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PERFORMANCES NATATOIRES CHEZ DEUX ÉCOTYPES D'OMBLE DE FONTAINE LACUSTRES (*SALVELINUS FONTINALIS*) : CONTRAINTES MÉTABOLIQUES ET MORPHOLOGIQUES

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AVANT-PROPOS

Ce mémoire comprend trois chapitres. Le premier chapitre est la présentation de la problématique générale du projet ainsi qu'une rétrospective de la littérature, préalablement présentée dans le cadre du séminaire 1 (ECL-6005), mise à jour. Le second et le troisième chapitre sont les articles issus de mon projet de maîtrise et soumis pour publication dans le périodique scientifique *Journal of Experimental Biology*. Le premier article compare les performances à la nage et le métabolisme de deux écotypes d'ombles de fontaine (*Salvelinus fontinalis*) et met en relation ces performances avec les variations morphologiques retrouvées chez ces écotypes. Le second article compare l'importance des voies métaboliques de production d'énergie, via l'activité de huit enzymes, chez ces mêmes deux écotypes. L'auteur de ce mémoire a été le protagoniste de toutes les étapes de la démarche scientifique, y compris la rédaction des articles.

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ANCOVA : analyse de covariance ; angl. « *analysis of covariance* »

ANOVA : analyse de variance ; angl. « *analysis of variance* »

CCO : cytochrome c oxydase

CPK : créatine phosphokinase ; angl. « *creatine phosphokinase* »

CS : citrate synthase

DFA : analyse en fonction discriminant ; angl. « *discriminant function analysis* »

GLM : modèle linéaire général ; angl. « *general linear model* »

GPT : alanine aminotransférase ; angl. « *alanine aminotransferase* »

HOAD : β-Hydroxyacyl-CoA déshydrogénase ; angl. « *β-Hydroxyacyl-CoA dehydrogenase* »

LDH : lactate déshydrogénase ; angl. « *lactate dehydrogenase* »

LL : ombles issues du croisement entre un mâle et une femelle d'écotype littoral (L)

LP : ombles issues du croisement entre un mâle littoral (L) et une femelle pélagique (P)

MANCOVA : analyse multivariée de covariance ; angl. « *multivariate analysis of covariance* »

$\dot{M}O_2$: consommation d'oxygène

$\dot{M}O_{2\,max}$: consommation d'oxygène maximale

NetCOT : coût à la nage net ; angl. « *net cost of swimming* »

PFK : phosphofructokinase

PK : pyruvate kinase

PL : ombles issues du croisement entre un mâle pélagique (P) et une femelle littorale (L)

PP : ombles issues du croisement entre un mâle et une femelle d'écotype pélagique (P)

SMR : taux métabolique standard; *angl.* « *standard metabolic rate* »

TCOT : coût total à la nage; *angl.* « total cost of transport »

TCOT(U_{opt}) : coût total à la nage à la vitesse de nage optimale ; angl. *« total cost of swimming at the optimal speed »*

U_{crit} : vitesse de nage critique ; angl. « *critical swimming speed* »

U_{opt} : vitesse de nage optimale ; angl. « *optimal swimming speed* »

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RÉSUMÉ

Introduction

Le polymorphisme trophique est commun chez les vertébrés et est particulièrement bien documenté chez les poissons. Dans les lacs de l'hémisphère nord, on retrouve des populations de poissons constituées de plusieurs formes occupant des niches trophiques distinctes. Chez l'omble de fontaine (*Salvelinus fontinalis*, Mitchill) du Bouclier Laurentien, on retrouve un polymorphisme associé à l'exploitation de niches trophiques distinctes. Un écotype (ou forme) «littoral» se retrouve en eau peu profonde et se nourrit principalement de zoobenthos. L'écotype «pélagique» se retrouve en eau plus profonde, est spécialisé dans l'exploitation de la zone pélagique et s'alimente principalement de zooplancton. Associées à ces différences d'utilisation de l'habitat, les deux écotypes démontrent des différences morphologiques : les individus littoraux sont généralement plus trapus, ont de plus longues nageoires dorsales et pectorales et un pédoncule caudal plus haut que les individus pélagiques.

Basés sur des comparaisons morphologiques interspécifiques, plusieurs auteurs suggèrent que ces différences morphologiques visent à accroître l'efficacité d'exploitation de chacun des habitats. Toutefois, les évidences expérimentales supportant cette hypothèse sont rares voir inexistantes. De plus, si les coûts d'exploitation de chacun des habitats diffèrent et que les variations morphologiques sont des adaptations visant à réduire ces coûts, d'autres adaptations sont susceptibles d'être présentes entre les écotypes. Les performances locomotrices favorisant l'acquisition de nourriture ne sont effectivement pas sous le contrôle d'un seul aspect phénotypique (ex : morphologie) mais bien le résultat de l'ensemble des traits d'un phénotype. Notamment, certaines études font ressortir l'importance du taux métabolique standard (SMR) dans la détermination des coûts à la nage. Il existe aussi une littérature abondante faisant le lien

entre l'activité enzymatique (catalyseur de réactions chimiques responsable de la production d'énergie) et les performances à la nage chez les poissons.

Dans cette étude nous avons utilisé des ombles de fontaine littoraux et pélagiques capturés en milieu naturel et élevés au laboratoire pour répondre aux objectifs suivants : (1) déterminer si les écotypes de l'omble de fontaine diffèrent dans leur performances à la nage, (2) de mettre en relation les différences morphologiques et métaboliques (représentées par la consommation d'oxygène et l'activité enzymatique) observées entre les écotypes et leur performances à la nage et (3) d'évaluer l'importance des facteurs génétiques et environmmentaux dans les performances à la nage et le métabolisme.

Matériel et méthodes

Nous avons capturé des ombles littoraux (automne 2002, $N = 9$; printemps 2003, $N = 14$) et pélagiques (automne 2002, $N = 22$) dans leur zone respective du Lac Ledoux (Réserve Mastigouche, Mauricie, Québec) à l'aide de filets maillants (ci-après ombles sauvages). Nous avons également procédé à la récolte de produits sexuels sur les frayères du même lac pour former des familles de lignées pures (3 PP et 4 LL) et d'hybrides réciproques (2 PL et 2 LP ; les lettres en majuscules indiquent respectivement l'écotype des géniteurs mâles et femelles dans les croisements d'individus pélagiques (P) et littoraux (L) ; ci-après ombles élevés au laboratoire).

Les ombles de fontaines sauvages et élevés au laboratoire ont été soumis à la nage forcée dans un respiromètre à trois températures expérimentales, soit 10, 15 et 20°C. Le système de respirométrie était constitué de 8 respiromètres (tube dans lequel le poisson nage contre une vitesse de courant contrôlée) et de sondes à oxygène reliées via un oxymètre interfacé à un ordinateur. La consommation d'oxygène ($\dot{M}O_2$) des poissons durant l'activité a été déterminée à

toutes les heures tout en augmentant la vitesse de nage de 5 cm s^{-1} h^{-1} jusqu'à épuisement du poisson. De cette façon nous avons estimé la vitesse de nage critique (U_{crit} ; vitesse maximale à laquelle un poisson peut nager pour une heure complète), le SMR (extrapolation de MO_2 à vitesse de nage = 0), la consommation d'oxygène maximale ($MO_{2\ max}$; MO_2 estimé à U_{crit}), l'étendue métabolique (différence entre $MO_{2\ max}$ et SMR), le coût à la nage net (NetCOT ; proportionnel à pente de la relation MO_2 - vitesse de nage) et le coût à la nage total à la vitesse de nage optimal (TCOT(U_{opt}) ; coût minimal pour déplacer 1 kg de poisson sur 1 km).

Nous avons également mesuré 16 caractères morphologiques sur chaque poisson. De plus, nous avons prélevé des échantillons de muscle blanc et rouge sur les individus pour mesurer l'activité de huit enzymes représentant diverses voies métaboliques aérobies et anaérobies. Les essais (i.e. dosages enzymatiques) ont été faits à la même température d'acclimatation (et de respirométrie) du poisson, soit à 10, 15 ou 20°C. Les enzymes mesurées sont les suivantes : *enzymes aérobies*, cytochrome c oxydase (CCO), citrate synthase (CS), β-Hydroxyacyl-CoA déshydrogénase (HOAD) et alanine aminotransférase (GPT) ; *enzymes anaérobies*, phosphofructokinase (PFK), pyruvate kinase (PK), lactate déshydrogénase (LDH) et créatine phosphokinase (CPK).

Résultats

Pour les individus élevés au laboratoire, nos résultats indiquent que les individus provenant des lignées pures (LL et PP) sont de meilleurs nageurs dans le test de U_{crit} que les individus hybrides. Toutefois, les coûts à la nage (NetCOT et TCOT(U_{opt})) et $MO_{2\ max}$ ne différaient pas significativement entre ces écotypes. LL avait un SMR inférieur mais une étendue métabolique supérieure aux autres écotypes. Pour les ombles sauvages, les individus pélagiques étaient plus performants que les individus littoraux (prélevés à l'automne et et au

printemps ; ci-après « automne » et « printemps ») lors du test de U_{crit}, performance supérieure accompagnée d'un NetCOT inférieur aux individus littoraux (printemps). Le NetCOT des individus littoraux (automne) était intermédiaire mais pas significativement différent de celui des individus pélagiques et littoraux (printemps). TCOT(U_{opt}) et l'étendue métabolique était comparables entre les écotypes sauvages, mais les individus littoraux (printemps) avaient un SMR et un $MO_{2\ max}$ inférieurs aux deux autres écotypes. Pour les deux groupes d'omble de fontaine (élevés au laboratoire et sauvages), les performances à la nage et les indicateurs métaboliques augmentaient avec la température, sauf pour le NetCOT qui diminuait (effet marginal et non significatif pour SMR et NetCOT des individus sauvages). Les différences entre les meilleures et pires performances des écotypes étaient plus marquées pour les individus sauvages que pour ceux élevés au laboratoire.

Nous avons également trouvé que les individus provenant de mère littorale (LL et PL) étaient plus trapus que ceux provenant d'une mère pélagique (PP et LP) chez les ombles élevés au laboratoire. Aussi, les lignées pures (PP et LL) étaient différenciées des lignées hybrides (PL et LP) en étant plus fusiformes avec un pédoncule caudal plus haut et une tête plus longue. LL différait de PP en ayant une plus longue tête et une nageoire anale moins longue. Pour les ombles sauvages, les individus littoraux (printemps) étaient plus fusiformes, avaient une plus longue tête et un pédoncule caudal plus long que les individus pélagiques et littoraux (automne). Les individus de ce groupe avaient aussi la base de la nageoire anale plus longue que les individus pélagiques et une nageoire caudale plus courte que les individus littoraux (automne). Les individus littoraux (automne et printemps) avaient une nageoire dorsale plus longue (base) que les individus pélagiques. Nous avons également trouvé que la forme corporelle changeait durant la croissance et aussi avec la température d'acclimatation. De façon générale, les gros individus (masse supérieure) étaient plus trapus que les petits individus. Les individus élevés à

température élevée étaient aussi plus trapus avec une tête relativement plus grosse, un pédoncule caudal plus court mais plus haut et des nageoires (pectorales et caudales) plus longues.

Les résultats des dosages enzymatiques indiquent que, chez les ombles élevés au laboratoire, LL a une plus grande capacité aérobie (indiqué par CS et HOAD) que PP, alors que les hybrides (PL et LP) sont intermédiaires. Les hybrides (PL et LP) ont toutefois une meilleure capacité anaérobie que PP et LL tel qu'indiqué par une activité supérieure de la LDH. Pour les ombles sauvages, les individus littoraux (automne et printemps) ont généralement une plus grande capacité anaérobie (PFK, PK, LDH et CPK) alors que les individus pélagiques ont généralement une meilleure capacité aérobie (CS et HOAD). Dans les deux groupes d'ombles (élevé au laboratoire et sauvage), l'activité des enzymes aérobies (CCO, CS, HOAD et GPT) était supérieure dans le muscle rouge alors que l'activité des enzymes anaérobies (PK, LDH et CPK mais pas PFK) était supérieure dans le muscle blanc. L'activité enzymatique augmentait avec la température, excepté pour CCO qui ne démontrait pas de variation significative (pour les deux groupes).

Discussion

Les différences dans les performances de U_{crit} peuvent être expliquées par des variations morphologiques et métaboliques entre les écotypes. Pour les ombles élevés au laboratoire, un U_{crit} supérieur (PP et LL) était associé à un corps plus fusiforme et un pédoncule caudal haut, des caractéristiques morphologiques associées à la réduction des forces de traînée (fusiforme) et à la production d'une poussée efficace (pédoncule haut). De plus, les meilleurs nageurs (PP et LL) avaient une faible capacité anaérobie (indiqué par une faible activité de LDH), ce qui indique qu'il pourrait y avoir un compromis physiologique entre les performances aérobies (U_{crit}) et anaérobies (LDH). Similairement, les performances supérieures de U_{crit} des individus

pélagiques sauvages semblent être associées à de petites nageoires (dorsales, caudales et anales), caractéristiques diminuant les forces de traînée. Parallèlement, en ayant des nageoires plus développées, les individus littoraux voient leur coût à la nage net (NetCOT) augmenter plus rapidement lors de la nage soutenue. Toutefois, ce NetCOT élevé était compensé par un faible taux métabolique standard, résultant en des coûts énergétiques totaux (TCOT(U_{opt})) comparables entre les écotypes lorsqu'ils se déplacent à leur vitesse de nage optimale. Malgré cette apparente compensation, les individus littoraux vont voir leurs dépenses énergétiques augmenter plus rapidement que celles des individus pélagiques lorsque leur vitesse de nage s'éloignera de leur vitesse optimale, une conséquence de leurs coûts à la nage net (NetCOT) plus élevés. Conséquemment, les individus littoraux devraient utiliser des stratégies locomotrices impliquant une faible variance de vitesse de nage alors que les individus pélagiques seront moins affectés par l'utilisation d'une plus grande échelle de vitesse de nage. Aussi, il semble y avoir un compromis physiologique important chez les individus sauvages ; les individus pélagiques sont performants lors de U_{crit} et ont des capacités aérobies élevées (forte activité des enzymes aérobies : CS et HOAD) alors que les individus littoraux ont des capacités anaérobies élevées (forte activité des enzymes anaérobies : PFK, PK, LDH et CPK) et sont peu performants au test de U_{crit}. Une forte activité anaérobie des individus littoraux suggère qu'ils puissent être plus performants lors des départs rapides. Plusieurs études ont précédemment mis en relation ce type de performance et l'activité de certaines enzymes anaérobies dont PFK, PK, LDH et CPK.

Les différences dans les habilités locomotrices, la morphologie et le métabolisme sont en accord avec l'utilisation de l'habitat de chaque écotype en nature. Les individus pélagiques se nourrissent principalement de zooplancton dans la colonne d'eau alors que les individus littoraux se nourrissent principalement de zoobenthos en zone littorale. La zooplanctivorie

pourrait bénéficier d'une bonne capacité de nage prolongée, caractéristique facilitant la recherche du zooplancton distribué dans la colonne d'eau. Au contraire, la prédation sur des proies benthiques sollicite probablement une bonne capacité de manœuvre et d'accélération (départ rapide). Une bonne capacité d'accélération serait aussi favorable pour éviter les prédateurs terrestres en eau peu profonde.

Les différences morphologiques trouvées dans cette étude entre les écotypes des ombles élevés au laboratoire et sauvages étaient plus ou moins typiques de celles retrouvées en nature. Une des hypothèses possibles est la grande plasticité phénotypique des ombles. L'élevage dans des conditions semblables aurait créé une convergence des caractères plastiques. Nos résultats suggèrent aussi que la morphologie est modifiée durant la croissance et aussi en fonction de la température. Il est connu que les poissons deviennent plus trapus durant la croissance, adoptant une forme corporelle mieux adaptée pour s'alimenter de gros organismes (ex. : benthos et poissons). Un changement de forme corporelle avec la température est moins bien documenté. Nos résultats indiquent que les poissons élevés à faible température adoptent une morphologie de type pélagique (fusiformes, petites nageoires et pédoncule caudal étroit) alors que ceux élevées à forte température ont une morphologie semblable aux individus littoraux (trapus, grandes nageoires et haut pédoncule caudal). Ces modifications pourraient être une adaptation à l'augmentation de la viscosité de l'eau à faible température (traînée plus importante). La température de l'habitat pourrait donc jouer un rôle dans la différenciation morphologique des populations polymorphes mais sa contribution n'a pas été prise en compte (ni évaluée) jusqu'à ce jour.

De même, les différences dans les activités enzymatiques retrouvées chez les individus sauvages (les individus littoraux ont une grande activité des enzymes anaérobies et les individus

pélagiques ont une grande activité des enzymes aérobies) n'étaient pas retrouvées chez les individus élevés au laboratoire, suggérant une grande importance des facteurs environnementaux dans l'expression enzymatique. De plus, l'étendue des différences (performances, métabolisme et des enzymes) entre les écotypes était de loin supérieure chez les ombles sauvages que chez les ombles élevées au laboratoire, supportant l'hypothèse d'une grande influence de l'environnement sur les performances, la morphologie et le métabolisme chez l'omble de fontaine.

Conclusion

À notre connaissance, cette étude est la première à investiguer le rôle des variations morphologiques et métaboliques sur les performances à la nage des populations polymorphes. Les résultats présentés dans un premier article nous ont permis de vérifier l'existence d'un rôle fonctionnel de la morphologie sur les performances individuelles. Au moment de la rédaction de ce mémoire, une telle relation n'avait jamais été démontrée de façon directe pour differents écotypes au sein d'une même espèce ; les études antérieures basant leur interprétation des différences morphologiques observées sur des comparaisons interspécifiques. Dans un second temps, nous avons appuyé le rôle des différences morphologiques par des mesures physiologiques et métaboliques, mettant ainsi en évidence un compromis dans les voies métaboliques aérobies et anaérobies de production de l'énergie. De plus, il semble que non seulement des facteurs génétiques, mais également des facteurs environnementaux jouent un rôle important dans les performances à la nage et le métabolisme de l'omble de fontaine. L'intégration de ces connaissances suggèrent que les individus littoraux et pélagiques soient bien adaptés à l'exploitation de leur propre habitat, tant au niveau morphologique que

métabolique, mais au coût d'un compromis dans les performances et donc dans les options comportementales.

Les résultats obtenus lors de cette étude suggèrent que les deux écotypes puissent utiliser des styles de nage différents pour exploiter leur propre habitat. Malheureusement, une telle hypothèse s'avère difficile à vérifier sur le terrain étant donné la difficulté d'observation de l'espèce. Toutefois une vérification indirecte, via les capacités de nage prolongée et de départs rapides des deux écotypes semble une solution satisfaisante. Cette question a été adressée partiellement lors de cette étude, puisque seulement un test de nage prolongée a été conduit (test de nage critique) ; les capacités de départs rapides de ces formes n'étant pas connues à ce jour. Il serait fort intéressant dans de futurs travaux d'adresser cette question. Aussi, puisque la nage prolongée et de départs rapides sont soutenus par des fibres musculaires différentes (le muscle rouge est utilisé lors de la nage prolongée et le muscle blanc lors des départs rapides), il serait intéressant d'évaluer la proportion de ces deux types de muscles chez chacun des écotypes. Il est aussi suggéré dans cette étude que les facteurs environnemenaux ont une grande importance sur la morphologie et sur les performances elles-mêmes. Sur ce point, une expérience pouvant partitionner les facteurs environnmentaux des facteurs génétiques serait souhaitable. Il serait possible, par exemple, d'élever chacun des écotypes dans un environnement artificiel littoral et pélagique (tel que décrit dans Proulx et Magnan, 2004) puis les soumettre à des tests de nage (prolongée et/ou départs rapides). Ainsi il serait possible d'obtenir différent phénotypes d'un même écotype (la morphologie varie selon l'environnement) et donc de partitionner les composantes environnementales et génétiques des performances. Aussi il semble que la morphologie puissent être influencée non seulement par l'environnment physique mais aussi par l'environnement thermique et ce dans un laps de temps s'échelonnant sur quelques semaines seulement. Une expérience avec des ombles de pisciculture élevés à différentes températures

devrait permettre d'infirmer ou de confirmer une telle hypothèse, quoique les variations de formes dues aux taux de croissance inégaux entre les températures d'élevage devront être prises en considération.

PREMIER CHAPITRE

INTRODUCTION GÉNÉRALE

Problématique générale

La spécialisation trophique parmi les individus de la même espèce est bien documentée chez les vertébrés et serait une conséquence de la compétition pour la ressource (Robinson et Wilson, 1994). Ce «polymorphisme trophique» est un phénomène commun dans les lacs de l'hémisphère nord; plusieurs populations de poissons sont composées d'individus mieux adaptés dans l'exploitation de la colonne d'eau (écotype pélagique ou limnétique) et d'autres mieux adaptés dans l'exploitation de zone littorale (écotype benthique ou littoral) (Ehlinger et Wilson, 1988; Malmquist et al., 1992; Skúlason et Smith, 1995; Bourke et al., 1997; Svanback et Eklov, 2002). Dans les lacs du Bouclier Laurentien (Québec, Canada), l'omble de fontaine lacustre, *Salvelinus fontinalis* (Mitchill), démontre une ségrégation individuelle dans l'utilisation de l'habitat et dans la diète. Des études précédentes ont démontré que des individus littoraux se retrouvent en eaux peu profondes (0-2 m) et s'alimentent préférentiellement d'organismes zoobenthiques (> 90% de la masse sèche des contenus stomacaux) alors que des individus pélagiques se retrouvent en eaux plus profondes et s'alimentent principalement de zooplancton (Venne et Magnan, 1995; Bourke et al., 1997, 1999).Cette utilisation préférentielle de l'habitat est aussi reliée à des différences morphologiques subtiles ; les individus pélagiques sont plus fusiformes, ont des nageoires pectorales et dorsales plus courtes ainsi qu'un pédoncule caudal plus étroit que les individus littoraux (Bourke et al., 1997; Dynes et al., 1999; Proulx et Magnan, 2002; Marchand et al., 2003). L'absence de différentiation dans les caractères trophiques suggère que les traits associés à la nage sont plus importants que ceux associés à l'acquisition et à la manipulation de nourriture dans ces lacs (Dynes et al., 1999).

