content, and HSI [hepato-somatic index]). df is the degrees of freedom; F is the F-ratio.

	Condition factor			Visceral fat (%)			Muscle water content (%)			HSI (%)		
	df	F	*P*-value	df	F	*P*-value	df	F	*P*-value	df	F	*P*-value
Sampling time	1	359.7	< 0.001	1	39.6	< 0.001	1	0.5	0.49	1	0.1	0.92
Cross-type	7	20.6	< 0.001	7	5.9	< 0.001	7	16.3	< 0.000	7	17.2	< 0.000
Sampling time x Cross-type	7	15.0	< 0.001	7	6.6	< 0.001	7	8.4	< 0.001	7	10.4	< 0.001
Family (nested in Cross-type), random	53	3.4	< 0.001	53	6.1	< 0.001	53	3.7	< 0.001	53	3.7	< 0.001
Error	1147			1147			1147			1147		
Model R^2	0.51			0.36			0.37			0.39		
Adjusted R^2	0.48			0.33			0.34			0.35		

Table III. 2 : Summary of the mixed model statistics on sampling time x cross-types interactions for liver energy reserves traits (glycogen, protein, lipid, and total energy). df is the degrees of freedom; F is the F-ratio.

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

Table III. 3 : Body condition and energy reserves measured as condition factor, visceral fat (%), muscle water content (%), and HSI (hepato-somatic index; %) in the three purebred strains (bold) and their hybrids in December and March. Means ± SEM; n is the numbers of individuals. The different letters indicate significant differences among cross-types in December and March ($\alpha = 0.05$). In December, grey highlight indicates hybrids that had significantly more or less energy reserves than either parental line (non-additive effects). In March, grey highlight indicates hybrids that used significantly more or less energy reserves than either parental line during winter (non-additive effects).

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

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

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

Liver reserves

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

Table III. 4 : Liver energy reserves measured as glycogen (mg g^{-1}), protein (mg g^{-1}), lipid (mg g^{-1}), and liver total energy (kJ) in the three purebred strains (bold) and their hybrids in December and March. Means ± SEM; n is the numbers of individuals. The different letters indicate significant differences among cross-types in December and March ($\alpha = 0.05$). In December, grey highlight indicates hybrids that had significantly more or less energy reserves than either parental line (non-additive effects). In March, grey highlights indicate hybrids that used significantly more or less energy reserves than either parental line during winter (non-additive effects).

	December					March				
Cross	n	Glycogen (mg g^{-1})	Protein (mg g^{-1})	Lipid (mg g^{-1})	Total energy (kJ)	N	Glycogen (mg g^{-1})	Protein (mg g^{-1})	Lipid (mg g^{-1})	Total energy (kJ)
$D♀R♂$	67	45.5 ± 2.1^{bc}	58.7 ± 2.1^{c}	25.7 ± 1.2^{cde}	0.92 ± 0.06^{de}	66	71.2 ± 4.3^{fg}	48.5 ± 1.7^{ab}	26.1 ± 1.3^{cdef}	1.49 ± 0.14^{ef}
$D♀D♂$	**80**	$\mathbf{61.4 \pm 2.1^{ef}}$	$\mathbf{54.9 \pm 1.6^{abc}}$	$\mathbf{31.9 \pm 1.1^{f}}$	$\mathbf{1.72 \pm 0.13^{fg}}$	**79**	$\mathbf{91.2 \pm 4.3^{g}}$	$\mathbf{48.6 \pm 1.6^{ab}}$	$\mathbf{31.4 \pm 1.5^{ef}}$	$\mathbf{2.53 \pm 0.19^{g}}$
$D♀L♂$	67	56.8 ± 2.3^{def}	60.5 ± 1.9^{c}	27.2 ± 1.3^{cdef}	1.13 ± 0.08^{e}	69	65.3 ± 4.4^{def}	53.5 ± 1.6^{abc}	25.6 ± 1.2^{cde}	1.63 ± 0.18^{ef}
$L♀D♂$	88	50.1 ± 1.7^{cd}	57.5 ± 1.4^{c}	30.4 ± 1.3^{def}	1.21 ± 0.08^{e}	89	67.4 ± 3.5^{f}	47.7 ± 1.4^{a}	25.8 ± 1.1^{cd}	1.47 ± 0.12^{ef}
$L♀L♂$	**87**	$\mathbf{48.8 \pm 2.2^{cd}}$	$\mathbf{54.8 \pm 1.4^{abc}}$	$\mathbf{25.6 \pm 1.1^{cde}}$	$\mathbf{0.44 \pm 0.02^{b}}$	**87**	$\mathbf{19.8 \pm 2.1^{a}}$	$\mathbf{55.5 \pm 1.6^{bc}}$	$\mathbf{18.6 \pm 0.8^{a}}$	$\mathbf{0.26 \pm 0.02^{a}}$
$L♀R♂$	99	44.4 ± 1.6^{bc}	58.3 ± 1.5^{c}	24.9 ± 0.8^{c}	0.64 ± 0.03^{c}	97	35.0 ± 2.6^{b}	53.8 ± 1.7^{abc}	19.0 ± 0.8^{ab}	0.56 ± 0.05^{bc}
$R♀L♂$	59	61.1 ± 2.8^{def}	57.6 ± 1.7^{bc}	26.9 ± 1.4^{cdef}	0.72 ± 0.06^{cd}	59	48.8 ± 4.7^{bcde}	54.5 ± 1.9^{abc}	23.9 ± 1.3^{bc}	0.69 ± 0.07^{bcd}
$R♀R♂$	**49**	$\mathbf{57.4 \pm 3.3^{def}}$	$\mathbf{59.1 \pm 2.4^{c}}$	$\mathbf{24.2 \pm 1.4^{abcd}}$	$\mathbf{0.48 \pm 0.04^{bc}}$	**49**	$\mathbf{46.6 \pm 4.0^{bcde}}$	$\mathbf{55.2 \pm 2.2^{abc}}$	$\mathbf{22.7 \pm 1.2^{abc}}$	$\mathbf{0.48 \pm 0.04^{bc}}$

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

Relative liver protein concentrations (mg g^{-1} of liver) were similar among all cross-types in December (Tables III.2 and III.4). No change in relative liver protein was observed over winter for any of the purebred crosses (Table III.4). However, the $D_{♀}R_{♂}$ and $L_{♀}D_{♂}$ hybrids showed a significantly lower protein concentration in March than in December (Table III.4), suggesting the presence of non-additive effects. All others hybrids were similar to their parental lines (Table III.4).

Domestic fish had significantly higher relative total liver lipid concentration (mg g^{-1} of liver) in December than the Laval and Rupert fish (Tables III.2 and III.4). The relative liver lipid concentration in hybrids was generally not significantly different from those of their parental lines, the only exception being the $D_{♀}R_{♂}$ hybrids, which were closest to the paternal Rupert line (Table III.4). At the end of winter, only the $L_{♀}L_{♂}$ cross-type showed a significant decrease in relative liver total lipid concentration while no change was observed in the two other purebred crosses (Table III.4). The $L_{♀}R_{♀}$ hybrids also expressed a decrease in relative liver lipid concentration (Table III.4). No change in liver lipid concentration was observed in the other hybrids.

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

Additive genetic effects and heritability

Significant additive genetic variance estimates were obtained for all traits (Table III.5), except for the liver protein and lipid concentrations. However there were

notable differences among strains. In the domestic strain, additive genetic variances for visceral fat, muscle water content, HSI and liver total energy content were all significant and these traits showed medium to high values of heritability (see Table III.5). In the Laval strain, there was a significant additive genetic variance with medium heritability for the condition factor ($h^2 = 0.32$), visceral fat ($h^2 = 0.31$), HSI ($h^2 = 0.26$), and relative liver glycogen concentration ($h^2 = 0.42$). On the contrary, in the Rupert strain, the condition factor was the only trait for which a significant additive genetic component of variance was found, and for which heritability was high ($h^2 = 0.50$) (Table III.5).

Genetic and phenotypic correlations

Significant genetic covariances and phenotypic correlations were present between fish body and energy reserves (Table III.6). In domestic fish, significant genetic covariances and strong correlations were obtained between body mass and two energy reserve indices, the visceral fat ($r_G = 0.75$) and the total liver energy content ($r_G = 0.99$). These two energy reserves were also highly correlated to each other ($r_G = 0.69$; Table III.6). No significant genetic covariances were detected between body mass and any of the energy reserve traits in the Laval strain (Table III.6). However, in the same strain, significant genetic covariances and high genetic correlations ($r_G > 0.90$) were observed between the condition factor and two energy reserve indices, i.e., visceral fat and relative liver glycogen (Table III.6). These two energy reserve indices were also highly correlated with each other and with HSI (r_G of 0.94, 0.88 and 0.83 for relative liver glycogen vs. visceral fat, visceral fat vs. HSI, and HSI vs. relative liver glycogen, respectively) (Table III.6). In the Rupert strain, the condition factor was the only trait with significant genetic variance but no significant covariance was observed between body mass and condition factor ($COV_A = -0.01$).

Table III. 5 : Estimates of heritability ($h^2 \pm$ SE) and additive genetic variance ($V_A \pm$ SE) for the condition factor and the different energy reserves related traits in the three populations. Significant additive genetic variance estimates from the likelihood ratio test are in bold.

	domestic		Laval		Rupert	
	h^2	V_A	h^2	V_A	h^2	V_A
Condition factor	0.09 ± 0.10	0.001 ± 0.001	**0.32 ± 0.17**	**0.005 ± 0.003**	**0.50 ± 0.31**	**0.0044 ± 0.0035**
Visceral fat	**0.56 ± 0.25**	**0.481 ± 0.290**	**0.31 ± 0.17**	**0.340 ± 0.217**	0 ± 0	0 ± 0
Muscle water	**0.29 ± 0.18**	**0.256 ± 0.178**	0.03 ± 0.06	0.188 ± 0.472	0 ± 0	0 ± 0
HSI	**0.20 ± 0.14**	**0.024 ± 0.019**	**0.26 ± 0.15**	**0.021 ± 0.014**	0.05 ± 0.11	0.003 ± 0.006
Liver glycogen	0.08 ± 0.09	74.83 ± 88.07	**0.42 ± 0.20**	**164.90 ± 98.71**	0.11 ± 0.14	71.48 ± 96.78
Liver protein	0 ± 0	0 ± 0	0.01 ± 0.06	2.50 ± 11.63	0 ± 0	0 ± 0
Liver lipid	0.06 ± 0.08	8.46 ± 11.98	0.13 ± 0.11	10.18 ± 0.01	0 ± 0	0 ± 0
Total energy	**0.90 ± 0.29**	**1.973 ± 1.120**	0.04 ± 0.07	0.001 ± 0.002	0.06 ± 0.11	0.004 ± 0.008

