Université de Montréal

Utilisation de l'énergie chez l'omble chevalier : importance des mécanismes dépendants de la densité, de la diversité intra-spécifique et de la présence de compétiteurs

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Cette thèse intitulée:

Utilisation de l'énergie chez l'omble chevalier : importance des mécanismes dépendants de la densité, de la diversité intra-spécifique et de la présence de compétiteurs

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Sommaire

Les organismes vivants utilisent les ressources de leur environnement pour croître et se reproduire. Ces ressources sont disponibles en quantités finies, se renouvellent à des taux finis, et sont distribuées de façons hétérogènes dans l'environnement, limitant la croissance et la reproduction des organismes qui en dépendent et définissant leurs habitats.

Cette thèse de doctorat comprend quatre objectifs: 1) comparer les estimations de taux d'activité obtenues par deux méthodes, 2) explorer les mécanismes de compétition intra-spécifique et inter-spécifique chez l'omble chevalier, 3) quantifier les réponses bioénergétiques de deux écotypes à des conditions environnementales similaires et 4) établir l'importance de la compétition inter-spécifique comme facteur ayant conduit à la divergence de ces deux écotypes. Les variables bioénergétiques utilisées dans cette thèse comprennent les taux de croissance, de consommation et d'activité. Cette thèse comprend quatre chapitres.

L'objectif du premier chapitre est de comparer les taux d'activité estimés par deux méthodes indépendantes (bioénergétique et comportementale). Les estimés du taux d'activité obtenus par les deux méthodes ont été semblables dans trois enclos sur six mais aucune relation globale entre les estimations n'a été trouvée. Les causes envisageables du désaccord observé sont les erreurs sur les estimations du taux de consommation (méthode bioénergétique). La méthode comportementale, lorsqu'elle est applicable, apparaît comme une alternative adéquate.

L'objectif du second chapitre est d'explorer les mécanismes de croissance dépendante de la densité chez l'omble chevalier en comparant l'intensité des relations entre, d'un côté, la densité de poissons et de l'autre, des estimations indépendantes des taux de croissance, de consommation et d'activité. Les résultats ont mis en lumière un effet négatif de la densité sur la croissance associée de façon concomitante à une diminution du taux de consommation et à une augmentation du taux

d'activité. Ces résultats indiquent que l'augmentation de l'activité peut être un mécanisme responsable de la diminution de la croissance à haute densité.

L'objectif du troisième chapitre est de quantifier les réponses bioénergétiques d'ombles chevaliers provenant de deux populations. Ces populations se sont avérées distinctes d'un point de vue morphologique et des différences marquées ont été observées dans leurs taux de croissance, leurs taux de consommation et dans leurs patrons spatiaux d'activité (*i.e.* où ces derniers sont actifs dans les enclos). Ces résultats indiquent que certaines caractéristiques des écosystèmes peuvent promouvoir l'apparition d'écotypes mieux adaptés pour l'exploitation des ressources de la zone littorale des lacs.

Les objectifs du quatrième chapitre sont 1) d'explorer les mécanismes bioénergétiques de la compétition inter-spécifique et 2) d'évaluer l'importance de cette compétition comme facteur amenant la divergence phénotypique chez l'omble chevalier. Les réponses bioénergétiques associées à la compétition inter-spécifique par la truite brune ont été quantifiées chez deux écotypes. Les résultats de cette étude suggèrent que 1) la compétition peut affecter la croissance des poissons par son effet négatif sur la consommation de nourriture et 2) que l'importance des coûts d'activité peut différer entre écotypes. Ces résultats offre peu de support à l'hypothèse selon laquelle l'absence ou la présence de compétition est à l'origine des processus par lesquels les deux écotypes se sont adaptés à leurs habitats respectifs.

Mots clés : activité, bioénergétique, compétition, omble chevalier (*Salvelinus alpinus* L.), polymorphisme.

Summary

Organisms use the resources found in their environment to grow and reproduce. These resources are available in finite amounts, renewed at finite rates, and distributed unevenly in the environment, thereby limiting growth and reproduction, and defining habitats.

This Ph. D. thesis is aimed toward bioenergetics and seeks four objectives: 1) to compare estimates of activity rate obtained using two approaches, 2) to explore the mechanisms of intra-specific and inter-specific competition in Arctic charr, 3) to quantify the differences between two ecotypes in their responses (*i.e.* bioenergetics) to similar environmental conditions, and 4) to establish the importance of inter-specific competition as a factor that promoted the divergence between these ecotypes. Bioenergetics encompass growth rate, consumption rate, and activity rate. The thesis is divided into four chapters.

The objective of the first chapter is to compare the estimates of activity rate obtained by two independent approaches (bioenergetic and behavioural) were similar. Estimates of activity rate obtained from both approaches were similar in three enclosures out of six, but there was no global relationship between estimates. The most likely cause of these discrepancies was errors on estimates of consumption rate (bioenergetic approach). The behavioural approach, when applicable, is proposed as an alternative to the bioenergetic approach.

The objective of the second chapter is to explore the mechanisms of density-dependent growth in Arctic charr by comparing the magnitude of the relationships between fish density and independent estimates of growth, consumption, and activity rates. The results of this study highlight a negative effect of fish density on growth rate, associated with concomitant decrease of consumption rate and increase of activity rate. The results indicate that increased activity may be an important mechanism for reduced growth at high density.

The objective of the third chapter is to quantify the responses, in terms of bioenergetics, of Arctic charr originating from two populations. Charr from the two populations were morphologically distinct and responded differently in terms of growth rate, diet, consumption rate, and spatial activity patterns (*i.e.* when and where fish are active in the enclosures). These observations suggest that ecosystems characteristics may allow charr to adapt morphologically and behaviourally into phenotypes (*i.e.* ecotypes) suitable to exploit the resources found within the littoral zone of northern lakes.

The objectives of the fourth chapter are 1) to explore the bioenergetic mechanisms of inter-specific competition and 2) to assess the importance of inter-specific competition in promoting the phenotypic (*i.e.* morphological and behavioural) divergence between ecotypes of Arctic charr. For these purposes, bioenergetic responses (*i.e.* growth rate, consumption rate, activity rate) of two ecotypes to inter-specific competition by brown trout were quantified. The results suggest that 1) inter-specific competition affects growth through its effect on food consumption, and that 2) the response to competition in term of activity rate may vary between populations. The results bring few support to the hypothesis that the ecotypes studied differed as a consequence of adaptive pressures imposed by brown trouts, leaving other ecosystems characteristics more credit as selective forces.

Keywords : activity, bioenergetics, competition, Arctic charr (*Salvelinus alpinus* L.), polymorphism.

Table des matières

Liste des tableaux

Chapitre 1

Chapitre 2

Chapter 3

Chapitre 4

Annexe 1

Liste des figures

Chapitre 1

Chapitre 2

Chapitre 3

Chapitre 4

Sigles et abréviations

SIGLES

NSERC : « Natural Sciences and Engineering Research Council of Canada », ou Conseil de recherches en sciences naturelles et en génie du Canada (CRSNG).

ABRÉVIATIONS

AIC : « Aikake information criterion », ou critère d'information d'Aikake – Mesure de la qualité d'ajustement d'un modèle statistique.

ANOVA : « Analysis of variance », ou analyse de variance – Technique statistique permettant de comparer les moyennes de deux groupes ou plus.

BPC : biphenyls poly-chlorés – Une classe de substances organo-chlorées.

DDE : dichloro-diphenyl-dichloroethylène – Une substance organo-chlorée.

GLM : « Generalized linear model », ou modèle linéaire généralisé – méthode statistique permettant d'estimer les relations entre des variables explicatives et une variable réponse distribuée selon divers modèles statistiques.

ICP-MS : « Inductively Coupled Plasma Mass Spectrometry », ou spectrométrie de masse d'un plasma couplé par induction – Technique d'analyse chimique permettant d'obtenir les concentrations d'isotopes appartenant à divers éléments.

Me-Hg^+ : méthyl-mercure – Substance organo-métallique neurotoxique pouvant s'accumuler dans l'organisme.

MEI : modèle énergétique intégré.

NHM : « numerical habitat model », ou modèle numérique d'habitat – Fonction(s) mathématique(s) utilisée(s) pour décrire et/ou prédire la qualité des habitats utilisés par les organismes d'une ou plusieurs espèce(s).

SDA : « specific dynamic action », ou métabolisme de digestion – La quantité d'énergie utilisée pour digérer, absorber et transporter les nutriments jusqu'à leur lieux de stockage dans l'organisme.

SMR : « standard metabolic rate », ou métabolisme standard – La quantité minimale d'énergie qu'un organisme poïkilotherme doit utiliser pour assurer le maintien de ses fonctions vitales de base.

SVC : « Stereo-video-cameras », ou caméras stéréoscopiques – Ensemble de caméras dont les champs visuels partagent un espace conjoint, permettant ainsi de déterminer la position des objets situés dans cet espace.

VHS : « Video Home System », ou système vidéo domestique - standard d'enregistrement de signaux vidéo analogiques sur bande magnétique.

« Les espèces qui survivent ne sont pas les espèces les plus fortes, ni les plus intelligentes, mais celles qui s'adaptent le mieux aux changements. »

(Charles Darwin)

« Je sais pourquoi tant de gens aiment couper du bois. C'est une activité où l'on voit tout de suite le résultat. »

(Albert Einstein)

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Introduction générale

PROBLÉMATIQUE

La croissance est un processus inhérent au cycle vital des organismes. Par sa croissance, l'organisme augmente sa taille, constitue les réserves nécessaires à sa survie et génère les produits sexuels nécessaires à sa reproduction. La croissance est à la fois liée aux variations de l'effectif (*i.e.* la dynamique) des populations et à sa productivité (effectif *x* croissance moyenne des individus). De plus, comme divers aspects de l'écologie d'un organisme peuvent être affectés par sa taille (*e.g.* besoins physiologiques, sélection d'habitat), l'étude de la dynamique avec laquelle la taille des organismes change dans le temps (*i.e.* taux de croissance) et de l'effet des conditions du milieu sur cette dynamique est un élément central dans plusieurs domaines des sciences environnementales. D'un point de vu comptable, la croissance représente le revenu net d'un organisme.

Les organismes hétérotrophes (*e.g.* animaux, fongus, saprophytes) doivent consommer de la nourriture afin d'acquérir les constituants nécessaires au maintien de leurs fonctions vitales et à leur croissance. La consommation est, conséquemment, un aspect fondamental de leur écologie. De plus, la consommation réalisée par l'ensemble des individus d'une population (effectif *x* consommation moyenne des individus) est une mesure de l'impact qu'aura une espèce sur son milieu et constitue un aspect fondamental de l'écologie des communautés et de l'étude des interactions trophiques. Les ressources énergétiques acquises par l'alimentation représentent le revenu brut de l'organisme et une fraction de ce revenu pourra être utilisée pour la croissance.

Les organismes doivent utiliser de l'énergie sous forme de mouvements (activité) afin de parcourir les distances séparant leurs habitats, pourchasser leurs proies, fuir leurs prédateurs, défendre un territoire, etc. Les ressources énergétiques utilisées pour l'activité ne seront plus disponibles pour la croissance. L'activité constituent donc, en quelque sorte, le montant investi par les organismes afin de survivre et de compléter leur cycle vital.

En plus de l'énergie investie sous forme d'activité, certaines quantités d'énergie seront perdues

(*e.g.* matières non-digestibles, composés chimiques non-utilisables) ou devront être utilisées par l'organisme pour maintenir ses fonctions vitales (*e.g.* homéostasie, régulation osmotique, conversion des éléments nutritifs). À l'instar des coûts d'activité, ces montants sont aussi soustraits du revenu brut de l'organisme (*i.e.* la consommation).

La bioénergétique est l'étude quantitative de la dynamique d'allocation de l'énergie acquise par la consommation entre les différents processus d'origines physiologiques (*i.e.* pertes, métabolisme au repos, et croissance) et comportementales (*i.e.* activité) inhérents aux stratégies adoptées par les organismes pour compléter leur cycle vital. Pour un ensemble de conditions environnementales donné, la consommation et l'activité peuvent être perçues comme des mécanismes influencés directement par le comportement (*i.e.* choix et compromis réalisés par l'organisme) alors que les besoins physiologiques sont des mécanismes influencés indirectement par le comportement (*i.e.* conditions environnementales rencontrées par l'organisme dans les habitats qu'il a sélectionnés). Dans cette perspective, la croissance réalisée sera la conséquence ultime de ces mécanismes d'origines comportementales et sera donc appelée à varier de différentes manières lorsque les conditions environnementales changeront.

La densité (*i.e.* le nombre ou la biomasse d'individus par unité d'habitat) est un facteur environnemental susceptible d'influencer l'allocation de l'énergie et la croissance. Lorsqu'un nombre grandissant d'individus partage un même ensemble de ressources, ces dernières peuvent éventuellement s'appauvrir (*i.e.* compétition d'exploitation). Elles deviennent alors difficiles à obtenir (diminution de la consommation) et il est de plus en plus coûteux de les acquérir en quantités suffisantes (augmentation de l'activité). Soumis à une proximité grandissante, certains individus peuvent manifester des comportements agressifs impliquant des coûts supplémentaires d'activité (*i.e.* compétition d'interférence) alors que les autres, étant l'objet d'attaques répétées, peuvent être reclus à des sources d'alimentation de qualités moindres. La densité peut donc affecter les mécanismes bioénergétiques de deux façons (*i.e.* diminution de la consommation et augmentation du taux

d'activité). Ainsi, les conséquences de la densité sur l'impact qu'aura une population sur son milieu (*e.g.* intensité d'exploitation des ressources alimentaires) ne sont pas visibles en observant seulement son effet sur la croissance. L'étude de l'effet de la densité sur l'allocation de l'énergie permet de répondre à ces questions.

Parce qu'elle est fonction de la physiologie et du comportement des organismes, la stratégie d'allocation de l'énergie peut être considérée comme un trait bio-écologique dont l'expression est propre aux individus d'une espèce ou à un sous-groupe d'individus au sein d'une espèce (*e.g.* sous-espèce, écotype). Les différences intra-spécifiques de stratégies d'allocation de l'énergie restent, à l'heure actuelle, peu étudiées et peu de mesures de leurs conséquences sur le bilan énergétique ont été rapportées.

À l'instar de la densité d'organismes appartenant à la même espèce (compétition intra-spécifique), la compétition inter-spécifique peut affecter, de façons similaires, l'allocation de l'énergie chez les individus d'une espèce. À l'heure actuelle, ce champ de connaissance reste cependant peu exploré. De plus, la possibilité que des différences intra-spécifiques de stratégies d'allocation de l'énergie puissent influencer la façon avec laquelle les individus répondent en terme de consommation, d'activité et de croissance à la présence de compétiteurs demeure inconnue.

Cette thèse a pour objectif général d'améliorer notre connaissance des effets de la compétition et des différences phénotypiques sur la croissance et les processus bioénergétiques à l'origine de la croissance. Dans la prochaine section, nous verrons en détails les outils actuellement disponibles en modélisation bioénergétique et comment ils peuvent être utilisés pour quantifier ces effets.

BIOÉNÉRGÉTIQUE

La bioénergétique (*anglais* : bioenergetics) est une discipline ayant pour objectif de quantifier les flux d'énergie acquis, utilisés et stockés par les organismes vivants. Les informations produites par la bioénergétique peuvent être utilisées afin de quantifier l'impact des organismes sur leur milieu, de

prédire ou de comprendre l'impact des conditions environnementales sur leur croissance et d'explorer divers aspects leurs cycles vitaux. L'énergie utilisée par les organismes, d'abord présente sous la forme de potentiels chimiques dans la nourriture qu'ils ingèrent (*i.e.* la consommation), est soit évacuée sous forme de déchets (*i.e.* les pertes fécales et d'excrétion), dissipée sous forme de travail on de chaleur (*i.e.* le métabolisme) ou, ultimement, stockée dans leurs tissus (*i.e.* la croissance; Brett et Groves 1979, Adams et Breck 1990, Hanson *et al.* 1997). Des modèles et analyses basés sur l'approche bioénergétique ont été utilisés dans le cadre d'études portant, entre autre, sur plusieurs espèces de poissons (Kitchell et Breck 1980, Stewart *et al.* 1981, 1983, Railsback et Rose 1999, Sherwood *et al.* 2000, Dineen *et al.* 2007), de reptiles (Wallace *et al.* 2006; sous-groupe des oiseaux : Derby et Lovvorn 1997, Bishop et Green 2001, Gremillet *et al.* 2001, 2003, Hebert et Morrison 2003, McNab 2003) et de mammifères (Zenuto *et al.* 2002, Humphries *et al.* 2004, Nespolo *et al.* 2005, Rosen *et al.* 2007).

Le budget énergétique s'appuie sur le principe de conservation de l'énergie et consiste à modéliser un organisme comme un système clos dans lequel entre, sortent et sont stockés des flux énergétiques (*i.e.* quantités d'énergie par unité de temps, de masse ou les deux). Chez les poissons d'eau douce ou d'espèces sténohalines, un ensemble synthétique de ces flux et les liens qu'ils entretiennent sont représentés par le modèle mathématique suivant:

$$C = F + E + SMR + SDA + A + G \tag{I.1}$$

où C représente la consommation, F et E représentent respectivement les pertes d'origines fécales (*i.e.* l'énergie ingérée qui n'est pas assimilée) et urinaires (*i.e.* l'énergie associée aux produits d'excrétion), SMR le métabolisme standard (*i.e.* l'énergie nécessaire au maintien de l'homéostasie), SDA le métabolisme associé à la digestion (*i.e.* les coûts mécaniques et biochimiques associés à la digestion, à l'assimilation, au transport et au stockage des constituants organiques), A le métabolisme d'activité et G la croissance. Les prochaines sous-sections seront consacrées aux méthodes utilisées pour estimer ces flux énergétiques *in situ* ou à l'aide de sous-modèles.

Croissance

La croissance est le processus par lequel l'énergie acquise par la consommation et qui n'est pas perdue ou utilisée pour le métabolisme se retrouve stockée dans les tissus. La mesure de la croissance réalisée dans un intervalle de temps requière que l'on connaisse la masse et la densité d'énergie (*i.e.* la quantité d'énergie par unité de masse) de l'organisme au début (respectivement w_0 et ED_0) et à la fin (respectivement w_F et ED_F) de l'intervalle :

$$G = w_F \cdot ED_F - w_0 \cdot ED_0 \qquad \text{(I.2)}$$

La densité d'énergie est estimée par calorimétrie sur différents types de tissus, ou encore sur un échantillon homogénéisé (organisme complet). Il est aussi possible d'estimer ED à l'aide de modèles. Par exemple, Hartman et Brandt (1995) ont proposé une série de 39 modèles utilisant le pourcentage de masse sèche sur la masse humide ($100 \cdot w_{sèche} / w_{humide}$) comme variable explicative. Ces modèles permettent de prédire ED avec fiabilité ($0.87 < R^2 < 0.99$) chez plusieurs espèces et familles de poisson.

Consommation

La consommation est la quantité d'énergie acquise par voie alimentaire. Elle représente le revenu énergétique brut de l'organisme et la pression qu'il exerce sur ses ressources alimentaires. Chez les poissons, la consommation peut être estimée *in situ* ou prédite à l'aide de modèles bioénergétiques (*i.e.* équation I.1). On compte trois méthodes pour estimer la consommation *in situ* : la méthode d'Eggers (1977), la méthode d'Elliott et Persson (1978) et la méthode des traceurs chimiques (Davis et Foster 1958). Les deux premières méthodes sont basées sur les taux d'élimination du contenu gastrique ou du tractus digestif complet (Boisclair et Marchand 1993). Lors de leur application, on pose généralement comme prémisse qu'à une température donnée, le taux instantané d'évacuation gastrique est proportionnel à la quantité de nourriture présente dans l'estomac (J) tel que :

(I.3) $$\frac{dJ}{dt} = -k \cdot J$$

où k est une constante de proportionnalité (estimée empiriquement) décrivant le taux d'évacuation gastrique et t est le temps. On estime la consommation journalière par la méthode d'Eggers (1977) comme :

(I.4) $$C = 24 \cdot \bar{J} \cdot k$$

où $\bar{J}$ est la moyenne journalière de la masse relative de nourriture présente dans l'estomac des poissons et où k est estimé sur une base horaire (h^{-1}). La méthode d'Elliott et Persson (1978) est quant à elle basée sur la somme des consommations réalisées dans une série de n intervalles de temps t, chacun d'une durée i :

(I.5) $$C = \sum_{t=1}^{n-i} C_t \quad , \quad \text{où} \quad C_t = \frac{(J_{t+i} - J_t \cdot e^{-k \cdot i}) \cdot k \cdot i}{1 - e^{-k \cdot i}}$$

où l'unité de mesure utilisée pour i est l'inverse de celle utilisée pour k (*e.g.* respectivement h et h^{-1}). Cette méthode est basée sur la prémisse que les taux de consommation sont constants dans les intervalles de temps utilisés. La méthode d'Eggers (1977) requière quant à elle que $\bar{J}$ soit un estimateur adéquat de l'espérance mathématique de J pour la population (*i.e.* la quantité relative de nourriture qui soit la plus probable de retrouver dans un poisson observé à n'importe quel instant dans la population). Cette dernière est relativement simple d'un point de vue mathématique et Boisclair et Leggett (1988) ont démontré qu'elle est robuste dans un large spectre de conditions environnementales.