Les différences morphologiques entre les écotypes semblent adaptatives puisque que chacune des formes serait plus apte à acquérir de la nourriture dans son propre habitat (ex : la forme benthique dans la zone littorale et la forme pélagique dans la colonne d'eau) (Ehlinger, 1990; Malmquist, 1992; Skúlason et al., 1993; Robinson et Wilson, 1994; Schluter, 1995, 1996; Robinson et al., 1996; Hatfield et Schluter, 1999; Proulx et Magnan, 2002). Toutefois cette hypothèse est principalement basée sur les relations établies entre la morphologie et les diverses aptitudes à la nage au niveau interspécifique (Gatz, 1979b; Webb, 1988; Harper et Blake, 1990). En effet, plusieurs traits morphologiques associés aux forces de traînée et de poussée tels que la forme corporelle, la profondeur du pédoncule caudal et la forme et la taille de la nageoire caudale peuvent affecter les performances à la nage (Webb, 1982; Webb et Weihs, 1986; Boily et Magnan, 2002). Toutefois, bien qu'il existe plusieurs exemples de corrélation entre la morphologie et l'utilisation de l'habitat, nous ne savons pas comment les variations morphologiques des populations polymorphes affectent les performances natatoires individuelles. De plus, si les variations morphologiques sont des adaptations visant à réduire les coûts d'exploitation de l'habitat, d'autres adaptations sont susceptibles d'être présentes chez les écotypes puisque l'efficacité énergétique devrait augmenter la valeur adaptative (angl. « *fitness* ») d'un individu (Priede, 1977). Par exemple, le taux métabolique standard (SMR) et l'activité enzymatique (catalyseurs énergétiques) peuvent significativement affecter les performances à la nage (Kolok, 1992; Pettersson et Brönmark, 1999; Garenc et al., 1999; Kolok, 1999; Boily et Magnan, 2002; Schaarschmidt et Jurss, 2003). Les départs rapides, sont fournis par le muscle blanc riche en enzymes glycolytiques alors que le muscle rouge riche en enzyme oxydatives est utilisé durant la nage soutenue (Driedzic et Hochachka, 1978; Altringham et Ellerby, 1999; Norton et al., 2000). Ces relations suggèrent donc que les capacités métaboliques des muscles soient partiellement déterminantes des performances à la nage.

Dans cette étude nous avons utilisé l'omble de fontaine littoral et pélagique capturés en milieu naturel et élevés au laboratoire pour répondre aux objectifs suivants : (1) déterminer si les écotypes de l'omble de fontaine diffèrent dans leurs performances à la nage et (2) de mettre en relation les différences morphologiques et métaboliques (représentées par la consommation d'oxygène et l'activité enzymatique) observées entre les écotypes et leurs performances à la nage et (3) d'évaluer l'importance des facteurs génétiques et environmmentaux dans les performances à la nage et le métabolisme.

Rétrospective de la littérature

Polymorphisme trophique

Définition

Le polymorphisme trophique est défini comme étant l'occurrence intra-spécifique de formes distinctes (i.e. d'écotypes) démontrant diverses utilisations de la niche écologique, habituellement par des différences dans l'alimentation (Smith et Skúlason, 1996). Le polymorphisme trophique chez les poissons est fréquent dans les lacs de l'hémisphère nord récemment soumis à une période de glaciation (10 000 à 15 000 ans) (Schluter et McPhail, 1993; Robinson et Wilson, 1994) et serait d'une grande importance évolutive, menant même à la spéciation (Robinson et Wilson, 1994; Smith et Skúlason, 1996).

Mécanismes

En situation d'allopatrie, l'accroissement naturel des populations provoquerait une augmentation de la compétition intraspécifique (Malmquist et al., 1992; Bourke et al., 1999). Sous de telles conditions, la variabilité phénotypique entre les individus devrait augmenter pour atténuer l'effet de la compétition (Van Valen, 1965). Il est d'ailleurs reconnu que les

modifications comportementales ont de forts impacts sur l'efficacité de la quête alimentaire (Dill, 1983; Ehlinger, 1989). Dynes et al. (1999) suggèrent que la ségrégation alimentaire peut se produire par flexibilité comportementale des individus, caractéristique importante pour l'adaptation à la variabilité des ressources (Skúlason et al., 1993). Par la suite, la compétition pour les ressources favoriserait la diversification morphologique et l'effet néfaste de la compétition diminuerait en fonction de la distance morphologique des phénotypes spécialisés et intermédiaires (Schluter, 1994). L'isolement reproducteur viendrait ensuite par sélection divergente en faveur d'un phénotype plus compétitif (Schluter et McPhail, 1993; Skúlason et Smith, 1995; Ruzzante et al., 1998; Lu et Bernatchez, 1999), suivi de l'apparition de différences génétiques entre les écotypes, phase initiale de la spéciation (Schluter, 1996; Orr et Smith, 1998).

Plasticité phénotypique

La plasticité phénotypique est considérée comme un élément majeur de la différentiation polymorphe et de la ségrégation alimentaire (Scheiner, 1993; Smith et Skúlason, 1996; Schluter, 1996). Pour un génotype donné, toute modification de l'expression phénotypique sous influence environnementale est définie comme de la plasticité phénotypique (Scheiner, 1993). Le comportement, un élément plastique, est plus variable entre les individus d'écotype distinct qu'au sein d'un même écotype (Ehlinger et Wilson, 1988), ce qui suggère qu'il puisse avoir une base génétique (Meyer, 1989; Skúlason et al., 1993). De plus, certaines différences morphologiques chez les populations polymorphes sont aussi déterminées génétiquement (Robinson et al., 1996) alors que d'autres sont principalement le résultat de la plasticité phénotypique (Mittelbach et al., 1999; Proulx et Magnan, 2004). La plasticité phénotypique

serait d'une grande importance évolutive face à la stochasticité environnementale (Hutchings, 1996).

Évidences de polymorphisme chez l'omble de fontaine

Niche trophique et alimentation

Dans une première étude, Venne et Magnan (1995) ont observé que les individus 0+ de l'omble de fontaine se distribuaient en deux groupes ; un groupe « littoral » se retrouvait à une profondeur de 0 et 2 mètres et un groupe « profond » se retrouvait entre 3 et 6 mètres. Lors d'une étude de suivi télémétrique, Bourke et al. (1997) rapportent que 50% des individus se retrouvent principalement dans la zone benthique (ombles benthiques), 18% dans la zone pélagique (ombles pélagiques) et 32% voyagent régulièrement entre les deux zones (individus généralistes). Similairement, 41.3 % des individus se nourrissent presque exclusivement de zoobenthos (> 90% du contenu stomacal, poids sec) alors que 18% se nourrissent de zooplancton (Bourke et al., 1999). L'utilisation de niches trophiques distinctes semble aussi impliquer des différences dans l'utilisation des températures puisque Marchand (2000) rapporte un préférendum thermique différent entre les deux écotypes, où celui des individus littoraux est légèrement plus élevé (13.2 ± 2.8 °C) que celui des individus pélagiques (11.6 ± 2.7 °C).

Morphologie

Certaines différences au niveau de la coloration et de la morphologie ont été trouvées entre les écotypes en milieu naturel. Les individus pélagiques ont une coloration rougeâtre, sont plus fusiformes, ont une tête plus allongée, un pédoncule caudal plus étroit, des nageoires pectorales et une nageoire dorsale plus courtes que les individus littoraux (Bourke et al., 1997; Dynes et al., 1999; Marchand, 2000; Proulx and Magnan, 2002; Marchand et al., 2003). En

milieu lotique, les individus exploitant les habitats avec beaucoup de courant sont plus fusiformes et ont une nageoire caudale plus haute (McLaughlin et Grant, 1994). Ces caractéristiques morphologiques sont associées à la nage soutenue et de croisière ; de courtes nageoires et une faible surface corporelle réduiraient la force de traînée nuisible à l'avancement du poisson (Gatz, 1979b; Webb, 1982, 1984a,b; Webb et Weihs, 1986; Pettersson et Brönmark, 1999). Pour leur part, les individus littoraux seraient adaptés à la nage de type manœuvre puisqu'ils possèdent de plus longues nageoires pectorales et dorsales (Bourke et al., 1997; Dynes et al., 1999; Proulx et Magnan, 2002; Marchand et al., 2003), caractéristiques associées à ce type de nage (Gatz 1979a,b; Webb 1982, 1984a,b; Drucker et Lauder, 2003; Walker, 2004; Lauder et Drucker, 2004).

Au laboratoire, Proulx et Magnan (2004) démontraient que certains caractères morphologiques sont hérités des parents mais que ces traits réagissent à l'environnement. Ces auteurs ont également montré que le dimorphisme sexuel jouerait un rôle significatif dans la différentiation morphologique chez les ombles de fontaine. Les mâles auraient une tête plus robuste (plus longue et profonde), une machoire inférieure plus longue, une bouche plus large et un museau plus long que les femelles. Les mâles auraient également une croissance plus rapide (masse et longueur totale supérieures à la fin de l'expérience) que les femelles. Finalement, ces auteurs ont aussi trouvé que certains caractères morphologiques sont sous contrôle purement environnemental et ne sont pas fixés une fois que le poisson a adopté une certaine stratégie alimentaire.

Différentiation génétique

La découverte de différences au niveau génétique entre les deux écotypes dans un lac de la réserve Mastigouche (Lac Bondi) suggère un isolement reproducteur partiel où les échanges

génétiques ne sont plus aléatoires dans la population (Dynes et al., 1999). Bourke et al. (1997) suggèrent aussi un certain isolement reproducteur d'après la sélection de site de fraye des individus pélagiques et littoraux.

Performances en enclos

Lors d'une expérience en enclos, Proulx et Magnan (2002) ont montré que le contenu protéique et lipidique des ombles de fontaine littoraux diminuait lorsque contraints à la zone pélagique. Similairement, les résultats de Marchand et al. (2003) indiquent que les individus littoraux passent beaucoup plus de temps à s'alimenter que les individus pélagiques dans ces mêmes enclos. Les résultats de ces études supportent l'hypothèse que les individus littoraux dépensent plus d'énergie que les individus pélagiques lorsque contraints à s'alimenter sur le zooplancton en enclos pélagique et donc que la diversification trophique serait adaptative chez l'omble de fontaine.

Importance du métabolisme

Efficacité énergétique

Pour bien comprendre la bioénergétique des poissons nous devons voir comment l'énergie acquise est répartie dans les composantes physiologiques majeures du budget énergétique. Sous une forme générale, le budget énergétique peut être exprimé ainsi :

$$I = E + M + P \qquad (1)$$

où I est l'énergie ingérée, E est l'énergie perdue par les fèces et les produits d'excrétion, M est l'énergie perdue par le métabolisme (maintien des fonctions physiologiques de base, activité,

digestion et l'assimilation de la nourriture) et P correspond à l'énergie conservée pour la production (croissance somatique et production de gamètes) (Jobling, 1993).

Toute énergie sauvegardée des dépenses excrétoires et métaboliques pourrait être investie dans la fraction « production ». Pour un milieu donné, la taille adulte des poissons et leur taux de croissance devraient être optimisés puisque les poissons plus gros sont moins susceptibles à la prédation, sont de meilleurs compétiteurs (Forseth et al., 1994) et les grosses femelles, plus fécondes (Moyle et Cech, 1996). Par conséquent, la sélection naturelle devrait favoriser les individus maximisant leur fitness en ayant les meilleurs compromis métaboliques (Priede, 1977).

Métabolisme aérobie

Métabolisme standard (SMR)

Le taux métabolique d'un poisson au repos et à jeun en dessous duquel ses fonctions biologiques sont compromises s'appelle le taux métabolique standard (de l'anglais : *standard métabolique rate (SMR)*). Les dépenses énergétiques dues au métabolisme standard sont la conséquence d'une multitude de processus biochimiques comblant deux fonctions principales : (1) l'approvisionnement (système respiratoire et cardiovasculaire fournissant de l'oxygène aux différents tissus de l'organisme) et (2) la maintenance cellulaire (transport des ions et synthèse/remplacement des constituants cellulaires tels que lipides et protéines) (Jobling, 1993).

Autrefois, le SMR fut considéré chez les animaux comme un trait invariable de l'espèce, mais il existe maintenant plusieurs preuves qu'il peut varier au sein des individus d'une même espèce (Piersma et Lindström, 1997; Cutts et al., 1998; Pettersson et Brönmark, 1999; Boily et Magnan, 2002). Le SMR augmente avec la température environnementale (jusqu'à un

maximum) et la masse de l'individu (Bernatchez et Dodson, 1985; Beamish, 1990; van der Lingen, 1995; Hop et Graham, 1995; Sepulveda et al., 2003) et le niveau de stress (Sloman et al., 2000). Certains auteurs ont également démontré que, chez quelques espèces de salmonidés, le SMR était supérieur chez les individus dominants (Metcalfe et al., 1995; Cutts et al., 1998, 2001; Yamamoto et al., 1998).

Coût à la nage

Le coût relié à la nage est la somme du taux métabolique standard et de l'énergie requise pour produire la poussée, pour accélérer et pour surpasser les forces de traînée (Jobling, 1993). La nage est une activité très exigeante et les dépenses énergétiques d'un poisson nageant à grande vitesse peuvent surpasser par un facteur de 10 à 15 fois celles d'un poisson au repos (Beamish, 1978). L'énergie allouée à la nage a un impact majeur sur les gains énergétiques nets selon les différentes stratégies d'acquisition des ressources (Webb, 1993). La nage de routine impliquant des mouvements spontanés, comme ceux requis pour attaquer certain type de proies, est l'activité la plus coûteuse chez les poissons en nage libre (Boisclair et Tang, 1993; Krohn et Boisclair, 1994; van der Lingen, 1995; Hughes et Kelly, 1996). Le coût à la nage varie avec une multitude de facteurs dont la vitesse (Boisclair et Tang, 1993; Jobling, 1993; Videler, 1993; Tang et Boisclair, 1995; Leonard et al., 1999b), le type de nage (Korsmeyer et al., 2002), la température (Tang et Boisclair, 1995; Tang et al., 2000), le SMR (Pettersson et Brönmark, 1999; Boily et Magnan, 2002) ainsi que la taille et la morphologie de l'organisme (Boisclair et Tang, 1993; Vogel, 1994; Tang et al., 2000; Boily et Magnan, 2002).

Performance à la nage

Les performances natatoires des poissons sont généralement classifiées en trois catégories majeures : soutenue, prolongée et départ rapide (*angl. : burst*) (Beamish, 1978). Les

performances soutenues peuvent être maintenues pour une longue période (>200 min), alors que les performances de départ rapide ne peuvent être maintenues que pour une très courte période de temps (<20 s.; anaérobie) et sont celles où le poisson atteint la vitesse maximale. La nage prolongée dure entre 20 s et 200 min (Beamish, 1978), est principalement aérobie et se termine par la fatigue du poisson. Le test de nage critique (U_{crit} ; Brett, 1964) est une évaluation de la performance à la nage prolongée (Beamish, 1978) et est utilisé pour déterminer la capacité de nage générale des poissons (pour revue de littérature, voir Beamish, 1978; Kolok, 1999; Plaut, 2001; Nelson et al., 2002).

Il est intuitif de croire que les poissons nageant plus régulièrement (pour s'alimenter par exemple) ont des performances de nage critique accrues. Quelques études sur l'effet de l'entraînement sur les performances à la nage vont en ce sens (ex. : Houlihan et Laurent, 1987; Farrell et al., 1990; Young et Cech, 1994; Davison, 1997), alors que d'autres ne démontrent pas d'effet de l'entraînement sur le U_{crit} chez les poissons (Farrell et al., 1991; Gallaugher et al., 2001). De même les poissons soumis à de forte vitesse de courant sont plus performants lors du test de U_{crit} que ceux provenant de zone à faibles vitesses de courant (Bernatchez et Dodson, 1985; Nicoletto et Kodric-Brown, 1999; Nelson et al., 2003).

Métabolisme anaérobie

L'énergie pour les activités de départs rapides et de sprints est fournie par les muscles à contractions rapides (blancs) via les voies métaboliques anaérobies (Beamish, 1980), principalement par la glycolyse et implique la production de lactate (Milligan et Girard, 1993; Milligan et al., 2000; Sugita et al., 2000, 2001). Le métabolisme anaérobie peut aussi supporter des activités d'intensités intermédiaires se situant entre le sprint et la nage soutenue mais ne peuvent être maintenues que pour quelques minutes avant la fatigue (Webb, 1993). En fait, une

proportion de plus en plus importante de muscle blanc est recrutée avec l'augmentation de la vitesse de nage à partir d'un certain seuil correspondant à 70-95 % de la vitesse de nage critique chez les salmonidés (Johnston et Moon, 1980; Wilson et Egginton, 1994; Burgetz et al., 1998; Beddow et McKinley, 1999).

La production d'énergie anaérobie varie selon les espèces, la taille, la température et les saisons (Goolish, 1991a; McDonald et al., 1998). Les espèces ayant des comportements alimentaires par embuscade (angl. « *sit-and-wait* ») auraient un potentiel de production et une utilisation plus importante de ce type d'énergie que celles recherchant activement leur nourriture (Goolish, 1991b). Le coût du métabolisme anaérobie lors d'activités d'intensités sous-maximales est considérable. Chez la truite arc-en-ciel (*Oncorhynchus mykiss*) la nage soutenue à plus de 80 % de U_{crit} représente un coût énergétique important puisque la portion anaérobie de l'exercice représente de 33% à 65% de la consommation totale d'oxygène, lorsque l'on inclut le coût du rétablissement et de la gluconéogenèse (synthèse du glucose) (Burgetz et al., 1998). Par conséquent, les activités spontanées ayant un fort potentiel anaérobie devraient être utilisées d'avantage lors de l'attaque des proies et la fuite d'un prédateur et moins dans la recherche et la manipulation des proies, qui implique probablement des processus aérobies moins coûteux (Sherwood et al., 2002).

Activité enzymatique et performance individuelle

Les enzymes métaboliques représentent une approche intéressante pour quantifier les niveaux d'activités des poissons sur une base individuelle et à court terme et donc, pour évaluer les bases énergétiques de différents modes alimentaires (Newsholme et Crabtree, 1986; Johnston et Ball, 1997). Les enzymes peuvent être séparées en deux groupes selon leur appartenance à des voies métaboliques requérant ou non de l'oxygène (aérobie vs. anaérobie). Les muscles

rouges utilisés lors de la nage soutenue (et prolongée) sont riches en enzymes des voies aérobies mais pauvres en enzymes anaérobies alors que c'est l'inverse pour les muscles blancs (Driedzic et Hochachka, 1978; Norton et al., 2000). La nage prolongée peut être reliée à la fois aux capacités métaboliques du muscle rouge et du muscle blanc (Martinez et al., 2003).

Enzyme des voies aérobies

Il existe plusieurs mécanismes métaboliques pouvant répondre à l'accroissement de la demande énergétique. Parmi ces mécanismes, plusieurs études font ressortir des compensations métaboliques reliées à l'effort de nage, notamment au niveau de l'activité enzymatique (Farrell et al., 1990; Couture et Guderley, 1990; Leonard et McCormick, 1999) et par accroissement de la densité mitochondriale (Johnston et al., 1998). Chez plusieurs espèces, l'activité de certaines enzymes aérobies est corrélée avec le niveau d'activité du poisson (Dickson et al., 1993), avec les performances de U_{crit} ou d'épreuve d'endurance (ex. : Farrell et al., 1991; Kolok, 1992; Martinez et al., 2003) et s'accroît avec l'intensité de l'activité physique, comme c'est le cas lors de l'entraînement (Farrell et al., 1990) et des migrations (Couture et Guderley, 1990; Leonard et McCormick, 1999). Les exemples incluent des enzymes telles que la citrate synthase (CS) (Farrell et al., 1990; Couture et Guderley, 1990; Dickson et al., 1993; Leonard et McCormick, 1999; Schaarschmidt et Jurss, 2003), la β-hydroxyacyl coenzyme A déshydrogénase (HOAD) (Farrell et al., 1990, 1991; Leonard et McCormick 1999), la cytochrome *c* oxydase (CCO) (Couture et Guderley, 1990; Kolok, 1992; Martinez et al., 2003), la carnitine palmitoyl transférase (CPT) (Couture et Guderley, 1990), la glutamate-oxoloacétate transaminase (GOT) (Couture et Guderley, 1990) et l'alanine aminotranférase (GPT) (Leonard et McCormick, 1999). Ces enzymes sont des déterminants importants du métabolisme aérobie. Toutefois, Martínez et

al. (2003) indiquent que l'endurance de nage est reliée à la fois à la capacité oxidative (CCO) mais aussi à la capacité glycolytique (lactate déshydrogénase, LDH).