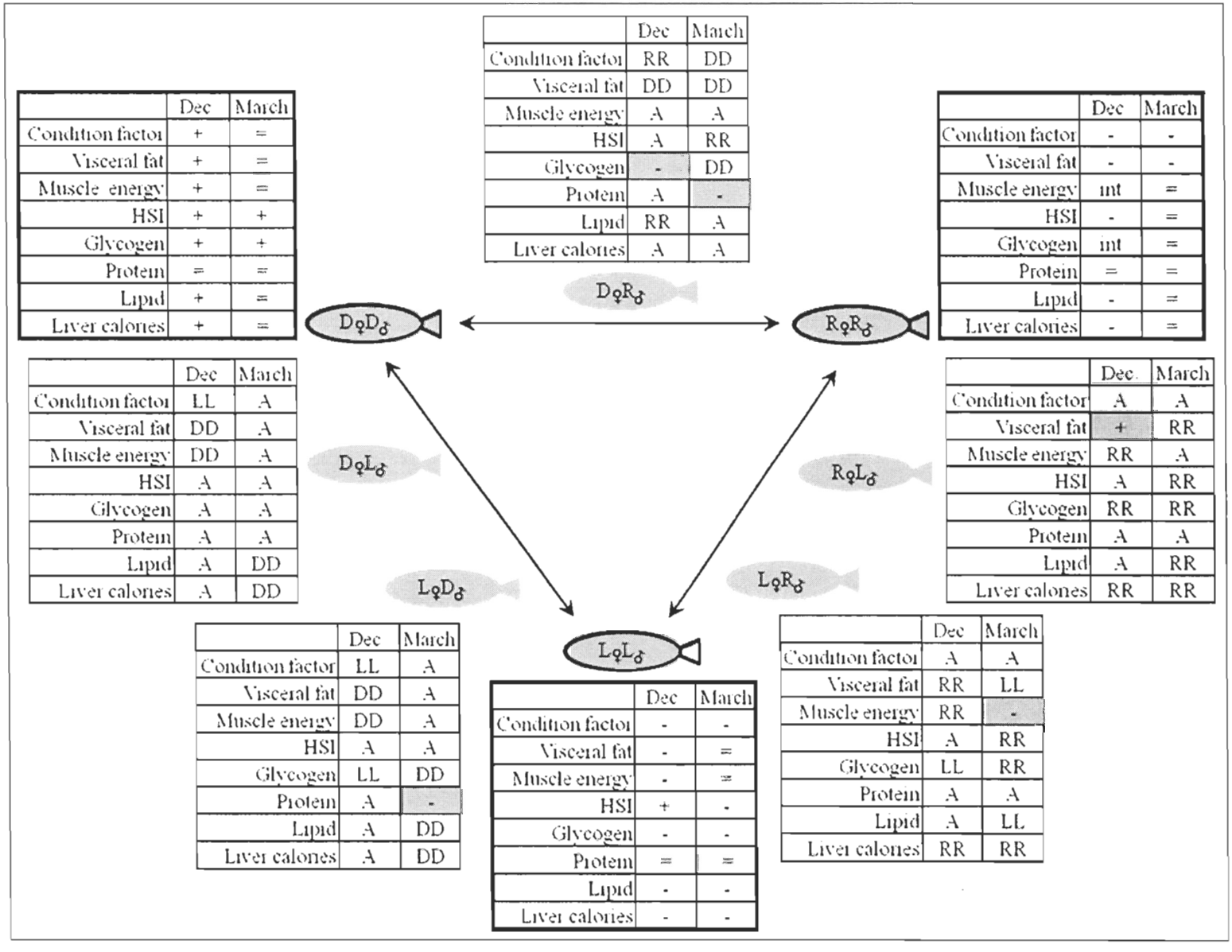
Table III. 6 : Estimates of genetic (below diagonal) and phenotypic (above diagonal) correlations with standard error (± SE) and genetic covariance (in italic below diagonal and genetic correlations) for body mass, condition factor and the different energy reserves for which heritabilities were significant in all strains. Significant genetic covariances (from the likelihood ratio test) are in bold and asterisks indicate marginally non-significant covariances.

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

DISCUSSION

The main objective of this study was to investigate the genetic basis of energy accumulation and mobilization in three strains of brook charr and their hybrids. These three strains did not undergo differential winter mortality. They all coped with winter conditions using different energy strategies: accumulation of high energy reserves before winter, the use of liver energy during winter, or the use of visceral fat (Fig. III.2). An additive genetic basis was present for traits related to body condition and energy storage/use in the domestic and the Laval strains but not in the Rupert, and it seems that each strain had its own genetic architecture underlying energy reserves. In hybrids, the occurrence of non-additive effects was overall very low.

The different strains had different energy strategies to support winter temperature constraints. Domestic fish accumulated high amount of energy reserves before winter and kept accumulating liver glycogen during winter despite lower amount of food being available compared to the others seasons. Hepatic glycogen reserves play an important role in fish metabolism, and glycogen is the first form of energy that is being accumulated after starvation (Rios *et al.*, 2006; Heermann *et al.*, 2009). Therefore, the domestic strain seemed to be relatively unaffected by low winter temperature conditions. Laval fish had accumulated low energy reserves by the onset of winter and seemed to have suffered energy costs during the coldest months since their condition factor had decreased by March. However, Laval fish are anadromous and anadromous fish have generally a low condition factor and are more streamlined than freshwater fish (Morinville & Rasmussen, 2008). Therefore, the condition factor decrease during winter may represent the cost of a limited energy storage prior to winter. On the other hand, anadromous fish overwinter away from their main feeding area and therefore may be not adapted to feed and accumulate energy during winter. It should be noted that mortality was not greater in Laval fish than in the other cross-types surveyed. During winter, the strategy of the Laval fish was thus to mobilize liver glycogen and lipids which resembles to the general pattern of energy mobilization during starvation or limited energy intake in fishes (golden perch, *Macquaria*



	Dec	March
Condition factor	+	=
Visceral fat	+	=
Muscle energy	+	=
HSI	+	+
Glycogen	+	+
Protein	=	=
Lipid	+	=
Liver calories	+	=

	Dec	March
Condition factor	RR	DD
Visceral fat	DD	DD
Muscle energy	A	A
HSI	A	RR
Glycogen	-	DD
Protein	A	-
Lipid	RR	A
Liver calories	A	A

	Dec	March
Condition factor	-	-
Visceral fat	-	-
Muscle energy	int	=
HSI	-	=
Glycogen	int	=
Protein	=	=
Lipid	-	=
Liver calories	-	=

	Dec	March
Condition factor	LL	A
Visceral fat	DD	A
Muscle energy	DD	A
HSI	A	A
Glycogen	A	A
Protein	A	A
Lipid	A	DD
Liver calories	A	DD

	Dec	March
Condition factor	A	A
Visceral fat	+	RR
Muscle energy	RR	A
HSI	A	RR
Glycogen	RR	RR
Protein	A	A
Lipid	A	RR
Liver calories	RR	RR

	Dec	March
Condition factor	LL	A
Visceral fat	DD	A
Muscle energy	DD	A
HSI	A	A
Glycogen	LL	DD
Protein	A	-
Lipid	A	DD
Liver calories	A	DD

	Dec	March
Condition factor	-	-
Visceral fat	-	=
Muscle energy	-	=
HSI	+	-
Glycogen	-	-
Protein	=	=
Lipid	-	-
Liver calories	-	-

	Dec	March
Condition factor	A	A
Visceral fat	RR	LL
Muscle energy	RR	-
HSI	A	RR
Glycogen	LL	RR
Protein	A	A
Lipid	A	LL
Liver calories	RR	RR

Figure III. 2 : Summary schema of energy reserves accumulated in December (Dec.) and their use during winter (March) in the three purebred strains (bold) and their hybrids. In purebred strains: for December, "+" indicates significantly more energy than in the others strains, "-" significantly less, "=" indicates similar energy, and "int" intermediate energy compared to the others strains; for March, "+" indicates significantly more energy in March than in December, "-" significantly less, and "=" indicates no difference. In hybrids, "A" indicates intermediate energy compared to parental lines (i.e., additive effects), "DD" or "LL" or "RR" indicates dominance of the parental line mentioned and grey highlight indicates non-additive effects, with "+" (or "–") when the hybrid outperformed (or underperformed) both parental lines.

ambigua, Collins & Anderson, 1995; Traira, *Hoplias malabaricus*, Rios *et al.*, 2006). In contrast, the strategy of the Rupert fish, which also had relatively low energy reserves accumulated by the end of autumn, was to mobilize visceral fat during winter. A similar preferential use of visceral fat has been seen in starved gilthead seabream (*Sparus auratus*; Ibarz *et al.*, 2010).

These different strategies seemed to be, at least in part, under genetic control. Additive genetic effects have been observed in energy reserves and, when significant, heritabilities varied from medium to high (about 0.20 to 0.90). The genetic basis of liver energy reserves is documented here for the first time (h^2 from 0 to 0.90 depending on the strain and the energy reserve type). For the other traits (i.e., condition factor, muscle water content, visceral fat), our significant estimates were in the upper range of heritability estimates documented in various cultured fish (condition factor: 0.10-0.20; muscle water content: 0.09-0.36; visceral fat: 0.18-0.68 in gilthead seabream, *Sparus auratus*, Navarro *et al.*, 2009; coho salmon, *Oncorhynchus kisutch*, Neira *et al.*, 2004 ; sea bass, *Dicentrarchus labrax*, Saillant *et al.*, 2009 ; rainbow trout, *O. mykiss*, Tobin *et al.*, 2006). This may be partially due to our full-sib design, which will overestimate the additive genetic variance by including other variance sources (common environment or maternal variance, and some portion of dominance variance) (Falconer & Mackay, 1996; Perry *et al.*, 2004a). However, most of the studies mentioned above also used full-sib families to estimate heritabilities. In addition, genetic correlations for some of the traits measured in the present study were consistent with those previously observed in gilthead seabream and sea bass for which estimates varied from low to highly significant depending on the traits (r_G between condition factor and muscle water content: -0.27 to 0.51; r_G between condition factor and visceral fat: 0.69-0.87; r_G between muscle water content and visceral fat: 0.08 to 0.11, Navarro *et al.*, 2009; Saillant *et al.*, 2009).

Energy reserves related-traits were therefore generally heritable in brook charr, but each strain had its own genetic basis characteristics. In the strategies of the domestic and Laval strains, energy reserves had heritable genetic basis while the strategy of the Rupert

strain did not. Moreover, the domestic and the Laval strains had their own combination of heritability in their energy reserve related-traits (significant heritability for visceral fat, muscle water content, HSI and total liver energy for the domestic strain while the Laval strain had significant heritability for condition factor, visceral fat, HSI and liver glycogen). The three strains showed also their own pattern of genetic correlations among the heritable traits measured. These three strains then expressed three different global genetic basis which indicate that they were quite divergent in their genetic architecture related to energy. The only other study which compared genetic basis in energy related-traits did not find differences between two populations of Coho salmon, *O. kisutch,* produced for aquaculture (Neira *et al.*, 2004).

Such divergence in genetic architecture and strategies in energy accumulation and mobilization can be potentially attributed to the adaptive response to distinct natural environments (Collins & Anderson, 1995; Hurst, 2007; Binner *et al.*, 2008). The Laval strain is anadromous and originates from a population that migrates from freshwater in winter for reproduction to saltwater in summer for feeding. The Rupert strain originates from a northern lacustrine population subjected to harsh winter conditions. The domestic strain was reared under artificial environments with mild general conditions for about 100 years. Fluctuations in food abundance and winter conditions in these three environments could thus have influenced the strategies of energy storage and metabolism among strains to deal with seasonal changes and local patterns (Collins & Anderson, 1995; Hurst, 2007; Finstad *et al.*, 2010). Such differences had also been observed among populations on a latitudinal cline and therefore could evolve in response to the environment, either through adaptive phenotypic plasticity or genetic drift (Schultz & Conover, 1997; Hurst, 2007; Stelkens *et al.*, 2009). In addition, the differences in gene expression due to local adaptations to a specific habitat can create variations in the genetic architecture and induce genetic divergence (Wilson *et al.*, 2003; Jensen *et al.*, 2008).

Surprisingly, no additive genetic basis related to the use of energy reserves were found in the Rupert strain. The lower number of families studied in this strain may have

partially caused the absence of significant effect. However, significant heritability was found for one trait, and then other factors may explain the absence of heritable genetic basis. As heritability is an indicator of the relative importance of genes and environment in the variation of traits (Visscher *et al.*, 2008), its absence may suggest that environmental effects are mainly involved in the observed phenotypic variation of energy reserves related-traits in this strain. Alternatively, the additive genetic variance of traits submitted to strong selection pressure for a long period of time could highly be reduced due to fixation of beneficial alleles (Uller *et al.*, 2002; Teplitsky *et al.*, 2009). In the Rupert strain, the absence of heritability could then also reflect adaptation of this trait.