Les méthodes d'Eggers (1977) et d'Elliott et Persson (1978) sont simples d'un point de vue méthodologique mais requièrent un effort d'échantillonnage important et beaucoup de travail de laboratoire (*e.g.* dissection, pesées). De plus, les poissons sont généralement sacrifiés lors du prélèvement de leur contenu gastrique, une situation incompatible avec certains protocoles expérimentaux. Estimer la consommation en utilisant un traceur chimique permet d'éliminer certaines de ces contraintes. Par exemple, Davis et Foster (1958) ont proposé l'utilisation de certains radio-

isotopes comme traceurs pour estimer la consommation. Ces traceurs sont détectables en petites quantités, par radio-spectrométrie (*i.e.* la mesure de l'intensité des radiations α, β ou γ d'une énergie donnée). Suite aux travaux de Davis et Foster (1958), le césium-137 (^{137}Cs) a été utilisé comme traceur chimique pour estimer la consommation chez la carpe (*Cyprinus carpio*, Kevern 1966), le crapet arlequin (*Lepomis macrochirus*, Kolehmainen 1974), la truite arc-en-ciel (*Oncorhynchus mykiss*, Hakonson *et al.* 1975), la truite brune (*Salmo trutta*, Forseth *et al.* 1992) et le saumon de l'Atlantique (*Salmo salar*, Kennedy *et al.* 2004). D'autres traceurs chimiques comme le mercure (Trudel *et al.* 2000) et certains contaminants organiques persistants (*e.g.* les BPC et le DDE; Borgman et Whittle 1992) ont aussi été proposés.

Les substances susceptibles d'être utilisées comme traceur chimique de la consommation doivent posséder sept propriétés, soit: 1) être utilisables en deçà de son seuil de toxicité, 2) être absorbées exclusivement, ou dans une large proportion, par voie alimentaire, 3) s'accumuler dans l'organisme, 4) être mesurables avec assez de précision dans l'organisme et dans sa nourriture, 5) avoir une dynamique d'élimination qui puisse être prédite, 6) se retrouver dans des concentrations qui soient stables dans la nourriture et 7) être absorbées par l'organisme dans des proportions qui soient, elles aussi, stables ou qui puissent être prédites.

La prémisse générale de la méthode des traceurs chimiques est de considérer la quantité de nourriture consommée dans un intervalle de temps comme étant une proportion directe de la charge de traceur ingérée (Q_I) dans ce même intervalle. On estime Q_I par unité de temps comme la somme de la charge de traceur mesurable (Q_M) et la charge de traceur éliminée (Q_E) tel que :

$$\frac{dQ_I}{dt} = \frac{dQ_M}{dt} + \frac{dQ_E}{dt} \qquad \text{(I.6)}$$

De façon générale, la méthode d'estimation consiste à intégrer la somme des fonctions décrivant l'augmentation de la charge et l'élimination du traceur chimique dans le temps, respectivement $Q_M(t)$ et $Q_E(t)$, dans un intervalle $[t_1, t_2]$, soit :

(I.7) $$Q_{I;t_1,t_2}=\int_{t_1}^{t_2} Q_M(t)+Q_E(t)dt$$

La consommation de nourriture associée à l'absorption d'une quantité de traceur Q_I est estimée pour un ensemble d'items j, chacun représentant une proportion p_j de la diète et contenant une concentration de traceur $[Q]_j$ lequel est absorbé dans une proportion α_j, telle que :

(I.8) $$C=\frac{Q_I}{\sum_j (\alpha_j \cdot [Cs]_j \cdot p_j)}$$

De plus, le calcul de $Q_M(t)$ et $Q_E(t)$ demande de poser certaines prémisses quant à la dynamique temporelle de la variation de Q_M (considérée comme constante lorsqu'on dispose seulement de mesures à t_1 et t_2) et à la trajectoire de croissance de l'organisme (linéaire : Forseth *et al.* 1992, exponentielle : Rowan et Rasmussen 1996; voir Gingras et Boisclair 2000).

Dans une population où les charges de traceur sont en équilibre ($Q_{M,t+1} \simeq Q_{M,t}$), la réponse de la méthode des traceurs est influencée principalement par le modèle d'élimination ($Q_E(t)$). L'importance du modèle d'élimination décroît lorsque les organismes sont placés dans un milieu plus riche en traceur ($Q_{M,t+1} > Q_{M,t}$; Forseth *et al.* 1992). Un approche par enrichissement en traceur permet donc d'améliorer la sensibilité de cette méthode. Gingras et Boisclair (2000) ont conclu que la méthode du césium rend des estimations de consommation similaires à la méthode de Eggers (1977) chez la perchaude (*Perca flavescens*) pour des périodes supérieures ou égales à 40 jours (sans enrichissement en traceur). Les méthodes utilisant un marqueur ont l'avantage de produire des estimés individuels de consommation intégrés sur une période de temps allant d'un mois à plusieurs années, selon la qualité des données disponibles. Cette méthode (utilisant le Cs stable : ^{133}Cs) pourrait produire des estimés fiables sur des périodes aussi courtes que deux ou trois semaines en conditions expérimentales (milieu enrichi en Cs; Torbjørn Forseth, communication personnelle).

Pertes, métabolisme standard et métabolisme de digestion

Les pertes fécale et d'excrétion et les métabolismes standard et de digestion sont mesurés expérimentalement en utilisant divers protocoles (Brett et Grove 1976, Elliott 1976a, Jobling 1994). Les pertes fécales (F) incluent principalement les matières non assimilables (*e.g.* cellulose, chitine, certains oligosaccharides et polypeptides), les déchets évacués par la bile et cellules détachées du tube digestif. Les pertes d'excrétion (E) représentent l'énergie associée aux substances qui ne peuvent pas être utilisées par l'organisme (*e.g.* déchets). Les pertes fécales et urinaires sont estimées *in situ* à l'aide de modèles mathématiques utilisant généralement la consommation (C), température (T), la masse du poisson (W, Elliott 1976b) :

(I.9) $$F = C \cdot a_F \cdot T^{b_F} \cdot e^{c_F \cdot C/C_{MAX}} \text{ et } U = C \cdot a_U \cdot T^{b_U} \cdot e^{c_U C/C_{MAX}} \text{ où } C_{MAX} = a_M \cdot W^{c_M} \cdot e^{b_M T}$$

où C_{MAX} représente la consommation maximale du poisson (*i.e.* nourrit à satiété) et les constantes $a_{(F, U \text{ et } M)}$, $b_{(F, U \text{ et } M)}$ et $c_{(F, U \text{ et } M)}$ sont estimés empiriquement (expériences de laboratoire).

Le métabolisme standard et le métabolisme de digestion sont mesurés en laboratoire par calorimétrie ou par respirométrie (*i.e.* mesure de la consommation d'oxygène). De façon analogue aux pertes fécales et urinaires, ces compartiments du bilan énergétique sont estimés *in situ* à l'aide de modèles empiriques s'appuyant sur la consommation de nourriture, la masse du poisson et la température. Le métabolisme de digestion est lié à la digestion, l'assimilation, au transport et au stockage des constituants organiques (*e.g.* sucres, lipides, protéines) et peut être estimé comme une proportion (a_D) de l'énergie absorbée ($C - P_F$, Stewart *et al.* 1983) :

(I.10) $$SDA = a_D \cdot (C - F)$$

Le métabolisme standard est généralement mesuré par respirométrie sur des poissons en état de jeûne ($SDA \simeq 0$; 24-48 heures depuis leur dernier repas) suivant deux méthodes. La première consiste à forcer les poissons à nager contre des courants d'eau de différentes vitesses et considérer le métabolisme standard comme étant l'ordonnée à l'origine de la relation entre la consommation

d'oxygène (en ordonné) et la vitesse (en abscisse). La seconde méthode consiste à mesurer directement la concentration l'oxygène chez des poissons immobiles et requière l'utilisation d'un respiromètre à échanges contrôlés (*anglais* : Flow-through respirometer; Lyytikäinen et Jobling 1998). Le métabolisme standard est estimé *in situ* comme une fonction de la masse et de la température par exemple (Elliott 1976b) :

(I.11) $$SMR = a_S \cdot w^{b_S} \cdot e^{c_S \cdot T}$$

où a_S, b_S et c_S sont estimés empiriquement.

Métabolisme d'activité

Le métabolisme d'activité est affecté par le comportement des poissons et représente une composante variable et parfois très importante de leur bilan énergétique (Boisclair et Leggett 1989b, Boisclair et Sirois 1993). On peut estimer le métabolisme d'activité des poisons en soustrayant le métabolisme standard aux mesures brutes de consommation d'oxygène ($SMR + A$) obtenues par respirométrie (Brett 1964, Beamish 1970). Le métabolisme d'activité peut être est estimé *in situ* à l'aide de modèles empiriques de coûts de nage. Ces modèles sont construits en utilisant la masse (w) et la vitesse de nage (v) comme variables prédictives et prennent généralement l'une ou l'autre des formes suivantes:

(I.12) $$A = a_A \cdot w^{b_A} \cdot v^{c_A} \quad , \quad A = a_A \cdot w^{b_A} \cdot e^{c_A \cdot v}$$

où a_A, b_A et c_A sont des constantes estimées empiriquement. Sur le terrain, les mesures de la vitesse de nage des poissons nécessaires à l'application de cette méthode peuvent être fournis par un système de vidéo-caméras configurées en paires stéréoscopiques tel que décrit par Boisclair (1992a). Cette méthode a été utilisée à plusieurs reprises (Aubin-Horth *et al.* 1999, Boisclair 1992b, Boisclair et Sirois 1993, Sirois et Boisclair 1995, Trudel et Boisclair 1996) en s'appuyant sur le modèle de coûts de nage de Boisclair et Tang (1993). À l'origine limitée à des environnements suffisamment éclairés pour permettre la détection des images par les vidéo-caméras, cette méthode peut aussi être adaptée pour des

environnements plus sombres ou totalement obscures (Chidami *et al.* 2007).

En utilisant le modèle de Boisclair et Tang (1993), Trudel et Boisclair (1996) ont obtenu des estimés de métabolisme d'activité semblables à ceux obtenus à partir d'un bilan énergétique dans des conditions expérimentales similaires, soit :

(I.13) $$A = C - (F + U + SMR + SDA + G)$$

où C a été estimée par la méthode d'Eggers (1977), F, U, SMR et SDA ont été estimés à l'aide de modèles empiriques et G a été mesuré directement. Une méthode semblable d'estimation du métabolisme d'activité, mais où la consommation était estimée à l'aide d'un traceur chimique (^{137}Cs), a été proposée par Rowan et Rasmussen (1996). Cependant, des estimés produits à l'aide de cette méthode, lors de cette étude ou d'études subséquentes, n'ont jamais été comparés à ceux obtenus par une autre méthode. Il importe de noter que la précision des estimés de métabolisme d'activité obtenus par ce type de méthodes est limitée par la fiabilité des mesures de terrain et des prédictions faites par les sous-modèles (Bartell *et al.* 1986, Rowan et Rasmussen 1996). De plus, les estimés obtenus à l'aide du bilan énergétique (*e.g.* A, C, G) ne sont pas indépendants d'un point de vue statistique (Boisclair et Leggett 1989b), il peut être discutable de les inclure conjointement dans une même analyse (*e.g.* pour estimer la relation entre C et A ou entre G et A).

D'autres méthodes basées sur des relations impliquant la consommation (Kerr 1982), l'abondance de nourriture (Boisclair 1992b, Sirois et Boisclair 1995), les conditions environnementales (Boisclair et Rassmussen 1996) ou le métabolisme standard (Kitchell *et al.* 1977) ont été proposées pour évaluer le métabolisme d'activité. Cependant, Boisclair et Leggett (1989b) ont mis en évidence que les approches de Kerr (1982) et de Kitchell et collaborateurs (1977) peuvent estimer de façon erronée les coûts d'activité en ne tenant pas compte de la variabilité parfois importante entre différentes populations d'une même espèce (Boisclair et Sirois 1993, Madon et Culver 1993). De plus, Boisclair (1992b) rappelle que l'absence de connaissance sur la forme des relations utilisées pour estimer le métabolisme d'activité à partir de l'abondance de nourriture impose des contraintes pratiques à leur

utilisation.

D'autres méthodes utilisant des mesures télémétriques du rythme cardiaque (Priede 1983, Armstrong *et al.* 1989, Lucas *et al.* 1991, 1993), des contractions musculaires (Weatherley *et al.* 1982, Rogers et Weatherley 1983, Hinch *et al.* 1996, Briggs et Post 1997, Geist *et al.* 2000) et de la fréquence des battements de queue (Lowe *et al.* 1998) ont aussi été proposées pour estimer l'activité *in situ* chez les poissons. Ces méthodes sont actuellement limitées par la taille des émetteurs (dictant la taille minimale des poissons sur lesquels ils peuvent être placés ou implantés), la durée de vie de la source d'énergie (*e.g.* pile) et le coût des équipements déployés. Elles pourraient être de plus en plus envisageables dans la mesure où ces obstacles techniques seront levés.

Allocation de l'énergie

Les poissons doivent acquérir de l'énergie, sous forme de consommation afin de croître. Ils doivent de surcroît dépenser de l'énergie sous forme de métabolisme d'activité pour acquérir leur nourriture, se déplacer à l'intérieur ou entre leur(s) habitat(s), éviter leurs prédateurs, se reproduire, défendre un territoire, se défendre, etc. De plus, leurs choix d'habitats physiques (*e.g.* température) et de nourriture peuvent aussi affecter les autres compartiments de leur bilan énergétique (SMR, SDA, F et E). Des facteurs comme la compétition intra-spécifique (Marchand et Boisclair 1998), la compétition inter-spécifique et les différences phénotypiques (morphologiques et comportementales) survenant au sein d'une même espèce (*i.e.* polymorphisme) peuvent donc affecter la croissance des poissons en influençant d'abord la consommation et l'activité.

Bioénergétique: contribution et utilisations

Dans la présente thèse, nous évaluerons, dans un premier temps, la validité de deux méthodes proposées pour estimer les taux d'activité de poissons sur le terrain. Certains des outils émanant de la bioénergétique et décrits précédemment seront utilisés pour 1) explorer les mécanismes de compétition intra-spécifique (processus dépendants de la densité) et inter-spécifique, 2) quantifier la grandeur des

différences entre deux écotypes d'omble chevalier et afin 3) d'évaluer l'importance de la compétition, par la truite brune, comme facteur à l'origine de l'apparition des différences de phénotypes entre ces deux écotypes.

COMPÉTITION

La compétition est l'interaction par laquelle la croissance, les probabilités de survie et l'aptitude à se reproduire (*i.e.* le fitness) d'organismes appartenant à une espèce donnée sont affectés par la présence d'organismes (les compétiteurs) appartenant à cette même espèce (compétition intra-spécifique) ou à une espèce différente (compétition inter-spécifique) et utilisant des ressources communes (Krebs 1994). Quantitativement, l'intensité de la compétition peut être décrite comme une fonction positive de la densité de compétiteurs (*i.e.* le nombre de compétiteurs pour une quantité donnée d'habitat), de la similarité de leurs besoins en ressources (*e.g.* nourriture, refuge) et négative de l'abondance de ces mêmes ressources. La compétition est donc associée aux processus dépendants de la densité tels la croissance dépendante de la densité (*anglais* : density-dependent growth).

Croissance dépendante de la densité

La croissance dépendante de la densité implique un ensemble de mécanismes fonctionnels (*i.e.* interactions entre les organismes et leurs ressources abiotiques et biotiques) ou de mécanismes comportementaux (*i.e.* interactions entre organismes partageant les mêmes ressources) à l'issue desquels la croissance des individus d'une population est affectée par la densité. La densité est définie comme le quotient du nombre d'individus d'une population occupant un même milieu et de la taille de ce milieu. Les mécanismes fonctionnels incluent ceux agissant par l'entremise d'une diminution de l'abondance des ressources (*e.g.* nourriture, refuges, sites de reproduction) par les compétiteurs. Les mécanismes comportementaux impliquent des interactions (*e.g.* intimidation, attaques) ayant pour objectif la mainmise sur l'accès aux ressources, soit en défendant un territoire (*i.e.* une source

d'approvisionnement), ou encore en nuisant à leur exploitation par d'autres individus.

Mécanismes bioénergétiques de dépendance à la densité

La croissance est, comme nous l'avons vu précédemment, le résultat de la consommation à laquelle est soustrait un ensemble de coûts associés à d'autres processus physiologiques tels l'activité. Par conséquent, les mécanismes fonctionnels et comportementaux à l'origine des phénomènes de croissance dépendante de la densité influenceront, préalablement la consommation (*i.e.* consommation dépendante de la densité) et l'activité (*i.e.* activité dépendante de la densité). Dans cette perspective, les organismes confrontés à une augmentation de la densité pourront adopter différentes stratégies d'allocation d'énergie. Ces stratégies auront pour but de maximiser leur croissance en modulant adéquatement leurs taux de consommation et d'activité. Pour illustrer les conséquences possibles de ces stratégies, prenons deux niveaux de densité (D_1, D_2, tel que $D_1 < D_2$), et autant de taux moyens de croissance (G), de consommation (C) et d'activité (A), chacun référencé par les mêmes indices. Nous explorerons quatre cas de figure ayant en commun une diminution, de D_1 vers D_2, de l'abondance de nourriture chez un organisme s'alimentant activement. 1) Dans le premier, l'organisme adopte une stratégie lui permettant de conserver un taux d'activité constant ($A_1 = A_2$), au prix d'un taux de consommation moindre ($C_1 > C_2$: la nourriture est moins abondante), en consentant à réduire sa croissance ($G_1 > G_2$). 2) Dans un second cas, l'organisme adopte plutôt une stratégie lui permettant de conserver un taux de consommation constant ($C_1 = C_2$), au prix d'une activité plus élevée ($A_1 < A_2$, pour exploiter plus d'habitat afin de compenser la diminution de l'abondance de nourriture), consentant, encore une fois, à réduire sa croissance ($G_1 > G_2$). 3) Dans un troisième cas, l'organisme adopte une stratégie visant à conserver son taux de consommation, mais sans y parvenir ($C_1 > C_2$), même au prix d'une activité plus élevée ($A_1 < A_2$), subissant une réduction plus importante de sa croissance ($G_1 >> G_2$). 4) Enfin, l'organisme peut adopter une stratégie lui permettant de conserver une croissance constante ($G_1 = G_2$), au prix de devoir augmenter à la fois ses taux de consommation ($C_1 < C_2$) et d'activité ($A_1 < A_2$). Dans les deux premiers cas de figure, la conséquence de la densité sur la

croissance est la même ($G_1 > G_2$). Cependant, l'impact de la population sur ses ressources alimentaires, lequel est proportionnel au taux de consommation moyen des individus, sera moindre dans le premier cas. Cette augmentation sera encore plus importante dans le quatrième cas de figure, où une augmentation de la consommation moyenne doit être réalisée afin de compenser l'augmentation du taux d'activité. Ce dernier cas de figure illustre que l'absence de croissance dépendante de la densité ne peut pas être perçue comme une preuve de l'absence de tout processus dépendant de la densité.

Formes des relations dépendantes de la densité

L'importance relative des réponses en terme de taux de croissance, de consommation et d'activité à l'augmentation de la densité peut varier en fonction des niveaux de densité eux-mêmes. En d'autres termes, la forme des relations entre, d'un côté, la densité (D) et, de l'autre, les taux de croissance (G_D), de consommation (C_D) et d'activité (A_D), n'est pas nécessairement linéaire ni monotone. Afin d'illustrer ces propos, nous récupérerons le cadre explicatif utilisé dans la sous-section précédente, auquel nous ajouterons un troisième niveau de densité (D_3, tel que $D_1 < D_2 < D_3$). Une augmentation de la densité de D_1 vers D_2 peut, tel que illustré précédemment (cas de figure #4), n'entraîner aucune baisse de la croissance ($G_1 = G_2$) mais une augmentation concomitante des taux de consommation ($C_1 < C_2$) et d'activité ($A_1 < A_2$). Pour continuer ce même exemple, une seconde augmentation de la densité, D_2 vers D_3 pourrait, cette fois-ci, entraîner une baisse de la croissance ($G_2 < G_3$) associée à une baisse de la consommation ($C_2 > C_3$; cas de figure #1), à une augmentation de l'activité ($A_2 < A_3$; cas de figure #2) ou aux deux à la fois (cas de figure #3). Dans cet exemple, différents mécanismes bioénergétiques sont impliqués selon les niveaux de densité auxquels l'organisme se trouve. Ce dernier exemple et les cas de figures mentionnés précédemment illustrent la complexité pouvant découler des mécanismes associés à la croissance dépendante de la densité.

Compétition inter-spécifique

À l'instar de la densité (*i.e.* compétition intra-spécifique), la compétition inter-spécifique (*i.e.*

associée à la densité d'une autre espèce) peut influencer la croissance par le même ensemble de mécanismes fonctionnels et comportementaux. De la même façon, l'effet de la compétition inter-spécifique sur la croissance des individus d'une espèce A est associé à l'effet de la présence et de la densité d'individus appartenant à une espèce B sur les taux de consommation et d'activité des individus de l'espèce A. De façon similaire à la compétition intra-spécifique, les effets de la compétition inter-spécifique sur les taux de consommation et d'activité peuvent être associés à la diminution des ressources utilisées conjointement par chacun des compétiteurs et à la protection des mêmes sources d'approvisionnement (*i.e.* des mêmes habitats).