Enzymes des voies anaérobies

Chez les poissons, la capacité anaérobie peut être estimée à partir de l'activité de certaines enzymes, dont la LDH (McDonald et al., 1998). En effet, l'activité maximale de cette enzyme glycolytique serait reliée au comportement alimentaire et associée au coût de l'activité chez les poissons (Sullivan et Somero, 1980; Childress et Somero, 1990). De la même façon, lors d'une activité intense de courte durée (ex. : 20 s) comme les départs rapides, l'activité de la phosphofructokinase (PFK) augmente très rapidement dans les muscles, indiquant une activation de la voie glycolytique pour fournir de l'ATP (Sugita et al., 2000). Toutefois, si l'activité intense est de longue durée (15 min), l'activité de la PFK diminue par inhibition causée par une diminution de pH et les poissons ne sont alors plus capables de nager (Sugita et al., 2001).

Il a été rapporté que les espèces plus actives ont une capacité de récupération musculaire supérieure après un exercice anaérobie (Castellini et Somero, 1981). Aussi, on rapporte chez ces espèces (Somero et Childress, 1990) une activité supérieure de la LDH (Sullivan et Somero, 1980; Goolish, 1991a; Dickson et al., 1993; Leonard et McCormick, 1999) et de la pyruvate kinase (PK) (Dickson et al., 1993), suggérant que ces espèces puissent avoir un potentiel anaérobie accru. De plus, puisque la capacité aérobie du muscle blanc semble importante pour minimiser le gradient de phosphocréatine (substrat énergétique) entre les mitochondries et les myofibrilles, une forte capacité aérobie du muscle blanc pourrait faciliter les départs rapides (Hubley et al., 1997). À titre d'exemple, l'activité de la CCO (aérobie) est fortement corrélée avec les performances de départ rapide chez les adultes de l'épinoche à trois épines

(*Gasterosteus aculeatus*), ainsi que celles de la créatine phosphokinase (CPK), de la PFK et de la LDH, des enzymes anaérobies (Garenc et al., 1999). Toutefois, un certain nombre d'études n'ont pu mettre en relation l'activité enzymatique et les performances de départs rapides (Gibb et Dickson, 2002; Odell et al., 2003), ce qui suggère que ces performances soient influencées par un ensemble de caractéristiques phénotypiques (ex : morphologie, cinétique musculaire, ampleur de la flexion corporelle, etc.) et non d'un seul aspect physiologique (voir Ghalambor et al., 2003)

Morphologie des phénotypes

Effet de la morphologie sur les performances natatoires

Les différences interindividuelles dans la morphologie peuvent expliquer en partie la variation dans les performances natatoires chez les poissons (Taylor et McPhail, 1985, 1986; Taylor et Foote, 1991; Hawkins et Quinn, 1996; Andraso, 1997; Boily et Magnan, 2002; Ojanguren et Braña, 2003). Puisque l'eau est un milieu visqueux, la morphologie des poissons est susceptible d'avoir une grande influence sur l'importance des forces servant à faire avancer le poisson et celles s'opposant à son déplacement (force inertielle et de traînée). C'est le cas car la force de traînée d'un poisson en nage continue est approximativement proportionnelle à sa surface totale et à sa vitesse au carré (Videler, 1993; Vogel 1994; Fuiman and Batty 1997; Sagnes et al. 2000).

La forme du corps et la morphologie des nageoires peuvent influencer les performances natatoires de trois façons : elles peuvent influencer l'habilité à produire de puissantes accélérations, peuvent affecter les coûts énergétiques de la nage soutenue, ou peuvent affecter l'habilité à manœuvrer précisément (Webb, 1982). En général, les poissons spécialistes de l'accélération (ex : Grand brochet, *Esox lucius*) ont de piètres performances en nage soutenue

par rapport aux généralistes (ex : Truite arc-en-ciel, *Oncorhynchus mykiss*) et vice versa (Webb, 1988; Harper et Blake, 1990). La spécialisation pour l'un de ces types de nage requiert des adaptations morphologiques et physiologiques particulières et semble compromettre la performance pour les autres types de nage réduisant ainsi les options comportementales (Reidy et al., 2000; Ojanguren et Braña, 2003 mais voir Domenici et Blake, 1997; Blake, 2004). Les études inter-spécifiques nous indiquent que (1) les spécialistes de l'accélération devraient avoir une hauteur corporelle importante jumelée à des nageoires ventrales et dorsales bien développées, (2) les spécialistes de la nage soutenue auraient un corps fusiforme, un pédoncule caudal étroit et une nageoire caudale étroite mais profonde et (3) les spécialistes de manœuvre auraient un corps compressé latéralement et de longues nageoires pectorales (Gatz, 1979b; Webb, 1982; Webb, 1984a,b; Webb et Weihs, 1986 mais voir Webb et Fairchild, 2001).

Bien qu'il semble y avoir un grand nombre d'évidences que les performances natatoires peuvent être liées à des différences morphologiques entre les espèces, les exemples au niveau intra-spécifique sont plus limités. Les cas retrouvés dans la littérature révèlent généralement des variations inter-populations associées aux migrations d'intensités différentes (Taylor et McPhail, 1985; Taylor et Foote, 1991), sont le résultat de compromis entre les vitesse de départs et le développement de structures défensives (Andraso, 1997; Bergstrom, 2002), reflètent différentes histoires de vie (Taylor et McPhail, 1986) ou résultent de mutations (Plaut, 2000). Par exemple, les comparaisons intra-spécifiques chez le saumon Coho, *Onchorhynchus kisutch* (Taylor et McPhail, 1985) et l'épinoche à trois épines, *Gasterosteus aculeatus* (Taylor et McPhail, 1986) révèlent que les individus plus trapus, c'est-à-dire au corps haut et large, ont de meilleures performances de départs rapides. Au contraire, les individus fusiformes sont plus performants lors de la nage prolongée (Taylor et McPhail, 1985, 1986; Taylor et Foote, 1991; Hawkins et Quinn, 1996). Aussi, les poissons possédant un pédoncule caudal long et haut sont plus

performants en nage prolongée (Hawkins et Quinn, 1996; Ojanguren et Braña, 2003). Une relation positive entre les performances de nage prolongée avec la longueur des nageoires pectorales, pelviennes et caudale est aussi connue (Plaut, 2000; Ojanguren et Braña, 2003), quoi que pour cette dernière, un maximum dans les performances est atteint par les poissons ayant une nageoire caudale de taille moyenne (Plaut, 2000).

Morphologie et coût à la nage

Plusieurs caractéristiques morphologiques associées à la force de traînée et à la production de la poussée comme la forme corporelle, la profondeur du pédoncule caudal et la taille ainsi que l'aspect de la nageoire caudale, sont susceptibles d'affecter le coût de la nage (Webb, 1982; Webb et Weihs, 1986). Dans une étude récente, Boily et Magnan (2002) ont mis en évidence la relation entre le coût à la nage et la forme corporelle : les individus plus trapus ont un coût à la nage plus élevé. Chez la perchaude (*Perca flavescens*), les individus avec une nageoire caudale haute et courte et ceux qui sont plus fusiformes ont un coût à la nage inférieur. Toutefois, il semble que le coût à la nage soit influencé par la morphologie chez la perchaude mais pas chez l'omble de fontaine où les coûts élevés à la nage des individus corpulents seraient reliés à un SMR élevé (Boily et Magnan, 2002). Le coût à la nage peut aussi être réduit par diminution du SMR de sorte que les individus corpulents ne souffrent pas de coûts à la nage accrus, du moins à faible vitesse de nage (Pettersson et Brönmark, 1999). À cet effet, les dépenses énergétiques augmenteraient plus rapidement avec l'augmentation de la vitesse de nage chez les individus qui ont une grande force de traînée (Webb, 1993; Pettersson et Hedenström, 2000).

Température

Due à la forte capacité thermique de l'eau (environ 3000 fois celle de l'air), la température corporelle des organismes aquatiques hétérothermes s'équilibre rapidement avec tout changement de température (Christiansen et al., 1991; Taylor et al., 1997). Conséquemment, en absence de spécialisations anatomiques pour maintenir un gradient de température, la température corporelle de la majorité des poissons est en équilibre avec celle de leur environnement (Christiansen et al., 1991; Taylor et al., 1997). De fortes variations de la température corporelle sont donc rencontrées pour les poissons sujets à des migrations (verticales, reproductrices,...) ou lors de changements de températures associés aux saisons ou à l'exploitation de niches écologiques différentes.

Effet sur le métabolisme et l'activité enzymatique

La température est l'un des facteurs abiotiques les plus importants influençant les vitesses de réactions biochimiques et a donc un impact substantiel sur les processus biologiques des organismes hétérothermes. Typiquement, le taux métabolique standard augmente par un facteur d'environ 2 à 3 pour tout gain de 10°C (i.e. Q_{10} = 2 à 3) pour atteindre un maximum, puis diminue ensuite avec l'augmentation subséquente de la température (Schimdt-Nielson, 1990; Beamish, 1990; Leonard et al., 1999). Cette situation représente une contrainte métabolique importante qui demande des compensations physiologiques ou biochimiques immédiates si l'animal doit maintenir une activité biologique constante. De façon générale, l'acclimatation temporaire ou l'adaptation permanente à de faibles températures améliore la capacité aérobie des muscles en augmentant la densité mitochondriale (Dunn, 1988; Johnston et al., 1998) l'activité spécifique (et/ou la concentration) des enzymes des voies oxydantes (Crockett et Sidell, 1990; Guderley et al., 1997; Cordiner et Egginton, 1997; Battersby et

Moyes, 1998; Hardewig et al., 1999). Ceci entraîne une utilisation supérieure des substrats lipidiques par rapport aux glucides puisque la voie glycolytique (voie de dégradation des glucides) ne démontrent généralement pas de compensations aux faibles températures (Crockett et Sidell, 1990; West et al., 1999 mais voir Pierce et Crawford 1997a,b). De même, l'acclimatation à la chaleur modifie l'activité des enzymes aérobies mais n'influence pas l'activité des enzymes glycolytiques (Hardewig et al., 2000).

Effet sur les performances à la nage

Chez les poissons, U_{crit} augmente avec la température jusqu'à un optimum avant de diminuer à plus forte température (Brett, 1964; Beamish, 1978; Bernatchez et Dodson, 1985; Peake et al., 2000 mais voir Myrick et Cech, 2000). La température optimale pour la nage soutenue se situerait près de l'extrémité supérieure de l'étendue ou du préférendum thermique d'une espèce donnée (Guderley, 1990), alors que les poussées accélératrices démontrent une certaine indépendance à la température (Beamish, 1978; Peake et al,. 2000). Finalement, chez plusieurs espèces, le coût à la nage augmente aussi avec la température (Tang et Boisclair, 1995; Tang et al., 2000 mais voir Beamish, 1990), mais est indépendant de celle-ci lorsque la vitesse de nage est élevée (Brett, 1964; Bernatchez et Dodson, 1985).

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DEUXIÈME CHAPITRE

PERFORMANCE NATATOIRE DE DEUX ÉCOTYPES D'OMBLE DE FONTAINE (*SALVELINUS FONTINALIS* M.) : CONTRAINTES MORPHOLOGIQUES, MÉTABOLIQUES ET THERMIQUES

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Swimming performance of two brook charr ecotypes (*Salvelinus fontinalis* M.): Morphological, metabolic, and thermal constraints

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Keyword : Swimming cost, critical swimming speed, oxygen consumption, respirometry, fish polymorphism, morphology, hybrids, temperature, adaptation.

Summary

Trophic polymorphism is common in fish and is reflected by individual differences in habitat use, food preference, and morphology. The significance of morphological variations among ecotypes is mainly based on knowledge at the interspecific level and are thought to reflect individual specializations to habitat use. However, direct evidence supporting this hypothesis are scarce and other adaptations (e.g., physiological ones) are likely to occur if there is a differential cost in habitat exploitation. The objectives of this study were (1) to determine whether littoral and pelagic ecotypes of brook charr, *Salvelinus fontinalis*, differ in their swimming performances, and if so (2) to investigate the functional significance of morphological and metabolic variations on their swimming performances. We submitted littoral and pelagic laboratory raised (pure and hybrids) and wild individuals to forced swimming in respirometers at 10, 15, and 20°C, and we measured 16 morphological characters on each fish. Our results indicate that wild pelagic charr are better swimmers than littoral ones as indicated by the critical swimming test (U_{crit}). Laboratory-raised pure littoral and pure pelagic individuals also had higher U_{crit} performances than hybrids. The differences were related to morphological traits associated with drag and thrust. Wild littoral individuals had a higher net cost of transport than pelagic ones. However, this cost was compensated by a lower standard metabolic rate, resulting in a comparable total cost of transport between ecotypes when they swam at their optimal swimming speed. Furthermore, the swimming and metabolic performances of laboratory-raised ecotypes were more homogenous than those of wild fish, suggesting an important environmental effect in the performances themselves. Taken together, our results suggest that morphological variations are adaptive in the polymorphic brook charr system and that pelagic individuals are better adapted than littoral individuals to forage in the open-water habitat.

Introduction

Trophic specialization among individuals of the same species is well known in vertebrates and is thought to be a consequence of resource competition (Robinson and Wilson, 1994; Skúlason and Smith, 1995). Such resource polymorphism is common in lakes of the Northern hemisphere; many fish populations are composed of individuals that feed in the open water (pelagic or limnetic ecotype) and others that feed in shallow waters (benthic or littoral ecotype) (Ehlinger and Wilson, 1988; Malmquist et al., 1992; Bourke et al., 1997; Svanback and Eklov, 2002). Brook charr *Salvelinus fontinalis* (Mitchill) exhibit individual differences in habitat use and diet in lakes of the Canadian Shield (Québec, Canada). Previous studies have shown that littoral individuals are found in shallow water (0-2 m) and feed mainly on zoobenthos (> 90% of stomacal content, dry weight) while pelagic individuals are found in deeper waters (3-6 m) and feed mostly on zooplankton (Venne and Magnan, 1995; Bourke et al., 1997, 1999). This habitat use preference is also related to subtle morphological differences, with pelagic individuals having shorter pectoral and dorsal fins and a shallower caudal peduncle than littoral ones (Bourke et al., 1997; Dynes et al., 1999; Proulx and Magnan, 2002). Proulx and Magnan (2004) found that such a morphological differentiation is gentically but also environmentally determined. The lack of differentiation in trophic-related morphology suggests that traits associated with swimming demands are more important than those related to food acquisition and manipulation in those lakes (Dynes et al., 1999).

Morphological differences among ecotypes appear adaptive since it is generally observed that each ecotype seems better adapted than the other to forage in its own habitat (e.g., benthic form in the littoral zone and planktivorous form in the open-water habitat) (Ehlinger, 1990; Malmquist, 1992; Skúlason et al., 1993; Robinson and Wilson, 1994; Schluter, 1995, 1996;

Robinson et al., 1996; Hatfield and Schluter, 1999; Proulx and Magnan, 2002). This hypothesis is mainly based on the usual relationships established between swimming ability and morphology at the interspecific level (Gatz, 1979; Webb, 1988; Harper and Blake, 1990). Many morphological traits associated with hydrodynamic drag and thrust forces, such as body shape, caudal peduncle height, and caudal fin shape, are known to affect swimming performance (Webb, 1982; Webb and Weihs, 1986; Boily and Magnan, 2002). However, although there are many examples of correlations between habitat use and morphology, it is unclear how morphological differentiation in polymorphic populations affects individual swimming performance. Furthermore, other related physiological traits such as standard metabolic rate (SMR) can significantly affect swimming costs (Pettersson and Brönmark, 1999; Boily and Magnan, 2002) and be under selective pressure (Priede, 1977).

The goal of the present study was to investigate the relationship between morphology and swimming performance in polymorphic brook charr. Experiments were done with laboratory-raised (pure and hybrid) and wild individuals at three different temperatures to determine the relative contribution of environmental and genetic factors on swimming performance and metabolism. The following hypotheses were tested:

1. Ecotypes differ in their swimming performance. It is expected that pelagic individuals wich feed in the open water on zooplancton and have a more streamlined body shape will have better prolonged swimming capacity.

2. Hybrids are intermediate to the parental crosses in their swimming performances given that performances themselves are heritable;

3. Differences in swimming performance are related to morphological and physiological differences (e.g., SMR).

Materials and methods

Experimental fish and holding conditions

A) Laboratory-raised brook charr

In October 2002, littoral and pelagic brook charr were sampled on the spawning ground of Lake Ledoux, Mastigouche Reserve, (Québec) Canada (46°40'N, 73°20'W), using gill nets. Brook charr ecotypes were determined using allometric relationships between body and fin length obtained from previous studies (Bourke et al., 1997; Dynes et al., 1999). In the field, pelagic individuals were only selected if the length of both the pectoral and dorsal fins and the caudal peduncle were smaller than expected from the size-adjusted regression lines for the pelagic form while littoral ones were only selected if the length of both fins and the caudal peduncle were above the size-adjusted regression line for the littoral form. The artificial fertilization procedure was performed by dry method (Piper et al., 1982), and the sexual products of both ecotypes were used to produce full-sib as well as reciprocal maternal "hybrid" broods: 3 PP, 4 LL, 2 PL, and 2 LP (capital letters indicate male x female ecotype crosses from littoral [L] and pelagic [P] individuals).

Eggs were incubated at 6 ± 0.5°C in two ascending-current vertical incubators (model 5609-8 tray trout; MariSource, Milton, WA, USA) connected to a glycol cooling system (± 1°C). Light intensity (40 lux) and photoperiod (12:12) were held constant during the whole experiment. Ammonia (NH_3; $\mu g\ l^{-1}$), nitrites (NO_2; $mg\ l^{-1}$), and water hardness ($mg\ l^{-1}$ of $CaCO_3$) were estimated using standard procedures (APHA, 1989) and kept within the tolerance limits for salmonid aquaculture (MAPAQ, 1990). Water hardness and alkalinity were adjusted

to 65 mg l^{-1} $CaCO_3$ by adding calcium chloride ($CaCl_2$) and sodium bicarbonate (Na_2HCO_3). Hatchling occurred from 17 January to 26 February 2003.

Offspring were counted and transferred into eleven 76-litre tanks (one per brood). Upon yolk sac resorption, food (Biodiet starter, Corey #0.7, and Corey #1) was distributed continuously for 12 hours a day from an overhead automatic feeding system. Fish were transferred to larger tanks (600 and 900 l) at 4 months and were fed *ad libitum* once a day.

B) Wild experimental fish

Wild juvenile brook charr were also captured in Lake Ledoux from 16 September to 2 October 2002 using multifilament gillnets (10 m long x 1.8 m deep, 15.9 mm stretched mesh). Gillnets were inspected every 10 to 15 minutes to minimize fish injury. Littoral individuals were sampled between 1 and 2 m of depth in a shallow zone of the lake while pelagic individuals were sampled between 3 and 6 m of depth in the deep zone (Bourke et al. 1997). Due to mortality during transportation (N=8) and during the first ten days in the laboratory (N=30), only a few littoral individuals (N=9) were available. We thus sampled another group of fish between 2 and 9 June 2003 (N=14). Wild fish were acclimated for at least two months to laboratory conditions at 8°C before the experiments. Water velocity inside each tank (all groups) was maintained under 15 cm s^{-1} to minimize the training effect (McDonald et al., 1998). A given fish was used only once in the experiments described below.

Experimental system

We used eight modified Blazka type (3.37 ± 0.03 l) respirometers similar to those described by Beamish et al. (1989) to assess oxygen consumption and swimming performances of our experimental fish. Respirometers were connected to an open-flow system with filtered

and oxygenated water circulating at a flow rate that we varied depending on the experimental water temperature and fish size (from 30 to 150 ml min^{-1}). The flow rate was controlled using small valves and was measured at the beginning and end of an experiment. Solenoid valves were used to redirect circulating water to sampling chambers containing oxygen probes (Probe 125/05; Instech Labs, Plymouth meeting, PA, USA) so that the oxygen concentration of the water leaving and entering each respirometer was determined once every hour. A fifteen-minute delay between oxygen measurements was allowed to insure a complete water change in the probe chamber. A software (Datacan V; Sable Systems International, Las Vegas, NV, USA) controlled the solenoid valves and recorded oxygen concentrations measured with an oxymeter (ReadOx-4, interfaced to the computer with a UI 2 interface; Sable System international). Oxygen probes were calibrated daily using the Winkler method modified for small volumes (APHA, 1989).

Water velocity (10 to 50 cm s^{-1}) inside each swimming chamber was adjusted by modifying the voltage applied to a submersible pump. The relationship between the applied voltage and the velocity was determined every week using a miniature current meter (OTT C2, propeller 5-123258; Kempten, Germany). The water velocity profile in the respirometer was uniform and the flow approximately rectilinear (Beamish et al., 1989). Respirometers were submerged in a temperature-controlled water tank (± 0.5°C). A mildly electrified grid (5 V) downstream of the swimming chamber kept the fish swimming against the current. Fish generally swam in the upstream shaded section during the experiment, rarely touching the electrified grid.