We observed a very limited occurrence of non-additive effects in hybrids. Non-additive effects that have been reported in hybrids mostly occur when parental lines are divergent and adapted to their own environments (Stelkens *et al.*, 2009). In the present study, the purebred strains showed strong divergence in their genetic architecture and thus non-additive effects should be expected, especially outbreeding depression (Bieri & Kawecki, 2003). Outbreeding depression occurs in first generation when the genetic composition of populations diverges and hybrid formation disrupts gene complex associations (Cooke *et al.*, 2001; Tymchuk *et al.*, 2007; Stelkens *et al.*, 2009). Bieri and Kawecki, (2003) indicated that, in presence of genetic divergence, a low occurrence of non-additive effects may suggest the absence of divergent evolution in coadapted gene complexes. Other effects related to genetic architecture (e.g., pleitropy or other genetic linkage) should be explored to explain these results.

In contrast to March, in December, hybrids showed more frequently intermediate or similar performance to their parental lines in energy reserves related-traits for which significant heritability was found. This was irrespective to the cross direction and suggests that the genetic control of energy reserves is more important for energy accumulation than for energy mobilization. Other studies have suggested that energy reserves stored before winter are one of the main factors involved in winter resistance (rainbow trout, *O. mykiss*, Biro *et al.*, 2004; perch, *P. fluviatilis*, Eckmann, 2004; Huss *et al.*, 2008). This could

explain why we found a closer genetic relationship with energy accumulation. On the other hand, energy reserves related-traits which had no significant heritability also seemed to influence some of the hybrids' performance. For example, hybrids between the Laval and the Rupert line expressed more dominance for the Rupert traits while these traits did not show significant additive variance. In these cases, the genetic basis of parental lines did not seem to reflect the phenotypic variation of hybrids. Even though the knowledge of the genetic basis of phenotypes had increased recently, the link between genotypes and phenotypes is still a black box (Rasmuson, 2002). Some others mechanisms may have participated to modify the phenotypic expression. However, this hypothesis requires further investigations.

In general, the different strategies adopted to limit winter costs are typically linked to the size of individuals (Cargnelli & Gross, 1997). In the present study, this does not seem to be the case as significant correlations with mass were found only in the domestic population. Our results were obtained under laboratory conditions (i.e., indoors, food given twice a week), which are relatively mild conditions during winter. In natural conditions, winters are harsher (lower food availability, ice cover, etc.). Starvation is one of the main causes of energy depletion and mortality in fish (Post & Evans, 1989; Schultz *et al.*, 1998; Eckmann, 2004; Rios *et al.*, 2006; Hurst, 2007). Studies that compared groups of fish with and without feeding revealed that there was more mortality and energy depletion in absence of feeding (Biro *et al.*, 2004; Pangle *et al.*, 2004; Huss *et al.*, 2008; Heermann *et al.*, 2009). In our study, the absence of starvation may thus explain the absence of mortalities in presence of different strategies of energy use. As charr production in Québec is essentially aimed at supporting recreational fisheries through stock enhancement, a similar study done under natural (and harsher) conditions could permit to have a better knowledge of the different winter resitance of the three strains and thus be of great economic interest.

CONCLUSION

In summary, the genetic regulation of energetic strategies to cope with winter constraints is complex. Each strain studied had its own phenotypic strategy controlled by its

own genetic architecture, which seemed to be related to local adaptations to distinct environments. On the other hand, in the presence of such genetic divergence, the absence of non-additive effects in hybrids suggests the absence of divergent evolution of the genetic basis and therefore would point out to the presence of genetic complex associations in energy processes. In addition, parental heritable traits were mainly observed in hybrids during pre-winter energy accumulation. This would suggest a more rigid genetic control on energy accumulation than on energy utilization. The different energy strategies of these strains could result from local adaptation but this deserves further investigations.

CHAPITRE 4

ANALYSES DE LA GÉNÉTIQUE QUANTITATIVE DE LA RÉPONSE PHYSIOLOGIQUE AU STRESS CHEZ TROIS SOUCHES D'OMBLES DE FONTAINE (*SALVELINUS FONTINALIS*) ET LEURS HYBRIDES

RÉSUMÉ

La sélection pour la résistance au stress a été identifiée comme un des principaux objectifs des programmes d'amélioration génétique dans la production de poisson. Cependant, peu d'études ont cherché à comprendre comment l'hétérosis (la vigueur hybride) pouvait être utilisée pour améliorer cette performance. Trois souches d'omble de fontaine (*Salvelinus fontinalis*) et leurs hybrides réciproques, ont été soumis à un stress de transport afin d'évaluer leur résistance au stress. Les réponses primaires (cortisol) et secondaire (glucose, osmolalité, et hématocrite) de stress ont été mesurées pour chaque croisement. Une forte héritabilité a été observée pour les deux niveaux de réponses : $h^2 = 0.60$ ($\pm$ 0.20) pour la concentration de cortisol plasmatique et 0.61 ($\pm$ 0.20) pour celle de glucose. La souche Rupert s'est avérée être la moins sensible au stress aux deux niveaux de réponses. Un effet hétérosis a été observé seulement pour l'osmolalité plasmatique de l'hybride $D_{♀}R_{♂}$ qui a augmenté après l'exposition au stress (variation 6 fois plus grande que celle des lignées parentales). De la dépression de croisement a aussi été observée chez cet hybride, avec une augmentation de 27% de la concentration de glucose plasmatique, et chez l'hybride $R_{♀}L_{♂}$ avec une diminution de l'osmolalité plasmatique 5 fois plus importante comparativement aux lignées parentales. L'hybridation a donc montré un effet limité et même négatif sur la résistance au stress chez cette espèce. Ces résultats indiquent que l'utilisation de lignées pures a un bon potentiel pour l'amélioration génétique de la réponse au stress mais que l'hybridation ne semble pas être une voie prometteuse.

Ce quatrième article, intitulé « *Quantitative genetic analysis of the physiological stress response of three brook charr (Salvelinus fontinalis) strains and their hybrids* », a été corédigé par moi-même ainsi que par ma directrice Céline Audet, et mes codirecteurs Louis Bernatchez et Dany Garant. Il va être soumis dans peu de temps dans *Journal of Fish Biology*. Ma contribution à ce travail a été l'essentiel de la recherche sur l'état de l'art, la mise au point et l'exécution du plan d'expérience, l'ensemble des analyses en laboratoires, des analyses statistiques et de génétique quantitative, ainsi que l'interprétation des résultats et la rédaction de l'article. Céline Audet a aidé à la mise au point de l'expérience, à la coordination de la recherche et à l'écriture du manuscrit. Louis Bernatchez a participé à la révision de l'article. Dany Garant a aidé à la réalisation des analyses de génétique quantitative et à la révision de l'article. Tous les auteurs ont lu et approuvé le manuscrit pour la soumission. Une version abrégée de cet article a été présenté au *Forum Québécois en Sciences de la mer* à Rimouski à l'automne 2009.

QUANTITATIVE GENETIC ANALYSIS OF THE PHYSIOLOGICAL STRESS RESPONSE OF THREE BROOK CHARR (SALVELINUS FONTINALIS) STRAINS AND THEIR HYBRIDS

ABSTRACT

Selection for stress resistance has been identified as a target for genetic improvement in fish production. However, few studies have investigated how heterosis (i.e., hybrid vigor) could be used to improve this trait. Three strains of brook charr (*Salvelinus fontinalis*) and their reciprocal hybrids were submitted to transport stress to measure stress resistance. Primary (cortisol) and secondary (glucose, osmolality, and haematocrit) stress responses were measured for each cross. High heritabilities were observed for both levels of stress response, with $h^2 = 0.60$ (± 0.20) for plasma cortisol and 0.61 (± 0.20) for plasma glucose. The Rupert strain appears to be the least sensitive to stress at the primary and secondary levels. Heterosis was observed only once: we found very low variation in plasma osmolality in the $D_{♀}R_{♂}$ hybrid (6 times more variation than in the parental strains). Outbreeding depression was also present in this hybrid, with a 27% increase of plasma glucose, and in the $R_{♀}L_{♂}$ hybrid with a decrease in plasma osmolality that was 5 times more pronounced than in parental strains. Thus hybridization has a limited or negative impact on stress resistance in this species. These results indicate a strong potential for genetic improvement in the stress response with the use of purebred crosses while hybridization does not seem promising.

KEYWORDS:

Stress resistance; heterosis; heritability; brook charr

INTRODUCTION

During aquaculture and stocking activities, fish are faced with several potential stressors. Capture and handling procedures, a highly crowded and confined farming environment, possible air exposure, variation in water quality, and transportation activities are all factors that may increase the stress level of organisms (Barton & Iwama, 1991; Iwama *et al.*, 1999; Barton, 2002; Hur *et al.*, 2007). Such stressors may disturb the organism's homeostatic equilibrium, and fish need to compensate by physiological and biochemical changes (Barton & Iwama, 1991; Iwama *et al.*, 1999; Barton, 2002). Three main levels of stress response have been identified (Barton & Iwama, 1991; Iwama *et al.*, 1999; Barton, 2002). The primary neuroendocrine response involves the release of stress hormones—catecholamines and cortisol—into the blood. Biochemical and physiological secondary responses are associated with the release of stress hormones that activate metabolic pathways resulting in the modification of blood chemistry and hematology, including a rapid release of glucose to provide sufficient energy, changes in osmolarity, and lysozyme activity. Finally, tertiary whole-organism and population responses are characterized by changes in the energy supply to the different biological pathways and in population productivity (Barton & Iwama, 1991; Iwama *et al.*, 1999; Barton, 2002), resulting in negative impacts on growth rate, reproductive success, disease and parasite resistance, saltwater tolerance, and survival (Barton & Iwama, 1991; Fevolden *et al.*, 1991; Pickering, 1993; Barton, 2002; Davis, 2006; Liebert & Schreck, 2006). Therefore, fish with reduced stress response may have an advantage in farming conditions compared to more stress-prone individuals (Fevolden *et al.*, 1991, 1993; Pickering, 1993).

Differences in the intensity of the stress response have been reported among families and strains of rainbow trout (*Oncorhynchus mykiss*) and Atlantic salmon (*Salmo salar*), among strains of fighting fish (*Betta splendens*), and among species of tilapia (*Oreochromis* spp.), guppy (*Poeciliopsis* spp.), and charrs (*Salvelinus* spp.) (Bulger & Schultz, 1982; Fevolden *et al.*, 1991; McDonald *et al.*, 1993; Pottinger & Moran, 1993; Cnaani *et al.*, 2004; Verbeek *et al.*, 2008). For example, brook charr (*Salvelinus fontinalis*) are less

sensitive to transport and net confinement stress (reduced ion loss) compared to lake trout (*Salvelinus namaycush*) (McDonald *et al.*, 1993). Furthermore, quantitative genetic studies have revealed a moderate to high degree of heritability of the cortisol response for different fishes including carp (*Cyprinus carpio*, 0.60, Tanck *et al.*, 2001) and rainbow trout (*O. mykiss*, 0.56 for North American lines, Weber *et al.*, 2008; 0.50 for European lines, Fevolden *et al.*, 2002). Given such additive genetic components, stress resistance—and more specifically variation in stress-induced cortisol concentration—has been identified as a trait of interest for genetic improvement (Fevolden *et al.*, 1991; Lankford & Weber, 2006). However, studies using selective breeding programs for disease resistance or growth that aim to improve fish performance via a lower cortisol response have met with limited success thus far (Lankford & Weber, 2006; Weber & Silverstein, 2007).

Another approach that can be considered for the genetic improvement of physiological traits is the production of hybrid crosses that may result in heterosis (i.e., hybrid vigor), which is the improved performance of first generation progeny compared to parental lines (Falconer & Mackay, 1996). Heterosis is the most important non-additive effect on cross performance and is usually stronger when parental lines are genetically distant from each other (Shikano *et al.*, 2000; Wang & Xia, 2002). This phenomenon is now being used in improvement schemes concerning traits of interest in aquaculture, including growth rate, survival, and salinity tolerance (Bentsen *et al.*, 1998; Shikano & Taniguchi, 2002a; Bryden *et al.*, 2004; Hena *et al.*, 2005). Until now, very few studies have investigated the importance of heterosis on stress response in fish (Campbell *et al.*, 1998; Bryden *et al.*, 2004).