Peu d'études ont évalué l'influence de la compétition inter-spécifique sur les taux de consommation (Hanson et Leggett 1986, Boisclair et Leggett 1989a) et l'impact de la compétition inter-spécifique sur le taux d'activité n'a, jusqu'à maintenant, jamais été quantifié. Cette connaissance a néanmoins une importance clé pour la compréhension de la manière avec laquelle les organismes affecteront leurs ressources alimentaires et croîtront en sympatrie.

Compétition et bioénergétique: contributions

Dans la présente thèse, les contributions fournies dans deux chapitres comblerons les lacunes actuelles dans la compréhension des impacts bioénergétiques de la compétition. Le deuxième chapitre sera entièrement dédié à l'étude de l'effet de la densité (compétition intra-spécifique) sur les taux de croissance, de consommation et d'activité. Le premier objectif du quatrième chapitre consistera à quantifier l'effet de la compétition inter-spécifique sur ces mêmes variables bioénergétiques.

POLYMORPHISME

On qualifie de polymorphe une espèce pour laquelle on peut reconnaître au moins deux groupes d'individus possédant des caractéristiques morphologiques, physiologiques et comportementales différentes (*i.e.* formes; Skúlason and Smith 1995, Smith and Skúlason 1996). Ces

différentes formes seront qualifiées d'écotypes (*gr.* οικος : maison et τυπος : impression) dans la mesure où les caractéristiques qui les distinguent sont couplées à des différences écologiques (*i.e.* des différences dans leur manière d'interagir avec l'environnement) liées aux habitats pour lesquels elles sont adaptées. Le polymorphisme a été rapporté chez de nombreuses espèces de vertébrés, incluant des espèces de poissons (Jonsson *et al.* 1988, Bourke *et al.* 1997, Keeley *et al.* 2005), d'amphibiens (Maerz *et al.* 2006, Pfennig *et al.* 2006) et de reptiles (Hatase *et al.* 2007; sous-groupe des oiseaux : Smith 1987, Galeotti *et al.* 2003). Le polymorphisme peut aussi bien se manifester entre différents écosystèmes qu'entre différents types d'habitats au sein d'un même écosystème.

Les différences observées entre les écotypes d'une espèce polymorphe apparaissent suite à l'adaptation des individus aux conditions prévalant dans leur milieu au cours de leur développement (plasticité phénotypique) et peuvent, à plus long terme, s'établir sur une base génétique (West-Eberhard 1986, 1989). Ces différences impliquent que les individus appartenant à des écotypes différents interagiront de façons différentes avec leur milieu et réagiront différemment lorsqu'ils seront ensuite confrontés à un même ensemble de conditions environnementales. Dans la prochaine sous-section, nous explorerons les processus à l'issue desquels les organismes d'une même espèce en viennent à utiliser différentes ressources et à s'adapter à cette utilisation. Nous explorerons par la suite les facteurs environnementaux susceptibles d'induire ces processus.

Processus de différentiation

Le polymorphisme peut être la conséquence de la plasticité phénotypique ou de l'action combinée de la plasticité phénotypique et de la sélection naturelle (directionnelle ou disruptive, West-Eberhard 1986, 1989, Robinson et Parsons 2000, Adams *et al.* 2003). La plasticité phénotypique regroupe un ensemble de mécanismes ontogénétiques (*i.e.* intervenant au cours du développement d'un organisme) à l'issue desquels un même génotype peut produire plusieurs phénotypes en réponse aux conditions environnementales. Ces différences de phénotypes peuvent être de nature morphologique,

physiologique ou comportementale et ont pour conséquence une adaptation plus adéquate des organismes aux conditions prévalant dans leur milieu. La plasticité phénotypique agit à l'échelle du temps de développement des organismes. À plus longue échéance, la sélection naturelle peut contribuer à sceller les différences de phénotypes en modifiant le contenu génique à l'échelle de la population. La sélection naturelle a pour conséquence une augmentation de l'importance démographique des individus possédant des génotypes mieux adaptés aux conditions rencontrées dans le milieu. Elle agit par triage des génotypes associés aux individus possédant les meilleurs succès reproducteurs (*i.e.* par l'entremise de gradients de sélection). Ce triage s'opère à la fois sur la base du matériel génétique disponible chez les individus ayant colonisé le milieu (*i.e.* les fondateurs) et, à une grande échelle de temps, sur le matériel génétique nouvellement apparu dans la population (*i.e.* mutations; Rice et Pfennig 2007).

Facteurs environnementaux

Les milieux accueillant les populations d'un espèce polymorphe peuvent différer par rapport à plusieurs facteurs environnementaux (*e.g.* structure des communautés, importance relative de divers types habitats, structure trophique, cycle d'abondance des proies, conditions physiques) et les causes possibles du polymorphisme sont donc diverses. Parmi ces causes, la compétition a été largement citée. Le phénomène de déplacement de caractère (*anglais* : character displacement; Brown et Wilson 1959) est un exemple bien documenté mettant en lumière l'importance potentielle de la compétition comme facteur pouvant conduire à la différentiation intra-spécifique. Considérons deux espèces utilisant des ressources semblables cohabitant sur une partie de leurs aires de répartition. Il y a déplacement de caractère lorsque les populations de ces espèces sont respectivement plus différentes dans les milieux où elles se retrouvent en sympatrie que dans ceux où elles vivent chacune en allopatrie (définition adaptée de Brown et Wilson 1959). Ce phénomène a été rapporté chez plusieurs espèces d'invertébrés (Chiba 1999), de poissons (Schluter et McPhail 1992, Robinson et Wilson 1994), d'amphibiens (Pfennig *et al.* 2006), d'oiseaux (Fjeldsa 1983, Schluter *et al.* 1985) et de mammifères (Dayan *et al.*

1990, 1992, Yomtov 1993, Dayan et Simberloff 1994, Simberloff *et al.* 2000, Rychlik *et al.* 2006). Dans cette perspective, Schluter (1994, voir aussi Schluter et McPhail 1992, 1993) a déjà mis en évidence que la présence de compétiteurs peut induire une gradient de sélection directionnel chez l'épinoche à trois épines (*Gasterosteus acculeatus*). Ce gradient de sélection, basé sur des traits morphologiques, indique que les individus les plus semblables à leurs compétiteurs croissent moins rapidement lorsque ces derniers sont présents. Les traits morphologiques sur lesquels s'appuient ce gradient de sélection sont liés à l'aptitude des individus cible à exploiter des proies différentes de celles consommées par leurs compétiteurs. Des résultats similaires ont aussi été rapportés chez l'omble chevalier en allopatrie ou en sympatrie avec la truite brune (Forseth *et al.* 2003). Ces études indiquent que la présence d'une espèce compétitrice peut rendre moins profitable l'utilisation de certaines ressources et induire la sélection de traits favorisant l'utilisation de ressources alternatives.

Mis à part la présence d'une espèce compétitrice, d'autres facteurs comme par exemple la présence et l'importance relative de différents types d'habitats dans le milieu, peuvent représenter des opportunités d'adaptation diverses et stimuler l'apparition du polymorphisme (Robinson *et al.* 2000). Peu d'études se sont cependant penchées sur l'importance de ces facteurs.

Réponses bioénergétiques

Nous avons vu que des groupes d'individus appartenant à une même espèce peuvent s'adapter au cours de leur développement (plasticité) ou à long terme (sélection naturelle) aux conditions environnementales prévalant dans leurs milieux respectifs. Les écotypes ainsi formés sont aussi susceptibles de différer dans leurs manières d'interagir avec leur milieu et de réagir différemment aux conditions environnementales qui leur sont présentées. De telles différences peuvent impliquer que ces écotypes auront leur propres stratégies d'allocation de l'énergie.

Une question demeure cependant quant à la grandeur de l'impact de ces différences sur les réponses, en termes de taux de consommation, d'activité et, ultimement, de croissance réalisées par les

individus appartenant à ces écotypes. La connaissance de la grandeur de ces différences de réponses est néanmoins importante car elle détermine à la fois la performance (*i.e.* leur aptitude à croître, survivre et se reproduire) des écotypes soumis à un ensemble particulier de conditions environnementales et les impacts qu'ils auront sur leurs ressources. Dans cette perspective, aucune étude n'a examiné la grandeur des différences entre écotypes sur un ensemble de variables bioénergétiques. De plus, l'influence de la présence d'une espèce compétitrice, lequel facteur est suspecté d'être prépondérant à l'émergence du polymorphisme, n'a jamais été quantifiée sur plusieurs variables bioénergétiques décrivant la réponse de différents écotypes.

Contributions à l'étude du polymorphisme

Dans la présente thèse, les contributions de deux chapitres apporteront des réponses à certaines questions prépondérantes de l'étude du polymorphisme. Le troisième chapitre sera consacré à quantifier les différences des réponses en terme de taux de croissance, consommation, d'activité (*i.e.* bioénergétiques) et de distribution spatiale et temporelle de l'activité (*i.e.* comportementales) entre deux populations morphologiquement distinctes d'omble chevalier. L'importance de l'absence ou de la présence de truite brunes (une espèce largement rapportée comme un compétiteur de l'omble chevalier) dans les lacs où ces populations (*i.e.* écotypes) d'omble chevalier proviennent, comme facteur prépondérant ayant conduit au polymorphisme, sera explorée dans le second objectif du quatrième chapitre. Pour réaliser ce dernier objectif, l'influence de la truite brune sur les variables bioénergétiques et comportementales mentionnées précédemment sera quantifiée simultanément chez deux écotypes d'omble chevalier.

Chapitre 1 :

Comparison between activity estimates obtained using bioenergetic and behavioural analyses

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ABSTRACT

The activity rate of Arctic charr (*Salvelinus alpinus*) held in 90 m^2 littoral enclosures was estimated using the bioenergetic (with consumption estimated using stable caesium; ^{133}Cs) and the behavioural approaches (with fish movements quantified using video-cameras). We found no statistically significant difference between values of activity rate obtained using the two approaches for three of the six experiments we performed. However, there was no relationship between estimates of activity rate obtained using the two approaches. Discrepancies may arise from the difficulty to meet assumptions regarding the temporal stability of the concentration of ^{133}Cs in fish diet and of the assimilation coefficient of this tracer. When fish remain in an area where their behaviour can be well described (*e.g.* enclosure, habitat patches of littoral zones, coral reefs), the behavioural approach appears more robust to estimate activity rate because it depends most on a variable that is easiest to estimate (the number of movements performed). When these conditions are not met (low fish densities or significant fish migrations), a reliable assessment of the concentration and the assimilation of ^{133}Cs in stomach contents appears critical to implement the bioenergetic approach based on this tracer.

RÉSUMÉ

Nous avons estimé les taux d'activité d'omble chevalier (*Salvelinus alpinus*) dans six enclos de 90m² installés dans la zone littorale d'une lac en utilisant une méthode bioénergétique (basée sur l'estimation des taux de consommation par une analyse de l'accumulation de césium stable; ^{133}Cs) et une méthode comportementale (basée sur l'estimation des mouvements de nage par des paires de stéréo-vidéo-caméras.) Nous n'avons pas trouvé de différences statistiquement significatives entre les taux d'activité estimés par l'une ou l'autre des méthodes dans trois enclos sur six. De plus, aucune relation n'a été décelée entre les estimés de taux d'activité produits par les deux méthodes. Il est possible que les différences dans les taux d'activité obtenus par ces deux méthodes aient été la conséquence du non-respect des prémisses liées à la stabilité temporelle de la concentration de Cs dans la diète des poissons, de même que dans les coefficients d'assimilation du marqueur. Lorsque la distribution des poissons est restreinte à des zones où leur comportement peut être décrit avec fiabilité (c.à.d. dans des enclos, des taches d'habitat, des récifs coralliens, etc.), la méthode comportementale semble la plus adéquate pour mesurer les taux d'activité car elle dépend principalement de variables faciles à estimer (le nombre de mouvements effectués). Par contre, dans les cas où le comportement des poissons est difficile à décrire avec fiabilité (basses densités de poissons, mouvements de migration), un suivi de la concentration et de la fraction assimilable de Cs dans le nourriture devra être effectué afin d'assurer que la méthode bioénergétique puisse être utilisée avec fiabilité.

INTRODUCTION

Bioenergetic models are mass-balanced equations that represent the energy budget ($kJ \cdot d^{-1}$) of an organism (Kitchell *et al.* 1977, Hewett and Johnson 1992, Hanson *et al.* 1997):

$$G = C - (F + E + SDA + SMR + ACT) \quad (1.1)$$

In these models, growth rate (G which, in Equation 1.1, includes energy reserves for reproduction) is the difference between consumption rate, and a series of energy losses (egestion: F; excretion: E) and expenditures (standard metabolic rate: SMR; specific dynamic action: SDA; activity rate: ACT). Bioenergetic models have been used to predict fish growth (Brandt *et al.* 1992, Rice *et al.* 1983, Weiser and Medgyesy 1991), to estimate the effect of fish on their prey (Kitchell and Breck 1980, Majkowski and Wairwood 1981, Stewart *et al.* 1981), to assess the role of fish on nutrient recycling (Kraft 1992, see Hansen *et al.* 1993 for a review), and to quantify the energy costs associated with heavy metal exposure (Sherwood *et al.* 2000).

Activity rate has long been recognized as the least understood component of bioenergetic models (Hewett and Johnson 1992, Ney 1993). Activity rate (the net cost of swimming at the exclusion of any other loss or expenditure) has been suggested to represent a variable and often important component of fish energy budget. Boisclair and Leggett (1989b) estimated activity rate of yellow perch (*Perca flavescens*) from three age classes in twelve lakes of the Eastern Township of Québec, Canada. Activity rate was estimated as the difference between consumption rate and the sum of growth rate, energy losses, and energy expenditures. In this study, consumption and growth rates were estimated in the field while other components of the bioenergetic equation were obtained using published empirical models (Hewett and Johnson 1992). Consumption rate was calculated by combining the results of surveys of fish digestive tract contents and experiments of evacuation rates (Eggers 1977). Boisclair and Leggett (1989b) found that perch activity rate ranged from 0% to 250% of SMR among their study lakes. Boisclair and Sirois (1993) estimated the activity rate of brook charr (*Salvelinus fontinalis*)

reared in *in situ* enclosures. They estimated activity rate using under water video-cameras that allowed them to assess the number and the velocity of the movements performed by fish. Fish movements were transformed in energy expenditures using an empirical relationship between swimming cost, fish mass, and swimming speed (Boisclair and Tang 1993). Activity rate of brook charr ranged 60% to 280% of SMR depending on the environmental conditions found in the enclosures in which they were held. These studies and others (see Boisclair 2001 for a review) are consistent with the suggestion that deficient modelling of activity rate may be responsible for the occasionally poor performance of bioenergetic models (Minton and McLean 1982, Wahl and Stein 1991, Madon and Culver 1993).

The development of reliable models of activity rate requires the repeated estimation of this component of bioenergetic models under variable environmental conditions (Sirois and Boisclair 1995, Boisclair and Rasmussen 1996). Approaches employed to estimate activity rate may be defined as 'bioenergetic' or 'behavioural'. Following the bioenergetic approach, activity rate is estimated as the difference between consumption rate and the sum of growth rate, energy losses, and energy expenditures associated with standard metabolism and digestion. Studies using the bioenergetic approach differ in the methods used to estimate consumption rate. Consumption rate over specified time periods may be estimated either from the interpolation of temporally punctual surveys of digestive tract contents and evacuation rates (Boisclair and Leggett 1989b, Post 1990, Fox 1991) or from the rate at which chemical tracers accumulate in the fish body (Caesium: Davis and Foster 1958, Kolehmainen 1974, Forseth *et al.* 1992; Mercury: Trudel *et al.* 2000). Following the behavioural approach, activity rate is estimated by interpolating data about fish behaviour transformed to energy expenditures using empirical relationships between fish mass, swimming speed, and respiration (Boisclair 1992a, b, Boisclair and Tang 1993). The bioenergetic approach based on a chemical tracer has been presumed to be superior to alternate approaches because it allows one to obtain consumption and activity rates that are integrated over a time interval (Rowan and Rasmussen 1996). The accuracy of the bioenergetic approach based on a chemical tracer to estimate consumption rate has been demonstrated (Forseth *et*

al. 1992, Gingras and Boisclair 2000). However, the ability of this approach to estimate activity rate remains to be assessed. In contrast, the behavioural approach has been shown repeatedly to provide realistic values of activity rate (Sirois and Boisclair 1995, Trudel and Boisclair 1996, Aubin-Horth *et al.* 1999). Unfortunately, the behavioural approach requires a sampling effort that is much larger than the bioenergetic approach (repeated sampling at 1-4 week intervals over a growing season instead of tracer concentration at the beginning and the end of this time interval). In this context, the corroboration of the bioenergetic approach based on a chemical tracer may improve our ability to develop models to predict fish activity rate. The purpose of this study was to compare activity rate estimated using the bioenergetic approach based on a chemical tracer to values estimated using the behavioural approach.

METHODS

Sites and enclosures

A total of six experiments were conducted in Lake Songsjøen, (western Norway; 63°19'26"N. - 9°39'55"E., elevation: 262 m above sea level, area: 70 ha) to estimate fish activity rate using the bioenergetic and the behavioural approaches. Lake Songsjøen is oligotrophic and holds populations of Arctic charr (*Salvelinus alpinus*) and Brown trout (*Salmo trutta*).

Experiments were conducted in two (2000) to four (2001) 9.5 m x 9.5 m square enclosures deployed 3 to 7 m from shore. Enclosures are further identified as E1 to E6. Depth at the shallow end of the enclosures ranged from 75 to 128 cm (average: 98 cm). Depth at the deep end of the enclosures ranged from 232 to 275 cm (average: 248 cm). The volume of the enclosures averaged 156 m^3, and ranged from 143 to 177 m^3. Enclosures were made of nets (7 mm mesh) attached to a frame anchored on the lake bottom. The bottom line of each net was sunk 10 to 30 cm into the sediments or anchored using gravel bags to prevent fish escape. The enclosures therefore allowed fish to feed on invertebrates

that may be found at the water surface, in the water column, and on or in the sediments.

Fish for study

Juvenile Arctic charr (age II+ and III+) were captured in two Norwegian lakes using minnow traps. Lake Våvatn (63°19'41"N. - 9°34'29"E., elevation: 298 m above sea level, area: 425 ha) is located 1.2 km upstream of Lake Songsjøen. Lake Øvre Nonshøtjønn (62°43'05"N. - 9°32'03"E., elevation: 1004 m above sea level, area: 3.5 ha) is located 68 km south of Lake Songsjøen. These lakes were selected because they contain populations of charr living under different environmental conditions (elevation, temperature, presence (Våvatn) or absence (Øvre Nonshøtjønn) of Brown trout, etc.). We performed the experiments at similar fish density, but using fish from Lake Våvatn at two different times (2000 and 2001), and from two different lakes at the same time (2001). This strategy was used because it allowed us to obtain among-year and among-population variability in activity rate. Arctic charr were collected in Lake Våvatn from May 17 to May 28 2000 and from June 3 to June 12 2001. Arctic charr were collected in Lake Øvre Nonshøtjønn only in 2001 (from May 25 to June 12). Charr were individually weighed (electronic balance, Mettler model BB1200, ±0.1 g) and marked using fin colour markers (Sigma-Aldrich alcian blue). These operations were conducted under anaesthesia (immersion in an emulsion of clove oil 25 $mg \cdot L^{-1}$ for 30 to 90 sec) to reduce the stress associated with fish handling. The fish were allowed to recover in aerated water for 15 min. The weight of the fish collected in Lake Våvatn in 2000 (N: 58; range: 12.4 to 35.9 g *fresh weight* [*fw*] ; average: 22.30 g *fw*) was less variable than in 2001 (N: 41; range: 13.0 to 55.5 g *fw*; average: 24.4 g *fw*). Fish collected in Lake Øvre Nonshøtjønn ranged from 10.2 to 93.5 g *fw* (N: 42; average: 37.32 g *fw*).

Experimental procedures

Experiments conducted in the two enclosures deployed in 2000 took place from June 4th to July 5th (E1) and from June 4th to July 3th (E2). At the beginning of the experimental period, snorkelling was performed to insure that no fish were present in the enclosures. Each enclosure was stocked with

20 fish from Lake Vålvatn (average density: 10.8 fish·100m^{-3}). Experiments conducted in the four enclosures deployed in 2001 began on June 20th and ended on August 2nd (E3, E5) or August 3th (E4, E6). At the onset of the experiments, E3 and E4 were stocked with 15 Arctic charr from Lake Vålvatn while E5 and E6 were stocked with 15 fish from Lake Øvre Nonshøtjønn (average density: 10.3 fish·100m^{-3}). Fish were distributed to minimize among-enclosure variations in average initial body mass. Arctic charr that were not stocked in the enclosures (18 fish from Lake Vålvatn in 2000, 11 fish from Lake Vålvatn in 2001, and 12 fish from Lake Øvre Nonshøtjønn in 2001) were used to estimate the initial ^{133}Cs content of charr (*i.e.* the initial Cs burden, see *Estimating consumption rate from Caesium*).

At the end of the experiments, fish were recaptured by dragging a seine three times inside each enclosure and killed by a 20 minutes immersion in clove oil emulsion (100 mg·L^{-1}). Each Arctic charr was identified, weighed, and dissected. The stomach contents of the fish taken from a given enclosure were analysed to assess diet and then pooled to obtain sufficient material for ^{133}Cs analysis. Fish tissues and stomach contents were frozen for ^{133}Cs burden analyses.