Experimental protocol

Fish were acclimated to the experimental temperature for at least two weeks prior to the experiments. The order of the experiments was arbitrarily set as 15, 10 and 20°C in order to limit the confounding effect between body size (growth) and water temperature in the statistical analyses.. The acclimation temperature was adjusted gradually at a rate of 1°C per day. On the day prior to the experiments, 48 h food-deprived fish were transferred to a respirometer between 16:00 and 18:00. Water velocity inside each respirometer was set to 10 cm s^{-1} overnight to allow fish to acclimate to the experimental conditions. The following morning, water flow was set to 15 cm s^{-1} and oxygen consumption rates were recorded while gradually increasing swimming speed by intervals of 5 cm s^{-1} per hour. When a given fish could no longer hold position, water velocity was brought back to 10 cm s^{-1} and the fish was left overnight in the respirometer. Rates of oxygen consumption were corrected for the associated consumption of each empty respirometer and for the time lag associated with the open-flow system (Niimi, 1978).

Morphological measurements

The following morning, fish were sacrificed with an overdose of eugenol. They were then weighed (± 0.1 g) and measured (total length, ± 1 mm). We measured sixteen morphological descriptors associated either to swimming performance or to brook charr trophic polymorphism (Bourke et al. 1997; Dynes et al., 1999) on the left side of the fish (Fig. 2.1). Morphological measurements (± 0.01 mm) were taken using a Mytutoyo digital calliper connected to a computer. Fish sex was determined by gonad inspection after morphological measurements were completed.

Response variables

Since we used a regression to estimate metabolic parameters (below), only data from fish that sustained a minimum of three swimming speeds and for which the logarithm of oxygen consumption, i.e., $\log_{10} \dot{M}O_2$, increased linearly with swimming speed were kept for further analysis. We rejected 10 of the 230 experimental fish used in this study (i.e., 4%) because they did not meet these criteria. Critical swimming speed (U_{crit}) was estimated using the model as establish by Brett (1964):

$$U_{crit} = U_{max} + (t/\Delta t)\Delta U \quad (1)$$

where U_{max} (cm s^{-1}) is the highest swimming velocity maintain for a complete hour, t is the time during which the fish could swim at exhaustion speed, Δt is the time between each velocity increment (60 min), and ΔU is the velocity increment (5 cm s^{-1}). One fish that was still swimming after 5 hours at the highest possible velocity (50 cm s^{-1}) was discarded because U_{crit} could not be estimated. Swimming speeds are expressed in body lengths per second (BL s^{-1}) and were corrected for the solid blocking effect produced by the fish (Bell and Terhune, 1970; Keen and Farrell, 1994).

Swimming costs ($\dot{M}O_2$) and standard metabolic rate (SMR) were estimated using the following model:

$$\log_{10} \dot{M}O_2 = \alpha + \beta U \quad (2)$$

where α and β are fitted constants and U is the swimming speed. Standard metabolic rate was estimated as 10^{α}. The active metabolic rate ($\dot{M}O_{2\,max}$) was estimated using equation (2) and replacing U by U_{crit}. Metabolic scope, i.e., the range through which the aerobic metabolic rate of

an animal can vary (Fry, 1947), was found by subtracting SMR from $\dot{M}O_{2\ max}$ for each fish. The total cost of transport at the optimal swimming speed (TCOT(U_{opt})) was estimated as:

$$TCOT(U_{opt}) = MR_{opt}\ M^{-1}\ U_{opt}^{-1} \quad (3)$$

where MR_{opt} is the metabolic rate when swimming at U_{opt}, M is the body mass (kg), and U_{opt} (km h^{-1}) is the swimming speed with the lowest energy cost per unit distance (Jobling, 1995). The relation between cost of transport per unit of distance travelled and swimming speed is U-shaped: it is high at low swimming speeds because of high standard metabolism cost (drag force is low but it takes more time to swim a given distance) and high at higher speeds because of increasing drag forces (Jobling, 1995) (see Fig. 5 as an example). U_{opt} was estimated as:

$$U_{opt} = \frac{1}{\beta_{ln}} \quad (4)$$

where β_{ln} is the same as β but using ln instead $\log_{10}$ in equation (1) (Pettersson and Brönmark, 1999). Net cost of transport (NetCOT), or incremental cost of swimming, was estimated individually by subtracting SMR from each $\dot{M}O_2$ value, then plotting the obtained $\log_{10}$ $\dot{M}O_2$ against swimming speed. The slope of the linear regression is proportional to the mean NetCOT for the fish (Sepulveda and Dickson, 2000). All $\dot{M}O_2$ data were converted in to Joules (J) using the oxycalorific equivalent of 14.1 J mg^{-1} O_2 (Videler, 1993). SMR, $\dot{M}O_{2\ max}$, and metabolic scope are expressed in kJ kg^{-1} hr^{-1} whereas TCOT(U_{opt}) and NetCOT are express in kJ kg^{-1} km^{-1}.

Statistical analysis

We performed a discriminant function analysis (DFA) on the size-adjusted residuals of the morphological characters to detect which ones best described the ecotypes (Legendre and Legendre, 1998). Morphological measurements were adjusted for size variation by applying the

Aitchison (1986) log-ratio transformation. We built a discriminant function with all morphological descriptors from laboratory-raised charr to describe the overall shape of the fish. We used the jackknifed method of classification to cross-validate group attribution. Unlike a normal classification matrix, a jackknifed matrix excludes the data while the coefficient used to assign ecotype-group is computed, which makes the method more accurate (Wilkinson, 1998). Since our experiments lasted approximately 6 months, fish morphology was likely to vary between the beginning and end of the experiments. A multivariate analysis of covariance (MANCOVA) indicated highly significant effects of Ecotype, Body mass, and Temperature (see Results section) on Aitchison-adjusted morphological variables. To compare morphology of all fish on the same basis, and since body size differed among ecotypes (Table 2.1), the Aitchison log-ratio of each morphological character was then transformed into a shape variate (regression residuals) by expressing it as the deviation of individuals from the pooled within-group regression line describing the relationship between the character (as the dependent variable) and body mass and experimental temperature (independent variables) (Reist, 1986). This deviation, orthogonal to body mass and experimental temperature, should be approximately independent of these variables and reflect the residual variation resulting from measurement error and biological deviation of individuals from the predicted character–fish size relationship (Kuhry and Marcus, 1977). To evaluate the parental contribution to offspring morphology, we also computed Pearson correlation coefficients for each morphological character studied (size adjusted as described above) between the mean character size of each family (N=11) and the size of that character for parental males and females (separately).

We performed an analysis of variance (ANOVA) on the size-adjusted residuals of each morphological character measured (described above) to determine morphological differences in wild brook charr. DFA was not used for wild brook charr morphology due to the low sample

size in each group (N ranged between 9 and 22 per group, see Table 1). Although we recognize it as an important issue (Peres-Neto, 1999), we did not attempt to correct probability values for multiple tests given that well-established standard corrections such as Holm's sequential Bonferroni correction can be extremely conservative (Peres-Neto et al., 2003; Moran, 2003).

We used the multivariate general linear model (GLM procedure; SAS Institute Inc., Cary, N.C.) to test the effects of Ecotype, Water temperature, Body mass, and all possible two-way interaction terms (Ecotype x Temperature, Ecotype x Body mass, Temperature x Body mass) on metabolic rates and swimming performance indices of laboratory-raised brook charr. No interaction terms were included in the statistical model of the wild group because of missing cells in the experimental design (i.e., experiments were not done at all experimental temperatures for all groups; see Table 2.1). A preliminary test indicated a significant effect of Sampling date (MANCOVA, nested Sampling date in Ecotype; P=0.0362) on metabolic rates and swimming performances of the wild littoral group. Hence, both samples of littoral individuals were treated as distinct groups, i.e., littoral (fall) and littoral (spring). Univariate GLMs were used as post-hoc tests to further examine the effect of each factor on a given performance indicator. Pairwise comparisons with sequential Bonferroni corrections were done using least-square means for each significant factor. All analyses were performed using SAS for Windows (version 8.2).

Results

Morphological variation

Effect of body mass, water temperature, and sex

Our results indicate strong effects of Temperature (MANCOVA, Wilks' λ=0.2606, F=10.29, P<0.0001) and Body mass (MANCOVA, Wilks' λ=0.5154, F=10.09, P<0.0001) on Aitchison's adjusted morphological characters in laboratory-raised brook charr after controlling for the effect of Ecotype (MANCOVA, Wilks' λ=0.2501, F=6.33, P<0.0001). Based on the sign of the regression coefficients (not shown), fish length (total length, middle peduncle to anal fin end, middle peduncle to dorsal fin end) and body height and width as well as anal fin base increased while head height, head length, and caudal and pectoral fin length decreased with body mass in the laboratory-raised group. On the other hand, body height and width, head height and length, and caudal and pectoral fin lengths increased while pectoral and anal fin bases and middle peduncle to anal and to dorsal fin ends decreased with water temperature (Fig. 2.2). Caudal peduncle height and head width were significantly longer at 15°C than at 10°C and were intermediate at 20°C (Fig. 2.2). Total length was longer at 10 and 20°C than at 15°C (Fig. 2.2).

Similarly, we also found an effect of Temperature (Wilks' λ=0.1258, F=3.03, P=0.0003) and Body mass (Wilks' λ=0.3392, F=3.25, P=0.0045) after accounting for the effect of Ecotype (Wilks' λ=0.0706, F=4.61, P<0.0001) on Aitchison's adjusted morphological characters in the wild group. The signs of the regression coefficients (not shown) indicated that body height and width increased while caudal fin length, head height, and head length decreased with body mass. Body height and width as well as head height and width increased while pectoral fin base and middle peduncle to anal and to dorsal fin ends decreased with water temperature (Fig. 2.2). For

these reasons, body mass and temperature were used as covariables in the further morphological analyses (below). In contrast, the sex of individuals did not have any significant influence on fish morphology in wild or laboratory-raised brook charr (MANCOVA, $P>0.05$).

Ecotype comparisons and parental contribution to morphology

The DFA indicated that the four laboratory-raised ecotypes were significantly different morphologically (Wilks' $\lambda=0.3807$, $F=4.89$, $P<0.0001$; Table 2.2). Overall, 54% of the fish were correctly classified to their respective group (Jackknifed procedure), with the highest reclassification success being for hybrid ecotypes (PL 60.3%; LP 57.1%) and the lowest for LL and PP (respectively 51.4 and 45.8%). Factors 1, 2, and 3 accounted respectively for 50, 28, and 22% of the between-group variability. The first factor differentiated maternal pelagic (PP and LP) from maternal littoral broods (LL and PL), with the highest differentiation being between hybrids (Fig. 2.3). Examination of the standardized discriminant loadings indicated that fish length and body height best accounted for discrimination between groups; fish from the littoral maternal broods were shorter (total length, middle peduncle to anal fin end, and middle peduncle to dorsal fin end), stouter, and had a higher caudal fin than those from maternal pelagic broods (Table 2.2; Fig. 2.3). Morphological variation on the second factor represented differences between hybrids and pure crosses while the third factor differentiated mainly pure littoral and pelagic crosses, with hybrids being intermediate. Standardized discriminant loadings on those factors indicated that pure crosses were slender and had a longer head and a higher caudal peduncle than hybrids, and that pure littoral individuals had a longer head but a shorter anal fin than pure pelagic fish. Of the 32 correlation coefficients between morphological characters of the parents and offspring, only the correlation between the female and mean standardized total length of offspring was significant ($r=0.803$, $P=0.003$).

ANOVA results indicated that ecotypes of wild brook charr differed in 8 of the 16 morphological characters measured (Table 2.3). Littoral (spring) individuals were longer (total length), more slender (body height), and had a longer head and a longer caudal peduncle (middle peduncle to anal and dorsal fin ends) than both littoral (fall) and pelagic ones (Table 2.3). Littoral (spring) individuals had a longer anal fin base than pelagic ones (littoral [fall] individuals were intermediate) but a shorter caudal fin than littoral (fall) ones (pelagics were intermediate; Table 2.3). Littoral individuals (fall and spring) had a longer dorsal fin than pelagic ones (Table 2.3).

Metabolic rates and swimming performances

Variations of U_{crit}, NetCOT, TCOT(U_{opt}), SMR, $MO_{2\,max}$, and metabolic scope are shown in Fig. 2.4. Results of the multivariate GLM indicated a significant effect of Ecotype, Temperature, and Body mass on these response variables for both groups of charr (Table 2.4). Preliminary tests indicated that Sex did not have any influence on fish metabolism or swimming performance (MANCOVA, $P>0.05$). The interaction between Ecotype and Temperature (Ecotype x Temperature) was not significant, indicating that the effect of temperature on the response variables was not significantly different among ecotypes (Table 2.4, Fig. 2.4A). On the other hand, interactions involving Body mass affected the response variables in laboratory-raised brook charr (Table 2.4, Fig. 2.4A).

Critical swimming speed

LP individuals had a significantly lower U_{crit} than both PP and LL (pairwise comparisons, both $P<0.03$), with PL being intermediate but not significantly different from the other crosses in the laboratory-raised group (pairwise comparison, all $P>0.34$; Fig. 2.4A). U_{crit} significantly increased from 10 to 20°C in all crosses of laboratory-raised charr (Fig. 2.4A). The

sign of the regression coefficient (not shown) also indicated that U_{crit} (expressed in BL s^{-1}) significantly decreased with body mass in laboratory-raised charr. In the wild group, littoral individuals (both samples) had a significantly lower U_{crit} than pelagic ones (pairwise comparisons, both $P<0.0001$; Fig. 2.4B). U_{crit} also increased significantly with temperature (reaching a maximum at 15 and 20°C; Fig. 2.4B) and decreased with body mass in wild charr (coefficient not shown).

Cost of transport

NetCOT did not differ among laboratory-raised individuals crosses (Fig. 2.4A). However, NetCOT significantly decreased with increasing temperature (Fig. 2.4A) and body mass (coefficients not shown) in laboratory-raised individuals. NetCOT was significantly higher in wild littoral individuals (spring) than in wild pelagic ones (pairwise comparisons, $P=0.010$; Fig. 2.4B), with littoral (fall) individuals being intermediate but not significantly different from the two other wild ecotypes (pairwise comparisons, both $P>0.180$; Fig. 2.4B). NetCOT of wild individuals also significantly decreased with body mass (coefficient not shown).

TCOT(U_{opt}) did not differ among ecotypes in any group (Fig. 2.4A,B). TCOT(U_{opt}) increased significantly with temperature in laboratory-raised and wild charr (Fig. 2.4A,B). TCOT(U_{opt}) also decreased with body mass in laboratory-raised charr but not in wild ones (coefficients not shown).

Standard and active metabolism

The SMR of LP was significantly higher than the other crosses in laboratory-raised charr (pairwise comparisons, all $P<0.012$; Fig. 2.4A). Furthermore, the SMR of all crosses significantly increased with temperature (Fig. 2.4A) and decreased with body mass (coefficient

not shown). The significance of the interaction terms Ecotype x Mass (Fig. 2.4A) indicates that the effect of body mass on SMR was not the same across ecotypes; the difference between LP and the other crosses is highest at lower masses and decreases with increasing mass (i.e., a higher negative regression coefficient for LP). Similarly, the effect of body mass on SMR was not the same among temperatures (Temperature x Mass; Fig. 2.4A); the negative regression coefficient (not shown) between SMR and body mass was highest at 15°C. The SMR of wild littoral (spring) individuals was significantly lower than those of pelagic and littoral (fall) individuals (pairwise comparison, both $P<0.018$; Fig 2.4B). The SMR of wild individuals did not differ significantly among tested temperatures (Fig. 2.4B) but significantly decreased with body mass (coefficient not shown).

$\dot{M}O_{2\,max}$ did not differ among laboratory-raised ecotypes (Fig. 2.4A). However, the $\dot{M}O_{2\,max}$ of wild littoral (spring) individuals was significantly lower than that of pelagic individuals (pairwise comparison, $P=0.002$; Fig. 2.4B), with littoral (fall) individuals being intermediate but not significantly different from the two other wild ecotypes (pairwise comparison, both $P>0.183$; Fig. 2.4B). $\dot{M}O_{2\,max}$ significantly increased with temperature (reaching a maximum at 15 and 20°C) but was independent of body mass in both groups of charr (Fig. 2.4A,B).

The metabolic scope differed among ecotypes in laboratory-raised brook charr (Fig. 2.4A); LP had a lower metabolic scope than LL (pairwise comparison, $P=0.004$; Fig. 2.4A). No significant differences in metabolic scope were found among wild ecotypes (Fig. 2.4B). Metabolic scope significantly increased with temperature (reaching a maximum at 15 and 20°C) and was also independent of body mass in both groups of charr (Fig. 2.4A,B).

Discussion

Morphological variation

Effects of body mass and water temperature

Our results indicated that larger (as indicated by body mass) laboratory-raised and wild brook charr are stouter, shorter finned, and have a relatively lower and shorter head than small fish. Changes in body shape during ontogeny are known in fishes and likely result from different trait-specific growth rates (Martin, 1949). Previous studies have indicated that fish become stouter as they grow, a shape that optimizes foraging performance on larger food items such as macroinvertebrates and fish (Hjelm et al., 2001; Svanback and Eklov, 2002). Also, as rearing water temperature increased, we found that laboratory-raised and wild brook charr became stouter and developed bigger heads as well as shorter caudal peduncles and narrower fin bases. In addition, laboratory-raised charr exhibited relatively longer fins (pectoral and caudal) and deeper caudal peduncles at higher temperatures. These results suggest that habitat selection could have a potential effect on the body morphology of pelagic (streamlined with short pectoral fins and narrow caudal peduncle) and littoral (stout body shape with long pectoral fins and a deep caudal peduncle) ecotypes in nature. In fish, rearing temperature affects a number of meristic characters such as vertebrae and number of fin rays and supports (Schultz, 1926; Lindsey, 1954; Ali and Lindsey, 1974; McDowall, 2003). However, examples of changes in body shape with water temperature are scarce and poorly understood (Martin 1949; Barlow, 1961; Sweet and Kinne, 1964; Mitton and Koehn, 1976). Slow growing fish (cold water) are usually stouter and have smaller heads and shorter fins (Martin, 1949; Barlow, 1961; Mitton and Koehn, 1976), which is in accordance with our results. It is suggested that changes in body form with temperature may be produced by either a change in the slope of a trait-specific growth line

and/or through changes in body size at growth inflection (i.e., change in the slope of a trait's growth line during ontogeny) (Martin, 1949; Barlow, 1961; Ghalambor et al., 2003). Also, as water viscosity is higher at colder temperatures than at warmer ones (Videler, 1993; Vogel, 1994), fish could get an advantage by being more drag-efficient at higher water viscosity (Fuiman and Batty, 1997; Sagnes et al., 2000).

Ecotype comparisons and parental contribution to morphology

Our study shows that fish morphology differed across ecotypes in both groups of charr after correcting for the effect of body mass and water temperature on morphology. In laboratory-raised charr, we found that crosses produced from a littoral female (LL and PL) were stouter and had a higher caudal fin than those from a pelagic one (PP and LP) (Factor 1), and this was especially true for the hybrids. Also, we found that pure crosses were more slender and had a larger caudal peduncle than hybrids (Factor 2). Pure littoral individuals could be differentiated from pure pelagic individual by their longer heads and shorter anal fins (Factor 3). Wild ecotype individuals also differed morphologically. Compared to pelagic and littoral (fall) individuals, littoral (spring) individuals were the most streamlined and had the longest heads, caudal peduncles, and anal and dorsal fins, but the shortest caudal fins of the wild experimental brook charr. Besides, we found that both samples of wild littoral individuals (spring and fall) had longer dorsal fins than pelagic individuals.

As morphology is to some extent genetically determined in this brook charr system (but also environmentally; see Proulx and Magnan, 2004), we expected a morphological gradient in laboratory-raised charr where hybrids would be intermediate to littoral and pelagic individuals, based on the morphological characters selected in the field to differentiate them. We did not observe such a gradient in our experiment. In fact, most of the variation in the laboratory-raised

morphology (i.e., factor 1) was apparently due to a maternal effect on morphology, where maternal pelagic crosses were more streamlined than maternal littoral ones. Standardized total length, which contributes to streamlining, was the only morphological trait correlated between female parents and their offspring and might be heritable in this system. Very few examples of maternal effect on fish morphology are known (Heath et al., 1999; Holtmeier, 2001). Proulx and Magnan (2004) also observed that offspring morphology better correlates to maternal than to paternal morphology in their study with brook charr from the same study lake. The maternal contribution to morphology would be better investigated with experiments specifically designed to test this hypothesis; our experiment was not designed to do so.

An alternative hypothesis to the lack of differentiation based on the selected characters might be a consequence of our holding conditions. In our experiment, fish from all strains were held in the same conditions, which might have caused a morphological convergence given that charr morphology shows a high level of plasticity to the environment (Noakes, 1989; McLaughlin and Grant, 1994; Hutchings, 1996; Imre et al., 2002; Proulx and Magnan, 2002, 2004; Adams et al., 2003; Peres-Neto and Magnan, 2004). Furthermore, we found only one significant correlation, out of 36, between parental and offspring morphologies (female total length), indicating a weak effect of genetic factors on morphology compared to environmental factors. This conclusion is also supported by the results of Proulx and Magnan (2004).

Similarly, wild experimental brook charr morphology diverged somewhat from those of littoral and pelagic individuals found in the same system. Previous studies reported that wild littoral brook charr have longer pectoral and dorsal fins, a longer caudal peduncle, and are usually stouter than pelagic individuals (Bourke et al. 1997; Dynes et al. 1999; Proulx and Magnan, 2002; Marchand et al., 2003). These differences were not observed in our experimental

fish. Littoral (fall) and pelagic individuals appear to be more similar morphologically than were littoral (spring) and littoral (fall) ones (with the exception of dorsal fin base). Littoral (spring) individuals were held for only 46 ± 11 days before the experiments while littoral (fall) and pelagic individuals were held for 202 ± 8 days (mean ± S.D.). A longer holding time in identical conditions for the latter groups might have caused a greater morphological convergence as discussed above.