The main objective of this study was to test for the occurrence and to quantify the importance of heterosis in the physiological stress response by comparing three pure strains of brook charr and their F1 hybrids. More specifically, the effects of stress induced by transportation, a common activity in aquaculture that often results in mortality and one of the most stressfull events in brook charr production, were investigated. A second objective was to estimate heritability values for primary (plasma cortisol) and secondary (plasma

glucose, plasma osmolality and haematocrit) stress indicators for the first time in brook charr and to compare the observed values with other fishes. In this way, we planned to evaluate the relative merits of hybrid crosses and selective breeding for improving the response of brook charr to stress in an aquaculture context.

MATERIALS AND METHODS

Brook charr strains

Three genetically distinct strains of brook charr (Martin *et al.*, 1997) were used as parental lines. The Laval strain originates from a wild population of anadromous brook charr from the Laval River (48°44′N; 69°05′W) on the north shore of the St. Lawrence Estuary (QC, Canada). The fish used were third generation breeders reared in captivity at the Station aquicole ISMER/UQAR (Rimouski, QC, Canada). The Rupert strain originates from a freshwater resident wild population inhabiting the Rupert River system (51°05′N; 73°41′W) (QC, Canada). The fish used as breeders were also from the third generation produced in captivity at the Laboratoire régional en sciences aquatiques (LARSA, Université Laval, Québec, QC, Canada). The third group was a domestic strain largely used by the Québec fish farming industry. It originates from two strains (Nashua and Baldwin), and breeders were obtained from the Pisciculture de la Jacques Cartier (Cap-Santé, QC, Canada). The two wild strains were selected for breed improvement because adults from these populations exhibit late sexual maturation and large adult size.

Breeding design

Hybrid and purebred crosses were made from mid-November to the end of December 2005 at LARSA using eggs and milt obtained from the different fish rearing locations. Three purebred crosses were produced: ♀ domestic × ♂ domestic ($D_{♀}D_{♂}$), ♀ Laval × ♂ Laval ($L_{♀}L_{♂}$) and ♀ Rupert × ♂ Rupert ($R_{♀}R_{♂}$). Five hybrid and reciprocal hybrid crosses were also produced: $D_{♀}R_{♂}$, $D_{♀}L_{♂}$, $L_{♀}D_{♂}$, $L_{♀}R_{♂}$, and $R_{♀}L_{♂}$. It was not possible to obtain the $R_{♀}D_{♂}$ cross because of the long time lag in sexual maturation between these two strains (October for the domestic males and December for the Rupert females). All breeders were used only once. For each cross, 10 full-sib families were obtained through single-pair mating, but 8 of these 80 families were eliminated due to the limited number of individuals that could be pooled in each tank.

Family rearing

During the first six months, i.e., from egg incubation (January) to exogenous feeding (June), families were kept separate in recirculated fresh water. Water temperature was maintained at 6°C during egg incubation and at 8°C after hatching. All families were brought to 2136 degrees-days by the end of the summer and maintained at 10°C in recirculated fresh water. Photoperiod followed the natural seasonal cycle, and fish were fed according to commercial charts. In September, fish were transferred to the Station aquicole ISMER/UQAR where they were reared under natural temperature and photoperiod conditions in running dechlorinated fresh water. Fish were fed daily (1% w/w ration) with commercial dry pellets.

Stress exposure

A simulation of fish transfer procedures in transport bags was conducted in June 2007 to induce stress in 16-month-old fish. Twenty fish per cross were used for this experiment. The fish were captured in tanks, and we tried to have equal numbers of fish from the different families within each cross-type. Each transport bag (diameter: 30 cm; length: 100 cm) contained ten fish that were kept in 1/3 dechlorinated fresh water and 2/3 compressed oxygen (total number of bags: 16; total number of fish: 160). Transportation bags were kept in the dark and shaken every 30 min for 10 s. Fish were maintained in the bags for a total of 4 h, which is long enough to induce an intense stress response in brook charr (McDonald *et al.*, 1993). After 4 h, the bags were put into fresh water to let the temperature gradually decrease to the tank temperature and fish were then sampled. Twenty fish per cross were also sampled directly from fish tanks and used as controls. No mortality was observed in transport bags or rearing tanks during the experiment.

Sampling procedures

All samplings were made between 16:00 and 19:00 to avoid bias due to endocrine circadian rhythms. Stressed and control fish were anaesthetized in MS 222 (0.16 g L^{-1} [3-aminobenzoic acid ethyl ester]) and their body mass (to the nearest 0.1 g) and fork length

(0.1 cm) were measured (Tables IV.1 and IV.2). Blood was collected by caudal puncture using ammonium-heparinized syringes. A small quantity of blood was transferred to capillary tubes for haematocrit determination and the remainder was centrifuged at 7200*g* for 3 min. The plasma was drawn off, quickly frozen in liquid nitrogen, and then stored at -80°C until analysis. Plasma osmolality was measured with an Advanced Micro-osmometer 3MO, plasma glucose was measured by enzymatic determination (Alexander & Griffiths, 1993), and cortisol levels were measured using a cortisol ^{125}I RIA kit (MP Biomedicals, Orangeburg, NY, USA).

Statistical analyses

Data normality and homogeneity of variance were tested with Kolmogorov-Smirnov and Brown-Forsythe tests, respectively. Plasma cortisol concentrations were log transformed to obtain normality. The different variables were analyzed using two-way ANOVAs with cross-type, stress treatment, and stress treatment × cross-type interaction as fixed effects. The effect of dam and sire origin (domestic, Laval or Rupert) on each physiological variable after stress exposure was analyzed using two-way ANOVAs with dam and sire origin as factors. The presence of heterosis or outbreeding depression was determined by the presence of a significant difference between the mean performance of hybrids compared to the mean performance of both parental strains (Bryden *et al.*, 2004). Heterosis was expressed when there was a lower stress response in hybrids. A posteriori Tukey tests were used for mean comparisons when possible or replaced by Games and Howell tests when variances were not homogenous. The influence of fish mass on variables was examined using mass as a covariate in ANCOVAs. Analyses were made using Statistica 6.0 version for Windows (StatSoft, Tulsa, OK, USA). A significance level of $\alpha = 0.05$ was used in all statistical tests.

Heritability analyses

Our breeding design was used to fit animal models (Lynch & Walsh, 1998) with the ASReml software (V2.0; Gilmour *et al.*, 2006). Univariate analyses were used to

Table IV. 1 : Total mass (g) and length (cm) of the three purebred strains (bold) and their hybrids used as controls or for the stress challenge. Mean ± SE; n is the number of individuals; different letters indicate significant differences among cross-types ($\alpha = 0.05$).

	Control			Stressed		
Cross	n	mass	length	n	mass	Length
D♀R♂	20	41.87 ± 2.07^{de}	15.69 ± 0.25^{c}	20	49.26 ± 4.16^{de}	16.53 ± 0.43^{c}
D♀D♂	**20**	$\mathbf{58.24 \pm 5.48^{e}}$	$\mathbf{16.63 \pm 0.49^{c}}$	**20**	$\mathbf{61.53 \pm 5.25^{e}}$	$\mathbf{17.25 \pm 0.49^{c}}$
D♀L♂	20	37.82 ± 3.47^{cd}	15.02 ± 0.45^{bc}	20	39.12 ± 4.02^{cd}	15.38 ± 0.45^{bc}
L♀D♂	20	33.36 ± 2.39^{cd}	14.73 ± 0.34^{bc}	20	45.39 ± 4.05^{cd}	16.41 ± 0.41^{c}
L♀L♂	**26**	$\mathbf{15.59 \pm 1.01^{a}}$	$\mathbf{11.94 \pm 0.29^{a}}$	**30**	$\mathbf{14.03 \pm 0.70^{a}}$	$\mathbf{11.49 \pm 0.18^{a}}$
L♀R♂	20	24.48 ± 2.09^{bc}	13.56 ± 0.39^{ab}	20	31.85 ± 3.23^{bc}	14.93 ± 0.53^{bc}
R♀L♂	20	23.91 ± 2.25^{b}	13.53 ± 0.36^{ab}	20	21.27 ± 1.72^{b}	13.13 ± 0.33^{ab}
R♀R♂	**21**	$\mathbf{22.75 \pm 1.50^{b}}$	$\mathbf{13.20 \pm 0.28^{ab}}$	**20**	$\mathbf{22.42 \pm 1.48^{b}}$	$\mathbf{13.23 \pm 0.28^{b}}$

Table IV. 2 : Summary of two-way ANOVAs for body mass and length. df is degrees of freedom; MS is mean square; F is the F-ratio.

	Mass (g)				Length (cm)			
	df	MS	F	*P*-value	df	MS	F	*P*-value
Stress treatment	1	633.0	1.6	> 0.1	1	21.4	7.3	< 0.01
Cross-type	7	9455.7	49.9	< 0.001	7	137.2	46.6	< 0.001
Stress treatment × Cross-type	7	278.4	1.5	> 0.1	7	6.5	2.2	< 0.05
Error	321	189.4			321	2.9		
Model R^2	0.53				0.52			
Adjusted R^2	0.51				0.50			

decompose the phenotypic variance (V_P) of each trait for the whole fish population (including pure and hybrids crosses) into their additive genetic (V_A) and residual (V_R) variances. The model was the following:

$$y = \mu + C + A + e$$

where y is the phenotypic observation, μ is the overall mean, C is the fixed effect of the cross-type, A is the random additive genetic effect, and e is the random residual effect. The narrow-sense heritability (h^2) for each trait was estimated as the ratio of the additive genetic variance (V_A) to the total phenotypic variance (V_P): $h^2 = V_A/V_P$. The statistical significance of the additive genetic component for each trait was tested by re-running a restricted model where the additive variance was set to zero and then comparing the difference the in log-likelihood ratio between the original and the constrained model against the chi-square distribution (df = 1), where χ^2 = -2*difference in log likelihood.

RESULTS

Plasma cortisol response

We noted a stress response in every cross-type, as shown by a significant increase in cortisol between control and stressed fish (Table IV.3; Fig. IV.1). However, the intensity of the cortisol response was highly variable depending on the cross, with significant interactions observed between stress treatment and cross-types (Table IV.3; Fig. IV.1). All control fish had the same level of initial plasma cortisol (Fig. IV.1). The stress treatment in purebred crosses induced a significantly lower cortisol response in the Rupert fish than in Laval and domestic fish (Fig. IV.1A). In hybrids, when the Rupert strain was used as either dam or sire, an intermediate increase in cortisol was observed compared to parental lines (Fig. IV.1B; IV.1D). In crosses involving the domestic and the Laval strains, all hybrids and parental lines showed similar cortisol responses (Fig. IV.1C). These results are indicative of an additive response rather than a non-additive effect. Mass had no significant effect on this trait (Table IV.3).

Secondary stress response indicators

A significant interaction was observed between stress treatment and cross-type for glucose concentration (Table IV.3). Plasma glucose concentrations were similar for all controls (Fig. IV.2) while they were significantly higher after stress exposure in all cross-types (Table IV.3; Fig. IV.2). The glucose response was similar among the three purebred lines (Fig. IV.2A), and hybrids showed concentrations similar to their parental lines (Fig. IV.2C; IV.2D). The only exception was the D♀R♂ hybrid, which had a significantly higher glucose concentration after than before stress exposure (Fig. IV.2B), hence expressing outbreeding depression. Glucose concentration was 27% higher in this hybrid after stress exposure compared to the average glucose concentration in parental lines. There was no significant co-factor effect for mass (Table IV.3).

Table IV. 3 : Summary of two-way ANOVAs for cortisol, glucose, osmolality, and haematocrit. df is degrees of freedom; MS is mean square; F is the F-ratio.