Video sampling

We applied the behavioural approach using the method described by Boisclair (1992a) to estimate fish activity rate from swimming behaviour. Fish swimming behaviour was recorded with Stereo-Video-Cameras (SVC). These consisted of a pair of cameras (either Panasonic™ WV-BL602 or Panasonic™ WV-BP312) enclosed in a water-resistant case. Two SVC were used, each producing two images. Fish behaviour could therefore be observed simultaneously at two locations of an enclosure. The four images produced by the two SVC were assembled into a single image using a Quad image processor (Panasonic™ WJ-410). A time-date generator (Panasonic™ WJ-810) was used to add the exact time of filming to the images (± 0.001 sec). The resulting images were recorded using a VHS videocassette recorder (Panasonic™ AG-1330). SVC were positioned to adequately estimate fish behaviour and activity rate in different areas of the enclosures. Snorkelling performed outside the

enclosures indicated that, during summer 2000, charr were observed in the surface layer (surface to 1 m from the bottom) of the offshore third of the enclosures. Hence, in 2000, we defined two sampling zones (Zones A and B; Figure 1.1). Zone A consisted in the water volume formed by the shallowest two thirds of the enclosures, and the layer within 1 m from the bottom of the offshore third of the enclosures. Zone B comprised the volume defined by the surface layer (from 1 m above the bottom to surface) of the offshore third of the enclosures. The ratio of the volumes of Zones A and B was approximately 3:1. The SVC deployed to observe fish behaviour in Zone A were positioned 50 cm from the perpendicular sides of the enclosures (perpendicular to shore), 80 cm below water surface (40 to 80 cm above the bottom), and in the middle of the enclosure on the littoral-pelagic axis. These cameras were directed perpendicular to the side of the enclosures and parallel to water surface. The SVC sampling Zone B was positioned 50 cm from the middle of the deepest side of the enclosures, 180 cm below the surface. It was oriented perpendicular to the side of the enclosure and looking upward with an angle of 45° relative to water surface. Depending on the enclosure, the SVC sampling Zone B was thus between 50 and 100 cm above the bottom.

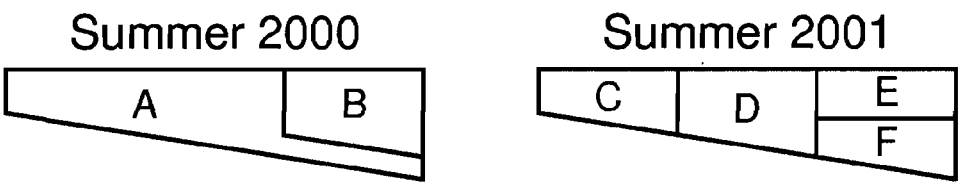

Figure 1.1 Zones sampled by the SVC in the enclosure during the summers 2000 and 2001.

Observations made in 2001 resulted in the definition of four sampling zones for that year (Zones C, D, E, and F; Figure 1.1). Zones C and D included, respectively, the water volume of the first and second shallowest thirds of the enclosures. Zone E was the volume defined by the surface layer

(surface to a depth of 1.1 m) of the offshore third of the enclosures. Zone F was the deepest layer (depth of 1.1 m to bottom) of the offshore third of the enclosures. Volume ratios of Zones C, D, E, and F were approximately 1:1.45:1:1.

The SVC deployed to observe fish behaviour in Zones C and D were positioned 50 cm from the perpendicular sides of the enclosures, 75 cm below the surface, and 3.15 m from the shallowest side of the enclosures. The SVC was oriented parallel to the surface, and was directed toward either Zone C or D (see the filming schedule below) by changing the angle relative to the enclosure side (45° to 60° shoreward for Zone C, and 75° to 85° offshore for Zone D). The SVC sampling Zones E and F were positioned 50 cm from the middle of the deepest side of the enclosures, and 110 cm below the surface (120 to 140 cm above the bottom). They were oriented perpendicularly with the side and directed upward with an angle of 20° to 30° relative to the surface when sampling Zone E, and downward with an angle of 10° relative to the surface when sampling Zone F.

Fish behaviour was quantified during two days in each enclosure. On any given sampling day, fish were filmed at 4:00 AM, 10:00 AM, 4:00 PM, and 10:00 PM. However, in 2001, the filming sessions were progressively shifted to 6:30 AM, 10:30 AM, 3:30 AM, and 8:30 PM from July 23th (sunrise: 3:15 AM, sunset: 9:30 PM) to August 3rd (sunrise: 4:45, sunset: 8:00 PM), because of the decrease in daylight hours. In 2000, Zones A and B were filmed simultaneously during 1h. However, in 2001, two of the four zones defined that year were filmed during 30 minutes, the SVC were repositioned (which would require 15-25 minutes), and the two other zones were filmed for 30 minutes. Hence, the filming schedule resulted in 48 h of films: Sixteen 1 h recordings of two zones (2 enclosures x 2 filming days x 4 hours of filming per day; Zones A and B were filmed simultaneously) in 2000, and sixty-four 30 min recordings of four zones (4 enclosures x 2 filming days x 8 periods of 30 minutes per day; pairs of zones filmed simultaneously were randomized) in 2001. A period of 5-10 min. was allowed after the positioning of the SVC before recording was started or resumed.

Analysis

Caesium analysis

Initial ^{133}Cs burden of charr was estimated using predictive models based on fish origin and size (see *Estimation of initial ^{133}Cs burden*). Final ^{133}Cs burden of charr was estimated for each individual fish. Each fish was weighed (g *fresh weight*; g *fw*), dried until no mass loss occurred (60°C for 24h to 48h), and weighed again to determine dry mass (g *dry weight*; g *dw*) and the proportion of dry matter. Dry fish were homogenized and a 300 mg sub-sample was taken and digested with HNO_3. Measurements of stable (^{133}Cs) caesium concentration ($ng \cdot g^{-1}$ *dw*) were made on the digested sample using a high resolution Inductively Coupled Plasma Mass Spectrometer (ICP-MS, Thermo Electron Corp. model Finnigan™ Element1). Cs concentrations per gram of dry fish tissues were converted to ^{133}Cs concentration per gram of fresh fish tissues ($ng \cdot g^{-1}$ *fw*) by multiplication with the proportion of dry matter. Cs burden in fish (ng) was obtained by multiplying ^{133}Cs concentration per gram of fresh fish tissue by the original fresh mass of the fish (g *fw*). Cs concentration in the food consumed by fish (pooled stomach contents) was evaluated following the same procedure. In this case, dry weight concentrations were used ($ng \cdot g^{-1}$ *dw*).

Video analysis

We converted the recordings from VHS videotapes to numeric format using a PC-based interface (ATI video acquisition interface, resolution: 640x480 pixels) to ease the use of computer-based image analysis tools. Image analysis began by an observation of each recording for actively swimming fish (velocity > 1 $cm \cdot s^{-1}$). For every second of filming, all moving fish were counted. Fish that were observed in only one camera of a given SVC were excluded from the count. Total moving fish second (*FS*, fish·s) is the sum of the number of the active fish observed within every seconds of a recording. Image analysis was performed with a software developed by the first author using XBasic Program Development Environment (2002, version 6.2.3). The analysis consisted in the manual

positioning (in raw pixel coordinates) of the head and tail of fish (see Boisclair 1992a for details). To minimize the effects of pseudo-replication, swimming velocity was estimated on a single, randomly selected, one second interval per fish passage. A fish passage is the complete displacement of a fish in the volume sampled by the SVC. A maximum of 100 velocity measurements were taken per hour of filming. Random sub-sampling was thus conducted when more than 100 fish passages where available per hour of filming. Boisclair (1992b) reported that this sample size is sufficient to obtain reliable estimates of the mean swimming velocity of Brook charr (*Salvelinus fontinalis*). We assumed that this finding is applicable to Arctic charr.

Computations

Estimation of initial Caesium burden

Because ^{133}Cs measurement requires killing the fish, the ^{133}Cs burden in fish at the beginning of the experiments was estimated from the ^{133}Cs concentration of the charr that were not used to stock the enclosures. We treated Arctic charr coming from Lake Våvatn in summer 2000 (Group 1), Lake Våvatn in summer 2001 (Group 2), and Lake Øvre Nonshøtjønn in summer 2001 (Group 3) as three distinct levels of treatment. Cs concentration ($\log_{10}$ transformed) of Arctic charr were different among groups ($F_{(2,38)} = 24.57$, $p = 1.42 \times 10^{-7}$). Moreover, ^{133}Cs concentration was not found dependent on the fresh body weight of the fish within every groups (Group 1: Pearson's $r = 0.17$, $t_{(16)} = 0.71$, $p = 0.49$; Group 2: $r = -0.19$, $t_{(9)} = -0.58$, $p = 0.57$; Group 3: $r = 0.29$, $t_{(10)} = 0.97$, $p = 0.35$). As a consequence, the initial ^{133}Cs burden (ng) of an Arctic charr belonging to one of the aforementioned groups was predicted by multiplying the mean ^{133}Cs concentration of that group (respectively 17.88, 19.42, and 27.79 $ng \cdot g^{-1}$ *fw* for Groups 1, 2, and 3) by its fresh body weight (g *fw*) at the beginning of the experiment.

Computation of activity rate using the bioenergetic approach

Calculation of activity (kJ) using the bioenergetic approach based on a chemical tracer was done by rearranging Equation 1.1 (see *Introduction*) to:

$$ACT = C - (G + F + E + SMR + SDA) \tag{1.2}$$

Activity rate was calculated for individual fish following five steps. First, for any given day i, we calculated the (linearly) interpolated body mass w_i (g *fw*) and ^{133}Cs burden Q_i (ng) of the fish. Second, we estimated ^{133}Cs elimination rate (k_i, d^{-1}) from w_i and mean daily temperature (T_i, °C) using the model of Ugedal *et al.* (1992). Daily food intake (I_i, $ng \cdot d^{-1}$) was calculated for each 1 day interval according to the method proposed by Forseth *et al.* (Equation 3b *in* Forseth *et al.* 1992). Food consumption for the complete duration of the experiment (C, kJ) was calculated as:

$$C = \frac{\left(\sum_i I_i\right) \cdot S}{[Cs]_f \cdot Eff} \tag{1.3}$$

where $[Cs]_f$ ($ng \cdot g^{-1}$ *dw*) is the concentration of ^{133}Cs in the diet of fish from each enclosure, and Eff is the assimilation efficiency of ^{133}Cs (the proportion of the ^{133}Cs found in the diet that is effectively assimilated by the fish), and S ($kJ \cdot g^{-1}$ *dw*) is the energy density of the diet. Energy density of the diet was estimated using the relative contribution (dry mass percentage) of prey items to fish diet from each enclosure and prey energy density ($kJ \cdot g^{-1}$ *dw*; Cummin and Wuycheck 1971). When no specific information about prey energy content was available, we employed values of the nearest taxonomic group. Third, growth (G, kJ) was obtained by multiplying predicted fish energy density ($kJ \cdot g^{-1}$ *fw*; Hartman and Brandt 1995, Equation #13 developed for Salmonids) by the body mass gained during the experiment, and by dividing this product by the duration of the experiment. Fourth, we estimated the maximum consumption (C_{MAX}, kJ) required to calculate F and E. C_{MAX} was estimated on a daily basis using values of w_i and T_i and was summed over the complete experimental period. Fifth, values of F (kJ), E (kJ), and SMR (kJ) were estimated on a daily basis using the models of Larsson and Berglund

(2005: C_{MAX}), Elliott (1976b: F and E), and Lyytikainen and Jobling (1998: SMR), and summed over the complete experimental period. SDA was assumed to represent 17% of assimilated energy (consumption rate minus fecal loss, Hewett and Johnson 1992). Because the experiments had different durations, estimates of energy compartments in Equation 1.2 were converted to rates ($kJ \cdot d^{-1}$) by dividing the number of experimental days. Models used to estimate C_{MAX} and SMR were developed from data on Arctic charr (Larsson and Berglund 2005, Lyytikainen and Jobling 1998) whereas models used to estimate k, F, E were borrowed from Brown trout (Ugedal *et al.* 1992, Elliott 1976b).

Calibration of the SVC

Calibration of the video-cameras was done underwater using a target consisting in a board having lines spaced both vertically and horizontally by 10, 20 and 30 cm. This target was placed at distances ranging from 40 cm to 240 cm from the cameras (increments of 40 cm). Calibration was done before the first filming day, and was repeated each four filming days. We estimated real length of objects (L, cm) from the relationship between virtual length (l, pixels) and parallax (*i.e.* the offset between images from the cameras in abscissa: Δx, pixels) using a non-linear function:

$$L = \frac{l}{\frac{c_1}{\Delta x + c_2} + c_3} \tag{1.4}$$

where c_1 is a scale parameter, and c_2 and c_3 are offset parameters estimated by least-squares non-linear regression of known distances between pairs of landmarks on the calibration target against values of Δx and l obtained from image analysis. The quotient of real and virtual length (L / l) was used to evaluate the distance between the target and the SVC (D, cm):

$$D = c_4 \cdot \frac{L}{l} + c_5 \tag{1.5}$$

where parameters c_4 and c_5 were estimated using linear regression of known values of distance of the calibration target and known values of L / l. Coefficients of determination associated with these

relationships (Equations 1.4 and 1.5) ranged from 92% to 99%.

Swimming cost model

The behavioural approach is based on the estimation of the energy spent swimming by fish per unit of volume observed using video-cameras. Energy spent swimming is estimated using the number of movements performed by fish per unit of time, fish mass, and fish swimming speed (Boisclair 1992a). The cost of swimming is determined using a swimming cost model implemented with fish mass and swimming speed (Boisclair and Tang 1993, Tang and Boisclair 1995, Tang *et al.* 2000). Datasets needed to estimate the parameters of these models are obtained by quantifying the oxygen consumption of swimming fish using respirometry experiments. We developed a new swimming costs model integrating datasets from Boisclair and Tang (1993, routine swimming), Tang and Boisclair (1995) and Tang *et al.* (2000). The resulting dataset consisted of results from 113 experiments for which oxygen consumption, body mass, and velocity of free-swimming fish (fish not forced to swim against a current nor constrained to swim in any given direction) were available. This dataset comprised four fish species: Goldfish (*Carassius auratus* L., Smit 1965: 54 experiments), Hawaiian flagtail (*Kuhlia sandvicensis* Steindachner, Muir *et al.* 1965: 11 experiments), Largescale mullet (*Liza macrolepsis*, Kutty 1969, 3 experiments), and Brook charr (Tang and Boisclair 1995, Tang *et al.* 2000: 45 experiments). The model predicting swimming costs was obtained by regressing (log-linear multiple regression) oxygen consumption rate of fish (VO_2, $mgO_2 \cdot h^{-1}$) against their body mass (M, g *fw*) and mean swimming speed ($\bar{v}$, $cm \cdot s^{-1}$):

$$\log_{10} VO_2 = b_0 + b_{MASS} \cdot \log_{10} M + b_{SPEED} \cdot \log_{10} \bar{v} \quad (1.6)$$

Parameters of this new swimming cost model are provided in *Results: Activity rate estimated using the behavioural approach.*

Evaluation of the volume sampled by video-cameras

The volume filmed by the SVC has the shape of a rectangle-base pyramid with a volume that increases as the distance from the cameras increases. In our study, this volume crossed the bottom of the littoral zone or the surface of the lake at an angle. Hence, the volume sampled by the SVC was calculated as the volume of a truncated rectangle-based pyramid. This volume began at 25 cm from the objective of the cameras (minimum distance to perceive a fish simultaneously in two cameras of a same SVC) and extended to the maximum distance of fish detection. The maximum distance of fish detection may vary with filming conditions (*i.e.* the zone sampled, the position and the orientation of the cameras, and the characteristics of the images such as pixel brightness and their frequency distribution) and with stochastic events (*e.g.* all fish swimming, by chance, near the video-cameras). The effect of these elements on the calculation of activity rate was considered by classifying each video recording according to the aforementioned filming conditions, by estimating the maximum fish detection distance for all video recordings belonging to a filming condition (pooling of the all the fish coordinates estimated for all video recordings obtained under a filming condition), and by adopting the highest value of maximum fish detection distance for a given filming condition as the maximum fish detection distance used to estimate the volume sampled by the video cameras under this filming condition. Hence, the volume sampled by the video-cameras for a given filming condition was identical for all video recordings obtained under this filming condition and was independent of the number of fish that moved during this specific video recording.

Computation of activity rate using the behavioural approach

The behavioural approach estimated the mean activity rate of fish within an enclosure over the complete duration of an experiment as the mean of the activity rate of fish in the different zones of an enclosure (two to four zones in 2000 and 2001 respectively), during four different times of the day (four filming sessions per day), and two days of filming. This was achieved in four steps. First, we estimated the *Active fish biomass* ($B_{z,t}$; $g \cdot m^{-3}$ *fw*) observed in the volume sampled by the SVC in each zone z of

an enclosure and for each combination t of time of day and day of filming as:

$$B_{z,t} = \frac{FS_{z,t} \cdot \bar{M}_t}{T_{z,t} \cdot V_{z,t}} \quad (1.7)$$

where $FS_{z,t}$ is the total number of moving fish-seconds (fish·s), $\bar{M}_t$ is the mean body mass of fish inside an enclosure (g *fw*: interpolated at the time of sampling), $T_{z,t}$ is the duration of the filming (s), and $V_{z,t}$ the observed volume of water (m^3). *Active fish biomass* is taken as a measure of the biomass of fish found in a zone at t weighted by the number of movements they performed per unit of volume and per unit of time. The number of $B_{z,t}$ values estimated for each enclosure was 16 in 2000 (two zones per enclosure x four filming sessions per day x two days of filming per enclosure) and 32 in 2001 (four zones per enclosure, x four filming sessions per day x two days of filming per enclosure). Second, when fish were observed swimming, we calculated the *Mean swimming cost* (MSC: $J \cdot g^{-1} \cdot h^{-1}$) in each zone z of an enclosure and for each combination t of time of day and day of filming using mean body mass, mean swimming speed, and coefficients of the swimming cost model (Equation 1.6) as:

$$MSC_{z,t} = 13.54 \cdot 10^{b_0} \cdot \bar{M}_t^{(b_{MASS}-1)} \cdot \bar{v}_{z,t}^{\,b_{SPEED}} \quad (1.8)$$

where 13.54 is the oxy-caloric coefficient ($J \cdot mgO_2^{-1}$, Elliott and Davison 1975). $MSC_{z,t}$ therefore represents the cost of swimming for a fish having the average weight and swimming at the average speed estimated in zone z of an enclosure and for the combination t of time of day and day of filming. When no fish were seen swimming in a zone at t, $MSC_{z,t}$ was assumed to be zero. The number of $MSC_{z,t}$ estimated was identical to that of $B_{z,t}$. Third, we calculated *Hourly activity rate* (A_t, $J \cdot g^{-1} \cdot h^{-1}$) in a complete enclosure for each combination t of time of day and day of filming as:

$$A_t = \frac{\sum_{z=1}^{n} (B_{z,t} \cdot MSC_{z,t})}{n \cdot B_{e,t}} \quad (1.9)$$

where $B_{e,t}$ ($g \cdot m^{-3}$ *fw*) is the mean biomass of fish in an enclosure per unit of volume (*i.e.* the sum of the interpolated body masses at t divided by the volume of the enclosure), and n is the number of zones

sampled in an enclosure (two in 2000, four in 2001). The numerator of this equation provided the sum of the cost of swimming in all zones z of an enclosure weighted by the *Active fish biomass* in each zone at t. The denominator of this equation averaged the sum of the cost of swimming over the zones sampled in an enclosure and over the biomass of fish present in this enclosure at t. Eight values of A_t (four filming sessions per day and two days of filming per enclosure) were estimated for each enclosure in 2000 and in 2001. Fourth, *Daily activity rate* (A_e, $J \cdot d^{-1}$) in an enclosure e over a complete experiment was estimated as:

$$A_e = 24 \cdot \bar{A}_t \cdot \bar{M}_e \quad (1.10)$$

where 24 is the number of hour in a day, $\bar{A}_t$ is the geometric mean of the *Hourly activity rate* estimated in an enclosure e, $\bar{M}_e$ is the mean body mass of charr (g *fw*) in this enclosure in the middle of the experiment (mean of the linear interpolation of individual fish mass).

Estimating the confidence intervals of activity rate

Confidence intervals around the activity rate obtained from bioenergetic approach were estimated by bootstrapping (Efron and Tibshirani 1993, 10 000 recalculations used in every cases). Confidence intervals on bioenergetic activity rate estimates were obtained following five steps. First, we calculated 10 000 bootstrapped sets of mean initial ^{133}Cs concentration in charr. For each individual fish, these sets of means were used in a second step to calculate pseudo-values of initial ^{133}Cs burden (see *Estimation of initial caesium burden*). Third, assuming that the error associated with the estimates of final ^{133}Cs burden in individual was low, we calculated 10 000 pseudo-values ^{133}Cs intake for each fish using the corresponding pseudo-values of initial ^{133}Cs burden. Fourth, we calculated 10 000 pseudo-values of consumption rate by including the error associated with ^{133}Cs concentration in food and ^{133}Cs absorption coefficient used for the method of Forseth *et al.* (1992). Pseudo-values of ^{133}Cs concentration in food were calculated by bootstrapping the values obtained in this study. Pseudo-values of ^{133}Cs absorption coefficient were normally-distributed random deviates using the means and

standard deviations published by Forseth *et al.* (1992). Fifth, we applied the pseudo-values of consumption rate on the calculation of the energy budget to obtain 10 000 pseudo-values of activity rate for each individual charr. The bilateral 95% confidence limits of activity rate were taken as the 2.5^{th} and 97.5^{th} percentiles of these pseudo-values. The error associated with the application of the models predicting k, C_{MAX}, F, E, SDA, and SMR were not included in error analysis because the variance / covariance of the parameters of these models were not available from original papers. The error analysis we performed may thus provide conservative values of 95% confidence limits of activity rate obtained using the bioenergetic approach. The confidence limits around activity rate obtained using behavioural approach were estimated using the standard error of the GLM models parameters.