Swimming performances and metabolism

We found that ecotypes differed in three indices of performance in laboratory-raised book charr (U_{crit}, SMR, and metabolic scope) compared to five in wild ones (U_{crit}, NetCOT, TCOT(U_{opt}), SMR, and $MO_{2\ max}$; TCOT(U_{opt}), was marginally significant). Furthermore, the magnitude of differences among ecotypes was always higher in wild than in laboratory-raised individuals. The higher response of wild ecotypes could be related to their shorter acclimation to laboratory conditions compared to laboratory-raised ones. Even in laboratory conditions, wild individuals might have retained specific morphological or physiological swimming traits necessary to exploit their own habitat in the field. Such characteristics would not have been stimulated or necessary in a controlled environment, explaining why the metabolic and swimming performances of laboratory-raised ecotypes were more similar than wild ones. Similarly, the difference in the response of littoral (spring) individuals when compared to littoral (fall) ones could also be related to acclimation time.

Critical swimming speed

Laboratory-raised pelagic and littoral brook charr were better swimmers than hybrids in the critical swimming test. Interestingly, pure lineages (PP and LL) and hybrids form two morphologically distinct groups (factor 2; Fig. 2.3); the pure crosses were more slender and had

a longer head and a higher caudal peduncle than hybrids. This suggests that the poor swimming performance of the hybrids is likely a consequence of their morphology since other studies have shown that a higher caudal peduncle increases thrust whereas a streamlined body reduces drag, resulting in higher critical swimming speeds (Webb, 1984; Taylor and McPhail, 1985, 1986; Taylor and Foote, 1991; Hawkins and Quinn, 1996). In the wild group, pelagic individuals were better swimmers than littoral ones. Again, critical swimming speed seems to be linked to morphology, as there is an apparent decrease in critical swimming speed with increasing fin development (dorsal fin base, caudal and anal fin length). Higher fin size increases surface area and results in higher drag force, and might therefore limit swimming ability (Jobling, 1995; Plaut, 2000). These differences in swimming ability of the wild charr are consistent with the habitat use of each ecotype in the field; pelagic individuals are mainly found in the water column and feed on zooplankton whereas littoral individuals are mainly found in the littoral zone and feed on zoobenthos (Bourke et al.,1997, 1999). Zooplanktivory probably requires prolonged swimming to find patchily distributed zooplankters in the water column, whereas benthic feeding more likely requires manoeuvring and burst attack to capture benthic prey (Bourke et al. 1997; Dynes et al. 1999). Well developed median fins (i.e. dorsal, anal, and caudal fin) aid in manoeuvring and may help in benthic prey foraging (Lauder and Drucker, 2004).

Cost of transport

The net cost of transport (NetCOT) and the total cost of transport at the optimal swimming speed (TCOT(U_{opt})) was comparable between laboratory-raised individuals. On the other hand the higher NetCOT of wild littoral (spring) individuals suggests that energy expenditure during locomotion increased more rapidly for those individuals than for pelagic

ones. Littoral (fall) fish also tended to have a higher NetCOT than pelagics. This pattern was expected because the morphology of both laboratory-raised and wild experimental fish has revealed that littoral individuals are usually more stout and have longer pectoral and dorsal fins (Bourke et al., 1997; Dynes et al., 1999; Proulx and Magnan, 2002, 2004; Marchand et al., 2003; present study), traits recognized to increase drag forces (Vogel, 1994; Jobling, 1995). Surprisingly, even though they should spend more energy during locomotion, littoral individuals did not have a higher total cost of transport than pelagic ones when swimming at their optimal swimming speed (U_{opt}). This finding could be explained by the fact that individuals from the littoral (spring) ecotype had a lower standard metabolic rate and a lower U_{opt} (inversely related to NetCOT), resulting in a comparable cost of transport between all wild ecotypes (Fig. 2.5A). Pettersson and Brönmark (1999) found similar results with crucian carp (*Carassius carassius*); stout individuals did not differ in the cost of transport, but the steeper slope between oxygen consumption and swimming speed (i.e., NetCOT) was compensated by a lower standard metabolic rate, an energy saving strategy for high-drag fish. In our experiment, littoral (spring) individuals were the most streamlined of the wild fish, which is inconsistent with hydrodynamic drag force predictions based on body shape and findings of previous studies (Petrell and Jones, 2000; Boily and Magnan, 2002). A possible hypothesis might be that other morphological characteristics of this ecotype (i.e., longer caudal peduncle, greater anal and dorsal fin base) may cause more drag than what streamlining could decrease, which could also explain their poor critical swimming performance.

Although littoral (spring) brook charr did not experience a higher cost of transport because of a low SMR, the extent to which they are able to swim close to their U_{opt} will determine the efficiency of this cost reduction strategy (Pettersson and Brönmark, 1999; Pettersson and Hedenström, 2000). By having a higher NetCOT, the TCOTs of littoral

individuals will increase dramatically when their swimming speed deviates from their U_{opt} (Fig. 2.5B). In contrast, the cost of transport for pelagic individuals will only be marginally affected by swimming over a broad range of velocities because their NetCOT is low. This suggests that littoral charr should generally show less variability in swimming speed and should consequently have a tendency to specialize in foraging strategies involving low-velocity variance (Pettersson and Hedenström, 2000). On the other hand, pelagic individuals should be more efficient foragers than littorals when feeding in patchily distributed food resources such as zooplankton in the open water (Pettersson and Hedenström, 2000). Proulx and Magnan (2002) showed that littoral individuals lost more body lipids and proteins when constrained to swim in pelagic enclosures, a possible consequence of higher energy required to forage on zooplankton due to their higher NetCOT.

Standard and active metabolism

Standard metabolism was first thought to be a determined trait in vertebrates, but there is now much evidence that it varies within species (Piersma and Lindström, 1997; Cutts et al., 1998; Pettersson and Brönmark, 1999; Boily and Magnan, 2002; present study). Lower SMR reduced the cost of swimming in littoral (spring) individuals, but this strategy is effective only over a small range of swimming velocities. Furthermore, this strategy likely involves other costs in terms of locomotion, digestion, and food conversion since low SMR is usually associated with low maximum workloads (Priede, 1985). Wild littoral individuals had a lower SMR but also a lower $MO_{2\ max,}$ resulting in a comparable metabolic scope. Consequently, critical swimming speeds were lower. Similarly, the laboratory-raised LL charr with lower SMR lead to a higher metabolic scope and associated higher U_{crit}.

Temperature

Swimming performance and metabolism increased with temperature (with the exception of NetCOT) in laboratory-raised charr, with higher values at 15 and 20°C, which is close to the thermal preferendum for this species (near 16°C; Coutant, 1977). We observed the same trend in wild charr. However, the lack of a significant relationship between swimming performance, metabolism, and temperature in wild experimental fish is probably a consequence of low sample size for this group, as *P*-values were marginally but not significant. Such a relationship between swimming performance, metabolism, and temperature is well documented (e.g., Beamish, 1978, 1980, 1990; Bernatchez and Dodson, 1985; van der Lingen, 1995; Leonard et al., 1999; Cooke et al., 2001; Dickson et al., 2002; MacNutt et al., 2004) and is likely a consequence of thermally sensitive biological and physical processes (Hazel and Prosser, 1974; Taylor et al., 1997) and water viscosity (Fuiman and Batty, 1997). Our results indicate that changes in water temperature affected both ecotypes (and their hybrids) in the same way since the interaction between ecotype and water temperature was never significant. This finding suggests that habitat selection in polymorphic brook charr is not a consequence of metabolic cost or swimming disadvantage caused by habitat water temperature for a given ecotype.

To our knowledge, this is the first study investigating the role of morphological differentiation and metabolism on the swimming energetics of trophic polymorphism. Our results indicate that there is a functional relationship between morphology and an individual's performance. Also, it seems that littoral individuals might suffer from a lower swimming efficiency, especially when swimming over a broad range of velocities, but that this lower performance is compensated by a low SMR. The extent to which the observed metabolic differences caused or are an adaptation to the ecotype's habitat segregation remains unknown.

Furthermore, the apparent energetic disadvantages during swimming for littoral individuals might well be offset by habitat properties (e.g., temperature, prey energy content) and associated foraging tactics themselves.

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Table 2.1. Body size of the laboratory-raised and wild experimental juvenile brook charr at the three selected temperatures. Data are mean weights and total lengths (TL) ± S.D., with sample size in parentheses.

	10°C		15°C		20°C	
	Mass (g)	TL (cm)	Mass (g)	TL (cm)	Mass (g)	TL (cm)
Laboratory-raised						
LL	8.9 ± 1.88[a] (22)	10.7 ± 0.80[a] (22)	6.8 ± 1.61[a] (20)	9.7 ± 0.75[a] (20)	12.1± 3.04[a] (22)	11.5 ± 0.93[a] (22)
PL	18.8 ± 5.06[b] (13)	13.4 ± 1.17[b] (13)	8.5 ± 2.83[a] (15)	11.0 ± 0.79[bc] (10)	18.9 ± 5.93[b] (12)	13.1 ± 1.23[b] (12)
LP	18.3 ± 6.07[b] (12)	13.4 ± 1.44[b] (12)	12.0 ± 1.98[b] (11)	11.6 ± 0.63[c] (11)	21.7 ± 5.04[b] (14)	13.8 ±1.05[b] (14)
PP	11.2 ± 3.18[a] (17)	11.5 ± 1.05[a] (17)	8.5 ± 2.83[a] (15)	10.3 ± 1.13[ab] (15)	13.3 ± 3.20[a] (16)	11.8 ± 0.87[a] (16)
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wild						
Littoral (fall)	N/A	N/A	24.6 ± 5.19[a] (9)	14.5 ± 10.5[a] (9)	N/A	N/A
Littoral (spring)	N/A	N/A	29.8 ± 5.98[a] (6)	15.7 ± 10.1[a] (6)	24.8 ± 7.37[a] (8)	14.9 ± 1.92[a] (8)
Pelagic	21.58 ± 4.83 (9)	14.0 ± 0.99 (9)	23.6 ± 6.82[a] (5)	14.4 ± 12.3[a] (5)	25.5 ± 7.93[a] (8)	14.3 ± 1.31[a] (8)
P	N/A	N/A	0.203	0.093	0.772	0.583

Note: N/A = not available.

For each temperature and size variable, means with different letters indicate significant differences as determined with an ANOVA followed by a sequential Bonferroni post hoc multiple-range comparison test ($P<0.05$).

Table 2.2. Results of the discriminant function analysis (DFA) used to compare morphological descriptors of laboratory-raised juvenile (0+) brook charr crosses. For all fish ecotypes, the male is listed first and the letter indicates the parent's ecotype: L, littoral; P, pelagic. Data are mean ± S.E.M. (mm) of the morphological character (adjusted for body mass with simple linear regression). Note that adjusted lengths of the characters are approximate because statistical analyses were performed on size- and temperature-adjusted Aitchison (1986) log-ratio transformations (see text). Values in bold indicate the highest loadings on each factor.

Descriptors	Ecotype				Standardized discriminant loadings		
	LL (*N*=63)	PL (*N*=35)	LP (*N*=36)	PP (*N*=48)	1	2	3
Total length	116.12 ± 0.32	113.97 ± 0.38	115.47 ± 0.39	115.75 ± 0.31	**0.509**	0.084	0.335
Anal fin height	14.17 ± 0.13	14.58 ± 0.16	14.59 ± 0.16	14.73 ± 0.13	0.155	-0.057	**-0.533**
Caudal fin height	28.63 ± 0.30	28.34 ± 0.37	26.73 ± 0.35	27.72 ± 0.28	**-0.473**	0.036	0.173
Body height	18.88 ± 0.07	19.58 ± 0.08	18.90 ± 0.08	18.96 ± 0.06	**-0.520**	**-0.417**	-0.319
Caudal peduncle height	9.45 ± 0.04	9.20 ± 0.05	9.05 ± 0.05	9.43 ± 0.04	-0.210	**0.505**	-0.109
Head height	14.73 ± 0.05	14.38 ± 0.06	14.18 ± 0.06	14.51 ± 0.05	-0.333	0.287	0.341
Anal fin base	9.85 ± 0.08	9.82 ± 0.10	9.79 ± 0.10	9.75 ± 0.08	-0.031	-0.132	0.188
Middle peduncle to anal fin end	21.20 ± 0.13	20.17 ± 0.16	20.87 ± 0.17	21.22 ± 0.13	**0.480**	0.378	0.073
Caudal fin length	10.80 ± 0.09	10.81 ± 0.11	10.81 ± 0.11	10.80 ± 0.09	0.033	-0.084	0.008
Dorsal fin base	11.70 ± 0.09	11.78 ± 0.11	11.67 ± 0.12	11.48 ± 0.09	-0.087	-0.283	0.327
Body width	11.42 ± 0.05	11.53 ± 0.06	11.50 ± 0.06	11.45 ± 0.05	0.030	-0.209	-0.043
Pectoral fin length	15.42 ± 0.09	15.63 ± 0.11	15.52 ± 0.12	15.59 ± 0.09	-0.013	-0.158	-0.291
Middle peduncle to dorsal fin end	45.08 ± 0.19	43.96 ± 0.23	45.72 ± 0.24	45.01 ± 0.19	**0.650**	-0.016	0.314
Head length	23.20 ± 0.10	22.30 ± 0.12	22.07 ± 0.12	22.79 ± 0.10	-0.211	**0.500**	**0.425**
Pectoral fin base	3.30 ± 0.03	3.31 ± 0.04	3.38 ± 0.04	3.37 ± 0.03	0.265	-0.074	-0.350
Head width	11.10 ± 0.05	10.89 ± 0.06	10.82 ± 0.06	11.06 ± 0.05	-0.093	0.219	0.044

Table 2.2. Continued and concluded

DFA statistics			
Eigenvalue	0.576	0.327	0.256
% of variance explained	49.72	28.22	22.06
Wilk's λ	0.381	0.600	0.796
Chi square	165.59	87.55	39.04
d.f.	45	28	13
P	<0.0001	<0.0001	0.0002

Table 2.3. Morphological descriptors of wild juvenile (0+ and 1+) brook charr individuals. Data are mean ± S.E.M. (mm) of the morphological characters (adjusted for body mass with simple linear regression). Note that the adjusted character lengths are approximate because statistical analyses were performed on size- and temperature-adjusted Aitchison (1986) log-ratio transformations (see text). Significant differences in morphology among ecotypes are in **bold**.

	Littoral (fall) (N=9)	Littoral (spring) (N=14)	Pelagic (N=22)	F	P
Total length	**143.83 ± 1.24^{a}**	**149.01 ± 0.92^{b}**	**143.50 ± 0.64^{a}**	**11.60**	**<0.001**
Anal fin height	18.45 ± 0.50	18.37 ± 0.36	18.05 ± 0.25	0.20	0.816
Caudal fin height	33.25 ± 1.37	31.03 ± 0.92	33.25 ± 0.70	3.11	0.056
Body height	**24.64 ± 0.32^{a}**	**22.54 ± 0.21^{b}**	**24.62 ± 0.17^{a}**	**36.78**	**<0.001**
Caudal peduncle height	11.58 ± 0.15	11.61 ± 0.11	11.67 ± 0.08	1.20	0.313
Head height	18.14 ± 0.22	18.35 ± 0.16	18.45 ± 0.11	2.32	0.112
Anal fin base	**11.94 ± 0.24^{ab}**	**11.92 ± 0.22^{a}**	**11.21± 0.15^{b}**	**3.84**	**0.030**
Middle peduncle to anal fin end	**24.78 ± 0.36^{a}**	**27.26 ± 0.28^{b}**	**25.89 ± 0.19^{c}**	**14.55**	**<0.001**
Caudal fin length	**12.56 ± 0.27^{a}**	**11.79 ± 0.18^{b}**	**12.11 ± 0.13^{ab}**	**5.38**	**0.009**
Dorsal fin base	**15.10 ± 0.26^{a}**	**15.43 ± 0.19^{a}**	**14.38 ± 0.13^{b}**	**9.74**	**<0.001**
Body width	13.95 ± 0.21	14.04 ± 0.15	14.22 ± 0.11	1.24	0.300
Pectoral fin length	20.42 ± 0.59	19.34 ± 0.40	19.23 ± 0.29	1.90	0.163
Middle peduncle to dorsal fin end	**54.69 ± 0.81^{a}**	**60.34 ± 0.64^{b}**	**56.94 ± 0.44^{a}**	**13.58**	**<0.001**
Head length	**29.08 ± 0.36^{a}**	**30.27 ± 0.27^{b}**	**29.34 ± 0.19^{a}**	**6.61**	**0.003**
Pectoral fin base	4.71 ± 0.14	4.89 ± 0.10	4.72 ± 0.07	0.84	0.441
Head width	13.74 ± 0.21	13.57 ± 0.15	13.72 ± 0.11	1.21	0.310

For each temperature and size variable, means with different letters indicate significant differences as determined by ANOVA followed by a pairwise comparison test (least-squares means) with sequential Bonferroni correction (P<0.05).

Table 2.4. Results of the multivariate GLM testing for the effect of ecotype, water temperature, body mass and two way interaction terms on the swimming performance and metabolic rates in laboratory-raised and wild juvenile brook charr. All performance data and body mass were $\log_{10}$ transformed.

	Laboratory-raised				**Wild**			
	Wilk's λ	*F* value	d.f.	*P*	Wilk's λ	*F* value	d.f.	*P*
Ecotype	0.649	4.050	18, 441	<0.001	0.221	5.25	12, 56	<0.001
Temperature	0.372	16.627	12, 312	<0.001	0.227	5.13	12, 56	<0.001
Body mass	0.030	838.7	6, 156	<0.001	0.033	138.38	6, 28	<0.001
Ecotype x temperature	0.810	0.940	36, 687	0.572	-	-	-	-
Ecotype x body mass	0.727	2.933	18, 441	<0.001	-	-	-	-
Temperature x body mass	0.860	2.034	12, 312	0.021	-	-	-	-

Figure legends

Fig. 2.1 Position of the sixteen morphological measurements used in this study. *HW* head width, *HL* head length, *HH* head height, *PFB* pectoral fin base, *PFL* pectoral fin length, *BW* body width, *BH* body height, *DFB* dorsal fin base, *MPD* middle peduncle to the end of the dorsal fin, *AFB* anal fin base, *AFH* anal fin height, *MPA* middle peduncle to the end of the anal fin, *CPH* caudal peduncle height, *CFL* caudal fin length, *CFH* caudal fin height, *TL* total length. Measures having two arrows (HW and BW) indicate the position where the width was measured.

Fig. 2.2 Morphological trajectories of laboratory-raised (open symbols) and wild brook charr (filled symbols) to rearing temperature. Different letters above each group series indicate a significant difference in the response variable among temperatures. Error bars are S.E.M.

Fig. 2.3 Distribution of morphological scores from the discriminant function analysis (DFA) of the four laboratory-raised brook charr crosses; LL (filled circles), PL (open circles), LP (open squares), and PP (filled squares). The confidence ellipse for each group is plotted for each factor (tension = 0.5, dashed line for hybrids and continuous line for pure crosses).

Fig. 2.4 Metabolism and swimming performance of (A) laboratory-raised brook charr: LL (filled circles), PL (open circles), LP (open squares), and PP (filled squares) male x female crosses and (B) wild brook charr captured in the littoral (fall, filled circles; spring, filled triangles) and pelagic zone (filled squares) of Lake Ledoux. Graphs are on the same scales and data were log transformed and size adjusted to a grand mean size of 15.2 g for comparisons of laboratory-raised and wild individuals. Different letters above each figure indicate a significant difference in the response variable among temperatures. Error bars are S.E.M.

Fig 2.5 Mass-adjusted total cost of transport as a function of (A) swimming speed and (B) deviation from the optimal swimming speed (U_{opt}) of wild brook charr captured in the littoral (fall, filled circles; spring, filled triangles) and pelagic zone (filled squares) of Lake Ledoux. Dotted lines in (A) indicate optimal swimming speed (U_{opt}). Data were size adjusted at a mean mass of 15.2 g.