	Cortisol ($\mu g\ dl^{-1}$)				Glucose ($mg\ ml^{-1}$)			
	df	MS	F	*P*-value	df	MS	F	*P*-value
Mass (co-variable)	1	0.2	1.7	> 0.1	1	0.2	2.2	> 0.1
Stress treatment	1	108.6	1132.0	< 0.001	1	28.4	410.8	< 0.001
Cross-type	7	0.2	2.2	< 0.05	7	0.3	4.2	< 0.001
Stress treatment × Cross-type	7	0.2	2.2	< 0.05	7	0.2	2.3	< 0.05
Error	300	0.1			289	0.1		
Model R^2	0.80				0.62			
Adjusted R^2	0.79				0.60			
	Osmolality ($mosm\ kg^{-1}$)				Haematocrit (%)			
	df	MS	F	*P*-value	df	MS	F	*P*-value
Mass (co-variable)	1	468.0	8.7	< 0.01	1	0.03	7.9	< 0.01
Stress treatment	1	127.0	2.4	> 0.1	1	0.02	6.4	< 0.01
Cross-type	7	303.0	5.6	< 0.001	7	0.01	1.9	> 0.05
Stress treatment × Cross-type	7	431.0	8.0	< 0.001	7	0.01	2.3	< 0.05
Error	274	54.0			278	0.01		
Model R^2	0.29				0.14			
Adjusted R^2	0.25				0.09			

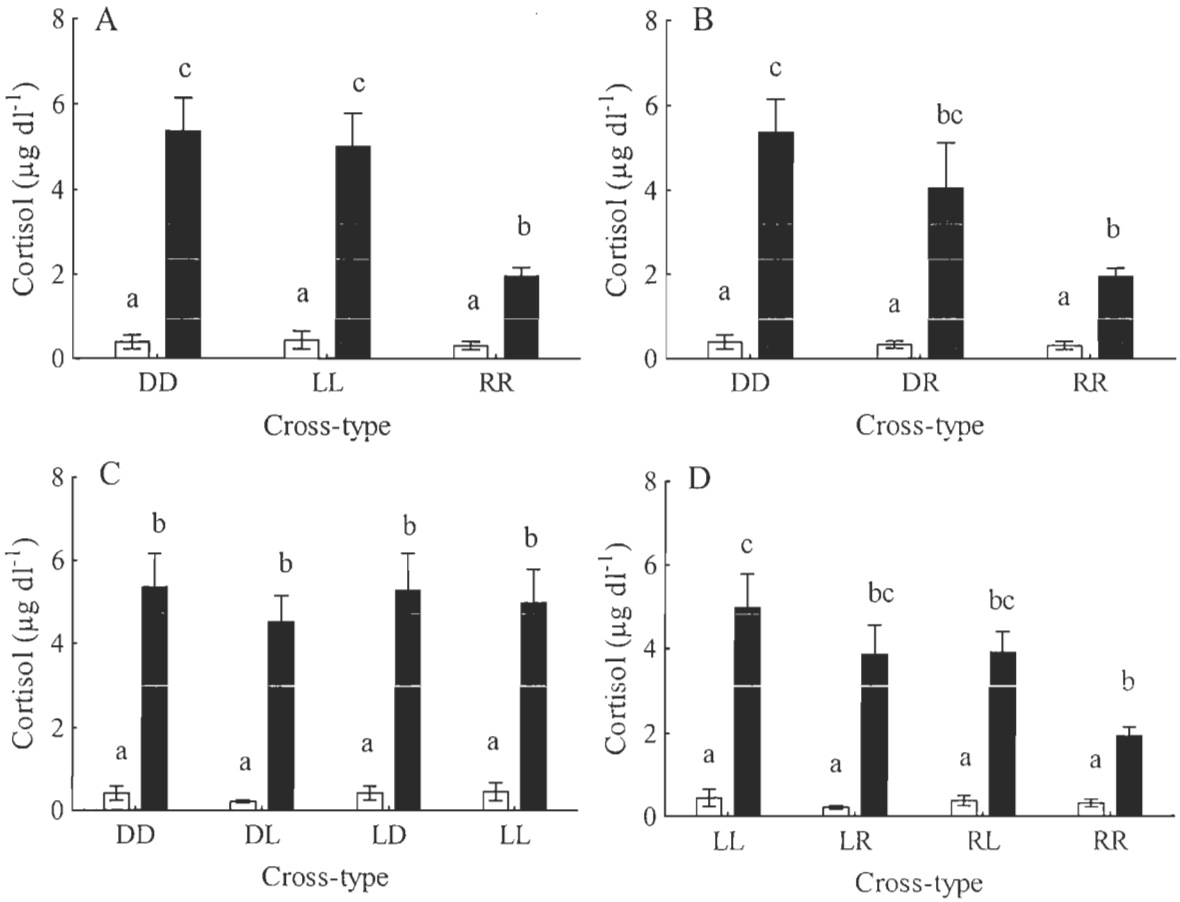


Figure IV. 1 : Cortisol (µg dl^{-1}) stress response in the three purebred strains (A) and hybrids between (B) domestic and Rupert strains, (C) domestic and Laval strains, and (D) Laval and Rupert strains. The first letter of the cross-type indicates the dam and the second letter the sire. Open bars are for controls and solid bars for stressed. Statistical analyses were made on log-transformed data but results are presented as mean ± SE. Different letters indicate significantly different means ($\alpha = 0.05$).

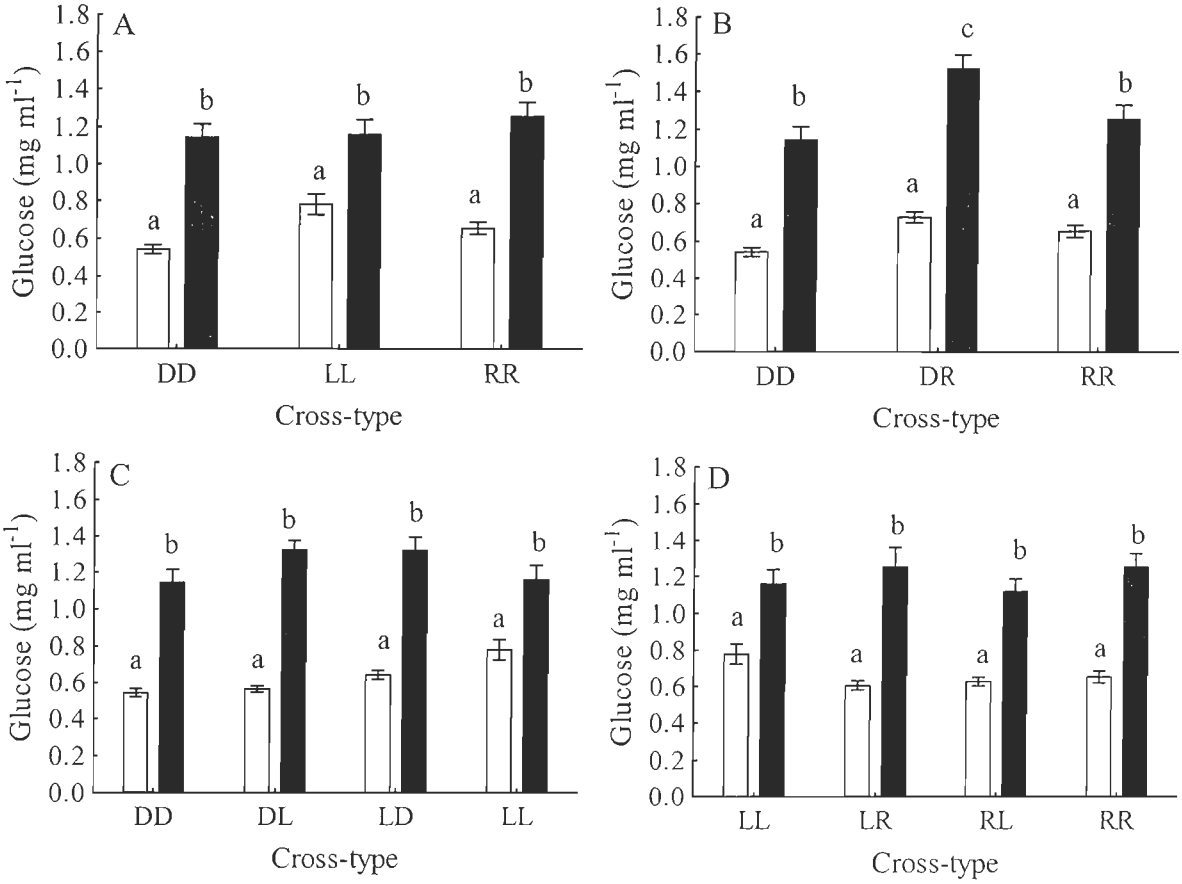


Figure IV. 2 : Plasma glucose (mg ml^{-1}) stress response in the three purebred strains (A) and hybrids between (B) domestic and Rupert strains, (C) domestic and Laval strains, and (D) Laval and Rupert strains. The first letter of the cross-type indicates the dam and the second letter the sire. Open bars are for controls and solid bars for stressed. Mean ± SE. Different letters indicate significantly different means ($\alpha = 0.05$).

A significant interaction was observed between stress treatment and cross-type in the plasma osmolality response to transport stress (Table IV.3; Fig. IV.3). In purebred lines, controls were not different (Fig. IV.3A). Following stress exposure, Laval fish had a significant higher plasma osmolality than controls while osmolality did not vary in the two other purebred lines (Fig. IV.3A). Pre-stress levels of plasma osmolality were similar to both parental lines in the $D_{♀}R_{♂}$ and $D_{♀}L_{♂}$ hybrids (Fig. IV.3B and IV.3C), similar to the Laval line in the $L_{♀}D_{♂}$ hybrid (Fig. IV.3C), and similar to the Rupert line in hybrids between the Rupert and the Laval lines (Fig. IV.3D). After stress exposure, heterosis was expressed in plasma osmolality in one hybrid: the $D_{♀}R_{♂}$ hybrid had a significant increase in plasma osmolality while no change was observed in the parental lines (Fig. IV.3B). The increase was about 6 times higher than the average osmolality change in parental lines. However, outbreeding depression was also observed in one other hybrid: the $R_{♀}L_{♂}$ hybrid had a decrease in plasma osmolality, a response significantly different from those of both parental lines (Fig. IV.3D). The decrease was about 5 times more pronounced than the average change observed in parental lines. No change was observed in osmolality in the $L_{♀}R_{♂}$ hybrids, similarly to the Rupert line (Fig. IV.3D) and hybrids between the domestic and the Laval strains behaved similarly to their maternal strain (Fig. IV.3C). The interaction between stress treatment and cross-type was significant for the blood haematocrit response (Table IV.3). Blood haematocrit was similar among controls and increased only in the domestic line after stress exposure (Fig. IV.4). For both plasma osmolality and blood haematocrit, the mass co-factor was significant (Table IV.3) but correlations were weak ($r = 0.15$ for both).

Heritability

Significant additive genetic variance and heritability were obtained at both stress response levels for the whole population. Heritability estimates for cortisol ($h^2 = 0.60 \pm 0.20$) and glucose ($h^2 = 0.61 \pm 0.20$) following stress exposure were high and significant (Table IV.4) while estimates were not significant for osmolality ($h^2 = 0 \pm 0$) and haematocrit ($h^2 = 46 \pm 0.25$) (Table IV.4).