Model comparison

Mean daily activity rates estimated with the bioenergetic approach were compared with values obtained with the behavioural approach using a major axis regression (type II regression; Legendre and Legendre 1998). Confidence limits of parameters such as the correlation coefficients (Pearson), regression slope and regression intercept were calculated using the pseudo-values of activity rate obtained from the bootstraps (bioenergetic approach) and GLM model parameters (behaviour approach). Only one pair of pseudo-values from each enclosure was allowed for every single recalculation of the parameters. The lower and upper 95% confidence limits of a given parameter were taken as the 2.5 and 97.5 percentiles of its pseudo-values. Expectation was that if the bioenergetic and the behavioural approaches produced similar estimates of activity rate, these estimates would be correlated, and the confidence intervals of their type II regression slope and intercept would include respectively 1 and 0.

Statistical analysis

Computations and statistical analysis were performed using R language (version 2.4.1; R Development Core Team 2007). Tests of the statistical significance of among-enclosure differences

were done using analysis of variance (ANOVA). When among-enclosure differences were statistically significant, a *post-hoc* test (Scheffé test: Scheffé 1953) was conducted to test for differences between every pairs of enclosures. Normality of the residuals of ANOVA and regression models was tested using Shapiro-Wilk's test of normality (Shapiro and Wilk, 1965). Homogeneity of within-group residual variance was tested using Bartlett's test (Snedecor and Cochran, 1989). Homogeneity of the residual variance along regression lines was assessed by examining the plots of residual values (y) as a function of predicted values (x). The analysis of the effect of experimental and environmental factors on *Active fish biomass* and *Hourly activity rate* was done using Generalized Linear Model (McCullagh and Nelder 1989; Quasi-Poisson likelihood model using logarithmic link function: Hastie and Pregibon 1992). This procedure was used because these variables featured an important level of skewness and over-dispersion. Statistical significance of the resulting deviance tables were calculated using F test. We used a statistical significance threshold of 5% for type I (α) error in all analyses.

RESULTS

The mean body mass of individual charr in the enclosures at the beginning of the experiments (summers 2000 and 2001) ranged from 21.38 (E2) to 24.02 g *fw* (E5) and the did not differ among enclosures (Table 1.1). At the beginning of the experiments, the density of charr (initial fish density) inside the enclosures averaged 10.64 fish·100m^{-3} and ranged from 9.95 (E3) to 11.44 (E2) fish·100m^{-3}. On average, 80% of the fish stocked were recaptured at the end of the experiments (from 60% in E2 to 95% in E1). At the end of the experiments, charr density (final fish density) averaged 8.52 fish·100m^{-3}, and ranged from 6.86 (E2) to 10.75 fish·100m^{-3}. The mean body mass of fish recaptured at the end of the experiments ranged from 24.23 (E3) to 35.06 g *fw* (E5). Final body mass differed among enclosures (individual fish within each enclosure were used as replicates), but differences between pairs of enclosures were too small to be detected by *post-hoc* tests. Individual growth rate averaged 203 mg·d^{-1} (*fw*), and ranged from –72.1 to 442 mg·d^{-1}. Only one fish (from E4) lost weight during the experiments.

Growth rate was not related to initial fish body mass (r = 0.099, $t_{(78)}$ = 0.877, p = 0.383) and differed among enclosures (individual fish within each enclosure were used as replicates). Fish in enclosure E3 (95 mg·d^{-1}) had growth rate respectively 2.6, 2.4, and 2.6 times lower than in enclosures E1, E2, and E5 (respectively 246, 232, and 244 mg·d^{-1}). Moreover, growth was positively influenced by initial and final fish density (respectively: *adjusted* R^2 = 0.15, $t_{(78)}$ = 3.88, p = 0.0002, and *adjusted* R^2 = 0.057, $t_{(78)}$ = 2.41, p = 0.02).

During summer 2000, the average water temperature was 11.5 °C, and ranged from 8.2 (June 4, 1st day of the experiment) to 15.8 °C (July 2). Water temperature increased throughout the experiment at a rate of 0.14°C·d^{-1}. During summer 2001, average water temperature was 16.3 °C, and ranged from 13.5 (August 2) to 19.6°C (July 9). In 2001, water temperature tended to decrease from the beginning to the end of the experiments (-0.042 °C·d^{-1}).

Table 1.1 Variables estimated in the experimental enclosures and results of statistical tests of among-enclosure differences.

Variable		Units	Mean	Range	Enclosures						Among-enclosures differences		
					E1	E2	E3	E4	E5	E6	F_{ν_1,ν_2}	ν_1,ν_2	p
Mass	Initial	g *fw*	22.14 [21.32, 22.99]	10.2 – 55.5	21.99 [20.19, 23.96]	21.38 [19.62, 23.29]	21.43 [19.41, 23.66]	21.24 [19.24, 23.45]	24.02 [21.75, 26.52]	23.21 [21.02, 25.63]	0.9275	5, 94	0.93
	Final		29.68 [28.63, 30.78]	15.2 – 65.0	30.01^a [27.94, 32.23]	27.49^a [25.12, 30.07]	24.23^a [22.15, 26.51]	28.26^a [25.73, 31.04]	35.06^a [32.16, 38.22]	33.38^a [30.62, 36.39]	2.3428	5, 74	0.05
Fish recaptured		Charr	13.3	11 – 19	19	12	12	11	13	13	---	---	---
Density	Initial	Fish ·100m^3	10.64	9.95 – 11.44	11.32	11.44	9.95	10.52	10.39	10.20	---	---	---
	Final		8.52	6.86 – 10.75	10.75	6.86	7.96	7.71	9.00	8.84	---	---	---
Growth rate		mg·d^{-1}	203 ± 10	-72.1 – 441.9	246^a ± 18	232^a ± 23	95^b ± 23	168^{ab} ± 23	244^a ± 22	199^{ab} ± 22	7.2688	5, 74	$1.38 \cdot 10^{-5}$
		kJ·d^{-1}	1.11 ± 0.06	-0.32 – 2.44	1.36^a ± 0.11	1.20^a ± 0.13	0.52^b ± 0.13	0.86^{ab} ± 0.15	1.42^a ± 0.13	1.14^{ab} ± 0.13	6.787	5, 72	$3.09 \cdot 10^{-5}$
Cs burden	Initial	ng	463 [441, 487]	253 – 1440	440 [367, 436]	368 [331, 408]	385 [347, 428]	369 [329, 414]	681 [616, 754]	675 [610, 747]	---	---	---
	Final		834 [776, 896]	311 – 4129	709^a [651, 771]	594^a [536, 659]	496^a [447, 550]	478a [427, 536]	1710^b [1548, 1889]	1722^b [1558, 1902]	33.739	5, 72	$< 2.2 \cdot 10^{-16}$
Cs Intake		ng·d^{-1}	13.24 [12.10, 14.48]	2.99 – 79.54	12.42 [11.28, 13.67]	9.62 [8.55, 10.82]	5.92 [5.26, 6.66]	5.76 [5.06, 6.55]	32.26 [28.82, 36.12]	31.81 [28.41, 35.62]	43.735	5, 72	$< 2.2 \cdot 10^{-16}$
Diet	Zoo-plankton	%	78	63 – 89	77	63	83	74	80	89	---	---	---
	Zoo-benthos		22	11 – 36	23	36	17	26	18	11	---	---	---

Variable	Units	Mean	Range	Enclosures						Among-enclosures differences		
				E1	E2	E3	E4	E5	E6	F_{ν_1,ν_2}	ν_1,ν_2	p
Consumption rate	$kJ \cdot d^{-1}$	5.32 [4.98, 5.69]	1.47 – 21.52	6.09^{ac} [5.53, 6.70]	4.72^{ab} [4.19, 5.31]	2.90^{b} [2.58, 3.26]	2.82^{b} [2.48, 3.21]	8.73^{c} [7.79, 9.77]	8.60^{c} [7.69, 9.63]	18.206	5, 72	$1.23 \cdot 10^{-11}$
C / C_{MAX}	%	34 [31, 37]	20 – 104	50^{a} [44, 55]	38^{a} [32, 44]	14^{b} [11, 18]	12^{b} [8.6, 16]	44^{a} [38, 50]	46^{a} [40, 53]	12.281	5, 72	$1.27 \cdot 10^{-8}$
Activity rate (bioenergetics)	$kJ \cdot d^{-1}$	1.41 [1.24, 1.58]	-0.71 – 8.50	1.65^{ab} [1.40, 1.93]	1.14^{b} [0.88, 1.44]	0.41^{bc} [0.20, 0.63]	-0.04^{c} [-0.22, 0.17]	2.81^{a} [2.42, 3.24]	2.99^{a} [2.58, 3.43]	16.210	5, 72	$1.11 \cdot 10^{-10}$
	SMR	2.19 [2.00, 2.38]	-0.90 – 6.11	3.20 [2.92, 3.49]	2.58 [2.23, 2.93]	0.56 [0.21, 0.91]	0.08 [-0.30, 0.47]	2.69 [2.36, 3.03]	3.06 [2.72, 3.40]	14.764	5, 72	$5.93 \cdot 10^{-10}$
Swimming speed	$cm \cdot s^{-1}$	13.79 [13.34, 14.26]	3.63 – 31.35	14.68^{ab} [13.56, 15.85]	16.22^{a} [15.08, 17.41]	10.64^{b} [9.78, 11.54]	10.48^{b} [9.70, 11.30]	15.11^{a} [14.28, 15.96]	16.72^{a} [15.63, 17.84]	8.3389	5, 97	$1.37 \cdot 10^{-6}$
Hourly activity rate	$kJ \cdot kg^{-1} \cdot h^{-1}$	2.18 [1.96, 2.43]	0 – 6.55	2.31 [1.78, 3.01]	1.72 [1.26, 2.33]	2.28 [1.74, 2.97]	2.59 [2.02, 3.32]	2.63 [2.05, 3.37]	1.58 [1.15, 2.18]	0.5689	5, 42	0.72

Variables are presented with their standard deviation (± 1 sd), or in the form: "mean [mean - 1 sd, mean + 1 sd]" for asymetric intervals.
Enclosures of equal means are labeled using superscripts a, b, and c. Enclosures labeled with two superscripts share similarities with both (*e.g.* ab is similar with both a and b).

Caesium intake

Predicted ^{133}Cs burden of charr at the beginning of the experiments (initial ^{133}Cs burden) ranged from 252 to 1440 ng (mean = 464 ng) whereas the ^{133}Cs burden of charr at the end of the experiments (final ^{133}Cs burden) ranged from 311 to 4129 ng (mean = 834 ng). Final ^{133}Cs burden differed among enclosures (Table 1.1). At the end of the experiments, charr from Lake Øvre Nonshøtjønn (mean = 1716 ng) contained, on average, 3 times more ^{133}Cs than charr from Lake Våvatn (mean = 562 ng). The ^{133}Cs daily intake of individual charr ranged from 3.0 to 79.5 $ng \cdot d^{-1}$ (mean = 13.2 $ng \cdot d^{-1}$). The mean daily ^{133}Cs intake of charr differed among enclosures (Table 1.1). Daily intake of ^{133}Cs for charr from Lake Øvre Nonshøtjønn (average: 32.0 $ng \cdot d^{-1}$) was 4 times higher than corresponding values for charr from Lake Våvatn (average: 8.0 $ng \cdot d^{-1}$). Among fish from Lake Våvatn, charr in enclosure E1 (12.4 $ng \cdot d^{-1}$) had daily ^{133}Cs intake 2.1 times higher than charr from enclosures E3 and E4 (summer 2001, average: 5.8 $ng \cdot d^{-1}$).

Stomach contents

Zooplankton crustaceans (mainly Cladorerans and Copepods) largely dominated the diet of charr in all experiments (80% to 90% of stomach contents *dw*). Chironomids were the second most

important prey item (10% to 15% of stomach contents). Energy densities used to transform consumption rate from a dry mass to an energy basis were 21.93 $kJ \cdot g^{-1}$ *dw* for Cladocerans, 24.22 $kJ \cdot g^{-1}$ *dw* for Copepods, 22.69 $kJ \cdot g^{-1}$ *dw* for Chironomids, and 20.18 $kJ \cdot g^{-1}$ *dw* for surface Insects (Cummin and Wuycheck 1971). For all other prey items, we used the mean value of Arthropods (19.77 $kJ \cdot g^{-1}$ *dw*). The estimated energy content of fish diet ranged from 21.01 to 23.36 $kJ \cdot g^{-1}$ *dw* among-enclosure (average = 22.47 kJ $\cdot g^{-1}$ *dw*).

Caesium concentration in fish diet averaged 96 $ng \cdot g^{-1}$ *dw* and varied up to 3.4-fold among enclosures (from 51 to 171 $ng \cdot g^{-1}$ *dw*). Cs concentration found in the stomach contents of Arctic charr from Lake Våvatn in 2000 (average = 127 $ng \cdot g^{-1}$ *dw*) was 2.4-fold higher than in 2001 (average = 52 $ng \cdot g^{-1}$ *dw*), whereas in 2001, ^{133}Cs concentration of the stomach contents of fish originating from Lake Øvre Nonshøtjønn (average = 109 $ng \cdot g^{-1}$ *dw*) were twice as high as that of Arctic charr from Lake Våvatn. Such high variation in the ^{133}Cs concentration of stomach contents may have originated from differences in the ^{133}Cs content of the consumed preys, and/or from the simultaneous ingestion of particulate matter. Because few differences were observed in diet composition (Table 1.2), we believe that the latter possibility deserves to be explored. Studies by Kolehmainen (1972) have shown that absorption of radioactive (^{137}Cs) caesium by Bluegill sunfish (*Lepomis macrochirus*) from Chironomid larvae was low when the larvae ingested contaminated sediments (containing clay 7-16% of total ingested ^{137}Cs were absorbed) or contaminated detritus (3.0%), but higher when the larvae ingested algae growing in contaminated water (68.7%). The same author found that « [...] Bluegill can absorb most of ^{137}Cs associated with tissues, but are able to absorb very little of ^{137}Cs that is in the detritus and on the clay in the alimentary canal of Chironomid larvae ». This assertion may hold true for stable ^{133}Cs as well. Consequently, food may contain substantial amounts of ^{133}Cs that are adsorbed to sediment particles and may not be available for absorption by fish. In such situation, estimates of ^{133}Cs absorption in the field may be overestimated by coefficients obtained from laboratory studies (*see* Forseth *et al.* 1992, Tucker and Rasmussen 1999).

We assessed this possibility using concentrations of Praseodymium (^{141}Pr), an element of the lanthanide group closely associated with sediment particles, and measured at the same time as ^{133}Cs during mass spectrometry analysis. ^{141}Pr has strong adsorptive properties for sediments particles (Kyker 1961, Zhang and Chai 2004), and have been used by Ellis and Huston (1968) as an inert tracer for estimation of absorption in ruminants. We assumed that the same would hold true for fish as well. Concentrations of ^{141}Pr in stomach contents of Arctic charr differed among-groups ($F_{(2,11)} = 14.92$, $p = 0.0007$). Charr from Lake Våvatn in summer 2000 (average = 515 ng·g^{-1} *dw*) had 1.8 times higher ^{141}Pr concentrations than in summer 2001 (mean = 283 ng·g^{-1} *dw*) indicating that charr from Lake Våvatn ingested more sediments in 2000 than in 2001. However, no such difference was found in summer 2001 between charr from Lake Våvatn and Lake Øvre Nonshøtjønn (average = 210 ng·g^{-1} *dw*). Moreover, concentrations of ^{141}Pr in the stomach contents of charr from Lake Våvatn in 2000 were positively related to ^{133}Cs concentrations ($R^2_{adj} = 91.1\%$, $F_{(1,4)} = 52.39$, $p = 0.002$). This relationship between ^{133}Cs and ^{141}Pr concentrations in the stomach contents for charr was not found in 2001 (Lake Våvatn: $F_{(1,2)} = 5.01$, $p = 0.155$; Lake Øvre Nonshøtjønn: $F_{(1,2)} = 0.005$, $p = 0.948$). Consequently, the total ^{133}Cs concentrations found in the stomachs of charr in 2000 may not reflect the true exposition of charr to ^{133}Cs because a substantial fraction of the ^{133}Cs found in the stomach of charr is likely bound to sediment particles. This situation may yield to an underestimation of consumption rate through an overestimation of ^{133}Cs absorption. We avoided this problem by substituting the ^{133}Cs concentration in stomachs of charr from Lake Våvatn in summer 2000 by the corresponding values available for charr from Lake Våvatn on summer 2001.

Consumption rate

The Cs-based daily consumption rate estimated for individual fish ranged from 1.47 to 21.5 kJ·d^{-1}. The general mean Cs-based daily consumption rate was 5.32 kJ·d^{-1}. Consumption rate differed among-enclosures (Table 1.1). Charr from enclosures E5 and E6 (Lake Øvre Nonshøtjønn, 2001: mean = 8.67 kJ·d^{-1}) had a consumption rate 2.5 times higher than charr from enclosures E2, E3, and E4

(mean = 3.48 $kJ \cdot d^{-1}$). Charr from enclosure E1 (mean = 6.09 $kJ \cdot d^{-1}$) consumed 2.1 times more food that charr in enclosures E3 and E4 (Lake Våvatn, 2001: mean = 2.86 $kJ \cdot d^{-1}$). Consumption rate represented 20-104% of the estimated maximum consumption rate and differed among-enclosures. C/C_{MAX} of charr from enclosures E1, E2, E5, and E6 (mean = 44%) was 3.4 times higher than that of charr from enclosures E3 and E4 (mean = 13%; Table 1.1). Two of the 80 fish analysed were associated with estimates of consumption rate that were either unrealistically low (consumption rate represented only 4% of C_{MAX} and was lower than the growth rate of the fish, one fish in E1) or high (consumption rate represented 148% of C_{MAX}, one fish in E4). Keeping in our analysis an individual fish that apparently grew more than it fed or fed 48% more than maximum consumption rate for this fish species and size (C_{MAX} model of Larsson and Berglund 2005) was not only thermodynamically and physiologically incorrect but that it potentially introduced in the literature incorrect values of activity rate. These two fish were therefore excluded from further analysis. Consumption rate and C/C_{MAX} were employed to estimate most components of the energy budget of the fish found in all enclosures (Figure 1.2).

Activity rate: bioenergetic approach

The mean activity rate per fish obtained from the bioenergetics approach was 1.41 $kJ \cdot d^{-1}$ (2.19 times SMR: x SMR), and ranged from -0.709 (-0.895 x SMR) to 8.50 $kJ \cdot d^{-1}$ (6.11 x SMR). Negative values of activity rate arise when the model of Equation 1.1 does not balance. This occurred for 8 of the 78 fish analyzed. The magnitude of the error around consumption rate was sufficient to explain the existence of negative activity rate. Negative values of activity rate estimated using the bioenergetic approach were taken to represent low values of activity rate and were not corrected during the comparison with activity rates estimated using the behavioural approach.

Mean activity rate per enclosure (Figure 1.2) ranged from -0.035 (E4) to 2.99 $kJ \cdot d^{-1}$ (E6; from 0.08 x SMR: E4 to 3.20 x SMR: E1), and varied significantly among enclosures (Table 1.1). Activity rate of charr from enclosure E1, E5 and E6 (mean = 2.98 $kJ \cdot d^{-1}$) was 13 times higher than activity rate

of charr from enclosures E3 and E4 (mean = 0.19 $kJ \cdot d^{-1}$). Moreover, activity rate of charr from enclosure E2 (mean = 1.14 $kJ \cdot d^{-1}$) was 6 times higher than that of charr from enclosures E3 and E4. Activity rate expressed in term of multiplier of *SMR* was 9 times higher for charr from enclosures E1, E2, E5, and E6 (mean = 2.88 x *SMR*) then for charr from enclosures E3 and E4 (mean = 0.32 x *SMR*). No differences in activity rate were found among enclosures E1, E2, E5, and E6, and between enclosures E3 and E4. The grand mean activity rate of all enclosures was 1.31 $kJ \cdot d^{-1}$ (2.03 x *SMR*), lower and upper 95% confidence limits were respectively 1.06 and 1.59 $kJ \cdot d^{-1}$ (1.73 - 2.39 x *SMR*).