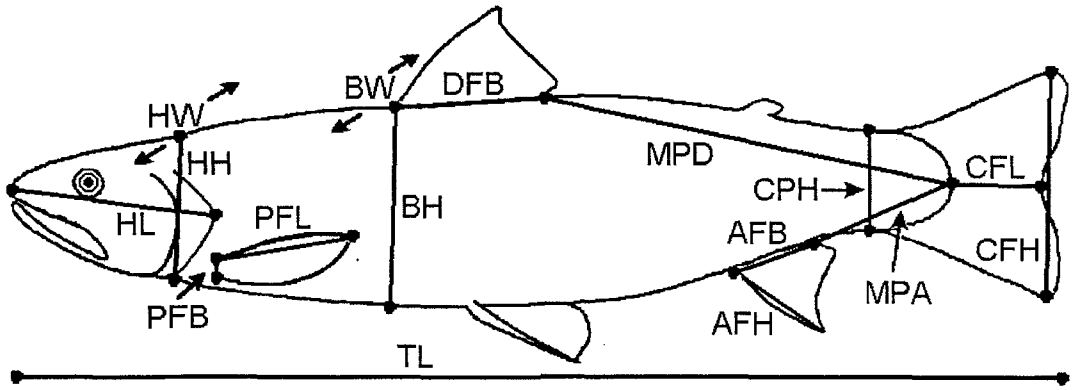


Fig. 2.1

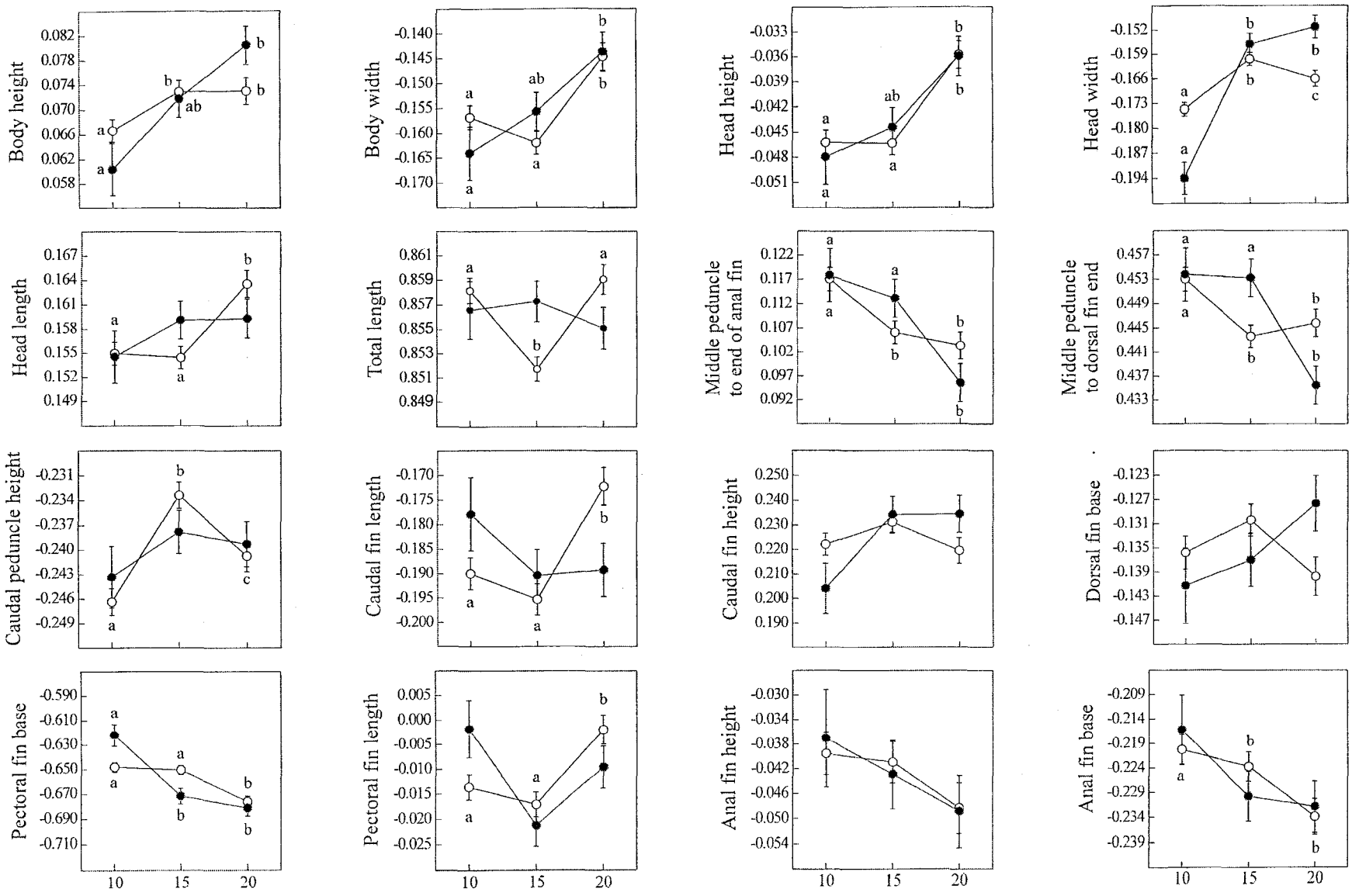

Body height
Body width
Head height
Head width
Head length
Total length
Middle peduncle to end of anal fin
Middle peduncle to dorsal fin end
Caudal peduncle height
Caudal fin length
Caudal fin height
Dorsal fin base
Pectoral fin base
Pectoral fin length
Anal fin height
Anal fin base
Temperature (°C)

Fig. 2.2

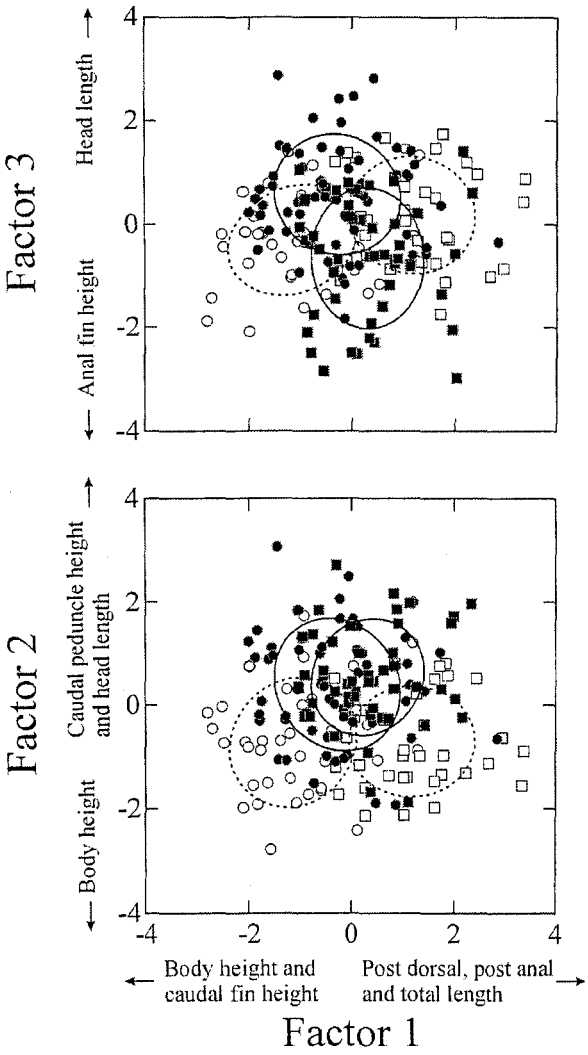
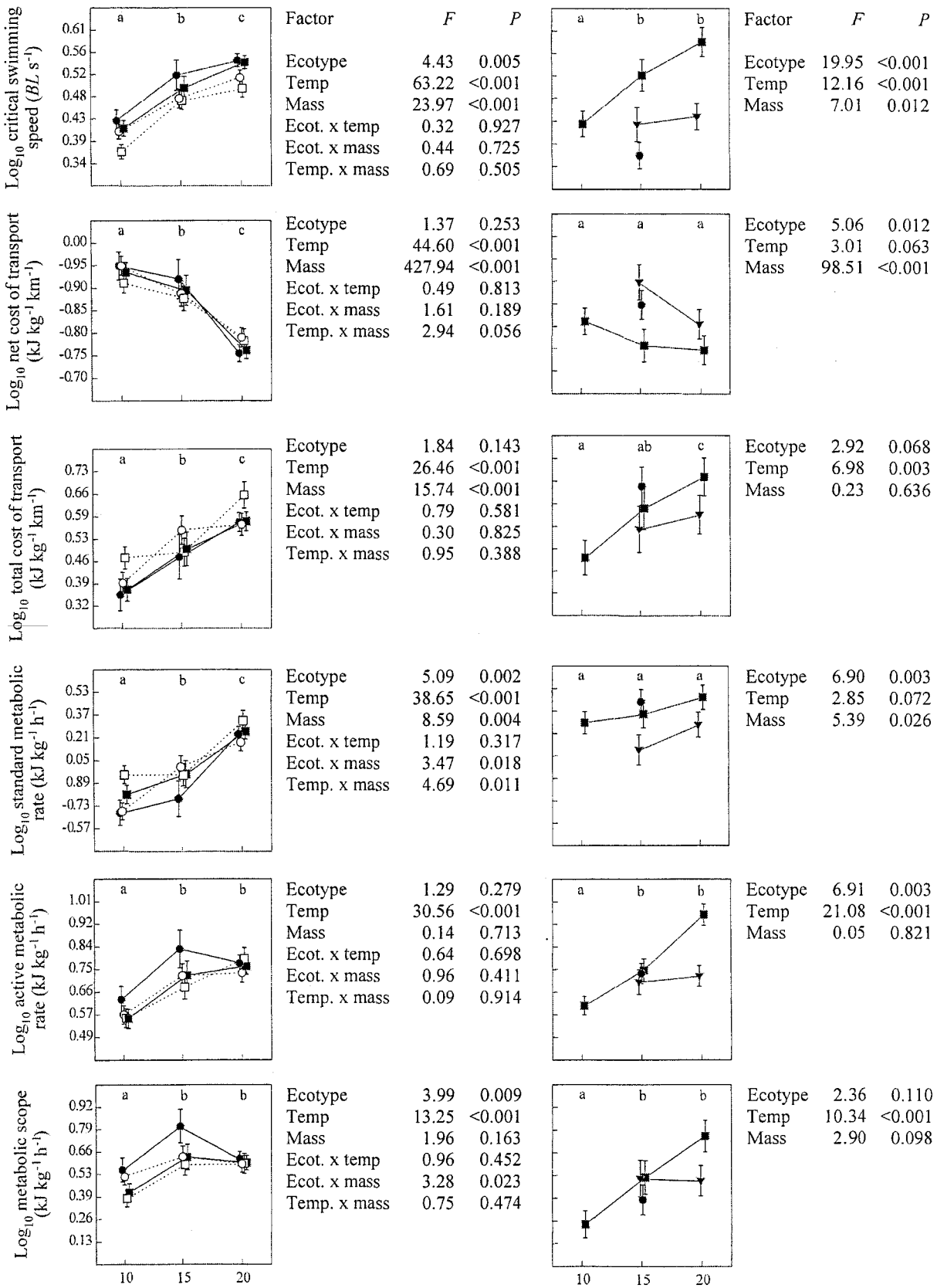

Factor 3
Head length
Anal fin height
4
2
0
-2
-4
Factor 2
Caudal peduncle height and head length
Body height
4
2
0
-2
-4
-4
-2
0
2
4
Body height and caudal fin height
Post dorsal, post anal and total length
Factor 1

Fig. 2.3



Laboratory-raised			Wild		
Factor	*F*	*P*	Factor	*F*	*P*
Ecotype	4.43	0.005	Ecotype	19.95	<0.001
Temp	63.22	<0.001	Temp	12.16	<0.001
Mass	23.97	<0.001	Mass	7.01	0.012
Ecot. x temp	0.32	0.927			
Ecot. x mass	0.44	0.725			
Temp. x mass	0.69	0.505			
Ecotype	1.37	0.253	Ecotype	5.06	0.012
Temp	44.60	<0.001	Temp	3.01	0.063
Mass	427.94	<0.001	Mass	98.51	<0.001
Ecot. x temp	0.49	0.813			
Ecot. x mass	1.61	0.189			
Temp. x mass	2.94	0.056			
Ecotype	1.84	0.143	Ecotype	2.92	0.068
Temp	26.46	<0.001	Temp	6.98	0.003
Mass	15.74	<0.001	Mass	0.23	0.636
Ecot. x temp	0.79	0.581			
Ecot. x mass	0.30	0.825			
Temp. x mass	0.95	0.388			
Ecotype	5.09	0.002	Ecotype	6.90	0.003
Temp	38.65	<0.001	Temp	2.85	0.072
Mass	8.59	0.004	Mass	5.39	0.026
Ecot. x temp	1.19	0.317			
Ecot. x mass	3.47	0.018			
Temp. x mass	4.69	0.011			
Ecotype	1.29	0.279	Ecotype	6.91	0.003
Temp	30.56	<0.001	Temp	21.08	<0.001
Mass	0.14	0.713	Mass	0.05	0.821
Ecot. x temp	0.64	0.698			
Ecot. x mass	0.96	0.411			
Temp. x mass	0.09	0.914			
Ecotype	3.99	0.009	Ecotype	2.36	0.110
Temp	13.25	<0.001	Temp	10.34	<0.001
Mass	1.96	0.163	Mass	2.90	0.098
Ecot. x temp	0.96	0.452			
Ecot. x mass	3.28	0.023			
Temp. x mass	0.75	0.474			

Fig. 2.4

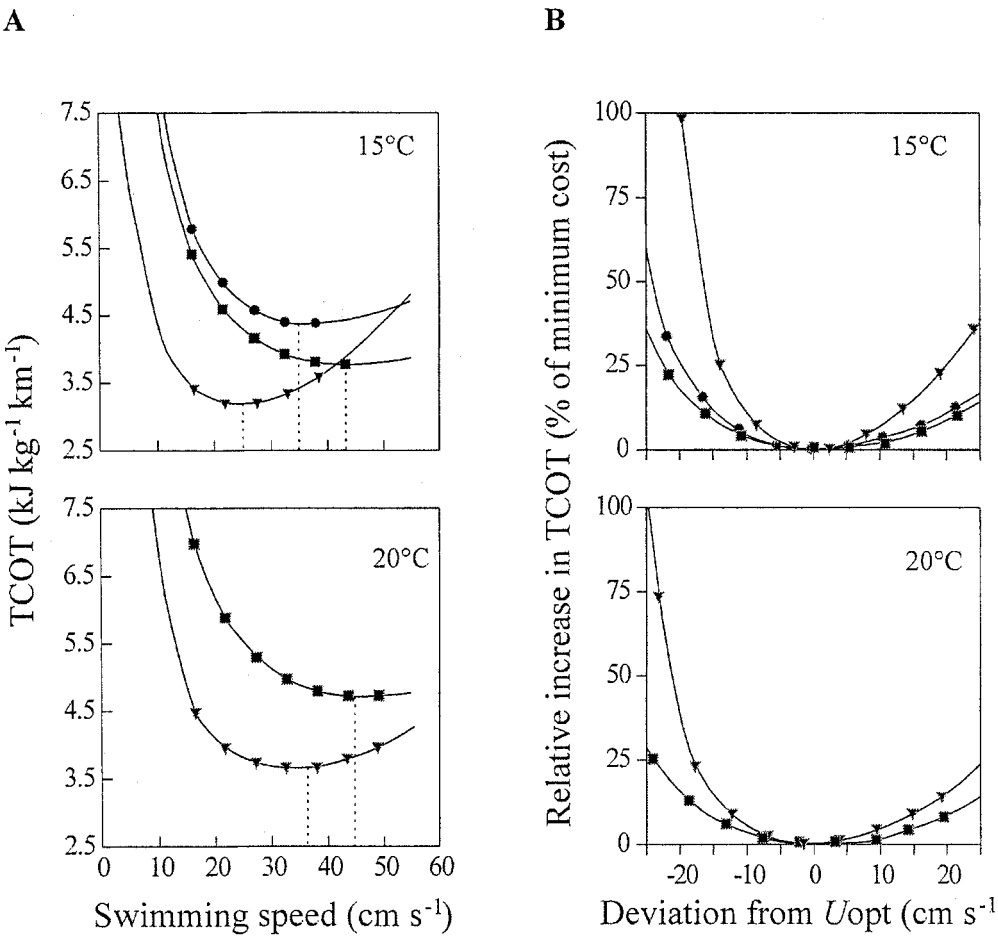

A
B
15°C
20°C
TCOT (kJ kg-1 km-1)
Swimming speed (cm s-1)
Relative increase in TCOT (% of minimum cost)
Deviation from Uopt (cm s-1)
7.5
6.5
5.5
4.5
3.5
2.5
0
10
20
30
40
50
60
100
75
50
25
-20
-10

Fig. 2.5

TROISIÈME CHAPITRE

MÉTABOLISME AÉROBIE ET ANAÉROBIE DES ÉCOTYPES LITTORAL ET PÉLAGIQUE DE L'OMBLE DE FONTAINE (*SALVELINUS FONTINALIS* M.) : RELATION AVEC L'UTILISATION DE L'HABITAT.

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Aerobic and anaerobic swimming metabolism of littoral and pelagic brook charr ecotypes (*Salvelinus fontinalis* M.): relationship with habitat use.

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Summary

Brook charr from the Canadian Shield display a resource polymorphism where littoral individuals feed mainly on zoobenthos in shallow waters and pelagic individuals on zooplankton in the open-water. These ecotypes show distinctive morphological characteristics suggesting they might use different swimming strategies to forage in their respective habitats. The main objective of this study was to determine if brook charr ecotypes differ in their muscular swimming metabolism as indicated by enzyme activities. To do so, we assayed 8 enzymes representative of aerobic and anaerobic metabolic pathways at 10, 15 and 20°C in the red and white muscle of pelagic and littoral individuals. More specifically, experiments were conducted with wild and laboratory-raised ecotypes and their hybrids. Our results indicate that wild individuals show a trade-off in their aerobic/anaerobic potential. Overall, wild pelagic individuals have greater CS and HOAD activities (aerobic) but lower PFK, PK, LDH and CPK activities (anaerobic) than littoral individuals. However, this pattern was less clear for laboratory-raised ecotypes. Pure laboratory-raised littoral individuals show higher CS and HOAD activities than pure pelagic individuals, which is contrary to what we found in wild ecotypes. Hybrids were intermediate in CS and HOAD but show the highest LDH activities. These results suggest that wild pelagic individuals should be better adapted for sustained swimming while littoral individuals should rely more on burst attacks to forage in their respective habitats. Furthermore, the magnitude of the difference observed between ecotypes was much less pronounced in the laboratory-raised charr (7 to 21%) than in wild charr (58 to 430%), suggesting that enzyme activities show a high degree of environmental plasticity.

Introduction

In freshwater lakes of the Northern hemisphere, many allopatric populations of fish are composed of discrete morphs usually specialised in exploiting either the benthic (benthic or littoral form) or pelagic (pelagic or limnetic form) habitats (e.g. Skúlason and Smith, 1995; Schluter, 1996; Svanback and Eklov, 2002). Brook charr (*Salvelinus fontinalis* Mitchill) from the Canadian Shield (Québec, Canada), exhibit such individual preference in habitat use and diet. A littoral ecotype is found in shallow water (0-2 m) and feeds mainly on zoobenthos (> 90% of stomacal content, dry weight) while a pelagic ecotype is found in deeper waters (3-6 m) and feeds mostly on zooplankton (Venne and Magnan, 1995; Bourke et al., 1997, 1999). This resource-based habitat segregation is related to subtle morphological differences; pelagic individuals are usually more streamlined, have shorter pectoral and dorsal fins and a shallower caudal peduncle than littoral individuals (Bourke et al., 1997; Dynes et al., 1999; Proulx and Magnan, 2002, 2004; Marchand et al., 2003). Streamlined body shape and short fins enhance prolonged swimming ability and should be energically efficient for foraging on patchily distributed ressources of the open water such as zooplancton. On the other hand, stout body shape and longer fins would likely improve manoeuvering or burst swimming performance, traits advantageous when exploiting spatially complex habitats such as the littoral zone (Webb, 1982, 1984; Taylor and McPhail, 1985, 1986; Taylor and Foote, 1991; Hawkins and Quinn, 1996).

Within a population, it is commonly observed that each ecotype appears better adapted to forage in its own habitat (e.g. benthic form in the littoral zone and pelagic form in the open-water habitat), suggesting a morphological and behavioural based trade-off in foraging efficiency (e.g. Ehlinger, 1990; Malmquist, 1992; Schluter, 1995; Robinson et al., 1996; Robinson, 2000; Proulx and Magnan, 2002; Svanbäck and Eklov, 2004). Swimming

performances, which are related to foraging efficiency and predator escape, are more likely a consequence of many interrelated traits and not of a unique phenotypic caracteristic such as morphology (Ghalambor et al., 2003). As an example, muscular metabolic capacities (i.e. enzyme activities) are often linked with swimming performance in fish (Kolok, 1992, 1999; Garenc et al., 1999; Schaarschmidt and Jurss, 2003). Burst swimming is mainly sustained by white muscle fibers, rich in glycolytic enzymes (anaerobic), whereas oxidative enzymes in red muscle fibers are mainly used during sustained swimming (Driedzic and Hochachka, 1978; Altringham and Ellerby, 1999; Norton et al., 2000). These relationships suggest that muscle metabolic capacities, at least, partly determine swimming performance.

In this study, we investigate whether the metabolic capacity of muscle types in polymorphic brook charr reflects swimming performance associated with habitat use. The activities of eight enzymes representative of aerobic and anaerobic metabolic pathways were determined in the red and white muscles at three acclimation temperatures. Measurements were made in laboratory-raised (pure and hybrid) and wild individuals to assess the relative importance of environmental and genetic factors on enzyme activity. More specifically, we test the following hypotheses:

1. Ecotypes differ in enzyme activities and show a physiological trade-off in aerobic/anaerobic metabolic capacities. It is expected that littoral individuals which mainly use burst swimming (and/or manoeuvering) will have a better anerobic capacity while the pelagic ecotype that uses sustained swimming will have a better aerobic capacity;

2. Hybrids are intermediate to the parental crosses in their enzyme activities given that enzyme activity is heritable;

3. Effects of acclimation temperature and muscle type on enzyme activities are not the same across ecotypes. It is expected that each ecotype is metabolically adapted to the different thermal regimes found in their respective habitats. Furthermore, red and white muscles should be utilized differently by littoral and pelagic ecotypes for burst and sustained swimming respectively.