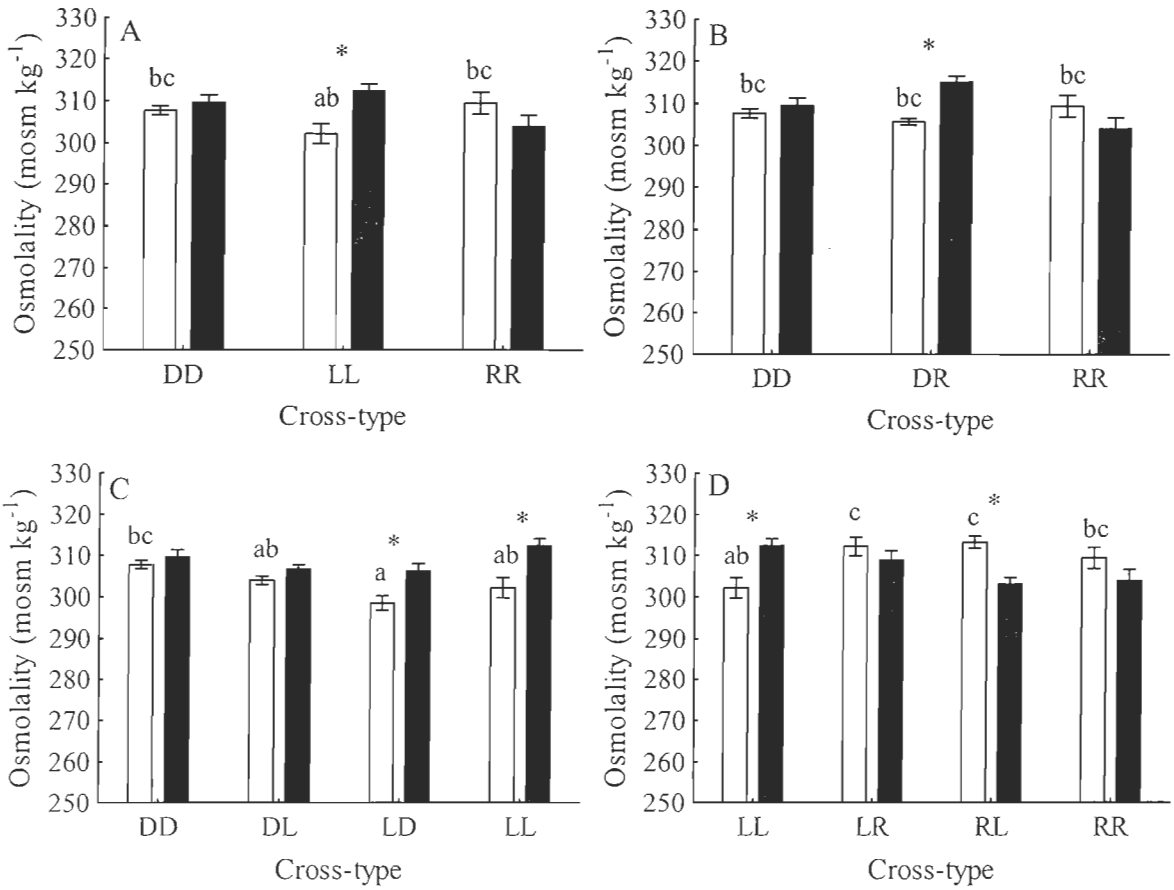


Figure IV. 3 : Osmolality (mosm kg^{-1}) stress response in the three purebred strains (A) and hybrids between (B) domestic and Rupert strains, (C) domestic and Laval strains, and (D) Laval and Rupert strains. The first letter of the cross-type indicates the dam and the second letter the sire. Open bars are for controls and solid bars for stressed. Mean ± SE. Different letters indicate significantly different means among controls and asterisks indicate significantly different means between control and stressed ($\alpha = 0.05$).

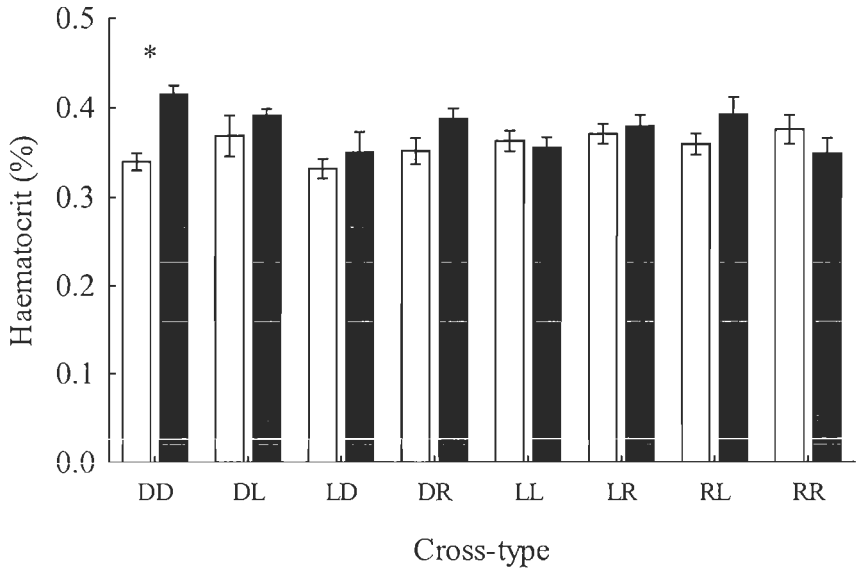


Figure IV. 4 : Haematocrit (%) stress response in the three purebred strains and their hybrids. The first letter of the cross-type indicates the dam and the second letter the sire. Open bars are for controls and solid bars for stressed. Mean ± SE. Asterisks indicate significantly different means between control and stressed ($\alpha = 0.05$).

Parental origin effects

Dam and sire origin significantly affected the stress response depending on the trait (Table IV.5). As was the case for heritability, the parental origin effect was strong for cortisol (Table IV.5). However, the results for the secondary response show different tendencies (Table IV.5). There were significant effects of both dam and sire origin in the cortisol response. Fish issued from the Rupert strain had lower plasma cortisol than other fish (Table IV.5). No significant dam or sire effect were observed for the glucose response (Table IV.5). There was a significant dam origin effect on the osmolality and haematocrit stress responses (Table IV.5). Progeny of Rupert dams had lower plasma osmolality following stress exposure than progeny of the other two strains when used as dams, and progeny of Laval dams had lower haematocrit after stress exposure than when domestic dams were used.

Table IV. 4 : Genetic components of the different traits in the stress responses. Estimates of total phenotypic (V_P), additive (V_A), and residual (V_R) variance components and heritability (h^2) with their standard errors (± SE); n is the number of individuals. *P*-values were obtained from a likelihood ratio test.

	n	V_P	V_R	V_A	h^2	*P*-value
Cortisol	159	0.14 ± 0.03	0.06 ± 0.02	0.08 ± 0.04	0.60 ± 0.20	< 0.05
Glucose	158	0.17 ± 0.04	0.07 ± 0.02	0.11 ± 0.06	0.61 ± 0.20	< 0.05
Osmolality	148	58.92 ± 7.04	58.92 ± 7.04	0	0	> 0.1
Haematocrit	146	0.004 ± 0.001	0.002 ± 0.001	0.002 ± 0.002	0.46 ± 0.25	> 0.1

Table IV. 5 : Dam and sire origin effects on the different traits after stress exposure. Physiological traits are expressed as mean ± SE. Different letters indicate significant differences among cross-types ($\alpha = 0.05$); *P*-value indicates the significance level.

	Dam				Sire			
	domestic	Laval	Rupert	*P*-value	domestic	Laval	Rupert	*P*-value
Cortisol ($\mu g\ dl^{-1}$)	4.64 ± 0.48^b	4.71 ± 0.46^b	2.89 ± 0.31^a	< 0.05	5.32 ± 0.58^b	4.48 ± 0.38^b	3.28 ± 0.44^a	< 0.01
Glucose ($mg\ ml^{-1}$)	1.33 ± 0.04	1.24 ± 0.05	1.19 ± 0.05	> 0.05	1.23 ± 0.05	1.21 ± 0.04	1.34 ± 0.05	> 0.05
Osmolality ($mosm\ kg^{-1}$)	310.42 ± 0.94^b	309.05 ± 1.14^b	303.52 ± 1.47^a	< 0.01	307.87 ± 1.25	307.57 ± 0.96	309.85 ± 1.33	> 0.05
Haematocrit (%)	0.40 ± 0.01^b	0.37 ± 0.01^a	0.37 ± 0.01^{ab}	< 0.01	0.39 ± 0.01	0.38 ± 0.01	0.37 ± 0.01	> 0.1

DISCUSSION

Our main objectives were to investigate the occurrence of heterosis and to estimate the heritability of primary and secondary stress indicators in brook charr. While our results indicate only little evidence of heterosis, relatively high heritability was found for endocrine and physiological responses. A third objective was to compare the stress response between strains of brook charr. Inter-strain differences in cortisol levels have been previously reported in rainbow trout (*O. mykiss*), Atlantic salmon (*S. salar*), and fighting fish (*B. splendens*), where the stress cortisol response varied by 1.25 to 2 times when the most sensitive population is compared to the least sensitive one (Fevolden *et al.*, 1991; Pottinger, 2006; Verbeek *et al.*, 2008). Our results indicate a similar range, with the Rupert strain response being about half those of the other purebred strains.

Purebred lines

As previously indicated based on the primary and secondary stress responses, the Rupert strain was less sensitive to stress while the Laval strain seemed to be the most sensitive. Indeed, only the Laval strain showed an osmoregulatory disturbance, which suggests severe stress (Davis, 2006). The domestic strain was the only one to show an increase in haematocrit, which may reflect a need for oxygen to compensate stress (Casillas & Smith, 1977). Some studies have revealed an impact of growth selection on stress performance, with a greater response to stress challenge and a longer stress recovery in heavier fish (Casillas & Smith, 1977; Lankford & Weber, 2006; Weber & Silverstein, 2007), while others observed no such correlations (Fevolden *et al.*, 1991; Millot *et al.*, 2009). Here, only weak correlations were present between mass and either primary or secondary stress responses, indicating a weak link and therefore a limited effect of body mass in the stress resistance in brook charr.

Non-additive genetic effects

There was no evidence for the influence of non-additive components on the cortisol response; this is similar to findings from studies on other species (channel catfish, *Ictalurus*

punctatus, Bosworth *et al.*, 2004; Chinook salmon, *Oncorhyncus tshawytsha*, Bryden *et al.*, 2004). Studies on hybrids have rarely provided evidence of non-additive effects, but they generally focused on survival or cortisol response (Bulger & Schultz, 1982; Bosworth *et al.*, 2004; Bryden *et al.*, 2004). However, heterosis related to survival time (tertiary response) was reported in F1 hybrids after salinity stress in *Poecilia reticulate* (Chiyokubo *et al.*, 1998) and heat stress in *Poeciliopsis monacha-occidentalis* (Bulger & Schultz, 1982).

A weak but significant non-additive component was present at the physiological level (secondary response), especially for plasma osmolality in $D_{♀}R_{♂}$ and $R_{♀}L_{♂}$ hybrids, but also for plasma glucose concentration in the $D_{♀}R_{♂}$ hybrid. The presence of non-additive components in hybrids generally indicates genetic divergence between the parental strains (Falconer & Mackay, 1996; Tymchuk *et al.*, 2007). Our observations of non-additive components only at the secondary level of response reveal the presence of genetic divergence in purebred strains at the physiological level rather than a neuroendocrine response to stress stimuli. The extents of non-additive genetic phenomena are also thought to be principally linked to the genetic distance between parental lines. If the lines are too genetically distant or adapted to their own environment, hybrids can show outbreeding depression with a breakdown of genetic complex associations; on the other hand, when the genetic distance between parental strains is closer, hybrids can express heterosis (Falconer & Mackay, 1996; Shikano *et al.*, 2000; Cooke *et al.*, 2001). Our results do not support these expectations according to genetic distance: (1) the Laval and Rupert strains were the most genetically distant strains (Martin *et al.*, 1997), and only one of their hybrids ($R_{♀}L_{♂}$) expressed outbreeding depression for osmolality; and (2) the $D_{♀}R_{♂}$ hybrid expressed either outbreeding depression (glucose) and heterosis (osmolality) while the two parental lines were more genetically similar. The results obtained on other hybrids do not support the hypothesis that the genetic distance would be the main effect involved in non-additive expression in our crosses. Other effects related to genetic architecture (e.g., epistasis, pleitropy, or genetic linkage) should be explored to explain our results. Overall, the presence of non-additive genetic effects only in secondary stress responses along with the

greater occurrence of outbreeding depression compared to heterosis suggest that the use of hybrids to improve stress resistance in aquaculture has limited potential.