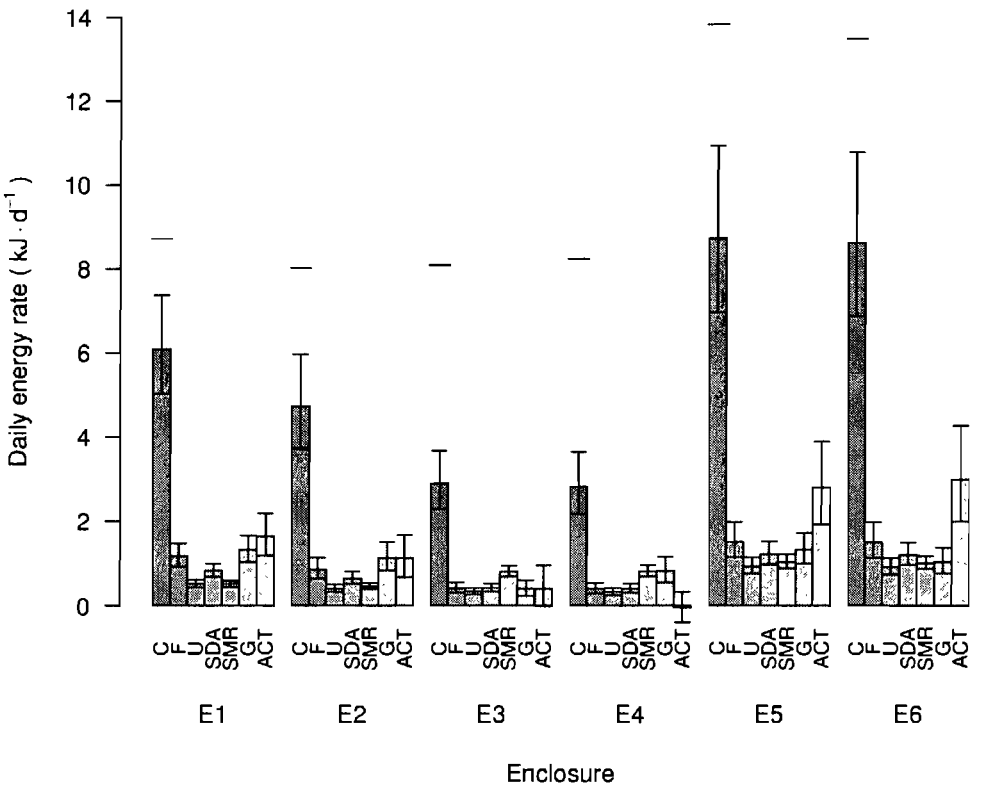

Figure 1.2 Bioenergetic budget for Arctic charr in enclosures E1 to E6. Mean estimates of the components are shown with their respective confidence intervals (95%). Black dashes over consumption rates represent the maximum consumption rates (C_{MAX}) estimated from the models of Larsson and Berglund (2005).

Activity rate: behavioural approach

Body mass of fish used to develop the swimming cost model ranged from 1.1 to 100 g *fw* and their swimming speed ranged from 0.363 to 13.5 $cm \cdot s^{-1}$. The (log_{10}) fresh body mass of fish explained 70.9% (adjusted R^2) of the variation in their log_{10} respiration rate ($F_{(1,112)} = 247.0$, $p < 2.2x10^{-16}$) and adding log_{10} swimming speed to the model increased the adjusted R^2 to 84.2% (Figure 1.3a; $F_{(2,111)} = 270.9$, $p < 2.2x10^{-16}$). Both predictors were positively related with respiration rate ($b \pm 1$ standard error, b_0: -1.411 ± 0.092; b_{MASS}: 0.915 ± 0.039; b_{SPEED}: 0.886 ± 0.096).

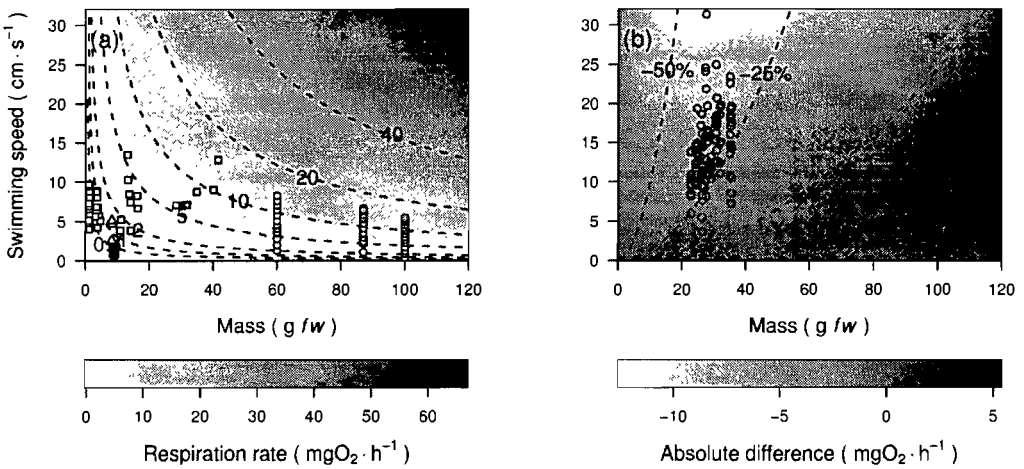

Figure 1.3 A) Swimming costs model used to estimate activity rate of charr using swimming behavioural method. Respiration rate (tones of grey of the background of points) of Goldfish (O), Aholehole (◇), Mullet (△), and Brook charr (□) are represented against their body mass (x-axis) and swimming speed (y-axis). Predictions of the model for any combination of body mass and swimming speed are displayed as tones of grey in the background of the plotting surface. B) Difference between predictions of the swimming costs model developed in this study and the model of published by Boisclair and Tang (1993). Absolute differences ($mgO_2 \cdot h^{-1}$) are displayed as background tones whereas relative difference (%) are represented by overlying isopleths (dashed lines). Data points are plotted over graph B.

The water volume sampled by the video cameras ranged from 0.1 and 4.8 m^3 (average = 0.6 m^3). Fish were observed in 126 of a total of 160 recordings (80%). Furthermore, it was possible to estimate swimming speed for 103 recordings (64%). The median value of fish-seconds (*FS*) observed

for a 1 hour recording was 28 fish·s·h^{-1} and the maximum was 1239 fish·s·h^{-1} (E1, Zone B, June 13, 2000, 10:00 AM). Mean *Active fish biomass* observed ($B_{z,t}$) was 1.17 g·m^{-3}, and values ranged from 0 to 9.14 g·m^{-3}, whereas estimates of biomass density in the enclosures ($B_{e,t}$) ranged from 2.26 to 3.69 g·m^{-3}. Charr used preferentially the deepest sections of the enclosures, avoiding shallow areas. In 2000, the active fish biomass in zone B (mean = 2.50 g·m^{-3}) were 21 times as high as in zone A (mean = 0.12 g·m^{-3}; $F_{(1,30)} = 28.55$, $p = 8.83 \times 10^{-6}$). Moreover, in 2001 *Active fish biomass* in zones E and F (mean = 1.70 g·m^{-3}) were 3 times as high as in zones C and D (mean = 0.56 g·m^{-3}; $F_{(3,124)} = 5.916$, $p = 0.000833$).

The mean swimming speed of charr was 13.79 cm·s^{-1} (range: 3.63 to 31.4 cm·s^{-1}). Swimming speed varied significantly among enclosures (Table 1.1). Fish from enclosures E2, E5, and E6 (mean = 16.01 cm·s^{-1}) swam 52% faster than fish from enclosures E3 and E4 (mean = 10.56 cm·s^{-1}). No differences in mean swimming speed were found among enclosures E1, E2, E5, and E6, and among enclosures E1, E3, and E4. Charr from Lake Våvatn observed in 2000 therefore swam at speeds similar to those of charr originating from Lake Øvre Nonshøtjønn observed in 2001 and both swam faster than charr from Lake Våvatn in 2001. Swimming speed greater than the maximum value of swimming speed used to develop the swimming cost model (13.5 cm·s^{-1}) were observed in a total of 55 recording (53% of the recordings where swimming speed could be estimated).

The mean value of *Hourly activity rate* was 2.18 kJ·kg^{-1}·h^{-1} (1.75 x *SMR*), and ranged from 0 to 6.55 kJ·kg^{-1}·h^{-1} (0 - 7.43 x *SMR*). *Hourly activity rate* did not differ among enclosures (Table 1.1) and time of day ($F_{(3,44)} = 2.7608$, $p = 0.053$; *SMR*: $F_{(3,44)} = 1.3823$, $p = 0.26$). *Daily activity rate* ranged from 1.15 (E2) to 2.38 kJ·d^{-1} (E5), and from 1.04 (E6) to 2.81 (E1) x SMR. Mean *Daily activity rate* (all enclosures) was 1.64 kJ·d^{-1} (1.75 x *SMR*), and lower and upper 95% confidence limits were respectively 1.32 and 2.03 kJ·d^{-1} (1.35-2.26 x *SMR*).

Comparison of activity estimates

There was no statistically significant relationship between estimates of activity rates obtained

from the bioenergetic and the behavioural approaches (Figure 1.4). The Pearson's correlation coefficient between estimates were 0.25 (0.45 x *SMR*) and the lower and upper 95% confidence limits of this coefficient were respectively -0.56 and 0.80 (-0.32 and 0.82 x *SMR*). The null hypothesis that both approaches rendered unrelated estimates in a per enclosure basis thus cannot be ruled out. The slope of the major axis behaved accordingly (0.10, 95% C.L.: -0.41 and 0.88; 0.25 x *SMR*, 95% C.L.: -0.23 and 1.00 x *SMR*). Finally, the intercept of the major axis was 1.27 $kJ \cdot d^{-1}$ (95% C.L.: -0.57 and 2.47 $kJ \cdot d^{-1}$; 1.51 x *SMR*, 95% C.L.: 0.01 and 2.46 x *SMR*). The best agreement between approaches was observed for experiment E1, E2 and E5 (both confidence limits crossing the 1:1 line). Estimates of Daily activity rate obtained using the behavioural approach were higher than corresponding values estimated using the bioenergetic approach in experiments E3 and E4. The opposite trend was observed for enclosure E6.

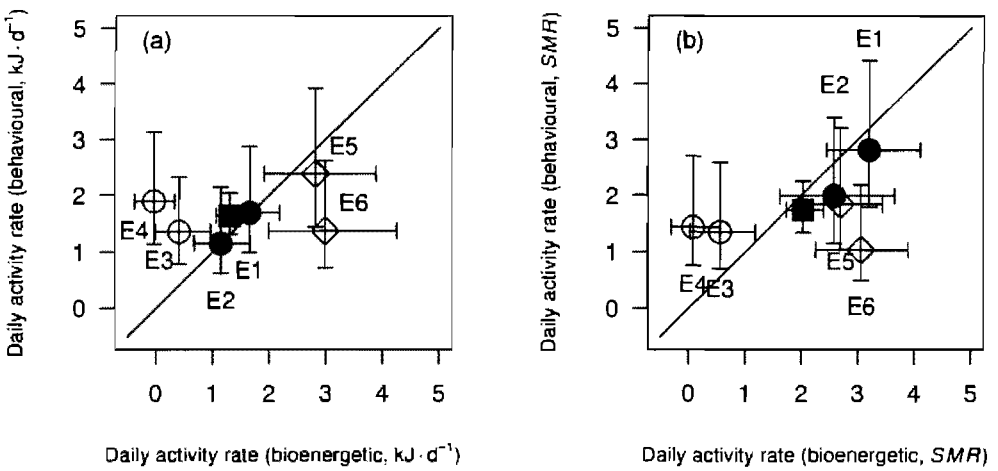

Figure 1.4 Comparison of the Daily activity rate estimates of charr from Lake Våvatn (summer 2000: closed circle; summer 2001: open circle), Lake Øvre Nonshøtjønn (diamond), and mean of the six enclosures (square) obtained using the behavioural (*y*-axis) and the bioenergetic approach (*x*-axis). Activity rate is presented in $kJ \cdot d^{-1}$ (A), or multipliers of SMR (B). Errors bars represent the 95% confidence limits around estimates. The graphs features a 1:1 line.

DISCUSSION

Daily activity rate estimated with the bioenergetic and the behavioural approaches were analogous in many respects. The mean *Daily activity rate* (1.31 $kJ \cdot d^{-1}$ for the bioenergetic approach and 1.63 $kJ \cdot d^{-1}$ for the behavioural approach) and the magnitude of the 95 % C.L. of the mean *Daily activity rate* (1.06- 1.59 $kJ \cdot d^{-1}$ for the bioenergetic approach and 1.32-2.03 $kJ \cdot d^{-1}$ for the behavioural approach) and of individual estimates of *Daily activity rate* obtained using the two approaches were similar (Figure 1.4a). In addition, the bioenergetic (0.08 to 3.20 x *SMR*) and the behavioural (1.04 to 2.81 x *SMR*) approaches provided values of *Daily activity rate* that are within the range of published estimates (0.02 to 3.99 x *SMR*; Sirois and Boisclair 1995, Trudel and Boisclair 1996, Aubin-Horth *et al.* 1999). Despite these conditions, Daily activity rate obtained using both approaches were significantly different for half of the experiments performed (E3, E4, E6). As a result, we found no statistically significant relationship between *Daily activity rate* obtained using the bioenergetic approach and corresponding values estimated using the behavioural approach. The discrepancies between the estimates provided by the two approaches may be best analysed by comparing the strengths and the weaknesses of these approaches.

Bioenergetic approach

The validity of estimates of activity rate obtained using the bioenergetic approach depends, first and foremost, on the validity of estimates of consumption rate. The estimation of consumption rate based on chemical tracers requires the adequate representation of the initial and final tracer concentration in fish tissues, the elimination rate of the tracer, and the concentration of the tracer in fish diet. As in most studies that employed the bioenergetic approach based on chemical tracers (Davis and Foster 1958, Forseth *et al.* 1992, Rennie *et al.* 2005), concentration of a tracer in fish tissues at the beginning of a time period was assessed with fish assumed to represent the initial state of the fish used to assess the concentration of the chemical tracer at the end of this time period (same species, size, and

origin). Given the content of most tracers in fish tissues, estimation of tracer concentration often requires the use of the complete fish, and hence the killing of the fish. The assumption described above is therefore unavoidable. In the present study, the elimination rate of ^{133}Cs by Arctic charr was predicted using the model of Ugedal *et al.* (1992). This model was based on radioactive ^{137}Cs elimination by Brown trout. Rowan and Rasmussen (1995) argued that the rate of radioactive ^{137}Cs elimination is independent of fish species. Although this claim has never been thoroughly tested, the use of this elimination rate model has been validated for Arctic charr (Forseth *et al.* 1991). Moreover, as ^{133}Cs nuclei are only 3% lighter than ^{137}Cs nuclei, it is reasonable to assume that the elimination rate of ^{133}Cs, through the isotopic kinetic effects, would only differ from the elimination rate of ^{137}Cs by a similar magnitude (Kolehmainen 1972). Consequently, it appears realistic to use the model of Ugedal *et al.* (1992) to estimate the elimination of stable ^{133}Cs for Arctic charr. Consumption rate estimated in the present study presumed that stomach contents at the end of the experiments (when fish were recuperated from the enclosures) are sufficient to obtain dependable concentrations of ^{133}Cs in fish diet during the experiment. Fish are generally not captured during experiments to minimize fish stress and environmental perturbations. Temporal variations of fish diet over a period of *ca* one month are possible and this may represent a weakness of the bioenergetic approach for experimental studies. This weakness may be circumvented but only at the expense of a significant increase in the number of experimental units (Boisclair 1992a; Marchand and Boisclair 1998) which somewhat reduces the advantage, over the behavioural approach, of the lower sampling effort required by the bioenergetic approach based on chemical tracers (Forseth *et al.* 1992, Rowan and Rasmussen 1996). The present study suggests that a representative survey of fish stomach contents is useful not only to insure a proper temporal assessment of the fish diet and its ^{133}Cs concentration but also to warrant an adequate appraisal of variations of the ingestion of material (sediments, detritus) that may contribute to ^{133}Cs concentrations in fish stomach but decrease the absorption of this tracer by fish. Substitution of ^{133}Cs concentrations in the stomach of fish from enclosures E1 and E2, by values obtained from enclosures E3 and E4 was based on the analysis of the concentration of ^{141}Pr in fish stomach contents, and applied

to compensate for the presence in the stomach contents of Cs bounded to sediments. This substitution increased estimates of consumption rate by 3-folds. However, such corrections were done only on the basis of the stomach contents on the last experimental day. Whether important quantities of sediments or detritus were present in the stomach contents of fish from different enclosures on different days is not known and could affect the results of the bioenergetic approach based on chemical tracers. Problems associated with adsorption may be expected to vary among tracers and their forms. Hg^{+} and Hg^{2+}, because of their affinity with clay, organic matter, and iron oxide, may be subjected to the same adsorption problem noted with ^{133}Cs. However, methyl mercury ($Me\text{-}Hg^{+}$) may be much less prone to this problem because it is generally associated with digestible particles such as proteins. It is presently impossible to identify why two of the 80 individual analyses of fish consumption rate provided aberrant values. However, it is worth noting that inclusion of these fish would not affect our finding about the lack of relationship between values of activity rate obtained using the bioenergetic and the behavioural approaches. The 95% C.I. of the correlation between values of activity rate obtained using both approaches were -0.56 - 0.80 without these two fish and would be -0.52 - 0.82 if the two aberrant fish would have been kept in the analyses.

The bioenergetic approach estimates Activity rate by subtracting a series of energy expenditures (Standard metabolic rate; Standard dynamic action) and losses (Fecal and Urinary) from Consumption rate. These energy expenditures and losses were computed using models developed for Brown trout feeding on invertebrates (*F* and *E*: Elliott 1976b), other Salmonid species (*SDA*: Hewett and johnson 1992), or Arctic charr itself (*SMR*: Lyytikäinen and Jobling 1998). The validity of activity rate estimates obtained using the bioenergetic approach also depends on the validity of these models for the species of interest. The effect of parameter or model borrowing from one species to another remains unresolved (Trudel *et al.* 2004, Trudel and Welsh 2005). As such, it is impossible to determine the extent to which the negative estimates of Activity rate provided by the bioenergetic approach (E3: three fish with negative activity rates; E4: five fish with negative activity rate) are related to

weaknesses described above about the estimation of Consumption rate or to parameter or model borrowing for *SMR*, *SDA*, *F* and *E*. However, the *SMR*, *SDA*, *F*, and *E* models used in the present study were implemented in the same manner in all enclosures, and in the advent of species specific models, these models would continue to be inputted with the same key variables (fish weight, water temperature, and Consumption rate). Given that the mass exponent of the empirical relationship generally used to represent these components of fish energy budget are the most stable parameters of bioenergetic models (thereby minimizing the effect of changing allometric relationships), and that the initial and final fish mass varied respectively by 41% and 35% (thereby minimizing the effect of changing allometric relationships) we would argue that the availability of species specific models would not change the relative position of Activity rates values obtained using the bioenergetics and the behavioural approaches (Figure 1.4).

The behavioural approach

Daily activity rate estimated using the behavioural approach could be affected by errors or biases on six key inputs: the mass of fish in the enclosure, the swimming speed of fish, the respiration predicted from the swimming cost model, the volume sampled by the SVC, the intensity of the filming schedule, and the number of fish-seconds estimated. Fish average mass on any given day was estimated by linear interpolation of the initial and the final fish mass. The bioenergetic approach was also implemented following a linear interpolation of fish mass. Hence, errors or biases about fish mass may not be responsible for the discrepancies between both approaches. Boisclair (1992a) showed that measurement error associated with swimming speeds estimated using SVC is ± 4.5% of mean swimming speed. Such measurement error would have an impact on the order of ± 8% on the estimates of mean swimming cost. Energy expenditures associated with swimming were obtained using a spontaneous swimming cost model developed using respiration data from four fish species other than Arctic charr. While this model is expected to adequately predict the swimming cost of fish performing changes in speed and direction (Boisclair 2001), the use of this model may be questioned because it

implies the inter-specific transfer of a model (model or parameter borrowing; Trudel *et al.* 2004, Trudel and Welsh 2005). However, studies using the behavioural approach and the swimming costs model of Boisclair and Tang (1993) were successful in producing activity estimates that allowed numerous authors to balance the bioenergetic equation implemented with independent values of growth and consumption rates for Brook charr (Boisclair and Sirois 1993, Sirois and Boisclair 1995, Marchand and Boisclair 1998), Dace (Trudel and Boisclair 1996), and Yellow perch (Aubin-Horth *et al.* 1999). Yet, none of these species were part of the dataset employed by Boisclair and Tang (1993) to develop their model. In the present study, the swimming cost of Arctic charr was estimated with a new model developed by combining the dataset of Boisclair and Tang (1993) with respirometry experiments performed with brook charr (Tang and Boisclair 1995, Tang *et al.* 2000). This is expected to represent, if anything, an improvement to the model of Boisclair and Tang (1993) because Arctic charr and brook charr belong to the same genus.

The volume sampled by the SVC were estimated using the geometric properties of the field-of-view of cameras and the maximum distance (from the SVC) beyond which fish detection was not possible as a consequence of water transparency and turbidity. The resulting polyhedron was further truncated to subtract the volume hidden by other obstacle (bottom, surface). These volumes were easy to estimate as obstacles were visible and their dimensions were straightforward to measure. On the other hand, the maximum distance for fish detection had to be deducted from the position of fish and, consequently, could only be estimated reliably if a sufficient number of fish are observed. Fish were absent in 20% of the recordings and 15 or less fish were observed in half of the remaining recordings. We assumed that grouping recordings performed in similar conditions would allow us to obtain a reasonable figure of maximum distance for fish detection and calculated sampled volumes accordingly.

The intensity of the filming schedule (4 h per day and 2 days per month) used in the present study was similar to that of numerous published studies that employed SVC (4 to 5 h per day and 3 to 10 days per month). These studies showed that this approach provided activity rate consistent with

other components of the bioenergetic equation. The number of movements observed within the field of view of the SVC (fish-seconds) was the most reliable variable estimated. Arctic charr were the only fish species present inside the enclosures and the quality of the images obtained insured their detection. No large moving object (> 10 cm) other than Arctic charr was observed on any recording. Variation of the number of fish-seconds alone explained 87% of the variability of all hourly activity rate values obtained ($F_{(1,101)} = 119.12$, $p < 2.2 \times 10^{-16}$). Body mass and swimming speed explained, respectively, 3.2% and 0.2% of the variation of hourly activity rate. This result is consistent with the suggestion that estimates of activity rate obtained using the behavioural approach may be primarily driven by the number of fish-seconds when fish are defined as active (Trudel and Boisclair 1996). This situation emphasizes that errors on fish mass, swimming speed, and predictions of respiration models may have relatively minor effects on the relative magnitude of among-hour or among-day variations of activity rate, and hence, on the relative position of estimates of Daily activity rate obtained using the bioenergetic and the behavioural approaches (Figure 1.4).