Materials and methods

Experimental fish and holding conditions

A) Wild experimental fish

Wild juvenile brook charr were captured in Lake Ledoux from September 16 to October 2, 2002 using multifilament gillnets (10m long x 1.8m deep, 15.9mm stretched mesh). Gillnets were inspected every 10 to 15 minutes to minimize fish injury. Littoral individuals were sampled at depths between 1 and 2 m in a shallow water zone of the lake while pelagic individuals were sampled at depths between 3 and 6 m in the deep zone (Venne and Magnan, 1995; Bourke et al., 1997). Due to mortality during transportation (N=8) and during the first ten days in the laboratory (N=30), only a few littoral individuals (N= 9) were available and a second sampling took place between June 2 and 9, 2003 (N=14). Wild fish were fed *ad libitum* once a day (Biodiet Corey #1) and were acclimated for at least one month to laboratory conditions at 8°C before proceeding with the experiments.

B) Laboratory-raised brook charr

In October 2002, littoral and pelagic brook charr were sampled on the spawning ground of Lake Ledoux, Mastigouche Reserve (Québec) Canada (46°40'N, 73°20'W) using gill nets. Brook charr ecotypes were determined using an allometric relationship between body and fin

length established in previous studies (Bourke et al., 1997; Dynes et al., 1999). In the field, individuals were designated as pelagic when the length of both fins and caudal peduncle were below that expected from the size-adjusted regression line for this form. Otherwise, individuals were designated as littoral, when these same parameters were above the size-adjusted regression line. The artificial fertilisation procedure was performed following the dry method (Piper et al., 1982), and the sexual products of both ecotypes were used to produce full-sib, as well as reciprocal maternal "hybrid" broods: 3 PP, 4 LL, 2 PL and 2 LP (capital letters indicate male x female ecotype crosses from littoral (L) and pelagic (P) individuals). Fertilised eggs were incubated at 6 ± 0.5°C in two ascending-current vertical incubators (model 5609-8 tray trout; MariSource, Milton, WA, USA) connected to a glycol cooling system (± 1°C). Hatching occurred from January 17 to February 26, 2003. Upon hatching, offspring were counted and transferred into eleven 76 litre tanks (one per brood). Upon yolk sac resorption, trout pellets (Biodiet starter, Corey #0.7, and Corey #1) were distributed continuously on a 12 hour-a-day basis from an overhead automatic-feeding system. Fish where transferred to larger tanks (600 and 900 l) at 4 months and were fed *ad libitum* with appropriate size trout pellets, once a day.

For both laboratory-raised and wild charr, light intensity (40 lux) and photoperiod (12:12) were held constant during the entire experiment. Ammonia (NH_3; $\mu g\ l^{-1}$), nitrites (NO_2; $mg\ l^{-1}$) and water hardness ($mg\ l^{-1}$ of $CaCO_3$) were estimated using standard procedures (APHA, 1989) and kept within the tolerance limits for salmonids (MAPAQ, 1990). Water hardness and alkalinity were adjusted to 65 $mg\ l^{-1}$ $CaCO_3$ by adding calcium chloride ($CaCl_2$) and sodium bicarbonate (Na_2HCO_3). Water temperature was gradually modified by 1°C per day until the selected experimental temperature was reached. The order of the experiments were arbitrarily set as 15, 10 and 20°C in order to limit the confounding effect between body size (growth) and water temperature in statistical analyses. As brook charr is a cold-water species, starting with the

lower temperature also limited mortality due to stress and disease. Fish were acclimatised to the experimental temperature for 2 weeks before sampling.

Tissue preparation

Fish were killed with an overdose of eugenol. White muscle (0.17 ± 0.04 g; mean wet mass ± S.D.) was sampled on the dorsal region anterior to the dorsal fin while red muscle (0.14 ± 0.06 g; mean wet mass ± S.D.) was entirely dissected from the lateral line area of the fish. Muscle samples were immediately frozen at -80°C and stored until analyses.

Immediately before the assay, muscles tissues were minced with a straight-edged razor blade on a frozen plastic cutting plate. Tissue extracts were prepared by homogenizing 0.05 to 0.37 g of sample in 5 volumes of 50 mM imidazole-HCl, 2 mM EDTA, 5 mM $MgCl_2$ and 1 mM gluthathione (pH 7.5) using a tissue grinder (model PowerGen 125, Fisher Scientific, Pittsburgh, PA, USA) for three periods of 10 seconds on ice. Between homogenizing periods (30 seconds), samples remained on ice. A volume of 5% Triton X-100 was added prior to centrifugation at 2000g for 5 minutes at 4°C. The supernatant was used for assays of enzyme activities.

Enzymatic assays

We assayed the activity of eight enzymes belonging to aerobic and anaerobic metabolic pathways. Cytochrome *c* oxydase (CCO) and citrate synthase (CS) are used as indicators of mitochondrial abundance and aerobic capacity (Somero and Childress, 1980; Couture and Guderley, 1990). β-hydroxyacyl coenzyme A dehydrogenase (HOAD) and alanine aminotransferase (GPT) are also aerobic enzymes and were used as indicators of lipolytic activity and protein catabolism respectively (Couture and Guderley, 1990; Mendez and Wieser, 1993; Davison, 1997). The glycolytic capacity was indicated by the activity of

phosphofructokinase (PFK), pyruvate kinase (PK) and lactate dehydrogenase (LDH, anaerobic end of glycolysis) (Somero and Childress, 1980). Creatine phosphokinase (CPK) is an anaerobic enzyme supporting bust swimming through rapid energetic phosphate liberation (Dobson et al., 1987; Sugita et al., 2000).

Enzyme activities were determined using an UV/Visible spectrophotometer (model Cary 100, Varian, Palo Alto, CA, USA) equipped with a thermostatted cell changer and were measured at the same temperature to which fish were acclimated (10, 15 and 20°C). Assays conditions were optimised for brook charr tissues. With the exception of CS and CCO, enzymes activities were measured by following the disappearance of NADH at 340 nm. CS was monitored at 412 nm to detect the transfer of sulphydryl groups from COASH to DTNB and cytochrome c oxydase was measured at 550 nm to follow the oxidation of reduced cytochrome c. The extinction coefficients used for NADH, DTNB and cytochrome c were 6.22, 13.6 and 19.1 $mmol^{-1}$ cm^{-1} respectively. All assays were run in duplicate and the specific activities are expressed in I.U. (µmol of substrate converted to product per minute) per g tissue wet mass. Assay order was randomised for each fish and are based on the following methods: CCO, GPT (Pelletier et al., 1994), CS, HOAD, LDH (Cordiner and Egginton, 1997), PFK (Guderley and Gawlicka, 1992), PK and CPK (Burness et al., 1999). Specific conditions were:

Cytochrome c oxydase (EC 1.9.3.1, CCO): Potassium phosphate 100 mM, reduced cytochrome c 0.05 mM; pH 7.5. Reactions were run against a control of 0.05 mM cytochrome c oxidized with 0.33% (w/v) potassium ferricyanide. The reduction of cytochrome c was carried out by the addition of sodium hydrosulfite and the solution was bubbled with air to eliminate the excess reducing agent (Hodges and Leonard, 1974).

Citrate synthase (EC 4.1.3.7, CS): Tris-HCl 100 mM, DTNB 0.1 mM, acetyl CoA 0.3 mM, oxaloacetate 0.5 mM (omitted for the control); pH 8.0.

β-Hydroxyacyl-CoA dehydrogenase (EC 1.1.1.35, HOAD): Imidazole-HCl 50 mM, EDTA 5 mM, NADH 0.1 mM, acetoacetyl CoA 0.1 mM (omitted for the control); pH 8.0.

Alanine aminotransferase (E.C. 2.6.1.2, GTP): Potassium phosphate 50 mM, L-alanine 400 mM, NADH 0.2 mM, pyridoxal 5-phosphate monohydrate 0.05 mM, lactate dehydrogenase 10 U ml^{-1}, α-ketoglutarate 10 mM (omitted for the control), pH 7.5.

Phosphofructokinase (EC 2.7.1.11, PFK): Imidazole-HCl 50 mM, NADH 0.15 mM, KCl 50 mM, ATP 2.5 mM, $MgCl_2$ 10 mM, α-glycerophosphate dehydrogenase 1U ml^{-1}, triosephosphate isomerase 1U ml^{-1}, aldolase 1U ml^{-1}, fructose-6-phosphate 5 mM (omitted for the control); pH 7.4.

Pyruvate kinase (EC 2.7.1.40, PK): Imidazole-HCl 50 mM, NADH 0.15 mM, ADP 5 mM, $MgCl_2$ 10 mM, KCl 50 mM, fructose 1,6-biphosphate 0.1 mM, LDH 10 U ml^{-1}, phosphoenolpyruvate 5 mM (omitted for the control); pH 7.4.

Lactate dehydrogenase (EC 1.1.1.27, LDH): Imidazole-HCl 50 mM, NADH 0.2 mM, pyruvate 1 mM (omitted for the control); pH 7.4.

Creatine phosphokinase (EC 2.7.3.2, CPK): Imidazole-HCl 50 mM, NADH 0.15 mM, $MgCl_2$ 10 mM, creatine 7.5 mM, phosphoenolpyruvate 5mM, pyruvate kinase 10 U ml^{-1}, lactate dehydrogenase 10 U ml^{-1}, ATP 5 mM (omitted for the control); pH 7.4.

Statistical analysis

We performed a repeated measures multivariate analysis of covariance (repeated measures MANCOVA) to determine differences in enzyme activities among ecotypes in wild and laboratory-raised charr separately. The models included Ecotype, Temperature and Body mass (covariate) as the independent variables and control versus Muscle type (red vs white) as the repeated measure (GLM procedure; SAS institute Inc., Cary, N.C.). The interactions involving Body mass other than Muscle type x Body mass were not significant in the repeated measures MANCOVA and were omitted. The interaction between Ecotype and Temperature (Ecotype x Temperature, Muscle x Ecotype x Temperature) was kept in the model in order to adjust for slight variations in slopes and to test a differential effect of temperature on enzyme activities between ecotypes. These interactions were not tested for wild individuals because of the missing cells in the design (i.e. experiments were not performed at all experimental temperatures for all groups; see Table 3.1). If an overall significant effect of the independent variables was found (using Wilk's λ), univariate repeated measures analysis of covariance (ANCOVA) were used as a post-hoc test to further examine the effect of each factor on a given enzyme activity. Pairwise comparisons with sequential Bonferroni corrections were performed using least-square means for each significant factor. All analyses were performed using SAS for Windows (version 8.2).

Results

Size-adjusted mean activities of CCO, CS, HOAD, GPT, PFK, PK, LDH and CPK for laboratory-raised and wild brook charr are presented in Fig. 3.1A,B. A first test showed that the relationship between body mass and enzyme activity was constant between laboratory-raised and wild groups (repeated measures MANCOVA, factor Group x Mass and Group x Muscle x

Mass, all $P>0.05$), indicating that both groups are comparable. This first test also indicated that sex did not affect enzyme activity in either group of fish (wild, Wilk's $\lambda=0.7027$, $F=1.45$, $P=0.2320$; laboratory-raised, Wilk's $\lambda=0.9787$, $F=0.35$, $P=0.9436$).

Ecotype comparison

A) Wild brook charr

Results from the repeated measures MANCOVA indicated that ecotype significantly affected enzyme activities in wild brook charr (Wilk's $\lambda=0.047$, $F=12.82$, $P<0.0001$). The effect of the ecotype on enzyme activities was not the same between muscle types as indicated by the significant interaction term, Muscle x Ecotype (Wilk's $\lambda=0.355$, $F=2.42$, $P=0.0111$). The effect of ecotype on enzyme activities across temperatures (i.e. Ecotype x Temperature and Muscle x Ecotype x Temperature interactions) was not tested due to missing cells in the design (see Materials and methods section). Univariate repeated measures ANCOVAs indicated that wild brook charr CCO activity was not significantly different across ecotypes (Table 3.2, Fig. 3.1A). The activity of CS was significantly higher for pelagic than for littoral (spring) individuals in both red and white muscles (Table 3.2; pairwise comparison, $P<0.0001$), while CS activity for littoral (fall) individuals was intermediate but not significantly different from the other ecotypes (pairwise comparison, both $P>0.06$; Fig. 3.1A). The significant Muscle x Ecotype interaction (Table 2) indicated that the effect of ecotype on HOAD activity differed between muscle types. Based on the pairwise comparison, HOAD activity in the red muscle was not significantly different across ecotypes (Table 3.2, Fig. 3.1A). In contrast, pelagic and littoral (fall) individuals had a significantly higher white muscle HOAD activity than littoral (spring) ones (Table 3.2; pairwise comparison, both $P<0.002$; Fig. 3.1A). GPT activity of both muscles did not differ between wild brook charr ecotypes (Table 3.2, Fig. 3.1A). The effect of ecotype on PFK activity

was not the same between muscle types as indicated by the significant Muscle x Ecotype interaction (Table 3.2). In the red muscle, PFK was not significantly different across ecotypes but for white muscle, it was significantly higher for littoral individuals (fall and spring) than for pelagic ones (Table 3.2; pairwise comparison, both $P<0.003$; Fig. 3.1A). The effect of ecotype on PK activity was also not equal between muscle types (significant Muscle x Ecotype, Table 3.2). Red muscle PK activity was significantly higher for littoral individuals (fall and spring) than for pelagic ones (Table 3.2; pairwise comparison, both $P<0.05$; Fig. 3.1A). In the white muscle, the activity of PK was significantly higher for littoral (spring) than for littoral (fall) and pelagic individuals (Table 3.2; pairwise comparison, both $P<0.0093$; Fig 3.1A). Red and white muscle LDH activity was higher for littoral (spring) than for littoral (fall) and pelagic individuals (Table 3.2; pairwise comparison, both $P<0.0001$; Fig. 3.1A). Finally, the effect of ecotype on CPK activity differed between muscle types (Muscle x Ecotype interaction, Table 3.2). CPK activity in the red muscle was higher for littoral (fall) than for pelagic (Table 3.2; pairwise comparison, $P=0.0396$; Fig. 3.1A), while that of littoral (spring) was intermediate but not significantly different from the other wild ecotypes (pairwise comparison, both $P>0.14$, Fig. 3.1A). CPK activity was not significantly different across wild ecotypes in the white muscle (Table 3.2; Fig. 3.1A).

B) Laboratory-raised brook charr

In the laboratory-raised brook charr, the repeated measures MANCOVA indicated a significant effect of ecotype on enzyme activities (Wilk's $\lambda=0.657$, $F=2.45$, $P=0.0002$). The effect of the ecotype on enzyme activities did not differ between muscle types and across temperatures as indicated by the non-significant interaction terms; Muscle x Ecotype (Wilk's $\lambda=0.780$, $F=1.41$, $P=0.0992$), Ecotype x Temperature (Wilk's $\lambda=0.693$, $F=1.04$, $P=0.4031$) and Muscle x Ecotype x Temperature (Wilk's $\lambda=0.698$, $F=1.02$, $P=0.4450$). The univariate

ANCOVAs indicated that CCO GPT, PFK, PK and CPK activities did not differ among ecotypes in the laboratory-raised charr (Table 3.3; Fig. 3.1B). CS activity was significantly higher for the LL group than for the PP one (Table 3.3; pairwise comparison, P=0.022) although this tended to vary with temperature (see Ecotype x Temperature interaction in Table 3.3; Fig. 3.1B). HOAD activity for the LP group was marginally but not significantly higher than for PP after applying the sequential Bonferroni probability correction (Table 3.3; pairwise comparison, P=0.0594; Fig. 3.1B) The Muscle x Ecotype interaction was significant for HOAD in the univariate ANCOVAs (Table 3.3) but was not in the MANCOVA. We thus considered the latter result as valid because the MANCOVA is more robust than univariate ANCOVA, which was used as a post hoc test. LDH activity was significantly higher for LP and PL (hybrids) than for LL and PP (Table 3.3; pairwise comparison, all P<0.05; Fig 3.1B).

Effect of muscle fiber type and body mass

A) Wild brook charr

The repeated measures MANCOVA indicated that muscle type (red vs white) (Wilk's λ=0.010, F=350.64, P<0.0001), body mass (Wilk's λ=0.492, F=3.69, P=0.0071) and the Muscle x Mass interaction (Wilk's λ=0.339, F=6.97, P=0.0001) significantly affected enzyme activities of wild brook charr. Activities of enzymes belonging to aerobic metabolic pathways (i.e. CCO, CS, HOAD, GPT) were always significantly higher in the red than in white muscle, whereas those from anaerobic pathways (i.e. PK, LDH, CPK but not PFK; Table 2) were significantly lower in the red than in the white muscle (Fig. 3.1A). Furthermore, the difference in enzyme activities between muscle fibers was more pronounced for aerobic enzymes, being 2 (GPT) to 6 (HOAD) times higher in the red than in the white muscle (Fig. 3.1A). Anaerobic enzymes were far less affected by the muscle type, their activities being only 0.8 (PFK) to 1.6

(LDH) times higher in the white than the red muscle (Fig. 3.1A). PK and LDH activities scaled positively with body mass in the wild group (coefficient not shown; Table 3.2). Furthermore, the effect of body mass was sometimes different across muscle type (Muscle x Mass interaction, see Table 3.2). Although sample size was low for CCO in the wild group (N=24), a negative relationship between CCO activity and body mass was observed (coefficient not shown). PK and LDH scaling was higher in white than in red muscle (coefficient not shown).

B) Laboratory-raised brook charr

In the laboratory-raised group, the repeated measures MANCOVA indicated a significant effect of Muscle type (Wilk's λ=0.005, F=2943.17, P<0.0001), Body mass (Wilk's λ=0.723, F=6.21, P<0.0001) and the Muscle x Mass interaction (Wilk's λ=0.480, F=17.62, P<0.0001) on enzyme activities. The activities of CCO, CS, HOAD and GPT were also significantly higher in the red than in the white muscle, whereas PK, LDH and CPK (not PFK) activities were generally lower in the red than in the white muscle (Fig. 3.1B). The difference in enzyme activities between muscle fibres was also more pronounced for aerobic enzymes, being 2 (GPT) to 6.5 (HOAD) times higher in the red than in the white muscle (Fig. 3.1B). Anaerobic enzymes were far less affected by the muscle type, their activities being only 0.8 (PFK) to 1.8 (LDH) times higher in the white than the red muscle (Fig. 1B). The activities of CS, HOAD, GPT, PFK, PK, LDH, and CPK (but not CCO) scaled positively with body mass in the laboratory-raised group (coefficient not shown; Table 3.3), although CS and GPT activities only scaled with body mass in the red muscle (white muscle, linear regression, P>0.05). Body mass scaling for PFK, PK, LDH and CPK was greater in the white than in the red muscle.

Effect of temperature

A) Wild brook charr

The repeated measures MANCOVA indicated that temperature significantly affected enzyme activities in wild charr (Wilk's λ=0.035, F=15.50, P<0.0001) and this effect was not significantly different between muscle type (Muscle x Temperature interaction, Wilk's λ=0.462, F=1.68, P=0.0902). Further examination of individual enzymes indicated that temperature did not affect CCO activity in wild individuals (Table 3.2; Fig. 3.1A). Overall activities of CS, HOAD, GPT, PFK, PK and LDH increased with temperature from 10 to 20°C, although the difference in activity between 15 and 20°C was not significant for CS and PFK (Fig. 3.1A).

B) Laboratory-raised brook charr

The repeated measures MANCOVA indicated a significant effect of temperature on enzyme activities of laboratory-raised charr (Wilk's λ=0.073, F=43.78, P<0.0001). The effect of temperature was however significantly different between muscle types, as indicated by the significant interaction, Muscle x Temperature (Wilk's λ=0.461, F=7.69, P<0.0001). As for wild charr, CCO activity of the laboratory-raised charr did not differ across temperatures (Table 3.3; Fig. 3.1B). Overall activities of CS, HOAD, GPT, PFK, PK, LDH and CPK increased with temperature from 10 to 20°C although the activity of CS and CPK was not significantly different between 15 and 20°C and the activty of PFK did not differ between 10 and 15°C (Fig. 3.1B). However, the effect of temperature on CCO, GPT, PFK, PK, LDH activities was not the same across muscle types (as indicated by the significant Muscle x Temperature interaction, Table 3.3); CCO, PFK, PK and LDH activities increased more rapidly with temperature in the red than in the white muscle (coefficient not shown; Fig. 3.1B). The significant interaction,

Muscle x Temperature (Table 3.3) also indicated that GPT activity increased more rapidly with temperature in the white than in the red muscle (coefficient not shown; Fig. 3.1B).