Additive genetic effects

The primary response to stress, i.e., cortisol response, seems to be principally under additive genetic control. The plasma cortisol concentration in hybrids was always intermediate to that of parental lines. Both dam and sire origin significantly affected this trait, indicating the importance of an additive genetic basis underlying this stress response. Other studies on hybrids also revealed additive effects on plasma cortisol level after exposure to stress: Bryden *et al.* (2004) exposed wild and farm Chinook salmon (*O. tshawytscha*) hybrids and purebred crosses to an "aerial emersion" stressor, and the cortisol response in hybrids was equal to both parental lines. The high additive component for cortisol regulation is supported by the high heritability estimate for this trait ($h^2 = 0.60 \pm 0.20$). The cortisol response to stress is already used for genetic improvement in selection programs on other fish species, especially in rainbow trout (*O. mykiss*), in which heritability lower than here has been found in the F1 generation (h^2 ranging from 0.41 to 0.56 depending on strain origin) (Pottinger & Carrick, 1999; Fevolden *et al.*, 2002; Overli *et al.*, 2005; Weber & Silverstein, 2007; Weber *et al.*, 2008). The selection procedure was based on the mean post-stress plasma cortisol response across five episodes of confinement stress testing on parental lines, with the highest responding (HR) or lowest responding (LR) individuals used to produce the next generation. This breeding program was repeated several times to obtain F2 and F3 generations in order to improve stress resistance and other possible related traits like growth or desease resistance (Pottinger & Carrick, 1999; Overli *et al.*, 2005; Ruiz-Gomez *et al.*, 2008). Our results suggest that such a program could also be applied in brook charr.

For the secondary stress response, plasma glucose concentration also displayed significant heritability estimates. This trait had high heritability ($h^2 = 0.61 \pm 0.20$), which is higher than values reported in previous studies on androgenetic carp (*C. carpio*, 0.19; Tanck *et al.*, 2001), Atlantic salmon (*S. salar*, 0.03; Fevolden *et al.*, 1993), and rainbow

trout (*O. mykiss*, 0.07; Fevolden *et al.*, 1993). The low heritability observed in carp could be related to the androgenetic design, i.e., the UV irradiation and heat shock treatment might induce additional environmental variation due to embryonic damage caused by the androgenetic shock treatment and therefore reduce heritability (Tanck *et al.*, 2001). On the other hand, our own estimates could have been inflated due to our full-sib design (Pante *et al.*, 2002). Nevertheless, the high heritability observed in brook charr may indicate high inter-species variations for the regulation of plasma glucose. No significant heritability was found for osmolality or haematocrit response. Until now, no study has documented the heritability of osmolality variations related to stress resistance, but a very low heritability for haematocrit was reported in clonal lines of ayu (*Plecoglossus altivelis*, 0.072; DelValle *et al.*, 1996).

In summary, the high heritability of stress response at both the primary (cortisol) and secondary levels (glucose) indicates good potential for selective breeding and improvement of stress resistance in brook charr through selection programs. The Rupert strain is particularly of interest in this regard. However, hybridization does not seem a promising avenue to improve stress resistance in brook charr.

DISCUSSION GÉNÉRALE

CONTRIBUTIONS DE L'ÉTUDE

Dans un premier temps, je me suis intéressée aux bases génétiques additives de différentes performances d'intérêt pour l'aquaculture de l'omble de fontaine, soit la croissance, l'absence de maturation sexuelle précoce, la survie, la mobilisation d'énergie durant l'hiver et la résistance au stress. J'ai alors pu mettre en évidence que la majorité des traits mesurés présentaient effectivement une base génétique additive, et que ces traits sont donc transmissibles. Avec une estimation d'héritabilité modérée à élevée (croissance : 0,20 à 0,80, réserves énergétiques : 0,20 à 0,90, résistance au stress : 0,60 à 0,61 selon le trait ou les souches), les composantes génétiques additives tiennent une place importante dans le contrôle des performances chez l'omble de fontaine et représentent une composante majeure dans l'évolution possible de ces performances. L'héritabilité de l'absence de maturation sexuelle précoce et de la survie n'a cependant pas pu être estimée car une seule mesure par famille a été obtenue pour ces traits. Néanmoins, l'observation des résultats phénotypiques a montré que les hybrides présentaient également un contrôle génétique additif important pour ces performances, tous les hybrides présentant des performances intermédiaires aux lignées parentales. Toutes ces performances ont donc une base génétique très héritable. L'omble de fontaine semble alors capable de transmettre efficacement des performances d'intérêt et donc de répondre à une sélection ou de s'adapter à un changement.

J'ai également mis en évidence que chaque souche peut avoir sa propre réponse à la sélection en explorant, séparément pour chacune d'elles, les différentes bases génétiques. En effet, les résultats présentés dans les différents chapitres de cette thèse (chapitres 2 et 3 surtout) montrent que les souches présentent des capacités phénotypiques qui leur sont

propres pour chaque performance et que ces capacités sont de plus contrôlées par une héritabilité (variance additive) et une architecture génétique spécifique à chacune des souches. Les résultats confirment donc la théorie voulant que les mesures d'héritabilité soient propres à chaque population, même au sein d'une espèce, contrairement à ce que souligne Visscher *et al* (2008). Ces derniers estiment en effet que les mesures d'héritabilités sont généralement identiques entre populations ou espèces proches. Il existe donc une grande divergence phénotypique et génétique entre les trois souches d'omble de fontaine, leur conférant des capacités évolutives différentes. L'isolement dans la nature entre les populations utilisées pour créer souches a eu lieu il y a environ 10 000 ans (Castric & Bernatchez, 2003). Un intervalle similaire a conduit à des divergences entre populations d'épinoche, *Gasterosteus aculeatus*, (Spoljaric & Reimchen, 2007) mais on sait que la divergence peut survenir dans un temps beaucoup plus court (Roberge *et al.*, 2006). Il semble donc nécessaire, dans le futur, de documenter les capacités d'une population spécifique ou alors de plusieurs populations d'une espèce pour connaitre les possibilités d'adaptation d'intérêt car il est difficile de généraliser ce que l'on retrouve chez une population à toute l'espèce.

Les résultats ont aussi permis de mettre en évidence un effet global de la domestication. La souche domestique est une souche qui a été maintenue en environnement d'élevage depuis 100 ans mais qui n'a jamais subie de sélection dirigée. Pourtant, cette souche a des capacités phénotypiques et génétiques complètement différentes des deux autres souches. La domestication a eu un effet sur sa croissance (nettement supérieure) et sur les bases génétiques de la croissance (héritabilité très élevée dans les deux environnements), mais aussi sur la maturation sexuelle (plus précoce), sur la mobilisation des réserves hivernales (stratégie spécifique d'accumulation d'énergie à l'automne qui continue durant l'hiver) et sur les bases génétiques de la mobilisation des réserves hivernales (architecture génétique spécifique). Chez d'autres salmonidés, le saumon atlantique et la truite brune, *Salmo trutta*, un effet de la domestication a également été observé sur la croissance (plus grande) en une centaine d'année (Petersson *et al.*, 1996). Des études récentes ont montré qu'une sélection artificielle peut modifier l'expression

génétique de plusieurs performances en seulement quelques générations comme chez le saumon atlantique (Roberge *et al.*, 2006), la truite arc-en-ciel (Tymchuk *et al.*, 2009), ou l'omble de fontaine (Sauvage *et al.*, 2010). Cependant, cette thèse révèle également qu'une simple domestication (sans sélection dirigée) peut modifier l'expression phénotypique de nombreux traits ainsi que leur contrôle génétique relativement rapidement.

Je me suis également intéressée aux effets non-additifs à savoir s'il était possible d'obtenir un effet hétérosis en croisant des populations génétiquement divergentes d'omble de fontaine, la présence de cet effet chez les salmonidés étant encore très controversée. En examinant toutes les performances, j'ai pu mettre en évidence qu'il existait effectivement un effet hétérosis chez l'omble de fontaine. Cependant, cet effet hétérosis est très variable et dépend de nombreux facteurs (souches parentales, orientation des souches, ontogenèse, environnement ; cf. chapitre 1). Néanmoins, notre étude a confirmé que la distance génétique entre les souches était un critère important pour l'obtention d'hétérosis et que l'utilisation d'hybrides entre populations d'une même espèce représente un éloignement génétique favorable à son expression comme Stelkens *et al*, (2009) l'avaient également démontré sur les cichlidés.

Un autre facteur qui pourrait influencer l'expression d'hétérosis dans les croisements est l'effet de la famille. Dans chacun des croisements j'ai étudié plusieurs familles plein-frères. Un effet spécifique des familles sur l'expression d'hétérosis est difficile à mettre en évidence car le concept d'hétérosis correspond à une comparaison entre un croisement hybride et ses lignées parentales. Cependant, j'ai observé une variabilité entre les familles avec pour certaines une masse similaire aux lignées parentales alors que d'autres présentaient une masse significativement supérieure. Il semblerait alors que les familles peuvent avoir un rôle important dans l'expression d'hétérosis d'un croisement. D'autres études ont d'ailleurs également montré un effet des familles dans l'expression d'hétérosis (Moav & Wohlfarth, 1976; Klupp, 1979). Même si, pour le moment, cet effet des familles est assez peu étudié, il serait intéressant de le prendre en compte et de l'examiner plus en profondeur, peut être par l'utilisation de marqueurs génétiques au niveau individuel qui

permettraient d'évaluer la distance d'apparentement entre les deux géniteurs. Il serait alors possible de réaliser des croisements entre individus génétiquement différents ce qui favoriserait l'expression d'hétérosis et aiderait également au maintien d'une grande variabilité génétique dans les populations.

Après avoir constaté la présence d'hétérosis pour la croissance, je me suis demandée s'il existait un lien avec les réserves énergétiques, à savoir s'il existait plus de réserves chez les hybrides (hétérosis) ce qui pourrait expliquer leur masse plus élevée. En effet, la croissance chez les poissons est définie comme étant une augmentation des contenus énergétiques du corps entrainant donc un gain de masse (Jobling, 1993). Cependant, un tel lien n'a pas été mis en évidence. Les hybrides qui présentaient de l'hétérosis pour la masse ne montraient pas d'hétérosis pour les réserves d'énergie. Cette observation est en accord avec des études précédentes sur les bases physiologiques de l'hétérosis qui expliquent que l'hétérosis interviendrait plus par l'équilibre des capacités des hybrides que par une capacité particulière des hybrides (Ahmadzadeh *et al.*, 2004; Tollenaar *et al.*, 2004). Il serait néanmoins intéressant de poursuivre l'étude des bases physiologiques de l'hétérosis chez les poissons en explorant de nouvelles pistes comme les processus enzymatiques de la conversion d'énergie. Des différences à ce niveau pourraient alors être une explication plausible du gain de masse chez les hybrides. L'énergie ne serait alors pas stockée mais directement utilisée pour la croissance des individus. L'étude des capacités enzymatiques de diverses voies métaboliques chez les hybrides présentant de l'hétérosis pourrait aider à mieux comprendre les bases physiologiques de ce phénomène.

Les résultats indiquent clairement que l'effet hétérosis n'était pas présent pour toutes les performances étudiées. Cet effet était principalement observé dans la croissance. La présence d'un effet hétérosis uniquement pour ce trait alors que les autres performances sont plus contrôlées par des effets additifs suggère que les trois lignées ont plus divergé au niveau du contrôle génétique de la croissance que du contrôle génétique des autres traits. La croissance semble donc avoir subi une pression de sélection particulière dans les environnements spécifiques de chaque souche, conduisant peut-être à la fixation d'allèles

différents. Ces résultats confirment que la divergence génétique entre populations se produit davantage sur des performances variables et particulièrement exposées à la sélection naturelle (tels que les traits morphométriques) plutôt que sur des traits liés à la valeur d'adaptation. Une différence d'expression d'hétérosis entre performances a également été observée chez d'autres espèces de poissons comme le guppy (Nakadate *et al.*, 2003) et le saumon chinook (Bryden *et al.*, 2004). L'expression de l'effet hétérosis est donc très imprévisible et il est alors nécessaire de vérifier son existence pour chaque performance d'intérêt et pour chacun des croisements.