Daily activity rate estimated using the behavioural approach may not only be affected by inputs to the models but also by the structure of the models. Equations 1.7 to 1.10 involve the product or the ratio of means of variables that may be argued to affect Daily activity rate through the 'fallacy of averages' (*e.g.* $\mu(A \cdot B) \neq \mu A \cdot \mu B$ when A and B are correlated; Wagner 1969). In our study, some variables were estimated on an individual basis (*e.g.* the mass of fish #1 at t in 2000) but the SVC did not allow us to identify fish individually and hence to assess many variables on an individual basis (*e.g.* FS of fish #1 in a particular zone z at time t). Consequently, the structure of the data does not permit us to assess or to correct the fallacy of averages using the solution proposed by Welsh *et al.* (1988; $\mu(A \cdot B) = \mu A \cdot \mu B + \mathrm{cov}(A,B)$). For instance, we have the individual mass fish #1 to #20 at any given time t of an enclosure in 2000 but we do not have the individual $FS / (T \cdot V)$ for fish #1 to #20 in zone z at t to which they should be paired to assess the covariance ($FS / (T \cdot V)$, M) to assess or to correct for the fallacy of averages in Equation 1.7. However, for each zone, time of day, and sampling

day we have $FS_{z,t} / T_{z,t} \cdot V_{z,t}$ and the coordinates of the head and of the tail of a sample of the fish that were observed in this zone at that time. We transformed the coordinates of the head and of the tail of fish in swimming velocities but these can also be transformed in fish length (Boisclair 1992) and, with a length weight relationship, in fish weight. This provided us with data on $FS / (T \cdot V)$, average fish mass (averaged over all fish observations) and average velocity (averaged over all fish observations) per zone and time of day. These data indicated that there is no correlation between $FS / (T \cdot V)$ and M ($-0.09 < R^2_{adj} < -0.01$; $0.40 < p < 0.99$), and between $A_{z,t}$ (estimated as $A_{z,t} = (B_{z,t} \cdot MSC_{z,t}) / B_{e,t}$) and M ($-0.07 < R^2_{adj} < -0.01$; $0.41 < p < 0.90$). Given that the fallacy of averages occurs only when the two variables involved are correlated, that the variables for which the existence of a correlation could be tested is insignificant or small in our study, and that, when correlations occur, the resulting bias is generally smaller than 20% (Welsh *et al.* 1988), we trust that the fallacy of averages may have a negligible impact on our interpretation about activity rate values that varied 0 to 53-folds between the bioenergetic and the behavioural approach.

CONCLUSION

The bioenergetic approach based on chemical tracers was developed to provide integrated values of consumption and, eventually, activity rates over extended periods of time, and this, with minimal sampling efforts. The quality of the consumption and activity rates obtained using this approach depends on the validity of numerous inputs and assumptions. For instance, the bioenergetic approach based on a chemical tracer assumes that the concentration of the tracer in the food and the assimilation of this tracer are constant over the time interval for which consumption and activity rates are estimated. As exemplified by the present study, the inclusion of sediments or detritus in fish diet may overestimate ^{133}Cs availability to fish and cause a 3-fold underestimation of consumption rate. Once the effect of sediments and detritus in fish diet is considered, the confidence limits of consumption rate ranged from ± 14% (E5) to ± 26% (E3 and E4). Estimates of activity rate obtained

using the bioenergetic approach represented from 0% (E4) to 32% (E6) of the consumption rate. Values of activity rate obtained using the bioenergetic approach were smaller than the width of the confidence intervals around estimates of consumption rate for 30 of the 80 individual charr analysed (38%). Similarly, Daily activity rate (mean activity rate within an enclosure) was smaller than the width of the confidence intervals of consumption rate for three of the six experiments (namely E2, E3, and E4). While the bioenergetic approach based on ^{133}Cs may provide realistic estimates of consumption rate, the errors associated with consumption rate and the uncertainties associated with the use of other components of the bioenergetic equation (F, E, SDA, and SMR) presently question the validity of this approach to estimate activity rate. This is best illustrated by the presence of negative values of activity rate for eight of the fish analysed and by the wide range of activity rate estimates (0.08 to 3.20 x SMR; Figure 1.4b) obtained under experimental conditions that were similar in many respects (same fish species, same fish origin, experiments in same lake with the same enclosures, approximately the same fish densities and biomass). The behavioural approach provides discrete values of activity rate over short time intervals (minutes to hours), a datum that cannot be obtained using the bioenergetic approach based on chemical tracers. The estimation of activity rate over time intervals of weeks to months with the behavioural approach requires more intense sampling and processing efforts than with the bioenergetic approach based on chemical tracers. The behavioural approach also involves the interpolation of hourly to daily activity rate and of daily to monthly activity rate. However, values of activity rate obtained using the behavioural approach depend mostly on a variable that is the easiest to estimate; the number of second fish are observed active (the number of moving fish-seconds of Equation 1.7). In addition, the behavioural approach cannot provide negative activity values. Finally, values of activity rate obtained under similar experimental conditions (same fish species, same fish origin, experiments in same lake with the same enclosures, approximately the same fish densities and biomass), as may be anticipated, did not vary significantly among each other and covered a relatively small range (1.04 to 2.81 x SMR; Figure 1.4b). The present study suggests that the behavioural approach may be more trustworthy than the bioenergetic approach implemented with ^{133}Cs to estimate

fish activity when fish are known to remain in an area where their behaviour can be well described (enclosures, littoral zones, coral reefs). Whether using tracers less subjected to the problem of adsorption would be sufficient to modify this interpretation remains to be tested. In addition, irrespective of the tracers used, isolation of activity rate using the bioenergetic approach requires dependable models of F, E, SMR and SDA. The present study also emphasizes that in other situations (low fish densities, fish performing movements or migrations over ranges that do not permit an adequate description of their behaviour), where the bioenergetic approach may be the only approach amenable, efforts should be deployed to adequately estimate the diet of the fish (in particular detritus or sediment contents) and the assimilation efficiency of the tracer.

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Chapitre 2 :

Mechanisms of density-dependent growth in Arctic charr

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ABSTRACT

We explored the mechanisms of density-dependent growth in Arctic charr (*Salvelinus alpinus* L.) by comparing their rates of growth, food consumption, and activity obtained independently under three different density treatments in a large scale enclosure experiment. The shape of the relationships between fish density and the rates of growth and consumption were investigated using three mathematical functions (linear, power and quadratic).

The growth and consumption rates of Arctic charr were negatively affected by fish density. The relationship between growth rate and fish density was best described by a linear function. On the other hand, the relationship between consumption rate and fish density was best described by a quadratic function, showing a transient increase in food consumption as density increases from the low (5.7 fish·100m^{-3}) to the medium (11.4 fish·100m^{-3}) density treatments. Finally, activity rate was positively affected by fish density.

These results suggest that increased activity may be an important mechanism for reduced growth of fish at high densities, and illustrated the potential complexity of the relationships between consumption, activity, growth and fish densities. Moreover, the transient increase in consumption rate observed as fish density increases from low to medium densities, coupled with increasing activity rate, also suggest that Arctic charr may, under these circumstances, have a greater *per capita* impact on their prey populations that would not translate into higher growth and production.

RÉSUMÉ

Nous explorons les mécanismes de croissance dépendante de la densité chez l'omble chevalier (*Salvelinus alpinus* L.) en comparant les taux de croissance, de consommation et d'activité obtenus de manières indépendantes et sous trois traitements de densités différentes dans des enclos expérimentaux. La forme des relations entre la densité et les taux de croissance et de consommation a été examinée à l'aide de trois fonctions mathématiques (linéaire, de puissance et quadratique).

Les taux de croissance et de consommation des ombles chevaliers ont été affectés négativement par la densité. La diminution du taux de croissance est décrite de façon plus appropriée comme une fonction linéaire de la densité. Par contre, la forme de la relation entre le taux de consommation et la densité est décrite de façon plus appropriée par la fonction quadratique; mettant en évidence une augmentation transitoire entre les traitements de basse (5.7 poissons·100m^{-3}) et de moyenne densités (11.4 poissons·100m^{-3}). Enfin, le taux d'activité est affecté positivement par la densité.

Ces résultats suggèrent qu'une augmentation du taux d'activité peut constituer un mécanisme clé expliquant la réduction de le croissance lorsque la densité augmente et illustrent la complexité des relations entre les taux de consommation, d'activité et de croissance et la densité de poissons. De plus, l'augmentation transitoire du taux de consommation observée lorsque la densité augmente entre des niveaux de basse et moyenne densité, ajouté à l'augmentation observée dans les taux d'activité suggèrent que l'omble chevalier aura, dans ces circonstances, un plus grand impact *per capita* sur les populations de ses proies. Cet impact accru ne sera pas couplé à une augmentation de la croissance et de la production.

INTRODUCTION

Knowledge about density-dependent growth in fishes is growing (Jenkins *et al.* 1999, Bohlin *et al.* 2002, Imre *et al.* 2005, Rosenfeld *et al.* 2005, Lobón-Cervia 2007). Contrasting results have been obtained for high and low density populations (Lobón-Cervia and references therein), and its relative importance is still a matter of debate (Beverton and Holt 1957, Elliott 1994, Rochet 2000, Rose *et al.* 2001), although many authors now regard it as being a key process in the regulation of fish populations (Post *et al.* 1999, Rose *et al.* 2001, Lorenzen and Enberg 2002). Understanding the mechanisms of density-dependent growth may help resolve the controversies, and provide new insights into the processes of density regulation and population dynamics in animal populations.

Reduced growth at high densities has been attributed to decreased food consumption due to competition. Resources become depleted by a high number of foraging individuals (Henderson 1985, Henderson and Brown 1985). In a large scale field study (12 lakes), however, Boisclair and Leggett (1989a) found a significant negative relationship between individual growth of yellow perch (*Perca flavescens*) and fish density, but no significant relationship between growth and consumption rates. As a logical conclusion, they suggested that the density effect resulted from differences in activity levels among populations. However, they had no independent estimate of activity to evaluate their hypothesis. Marchand and Boisclair (1998), on the other hand, found in enclosure experiments with 0+ brook charr (*Salvelinus fontinalis*) held at two densities that higher fish densities resulted in decreased food consumption and increased activity rates lending support to their earlier contention. However, their experiment did not establish the shape of the relationship. Knowledge of the shape of these relationships is useful to identify the range of fish density in which consumption or activity maybe expected to vary most. This information is crucial to adequately implement the effect of fish density on the predictions of bioenergetic models and to identify the range of fish density where density-dependent trophic interactions may (large increase of consumption and pressure on prey base with

small increase of fish density) or may not (stable and relatively low consumption and pressure on prey base with large change of fish density) dominate population dynamics (Rowan and Rasmussen 1996). Recently, Orpwood *et al.* (2006) provide further evidence for the importance of activity patterns for variation in fish growth, by exhibiting that juvenile Atlantic salmon (*Salmo salar* L.) modulated the amount of time they were active in responce to variation in food availability. This study, and similar studies on activity patterns of stream dwelling salmonids (*e.g.* Burns *et al.* 1997, Metcalfe *et al.* 1999, Imre and Boisclair 2004, Johnston *et al.* 2004), indicate that the trade-off between feeding and sheltering or reducing activity (to reduce predation risk) is an important part of the mechanisms creating variability in growth at different population densities.

Here we explored the mechanisms of density-dependent growth in Arctic charr (*Salvelinus alpinus*) by comparing independent estimates of growth, food consumption and activity rates under different density treatments in large scale enclosure experiments.

METHODS

Sites and enclosures

The enclosure experiment was conducted during summer 2000, in Lake Songsjøen, western Norway (Figure 2.1; 63°19'26" N. - 9°39'55" E.; 263 m above sea level; area = 0.70 km^2). Lake Songsjøen is oligotrophic and supports populations of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). During 24-28 May 2000, six square enclosures (9.5m x 9.5m surface area, 7 mm bar mesh size, denoted E1 to E6) were installed 3-7 m from the shoreline. The enclosures consisted of nets attached to a frame, and were positioned to minimize among enclosure variation in average depth and water volume. Depth at the shallow end of the enclosures ranged from 90 cm to 128 cm (average 113 cm), whereas depth at the deep end of the enclosures ranged from 268 cm to 285 cm (average 274 cm). The volume of the enclosures ranged from 167 m^3 to 178 m^3 (average 175 m^3). To prevent the fish

from escaping the enclosures, the netting was sunk into the sediments or secured with gravel bags over hard substrate along the lake bottom and extended 75 cm above the water surface. The absence of surface or bottom netting allowed the charr to feed on prey not only throughout the water column, but also at the water surface, along the lake bottom and within the sediments.

Experimental fish

During 25-30 May 2000, 158 juvenile Arctic charr (age II+ and III+; average size: 22.74 g, range:12.4-35.9) were captured in Lake Våvatn (Figure 2.1; 63°19'41" N - 9°34'29" E; 300 m above sea level; area = 4.25 km²) using baited minnow traps. Lake Våvatn is located 1.9 km upstream of Lake Songsjøen.

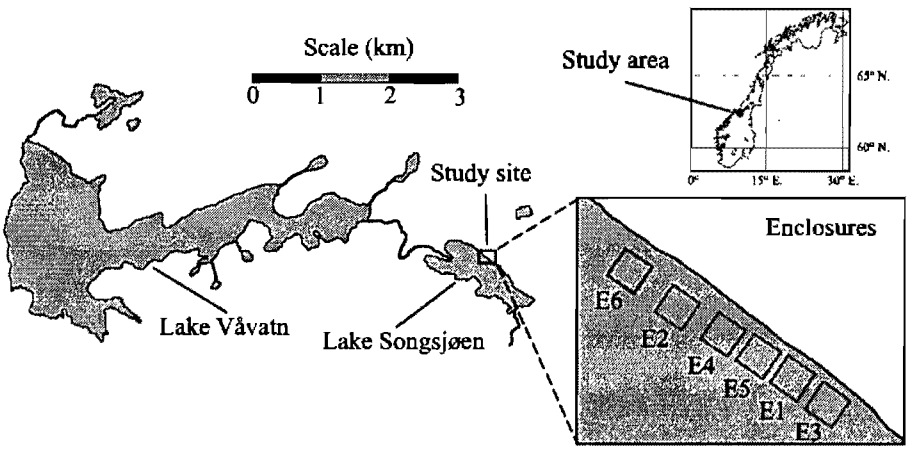

Figure 2.1 Study area, study site, and position of the experimental enclosures within the study site.

On 4 June, fish were anaesthetized using clove oil (25 mg·L^{-1}), weighed (electronic balance, Mettler™ model BB1200, ±0.1 g) and marked individually using alcian blue dye. Handling time was less than 90 s and the fish were allowed to recover for 15 min. in aerated water.

Experimental procedures

Fish growth, consumption and activity rates were assessed for three treatments (10, 20 and 40 charr per enclosure; hereafter referred to as low, medium and high density) with two replicates per treatment. Each enclosure was surveyed by snorkel to ensure that they were empty of fish prior to the experiment. On 4 June, charr were distributed among the enclosures so as to ensure similar among-enclosure mean and variance in body mass. The eighteen charr not stocked into the enclosures were sacrificed (by an overdose of anaesthetics) to provide a baseline estimate of ^{133}Cs concentration in charr at the beginning of the experiment (see *Caesium analysis and computation of consumption rate*). The experiments were terminated over three days because of the time required to recapture and process the fish (E4 terminated 3 July; E2, E5 and E6 terminated 4 July; E1 and E3 terminated 5 July). Charr were recaptured by dragging a seine three times within each enclosure and killed immediately by an overdose of clove oil (100 $mg \cdot L^{-1}$). They were identified individually, weighed, and dissected. The preys in the stomach contents of the fish taken from a given enclosure were identified to assess fish diet and the contents were pooled to obtain sufficiently large samples for ^{133}Cs analysis. All fish tissues and stomach contents were kept frozen (-80°C) for ^{133}Cs analysis.

Diet analysis

The diet was examined by analyzing the stomach contents of the fish at the end of the experiment and thus chiefly represents the last meal. Prey animals in the stomach contents were identified, counted and measured under a dissecting microscope. Crustaceans were identified to species whereas other animals were identified to family or order. For larger animals, all individuals were counted and measured, whereas for crustaceans representative sub-samples were counted and measured. Body length was measured on whole animals or specific body parts. In the latter case, regression equations were used to estimate body length, which was converted to dry mass using length-mass regressions (Breistein and Nøst 1997). The diet of each fish were expressed as proportion of dry mass by prey type, and the average mass of the prey animals in the diet of each fish was calculated.

For analyses, the different prey animals were grouped into 6 different categories: planktonic crustaceans (species of the genera *Daphnia*, *Bosmina*, *Holopedium*, *Bythotrephes*, *Polyphemus*, *Heterocope* and *Cyclops*), benthic crustaceans (*Eurycercus lamellatus* and *Sida crystallina*), mollusks (snails and mussels), aquatic diptera (larvae and pupae of the families Chironomidae and Ceratopogonidae), benthic insects (larvae, pupae and aquatic adults of other aquatic insects), and surface insects (terrestrial insects and adults of the aquatic Ephemeroptera, Trichoptera and Diptera).

Video sampling

The activity rate of charr was estimated from their swimming behaviour according to Boisclair (1992a). Fish swimming behaviour was recorded using Stereo-Video-Cameras (SVC), which consisted of a pair of cameras (either Panasonic™ WV-BL602 or Panasonic™ WV-BP312) enclosed side-by-side in a water-resistant (Plexiglas®) case, 10 cm from one another. Two SVC were used, each producing two images, allowing simultaneous observation at two locations of the enclosure. The four images produced by the two SVCs were assembled into a single image using a Quad image processor (Panasonic™ WJ-410). A time-date generator (Panasonic™ WJ-810) was used to add the time of filming to the images (± 0.001s). The resulting video sequences were recorded using a VHS videocassette recorder (Panasonic™ AG-1330).

Fish distribution was considered when positioning the SVC. Snorkeling performed outside the enclosures indicated that charr frequented the surface layer (surface to 1 m from the bottom) of the offshore third of the enclosures. Hence, we defined two sampling zones (zones A and B). Zone A included the entire water column within the shallowest two thirds of the enclosures, whereas zone B included the entire water column of the offshore third of the enclosures.

The SVC sampling zone A were positioned 50 cm from the perpendicular sides of the enclosures (*i.e.* perpendicular to shore), 80 cm below water surface (thus 40 to 80 cm above the bottom), and in the middle of the enclosure on the littoral-pelagic axis. These cameras were directed

perpendicular to the side of the enclosures and parallel to water surface. The SVC sampling zone B was positioned 50 cm from the middle of the deepest side of the enclosures, 180 cm below the surface. It was oriented perpendicular to the side of the enclosure and looking upward with an angle of 45° relative to water surface. Depending on the enclosure, the SVC sampling zone B was thus between 50 and 100 cm over the bottom.

Fish behaviour was quantified during two days in each enclosure. On any given sampling day, fish were filmed at 4:00 AM, 10:00 AM, 4:00 PM, and 10:00 PM. Zones A and B were filmed simultaneously during 1h. This filming schedule resulted in 48 h of film over the two zones (6 enclosures x 2 filming days x 4 hours of filming per day). Recordings began 5 minutes after the cameras were positioned.

Video analysis

VHS recordings were converted to numeric format using a PC-based interface (ATI video acquisition interface, resolution: 640x480 pixels) to ease computer-based image analysis. For every second of recording, all moving fish (velocity > 1 $cm \cdot s^{-1}$) that were observed simultaneously in both cameras of a given SVC were counted and summed over the duration of a recording (1h) to provide a measure of the total moving fish second (FS, fish·s). Image analysis was performed with software developed by the first author using XBasic Program Development Environment (2002, version 6.2.3). The analysis involved positioning (in raw pixel coordinates) the head and tail of fish (see Boisclair 1992a for details) through time. To minimize the effects of pseudo-replication, swimming characteristics were estimated on a single one second interval, randomly selected over the complete displacement of a given fish in the volume sampled by the SVC. A maximum of 100 measurements were taken per hour of filming. Random sub-sampling was thus conducted when more than 100 fish passages where available per hour of filming. According to Boisclair (1992b) this sample size is sufficiently large to obtain reliable estimates of the mean swimming velocity of brook charr. It was assumed that this is also true for other salmonids, such as Arctic charr.

Caesium analysis

Cs concentration was estimated for individual charr. Each fish was weighed (g *fresh weight*; g *fw*), and then dried until mass stabilized (60°C for 24-48 h) to determine its dry mass (g *dry weight*; g *dw*) and the proportion of dry matter. Dry fish tissues were then ground into a powder and a 300 mg sub-sample taken and digested with HNO_3. Measurements of ^{133}Cs concentration ($ng \cdot g^{-1}$ *dw*) were made on the digested sub-sample using a high resolution Inductively Coupled Plasma Mass Spectrometer (ICP-MS, Thermo Electron Corp. model Finnigan™ Element1).