Discussion

Ecotype comparison

Our results suggest a physiological trade-off in wild brook charr ecotypes where those having relatively high aerobic enzyme activities have relatively low anaerobic ones and vice versa. We found that wild pelagic individuals had higher aerobic enzyme activities (CS and HOAD), but lower anaerobic ones (PK, LDH, white muscle PFK and red muscle CPK) compared to littoral individuals. In contrast, littoral individuals (fall and spring) had lower aerobic enzyme activities than pelagic ones (except for littoral (fall) HOAD) but higher anaerobic activities, although littoral (fall) LDH and red muscle PK were intermediate and comparable to pelagic individuals. This suggest that wild pelagic individuals could be better adapted for aerobically fuelled swimming activities (e.g. sustained or prolonged swimming) but less suited for anaerobic activities (e.g. burst) compared to littoral ones. Previous studies found that myotomal aerobic enzymes activity (e.g. CCO, CS, HOAD and GPT) often correlate to critical swimming speed (aerobic swimming) or to the degree of activity of a fish (e.g. Couture and Guderley, 1990; Farrell et al., 1990, 1991; Dickson et al., 1993; Leonard and McCormick, 1999; Schaarschmidt and Jurss, 2003). In a related study, we found, that pelagic individuals (from the same experimental stocks) had higher critical swimming speeds (U_{crit}, prolonged swimming) than littoral ones (fall and spring) (S. Rouleau, H. Glémet and P. Magnan, manuscript submitted). In the same study, it was also found that SMR was lower for littoral (spring) (S. Rouleau, H. Glémet and P. Magnan, manuscript submitted). On the other hand, anaerobic enzymes such as PFK, LDH and CPK often correlate with burst swimming

performance (Garenc et al., 1999 but see alsoGibb and Dickson, 2002; Odell et al., 2003). Although burst swimming was not measured in our previous study, the higher anaerobic enzymes activities of wild littoral individuals suggest that they might be better adapted to this type of swimming. Such a trade-off in aerobic/anaerobic metabolic potential and performance has been observed between (Webb, 1988; Harper and Blake, 1990; Goolish, 1991) and within species (Reidy et al., 2000; Ojanguren and Braña, 2003 but see Peake et al., 2000).

In the wild, pelagic and littoral ecotypes of brook charr exploit different trophic niches that likely require different foraging strategies (Venne and Magnan, 1995; Bourke et al., 1997). Given that pelagic brook charr feed mainly on zooplankton (Bourke et al., 1999), sustained swimming ability providing high search rates might be advantageous in exploiting such a patchily-distributed resource (e.g. Webb, 1984; Ehlinger, 1990). In contrast, littoral brook charr feed mostly on zoobenthos (Bourke et al., 1999). Higher burst swimming capacity might either improve the capture success of such active prey and enhance predator evasion (especially from aquatic birds in this system) (Rand and Lauder, 1981; Webb, 1984; Blake, 2004). Interestingly, the observed differences in enzyme activities between littoral and pelagic wild brook charr correlates with morphological differences between the two ecotypes: pelagic brook charr exhibit streamlined body shape and short pectoral and dorsal fins while littoral ones had stout body shape with long pectoral and dorsal fins (Bourke et al., 1997; Dynes et al., 1999). Streamlined body shape and short fins are reported to be better suited for cruising in the open water habitat while stout body shape with long pectoral fins are better suited for burst swimming (fast-start) and manoeuvring (Webb, 1984; Blake, 2004; Lauder and Drucker, 2004). Our findings on enzyme activities (i.e. littoral individuals: mainly anaerobic and pelagic: aerobic) are thus consistent with the foraging strategies of the two ecotypes.

The aerobic/anerobic pattern of enzyme activity for wild brook charr (i.e. pelagic individuals: mainly aerobic and littoral individuals: anerobic) was not repeated for laboratory-raised charr. In the laboratory-raised group, we found that the PP had a low anaerobic capacity (low LDH activity) which is consistent with that of wild pelagic individuals, but PP also had a low aerobic capacity (low CS activity) compared to other laboratory-raised ecotypes. Furthermore, the LL ecotype had a low anaerobic capacity (low LDH) but a high aerobic capacity (high CS), which is contrary to that found for wild littoral individuals. Finally, LP and PL (reciprocal hybids) were intermediate in aerobic capacity (CS activity) as hypothesized, but had the highest anaerobic capacity (LDH) compared to pure crosses. In a related study with fish from the same experimental stocks, we found that the morphology of laboratory-raised individuals also differed from that of the wild ecotypes, and was not typical of ecotype morphology in the wild (S. Rouleau, H. Glémet and P. Magnan, manuscript submitted). However, the enzyme activities of laboratory-raised brook charr were consitent with measured U_{crit}; LP and PL which had the highest LDH activity also had the lowest U_{crit}. Furthermore, LP and PL were also stouter and had a narrower caudal peduncle than PP and LL, a shape not suited for prolonged swimming (Webb, 1984; Taylor and McPhail, 1985, 1986; Taylor and Foote, 1991; Hawkins and Quinn, 1996). Also, LL which have a higher aerobic but lower anaerobic capactity, exhibited the highest U_{crit}. PP was comparable in morphology and in U_{crit} performance to LL, but differed by having a low aerobic capactity (but similar anaerobic capacity). Even though laboratory-raised and wild individuals differed in their swimming capacity and enzyme activities, the observed swimming performances are consistent with measured enzyme activities and morphology, suggesting that fish phenotype (here enzyme activity and morphology) act as a whole on swimming performance (Ghalambor et al., 2003).

The observed differences in enzyme activities between laboratory-raised brook charr ecotypes were subtle when compared to those of wild charr. In the former, differences ranged from 7 to 21%, which is small when compared to wild charr, where differences ranged from 39 to 430%. This observation might be a consequence of a higher environmental over genetic influence on enzyme activities. Even if enzymatic activities are heritable in fish (Garenc et al., 1998; Pierce and Crawford, 1997a,b), they can also change relatively rapidly to meet environmental demands (e.g. Guderley et al., 1986, 1997; Couture and Guderley, 1990; Gamperl et al., 2002; Sherwood et al., 2002). A controlled rearing environment, from fertilisation to the time of the experiment, could have caused a metabolic convergence (or a lack of divergence) between laboratory-raised ecotypes thus explaining the small observed differences. For wild ecotypes, such a convergence could have been less pronounced than in laboratory-reared fish since they experience most of their "environmental acclimation" in the field and were kept under laboratory conditions for a shorter time period (154 ± 74 days vs 248 ± 26 days; mean ± S.D.). This hypothesis could also explain the observed differences between fall and spring wild littoral charr. For logistical reasons, littoral (fall) and pelagic individuals were held for 202 ± 8 days in the laboratory under identical conditions whereas littoral (spring) individuals were held for only 46 ± 11 days (mean ± S.D.) prior to tissue sampling. Overall, littoral (fall) charr enzyme activities were more similar to pelagic than were littoral (spring) ones. Littoral (spring) charr enzyme activities were generally intermediate to the other wild groups. On the other hand, even after a different acclimation time in the laboratory, both groups of wild littoral individuals (fall & spring) were alike for many of the other enzyme activities (i.e. CS, PFK, red muscle PK), suggesting differential time-dependent responses by discrete enzymes.

Muscle type

Aerobic enzyme activities were highest in the red muscle (CCO, CS, HOAD and GPT) while anaerobic ones were highest in the white muscle (PK, LDH and CPK but not PFK), supporting a well known relationship in fish (e.g. Driedzic and Hochachka, 1978; Norton et al., 2000). The effect of muscle type on enzyme activities was not the same across wild ecotypes, as indicated by the significant interaction between muscle type and ecotype, but not for laboratory-raised ones (which was marginally but not significantly different at the multivariate level). As discussed before, this difference might be a consequence of enzymatic phenotypic plasticity. Although pelagic and littoral individuals show a trade-off in aerobic/anaerobic potential, this trade-off was not associated to a particular type of muscle fibre: when an ecotype's enzyme activity was higher than the other ecotype, it was generally higher in both muscle types. This suggest that wild brook charr ecotypes invest in swimming related enzymes independently of muscle type.

Temperature

With the exception of CCO, all enzyme activities increased with temperature and reached a maximum at either 15°C or 20°C. As temperature increases, enzyme activities also increase since temperature directly influences the kinetics of biochemical reactions (Hazel and Prosser, 1974; Taylor et al., 1997). In this study, we were mainly interested by the differential response of ecotypes to temperature. Since the interaction between ecotype and water temperature was never significant, our results suggest that changes in water temperature will not differentially affect the energy production pathways for brook charr ecotypes (or hybrids) and that no genetically-determined compensation metabolism exist. Wild charr, on the other hand, tended to differ in LDH and CPK between temperatures. However this effect could not be tested

accurately due to missing cells in the design. Our results suggest that habitat selection in polymorphic brook charr (Bourke et al., 1997) is not a consequence of a physiological advantage (or disadvantage) gained through the influence of water temperature on a given ecotype. The results of a related study with fish from the same experimental stocks, where we investigated the influence of temperature on brook charr metabolism and swimming performances, goes in the same direction: the effect of temperature on metabolim (standard and active metabolic rate, aerobic scope for activity) and swimming performance (U_{crit}, net and total cost of transport) was the same across ecotypes (S. Rouleau, H. Glémet and P. Magnan, manuscript submitted).

A large number of studies have been performed on trophic polymorphism but few have attempted to assess the role of metabolism in habitat use. Our results support the hypothesis that polymorphic brook charr show metabolic adaptations to habitat use as indicated by enzymatic activities. It seems that wild littoral and pelagic individuals are metabolically well adapted to exploit their own resource but at the cost of an apparent trade-off between aerobic and anaerobic potential. This finding, coupled with morphological characteristics of both ecotypes, suggest that there is also a trade-off in swimming performances. The extent to which the observed metabolic differences are a direct result of habitat segregation is currently unknown, but the overall metabolic uniformity of laboratory-raised charr (as compared to wild ones) suggest an important role of environment in determining enzyme activity (environmental determinism on enzyme activities). Experiments specifically designed to investigate the relative role of environmental and genetic factors in determining the metabolic capacities of individuals are needed to fully understand the selective pressures acting on polymorphic populations.

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Table 3.1. Body size of the laboratory-raised and wild experimental juvenile brook charr at the three selected temperatures. Mean weight (g) and total length (TL; mm) ± S.D., are presented with sample size in parentheses.

	10°C		15°C		20°C	
	Mass (g)	*TL* (cm)	Mass (g)	*TL* (cm)	Mass (g)	*TL* (cm)
Laboratory-raised						
LL	8.9 ± 1.88[a] (22)	10.7 ± 0.80[a] (22)	6.8 ± 1.61[a] (20)	9.7 ± 0.75[a] (20)	12.1± 3.04[a] (22)	11.5 ± 0.93[a] (22)
PL	18.8 ± 5.06[b] (13)	13.4 ± 1.17[b] (13)	8.5 ± 2.83[a] (15)	11.0 ± 0.79[bc] (10)	18.9 ± 5.93[b] (12)	13.1 ± 1.23[b] (12)
LP	18.3 ± 6.07[b] (12)	13.4 ± 1.44[b] (12)	12.0 ± 1.98[b] (11)	11.6 ± 0.63[c] (11)	21.7 ± 5.04[b] (14)	13.8 ±1.05[b] (14)
PP	11.2 ± 3.18[a] (17)	11.5 ± 1.05[a] (17)	8.5 ± 2.83[a] (15)	10.3 ± 1.13[ab] (15)	13.3 ± 3.20[a] (16)	11.8 ± 0.87[a] (16)
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Wild						
Littoral (fall)	N/A	N/A	24.6 ± 5.19[a] (9)	14.5 ± 10.5[a] (9)	N/A	N/A
Littoral (spring)	N/A	N/A	29.8 ± 5.98[a] (6)	15.7 ± 10.1[a] (6)	24.8 ± 7.37[a] (8)	14.9 ± 1.92[a] (8)
Pelagic	21.58 ± 4.83 (9)	14.0 ± 0.99 (9)	23.6 ± 6.82[a] (5)	14.4 ± 12.3[a] (5)	25.5 ± 7.93[a] (8)	14.3 ± 1.31[a] (8)
P	N/A	N/A	0.203	0.093	0.772	0.583

Note: N/A = not available.

For each temperature and size variable, means with different letters are significantly different, as determined by ANOVA followed by a sequential Bonferroni post hoc multiple-range comparison test ($P<0.05$).

Table 3.2. Results of the univariate repeated measures ANCOVAs testing for the effect of ecotype, water temperature, body mass and two-way interaction terms on the enzyme activities in wild juvenile brook charr. CCO, cytochrome c oxydase; CS, citrate synthase; HOAD, β-Hydroxyacyl-CoA dehydrogenase; GPT, alanine aminotransferase; PFK, phosphofructokinase; PK, pyruvate kinase; LDH, lactate dehydrogenase. All enzyme activities and body mass were $\log_{10}$ transformed.

	Aerobic metabolism								Anaerobic metabolism							
Source	**CCO** (*N*=24)		**CS** (*N*=40)		**HOAD** (*N*=39)		**GPT** (*N*=40)		**PFK** (*N*=39)		**PK** (*N*=39)		**LDH** (*N*=40)		**CPK** (*N*=39)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between subject																
Ecotype	0.89	0.179	15.62	<0.001	9.60	0.001	1.84	0.174	9.00	0.001	18.65	<0.001	34.91	<0.001	3.69	0.036
Temp.	0.13	0.719	16.08	<0.001	40.93	<0.001	78.17	<0.001	30.77	<0.001	75.15	<0.001	26.15	<0.001	4.12	0.025
Body mass	0.37	0.549	1.77	0.192	1.79	0.191	3.71	0.062	1.08	0.306	25.71	<0.001	6.74	0.014	0.28	0.602
Within subject																
Muscle	563.01	<0.001	161.01	<0.001	520.78	<0.001	110.67	<0.001	0.10	0.759	29.51	<0.001	21.81	<0.001	27.84	<0.001
Muscle x ecotype	0.29	0.751	1.68	0.201	3.93	0.030	0.27	0.768	4.22	0.023	3.75	0.034	1.05	0.360	4.09	0.026
Muscle x temp.	1.06	0.316	3.53	0.041	0.90	0.415	0.03	0.969	2.52	0.096	0.92	0.407	0.67	0.520	2.15	0.132
Muscle x mass	6.83	0.017	0.22	0.639	0.00	0.961	1.06	0.311	0.20	0.659	29.44	<0.001	10.47	0.003	1.59	0.216

Table 3.3. Results of the univariate measures ANCOVAs testing for the effect of ecotype, water temperature, body mass and two-way interaction terms on enzyme activities in laboratory-raised juvenile brook charr. CCO, cytochrome c oxydase; CS, citrate synthase; HOAD, β-Hydroxyacyl-CoA dehydrogenase; GPT, alanine aminotransferase; PFK, phosphofructokinase; PK, pyruvate kinase; LDH, lactate dehydrogenase. All enzyme activities and body mass were $\log_{10}$ transformed.

	Aerobic metabolism								Anaerobic metabolism							
Source	**CCO** (*N*=159)		**CS** (*N*=156)		**HOAD** (*N*=159)		**GPT** (*N*=157)		**PFK** (*N*=155)		**PK** (*N*=158)		**LDH** (*N*=159)		**CPK** (*N*=159)	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between subject																
Ecotype	0.49	0.686	3.68	0.014	2.70	0.048	2.61	0.054	0.65	0.584	1.56	0.203	4.83	0.003	2.62	0.053
Temp.	0.38	0.685	25.87	<0.001	407.56	<0.001	223.13	<0.001	33.94	<0.001	121.70	<0.001	137.71	<0.001	13.71	<0.001
Body mass	1.20	0.276	4.16	0.043	6.56	0.012	10.36	0.002	4.76	0.031	33.19	<0.001	17.19	<0.001	8.52	0.004
Ecotype x temp.	0.87	0.518	2.06	0.061	1.76	0.112	1.97	0.074	1.01	0.422	0.66	0.683	0.35	0.909	1.80	0.104
Within subject																
Muscle	599.69	<0.001	12535	<0.001	7269.1	<0.001	3453.9	<0.001	2.42	0.122	79.97	<0.001	514.40	<0.001	164.32	<0.001
Muscle x ecotype	1.05	0.371	0.51	0.676	2.95	0.035	1.73	0.164	0.08	0.972	0.59	0.624	1.47	0.226	0.43	0.729
Muscle x temp.	3.53	0.032	0.19	0.824	2.86	0.061	15.57	<0.001	4.34	0.015	11.38	<0.001	18.47	<0.001	1.79	0.170
Muscle x mass	3.19	0.076	5.87	0.017	0.70	0.406	11.22	0.001	5.22	0.024	70.54	<0.001	44.77	<0.001	6.70	0.011
Muscle x ecotype x temp.	0.95	0.465	0.81	0.565	0.70	0.648	2.02	0.067	0.21	0.973	1.31	0.258	1.51	0.179	1.28	0.270

Figure legend

Fig. 3.1 Size-adjusted enzyme activities of (A) wild brook charr captured in the littoral (fall, circles; spring, and triangles) and pelagic (squares) zones of Lake Ledoux and (B) laboratory-raised brook charr crosses; LL (circles), PL (losanges), LP (triangles), and PP (squares); capital letters indicate male x female ecotype crosses from littoral (L) and pelagic (P) individuals. Filled symbols are for red muscle activities and open symbols for white muscle. CCO, cytochrome c oxydase; CS, citrate synthase; HOAD, β-Hydroxyacyl-CoA dehydrogenase; GPT, alanine aminotransferase; PFK, phosphofructokinase; PK, pyruvate kinase; LDH, lactate dehydrogenase. All data are in $\log_{10}(\mu M\ min^{-1}\ g\ wet\ mass^{-1})$. Both series of graphs have the same scale and data are size adjusted to a grand mean size of 15.20 g for comparison of laboratory-raised and wild individuals. Different letters on top of each graph indicate a significant difference in enzyme activity among temperatures. When the effect of temperature differed between muscle type (laboratory-raised only), letters on top and bottom of the graphs indicate nearest muscle type (i.e. letters on top are for red muscle CCO and GPT and white muscle PFK, PK and LDH). Error bars represent standard error of the mean (S.E.M.).

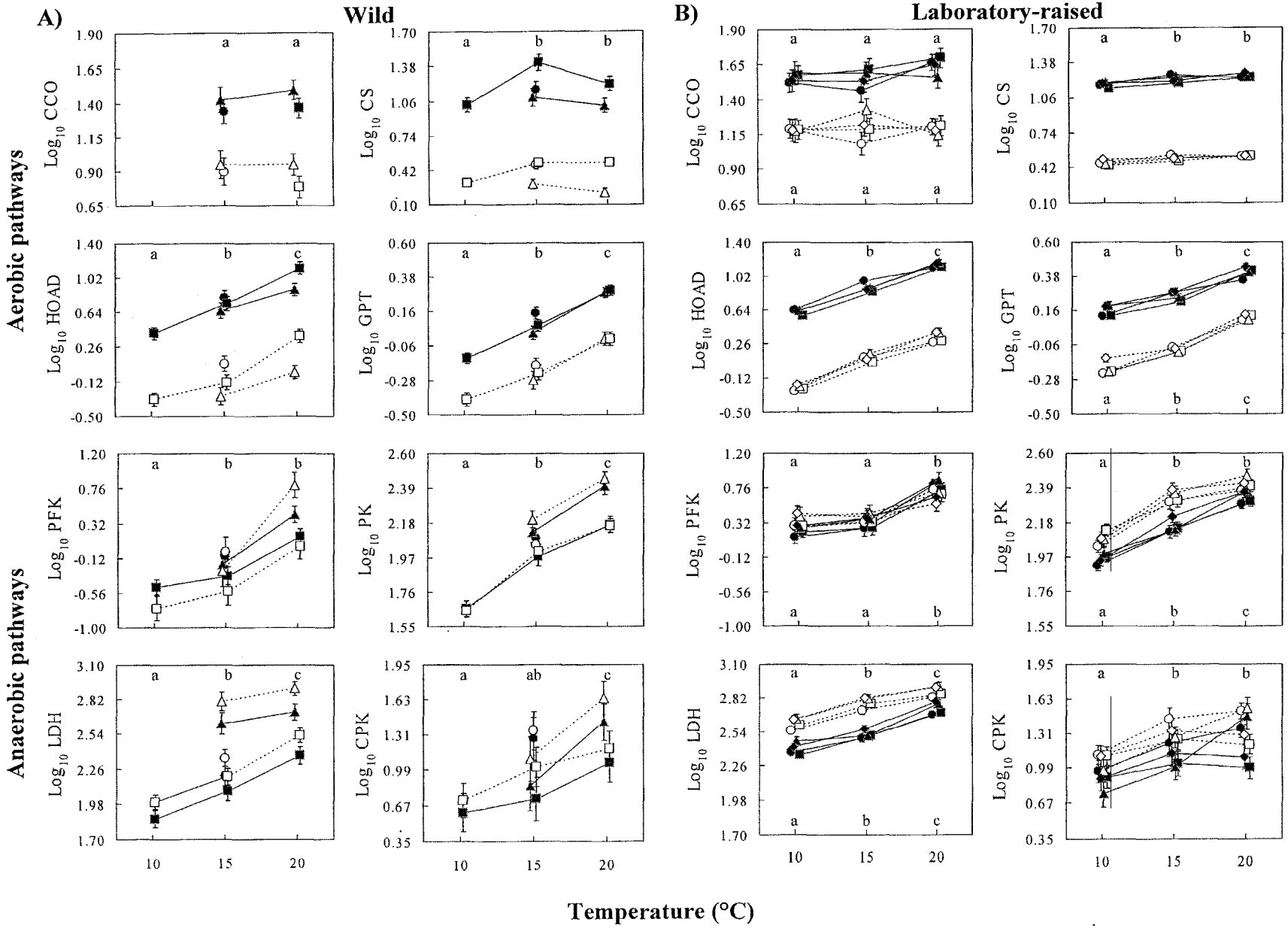
A)
Wild
B)
Laboratory-raised
Aerobic pathways
Anaerobic pathways
Log10 CCO
Log10 CS
Log10 HOAD
Log10 GPT
Log10 PFK
Log10 PK
Log10 LDH
Log10 CPK
Temperature (°C)

Fig. 3.1