Finalement, je me suis intéressée aux effets de l'environnement et nous avons montré qu'il existait effectivement des effets non négligeables de l'environnement sur l'expression des caractères phénotypiques et de leurs bases génétiques. J'ai observé que l'environnement peut modifier aussi bien les effets génétiques additifs que non-additifs dans l'expression de la croissance chez l'omble de fontaine. De plus, cette modification dépend du type de croisement effectué, j'ai donc mis en évidence que l'interaction gène x environnement tient une place importante dans le contrôle de ce caractère phénotypique. Chaque population peut ainsi avoir sa propre capacité d'adaptation de la croissance en réponse aux conditions environnementales. Une modification de l'environnement pourra donc conduire à une réponse imprévisible des populations autant par les effets génétiques additifs que non-additifs.

IMPLICATION POUR L'AQUACULTURE DE L'OMBLE DE FONTAINE

Dans un contexte de production, l'analyse des bases génétiques additives et non-additives est également essentielle pour connaitre les possibilités d'amélioration des performances par des programmes de sélection artificielle. Ainsi, avec l'ensemble des résultats obtenus, je peux maintenant apporter des réponses plus précises sur les capacités d'amélioration des productions d'omble de fontaine au Québec pour les différents traits selon les populations et les environnements.

- Tout d'abord, pour la croissance, chaque souche possède une héritabilité significative, donc qu'il est possible de faire de la sélection pour ce trait dans chacune des souches. Cependant, la souche domestique présente l'héritabilité la plus intéressante pour ce trait dans les deux environnements (environ 0,60) et comme cette souche est aussi celle ayant les capacités de croissance les plus fortes dans tous les environnements, elle représente la souche avec le potentiel d'amélioration le plus intéressant. Il serait alors particulièrement rentable de mettre en place des programmes de sélection basés sur les effets additifs chez cette souche. Toutefois, la présence d'effet hétérosis pour la croissance a aussi été remarquée, avec un effet stable dans le temps et les environnements chez les hybrides $L_{♀}R_{♂}$ (en moyenne 12%). Cependant, la croissance de cet hybride n'était pas plus importante que la croissance de la souche domestique. Cet effet hétérosis semble donc moins avantageux que d'utiliser les effets additifs chez les domestiques. Par contre, un effet hétérosis intéressant chez l'hybride $L_{♀}D_{♂}$ a également été observé. Cet hybride présentait des capacités de croissance supérieures à celles de la lignée domestique, dans l'environnement à température constante (hétérosis supérieur à 10%). L'effet hétérosis de cet hybride semble alors plus rentable à utiliser que les effets additifs chez la souche domestique dans un environnement à température constante. Pour utiliser un tel effet sur le long terme, il serait alors important de maintenir les deux lignées parentales comme stock de géniteurs, mais utiliser des productions d'hybrides F1 pour les fins commerciales.

- Pour l'absence de maturation sexuelle précoce, l'héritabilité n'a pas été mesurée, mais les différences phénotypiques semblent transmissibles. Pour cette performance, ce sont les souches Rupert et Laval qui présentent un avantage car elles montrent très peu de maturation précoce à 1+ quel que soit l'environnement d'élevage. Il semble alors possible de faire de la sélection pour ce trait dans ces souches.

- Pour les réserves énergétiques, les trois souches ont des stratégies différentes pour supporter les conditions hivernales mais seules les stratégies des souches Laval et domestique ont des bases génétiques transmissibles. Les hybrides ne présentent pas d'effets non-additifs. Il semble donc possible de faire de la sélection basée sur les effets additifs pour ces stratégies mais uniquement pour celles des souches Laval et domestique, soit pour une consommation des réserves hépatiques durant l'hiver (souche Laval) ou pour une accumulation de réserves à l'automne (souche domestique).

- Pour la résistance au stress, les réponses primaire et secondaire du stress (niveau de cortisol et glucose plasmatique, respectivement) ont montré des bases génétiques additives significatives. Les hybrides présentaient également essentiellement des effets additifs. De plus, la souche Rupert avait une meilleure résistance au stress que les deux autres souches dans les deux niveaux de réponse. Avec ces résultats, il semble possible de faire de la sélection pour améliorer la résistance au stress chez l'omble de fontaine, surtout en utilisant la souche Rupert.

L'ensemble de ces résultats confirme qu'il est possible d'améliorer la production d'omble de fontaine sur les différentes performances étudiées. Le résumé des avantages et de l'intérêt global des différents croisements est présenté au tableau D. 1. Les effets génétiques additifs semblent cependant être globalement plus exploitables que les effets non-additifs, mais aucune souche ne combine des capacités intéressantes pour toutes les performances. Dépendamment du trait que l'on souhaite améliorer et dans quel environnement, il faudra alors choisir la souche et le programme de sélection les plus appropriés. Il semble néanmoins possible d'effectuer des améliorations sur plusieurs traits en parallèle au sein d'une même souche (Perry *et al.*, 2004b). De tels programmes ont d'ailleurs déjà révélé des résultats intéressant chez la souche Laval en montrant qu'il était effectivement possible d'améliorer la croissance tout en réduisant l'incidence de la maturation sexuelle précoce (Bastien, 2010).

Tableau D. 1 : Résumé des principaux résultats génétiques (A = les effets génétiques additifs ; NA = les effets génétiques non-additifs) obtenus pour les différentes performances d'intérêt pour chacune des souches (en gras) et les différents croisements hybrides. « + » indique la présence d'un effet génétique avantageux et « - » indique la présence d'effets génétiques désavantageux.

		$D_♀R_♂$	$\mathbf{D_♀D_♂}$	$D_♀L_♂$	$L_♀D_♂$	$\mathbf{L_♀L_♂}$	$L_♀R_♂$	$R_♀L_♂$	$\mathbf{R_♀R_♂}$
Croissance									
env. à T° variable	A		+			+			+
	NA	-		-	-		+	+	
env. à T° constante	A		+			+			+
	NA	-		-	+		+	-	
Maturation sexuelle	A		-			+			+
	NA	-		-	-		+	+	
Réserves énérgétiques	A		+			+			-
	NA	-		-	-		-	-	
Résistance au stress	A		-			-			+
	NA	-		-	-		-	-	
Intérêt global		Faible	**Important**	Faible	Limité	**Important**	Notable	Limité	**Important**

PERSPECTIVES

Dans cette thèse, j'ai montré qu'il existait une importante héritabilité dans l'expression des performances, indiquant que l'omble de fontaine est capable de répondre à une sélection directe sur un trait. Cependant, le potentiel d'évolution d'une performance ne dépend pas simplement des bases génétiques du trait, mais aussi parfois des corrélations génétiques avec d'autres traits, par sélection indirecte (Falconer & Mackay, 1996). Des corrélations génétiques significatives et des sélections indirectes ont déjà été mentionnées pour plusieurs traits chez les salmonidés. Dans les milieux contrôlés, une amélioration de la résistance aux maladies via des programmes de sélection sur le cortisol a été suggérée (Fevolden *et al.*, 1991) et une amélioration possible de la qualité de la carcasse via une sélection pour la masse a déjà été soulignée (Quinton *et al.*, 2005; Kause *et al.*, 2007). En milieu naturel, le choix d'une stratégie de vie anadrome ou résidente est corrélé génétiquement avec la taille (Thériault *et al.*, 2007b). Il serait alors intéressant d'étudier plus en profondeur les corrélations génétiques entre les traits en plus de l'héritabilité de chacun pour avoir une vision plus globale du potentiel évolutif des populations.

Les estimations d'héritabilités dans cette thèse ont été réalisées à partir d'un plan de croisement basé sur des familles plein-frère (« full-sibs ») puisque que le projet prévoyait 9 croisements et 10 familles par croisement, ce qui était déjà assez complexe à réaliser. Le problème avec ce type de plan de croisement est qu'il est difficile d'obtenir une héritabilité non biaisée, les biais potentiels étant confondus dans l'effet des familles (effet de l'environnement proche, effets maternels, ou de dominance) (Falconer & Mackay, 1996; Perry *et al.*, 2004a). L'utilisation d'un plan de croisement en demi-frère (« half-sibs ») ou rectangulaire (beaucoup de mâles pour quelques femelles) serait alors plus approprié (Blanc, 2003). Les prochaines études sur l'héritabilité de performances devraient préférentiellement choisir ce genre de plan de croisement.

Le plan de croisement plein frère limite aussi l'estimation des effets non-additifs car les effets de dominance ne peuvent pas être estimés et les composantes d'épistasie sont ignorées (Blanc, 2003). L'utilisation d'un plan de croisement rectangulaire présenterait

alors un intérêt pour mesurer l'importance des effets non-additifs dans le contrôle génétique des performances. Il pourrait également donner des informations importantes sur les bases génétiques de la formation d'hétérosis car il permet de les décomposer. Ainsi, il aurait été possible de savoir laquelle des trois hypothèses (dominance, sur-dominance, épistasie) intervient dans l'expression d'hétérosis pour la croissance des ombles de fontaine. Avec les donnéesque j'avais, je n'ai pas pu répondre à cette question pour le moment. Cependant, Bougas *et al.*, (2010) ont réussi à montré par des analyses d'expression génétique que l'effet hétérosis était plus lié à un effet de dominance dans les croisements au cours des premiers stades de vie. Une alternative existe néanmoins pour mesurer de manière plus directe les bases de l'effet hétérosis. Wu & Li, (2002) ont démontré qu'il est possible de déterminer l'importance relative de chacune des hypothèses à l'aide de calculs relativement simples basés sur les mesures phénotypiques. Il serait alors très intéressant de faire ces calculs sur les données pour avoir notre propre réponse à cette question centrale sur les bases génétiques de l'hétérosis.

Dans ces chapitres, j'ai aussi montré que parfois les résultats sur les performances des hybrides ne correspondaient pas toujours aux résultats attendus sur la base des composantes génétiques additives ou non-additives estimées ou par rapport aux distances génétiques entre les souches. Il semblerait que d'autres phénomènes génétiques comme la pléiotropie (l'influence d'un gène sur plusieurs traits), l'épistasie (les interactions entre gènes) ou des processus épigénétiques (les modifications d'expression de gènes sans modification des séquences d'ADN) pourraient intervenir pour modifier le lien entre le génome et le phénotype. Des études sont actuellement en cours sur des générations F2 faites à partir de nos croisements d'omble de fontaine pour essayer de mieux comprendre ces mécanismes génétiques.

CONCLUSION

L'objectif général de cette thèse était de documenter les bases génétiques additives et non-additives ainsi que les interactions avec l'environnement afin de mieux comprendre le potentiel évolutif de différentes populations d'omble de fontaine. J'ai pu mettre en évidence que l'expression phénotypique de cette espèce était contrôlée par des interactions gènes x environnement (surtout pour la croissance), interactions qui impliquent aussi une base génétique additive importante. Cette thèse a également mis clairement en évidence que l'hétérosis était un phénomène présent chez l'omble de fontaine même s'il dépend de nombreux facteurs. J'ai aussi montré l'existence d'une divergence entre les populations sur le contrôle des phénotypes et donc que les capacités d'adaptation de l'omble de fontaine sont spécifiques à chaque population. Enfin, j'ai expliqué comment toutes ces nouvelles connaissances peuvent être utilisées à des fins commerciales. Suite à ce travail, il semble donc indispensable de continuer à étudier les bases génétiques et environnementales de performances dans plusieurs populations pouvant être soumises à des pressions de sélection car l'importance de ces composantes dans le contrôle d'expression phénotypique reste imprévisible. Cette étude n'est qu'un premier pas vers la compréhension du potentiel évolutif de l'omble de fontaine et du lien qui existe entre les bases génétiques et l'expression de phénotypes. Dans le futur, il sera essentiel de continuer à explorer de nouvelles pistes afin d'avoir une image encore plus précise des processus évolutifs, à travers les corrélations génétiques, et du lien qui unit le génotype au phénotype.

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