Computations

Growth rate

Growth rate (G, $kJ \cdot d^{-1}$) was calculated as:

$$G = \frac{(w_F - w_0) \cdot ED}{n} \tag{2.1}$$

where w_0 and w_F are the body mass of the fish (g *fw*) at the beginning and the end of the experiment, respectively; n is the duration of the experiment (day), and ED is fish energy density ($kJ \cdot g^{-1}$ *fw*) predicted from the proportions of dry matter according to the model of Hartman and Brandt (1995, Equation #13, developed for salmonids).

Consumption rate

Cs burden in fish (ng *fw*) was obtained by multiplying the ^{133}Cs concentration per gram of dry fish tissue by the proportion of dry matter and original fresh mass of the fish (g *fw*). Initial ^{133}Cs burden of the fish was estimated from the ^{133}Cs concentration (17.88 $ng \cdot g^{-1}$ *fw*) of the eighteen charr sampled at the start of the experiments and body mass at the start of the experiments (g *fw*). No statistically significant relationship was found between ^{133}Cs concentration and fresh fish weight ($t_{(16)} = 0.710$, $p = 0.488$). Final ^{133}Cs burden was estimated for each charr recaptured from low and medium density

enclosures. In the high density enclosures (E5 and E6), a subset of 20 charr was sampled randomly from among the recaptured fish of each enclosure. ^{133}Cs concentration in the food consumed by fish (pooled stomach contents) was evaluated using the same procedure as for body tissues and reported as the dry weight concentration (ng·g^{-1} *dw*).

Consumption rate was calculated for individual charr following the method proposed by Forseth *et al.* (1992). First, we calculated the (linearly) interpolated body mass w_i (g *fw*) and ^{133}Cs burden Q_i (ng) of the fish at any given day i. Cs elimination rate (k_i, d^{-1}) was estimated from w_i and mean daily temperature (°C) using the model of Ugedal *et al.* (1992) and daily ^{133}Cs intake (I_i, ng·d^{-1}) calculated as proposed by Forseth *et al.* (1992, their equation 3b). Mean daily consumption rate (C, kJ·d^{-1}) was then calculated as:

$$C = \frac{\sum_{i=1}^{n} I_i \cdot \sum_{j=1}^{m} (p_j \cdot S_j)}{[Cs]_f \cdot Eff \cdot n} \qquad (2.2)$$

where $[Cs]_f$ (ng·g^{-1} *dw*) is the concentration of ^{133}Cs in the diet of fish from each enclosure, and Eff is the assimilation efficiency of ^{133}Cs (the proportion of the ^{133}Cs found in the diet that is effectively assimilated by the fish), n is the duration of the experiment (day), p_j is the proportion (calculated dry mass percentage) of prey item j in fish diet, and S_j (kJ·g^{-1} *dw*) is the energy density of prey item j (kJ·g^{-1} *dw*). The energy densities of prey items were obtained from Cummin and Wuycheck (1971), and where species-specific energy densities were unavailable, generic values to the nearest taxonomic level were substituted. Energy densities used to transform consumption rate from a dry mass to an energy basis were 21.93 kJ·g^{-1} *dw* for cladocerans, 24.22 kJ·g^{-1} *dw* for copepods, 22.69 kJ·g^{-1} *dw* for chironomids, and 20.18 kJ·g^{-1} *dw* for surface insects. The mean value of arthropods (19.77 kJ·g^{-1} *dw*) was used for all other prey items. Because stomach contents were pooled, the energy density of the diet was estimated once for each enclosure.

Calibration of the SVC

Calibration of the SVC was done underwater using a target consisting of a board with lines spaced apart by 10, 20 and 30 cm. This target was placed at distances ranging from 40 cm to 240 cm from the SVC (increments of 40 cm). Calibration was done before the first filming day, and was repeated each four filming days. A non-linear function was used to estimate real lengths (L, cm) from virtual lengths (l, pixels) and parallax (*i.e.* the offset between images from the cameras in abscissa: Δx, pixels):

$$L = \frac{l}{\frac{c_1}{\Delta x + c_2} + c_3} \tag{2.3}$$

where c_1 is a scale parameter, and c_2 and c_3 are offset parameters estimated by least-squares non-linear regression of known distances between pairs of landmarks on the calibration target against values of Δx and l obtained from image analysis. The quotient of real and virtual length (L / l) was used to evaluate the distance between the target and the SVC (z, cm):

$$z = c_4 \cdot \frac{L}{l} + c_5 \tag{2.4}$$

where parameters c_4 and c_5 were estimated using linear regression of known values of distance of the calibration target and known values of L / l. Coefficients of determination associated with these relationships (Equations 2.3 and 2.4) ranged from 92% and 99%.

Volume sampled by the SVC

The volume filmed by a video-camera has the shape of a rectangle-based pyramid with a volume increasing with the distance from the camera. This volume crossed the bottom of the littoral zone or the surface of the lake at an angle. Hence, the volume sampled by the SVC was calculated as the volume of a truncated rectangle-based pyramid. This volume began at 25 cm from the objective of the cameras (minimum distance to perceive a fish simultaneously in two cameras of the same SVC)

and extended to a maximum distance of fish detection determined using the coordinates of the head and tail of the fish observed during filming. The volume sampled by the SVC for different recordings were grouped according filming conditions defined by the zone sampled, the position and the orientation of the cameras, and the characteristics of the images (pixel brightness and their frequency distribution). The volume sampled by a SVC for recordings during which no fish were observed was used as the average volume sampled by SVC when fish were observed under similar filming conditions.

Activity rate

Calculation of activity rate from swimming behaviour involved three steps. First, the *observed biomass density* ($B_{z,t}$: g·m^{-3} *fw*) of charr swimming actively in a zone z and at time t in the volume sampled by the SVC was calculated as:

$$B_{z,t} = \frac{FS_{z,t} \cdot \bar{M}_t}{T_{z,t} \cdot V_{z,t}} \quad (2.5)$$

where $FS_{z,t}$ is the total number of moving fish per second (fish·s), $\bar{M}_t$ is the mean body mass of fish inside the enclosure (g *fw*: linearly interpolated at the time of sampling), $T_{z,t}$ is the duration of the recording (s), and $V_{z,t}$ is the volume sampled by the SVC (m^3). We calculated the *mean swimming cost* (MSC: kJ·kg^{-1}·h^{-1}) in a zone z and at time t using mean body mass and swimming speed as:

$$MSC_{z,t} = 13.54 \cdot 10^{b_0} \cdot \bar{M}_t^{(b_1 - 1)} \cdot \bar{v}_{z,t}^{b_2} \quad (2.6)$$

where 13.54 is the oxy-caloric coefficient (J·mgO_2^{-1}, Elliott and Davison 1975), and parameters b_0, b_1, and b_2 ($b \pm 1$ standard deviation) are respectively −1.411 ± 0.092, 0.915 ± 0.039, and 0.886 ± 0.096, estimated from the swimming cost model developed by Guénard *et al.* (In press). Finally, we calculated hourly activity rate ($A_{z,t}$, kJ·kg^{-1}·h^{-1}) in zone z and at time t as:

$$A_{z,t} = \frac{B_{z,t} \cdot MSC_{z,t}}{B_{e,t}} \quad (2.7)$$

where $B_{e,t}$ ($g \cdot m^{-3}$ *fw*) is the *mean biomass density* of fish in the enclosure per unit of volume (*e.g.* the sum of the interpolated body masses at time t divided by the volume of the enclosure).

Statistical analyses

All computations and statistical analyses were performed using R language and environment (version 2.4.1; R Development Core Team 2007). Statistical significance of among-enclosures differences and relations with fish densities were examined by analysis of variance (ANOVA). Where applicable, between-enclosure differences were tested using a *post-hoc* test (Scheffé test: Scheffé 1953). Normality of the residuals was tested by Shapiro-Wilk's test of normality (Shapiro and Wilk 1965). When residuals were found to be non-normally distributed, the explanatory variable was transformed using the Box and Cox (1964) method prior to analysis. Homogeneity of within-group or residual variance was tested using Bartlett's test (Snedecor and Cochran, 1989), or by examining the plots of residual (y) and predicted values (x). Non-linearity in the relationships between performance and densities were explored by quadratic or power (typical for density-dependent growth relationships in fish; *e.g.* Jenkins *et al.* 1999) regressions. Model comparisons were based on adjusted R^2 comparisons (Ohtani 2000) or the Aikake information criteria (AIC, Aikake 1974). The non-linear model was regarded as significantly better when AIC improved by more than 2 units relative to the linear model (73 % probability that the model with the smallest AIC-value is better; Motulsky and Christopoulos 2004). As estimates of *active fish biomass* and *hourly activity rate* typically do not conform with a Gaussian distribution (high level of skewness and over-dispersion), the analysis of the effect of experimental factors (enclosures, density) on these variables were done using Generalized Linear Model (GLM; McCullagh and Nelder 1989, Quasi-Poisson likelihood model using logarithmic link function: Hastie and Pregibon 1992). Statistical significance of the resulting deviance tables were calculated using F-test based analysis of deviance. A statistical significance threshold of 5% for type I (α) error was used. Finally, type I error rates associated with multiple statistical inferences (*e.g.* contrasts obtained from GLM) were corrected sequentially using the Šidák inegality (Šidák 1967,

Wright 1992).

RESULTS

The body mass of charr at the beginning of the experiment were similar among enclosures (Table 2.1). Average stocking fish density was 5.7 fish·100m^{-3} (1.27 g·m^{-3}) in the low density enclosures, 11.4 fish·100m^{-3} (2.53 g·m^{-3}) in the medium density enclosures, and 23.2 fish·100m^{-3} (5.39 g·m^{-3}) in the high density enclosures. Water temperature ranged from 8.2°C (first day of the experiment) to 15.8°C (28 June) during the experiment, with a mean at 11.5°C.

Table 2.1 Variables estimated in the experimental enclosures and results of statistical tests of among-enclosure differences.

Variable		Units	Mean	Range	Enclosure						Among-enclosures differences		
					E1	E2	E3	E4	E5	E6	$F_{(5,v)}$	v	p
Mass	Initial	g *fw*	22.79	13.4, 33.6	22.25 ± 4.53	22.37 ± 5.95	22.53 ± 5.01	21.98 ± 5.39	22.00 ± 5.69	23.35 ± 5.64	0.1991	134	0.96
	Final		28.69	17.2, 42.2	31.83 ± 6.21	32.96 ± 4.40	30.40 ± 4.88	28.02 ± 5.72	28.22 ± 5.94	27.05 ± 5.28	2.4966	114	0.035
Fish Density	D_S	Fish ·100m^{-3}	---	---	5.7	5.7	11.3	11.4	22.5	24.0	---	---	---
	D_R		---	---	4.5	4.0	10.8	6.9	20.3	22.8	---	---	---
	D_M		---	---	5.1	4.9	11.0	9.2	21.4	23.4	---	---	---
Growth rate		kJ·d^{-1}	1.05	0.03, 2.53	1.54^{a} [1.35, 1.73]	1.78^{a} [1.69, 1.99]	1.34^{a} [1.23, 1.45]	1.16^{ab} [1.04, 1.29]	0.84^{b} [0.75, 0.93]	0.61^{b} [0.54, 0.69]	13.757*	76	1.46x10^{-9}
Cs burden	Initial	ng	396	240, 601	392	399	400	368	400	407	---	---	---
	Final		642	337, 1030	645 ± 57	666 ± 57	725 ± 36	607 ± 44	624 ± 35	597 ± 34	1.6343	77	0.16
Consumption rate		kJ·d^{-1}	4.95	1.20, 10.35	5.03^{ab} ± 0.57	5.43^{ab} ± 0.57	6.25^{a} ± 0.35	4.92^{ab} ± 0.43	4.53^{b} ± 0.34	4.00^{b} ± 0.33	5.5898*	76	1.94x10^{-4}
Growth efficiency		%	23.4	0.56, 51.0	31.6^{ab} ± 3.7	34.1^{a} ± 3.7	23.0^{ab} ± 2.3	25.3^{ab} ± 2.8	21.7^{ab} ± 2.2	17.8^{b} ± 2.2	5.3934*	76	2.68x10^{-4}
Swimming speed		cm·s^{-1}	14.36	3.5, 31.4	10.4^{a} ± 1.3	14.7^{ab} ± 1.6	14.8^{ab} ± 1.3	16.8^{b} ± 1.2	15.0^{ab} ± 1.4	14.5^{ab} ± 1.3	2.8774	65	0.021
Activity rate		kJ·kg^{-1}·h^{-1}	3.11	0, 33.4	3.21^{ab} [2.16, 4.75]	1.10^{a} [0.56, 2.15]	2.26^{a} [1.41, 3.61]	1.41^{a} [0.78, 2.56]	8.08^{b} [6.30, 10.35]	2.61^{a} [1.69, 4.04]	6.2312**	89	5.33x10^{-5}

Variables are presented with their standard deviation (± 1 sd), or in the form: "mean [mean - 1 sd, mean + 1 sd]" for asymetric intervals.
Enclosures of equal means are labeled using superscripts a and b. Enclosures labeled as "ab" share similarities with both a and b.
* After correcting the effect of body mass.
** After correcting the effect of sampling zone.

On average, 86% of the fish stocked were recaptured at the end of the experiments (range:

60% in E4 to 95% in E3 and E6). Missing fish may have escaped during or at the termination of the experiments when the enclosures were retrieved, or died during the experiment. Because experimental control over fish density is vital, we used both stocking density (D_S), recapture density (D_R) and mean density (D_M; the mean of stocking and recapture densities) when calculating density effects (Table 2.1).

Growth rate

The growth rate of the Arctic charr varied up to 84 folds among individuals, and was related to their initial body mass ($F_{(1,81)} = 5.1766$, $p = 0.026$, $R^2_{adj} = 0.048$), but slopes did not vary significantly among enclosures ($F_{(5,71)} = 0.3804$, $p = 0.86$) and body mass was included in further analyses involving growth rate. The growth rate of charr varied significantly among enclosures (Table 2.1), and differed among density treatments, but not between treatment replicates (Table 2.2). Charr reared in low (1.66 $kJ \cdot d^{-1}$) and medium (1.27 $kJ \cdot d^{-1}$) density enclosures grew 2.3 and 1.8 times faster, respectively, than charr reared in high density enclosures (0.72 $kJ \cdot d^{-1}$). The difference between low and medium density enclosures (1.3 times) was not statistically significant.

Table 2.2 Statistical tests of the differences among density treatments and between replicates of the density treatments.

Variable		Difference among density treatments and treatments replicates			
		$F_{(v1, v2)}$	v_1	v_2	p
Growth rate	Density	29.56	2	76	$3.19 \cdot 10^{-10}$
	Replicates	2.19	3		0.10
Consumption rate	Density	9.6042	2	76	$1.91 \cdot 10^{-4}$
	Replicates	2.2888	3		0.085
Growth efficiency	Density	12.2577	2	76	$7.97 \cdot 10^{-5}$
	Replicates	0.6507	3		0.59
Activity rate	Density	5.9078	2	89	0.004
	Replicates	6.4468	3		$5.33 \cdot 10^{-4}$

There were significant negative linear relationships between growth, initial body mass and the three estimates (release, recapture and mean) of fish density (Table 2.3, Figure 2.2a), explaining up to

43 % of the growth variation (R^2_{adj}). Adding density squared values did not improve explanatory power. Moreover, linear regression models between growth and densities (R^2_{adj} between 0.39 and 0.41) performed better than power models (R^2_{adj} between 0.31 and 0.34).

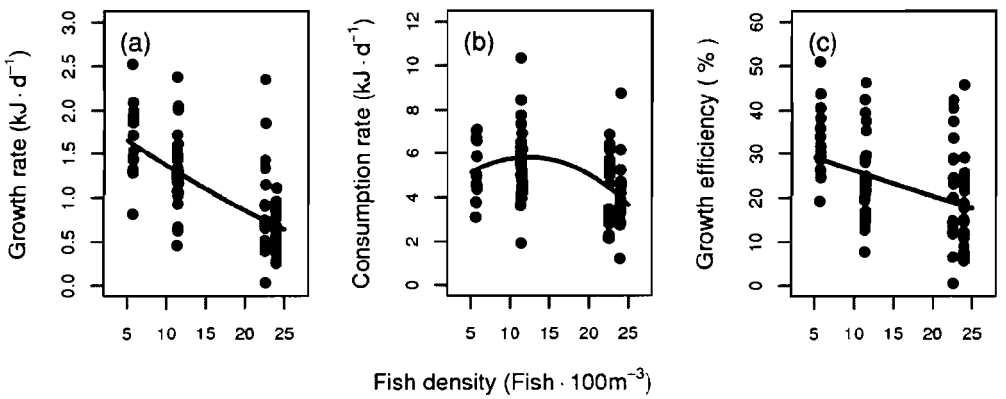

Figure 2.2 Relationships between growth rate (A), consumption rate (B), and growth efficiency (C) of Arctic charr and fish density (D_S) inside the experimental enclosures.

Table 2.3 Models (parameters ± 1 standard deviation) explaining growth rate, consumption rate, and growth efficiency (G_{EFF}) of Arctic charr (kJ·d^{-1}) as a function fish density and body mass (M_0).

Model	F_{v_1,v_2}	p	R^2_{adj} (%)
1. $G^{0.56*} = 1.67(\pm0.11) - 0.027(\pm0.004)\cdot D_S - 0.009(\pm0.004)\cdot M_0$	63.59	$9.08\text{x}10^{-12}$	42.0
2. $G^{0.55*} = 1.68(\pm0.11) - 0.026(\pm0.003)\cdot D_R - 0.010(\pm0.004)\cdot M_0$	63.57	$9.14\text{x}10^{-12}$	39.6
3. $G^{0.55*} = 1.64(\pm0.11) - 0.026(\pm0.003)\cdot D_M - 0.010(\pm0.004)\cdot M_0$	61.12	$1.84\text{x}10^{-11}$	41.1
4. $C = 1.50(\pm1.26) + 0.32(\pm0.17)\cdot D_S - 0.013(\pm0.005)\cdot D_S^2 + 0.10(\pm0.03)\cdot M_0$	10.131	$1.21\text{x}10^{-4}$	15.7
5. $C = 1.44(\pm0.99) + 0.38(\pm0.15)\cdot D_S - 0.017(\pm0.005)\cdot D_S^2 + 0.10(\pm0.03)\cdot M_0$	11.492	$4.16\text{x}10^{-5}$	17.9
6. $C = 1.37(\pm1.14) + 0.36(\pm0.16)\cdot D_S - 0.015(\pm0.005)\cdot D_S^2 + 0.10(\pm0.03)\cdot M_0$	10.665	$7.94\text{x}10^{-5}$	16.5
7. $G_{EFF}^{0.67*} = 14.61(\pm1.04) - 0.14(\pm0.03)\cdot D_S - 0.19(\pm0.04)\cdot M_0$	21.329	$1.46\text{x}10^{-5}$	16.2
8. $G_{EFF}^{0.67*} = 14.25(\pm1.00) - 0.13(\pm0.03)\cdot D_S - 0.19(\pm0.04)\cdot M_0$	21.499	$1.36\text{x}10^{-5}$	16.4
9. $G_{EFF}^{0.67*} = 14.44(\pm1.02) - 0.14(\pm0.03)\cdot D_S - 0.19(\pm0.04)\cdot M_0$	21.616	$1.30\text{x}10^{-5}$	16.4

F-statistics and adjusted R^2 are only reported for fish density, the number of degrees of freedom of the F statistics are $\nu_1 = 1$ and $\nu_2 = 80$ for models 1-3; 7-9, and $\nu_1 = 2$ and $\nu_2 = 79$ for models 4-6. F-statistics and p-values associated with the effect of initial body mass of charr are omited, but all statistical tests rejected the null hypothesis.

* Exponents used to normalize growth rate were obtained using the Box-Cox method (Box and Cox 1964).

Consumption rate

On average, the ^{133}Cs body burden of Arctic charr doubled during the course of the experiment, and among-enclosure differences in final ^{133}Cs body burden were not statistically significant (Table 2.1). Crustacean zooplankton (mostly cladocerans and copepods) dominated the diet of the charr, followed by aquatic diptera (Table 2.4). The diet varied somewhat among enclosures and replicates, but there were no significant treatment effects on mean prey size ($p < 0.05$). Energy density of food ranged from 21.92 (E6) to 22.06 (E5) $kJ \cdot g^{-1}$ *dw* (mean ± *SD* = 22.00 ± 0.047 $kJ \cdot g^{-1}$ *dw*). The mean (± *SD*) ^{133}Cs concentration in the diet was 55.25 ± 12.23 $ng \cdot g^{-1}$ *dw*. As zooplankton strongly dominated the diet, we used the ^{133}Cs absorption coefficient (0.816 ± 0.044) for zooplankton in Forseth *et al.* (1992) for the calculation of consumption rate.

Table 2.4 Diet composition (mean dry weight %) and prey size (geometric mean mg dry weight) in the experimental enclosures. See main text for details on grouping of prey animals.

Treatment		n	Diet composition				Mean Prey size (mg)
			Planctonic crustacea	Benthic crustacea	Aquatic Diptera	Other	
Low	E1	8	49.3	40.1	10.0	0.6	0.014
	E2	7	60.2	18.7	19.0	2.1	0.014
Medium	E3	19	77.1	12.7	10.1	0.0	0.013
	E4	12	62.7	18.7	16.4	2.2	0.019
High	E5	36	62.1	19.0	18.2	0.7	0.019
	E6	38	89.3	8.3	1.4	1.0	0.011

Consumption rate varied up to 8.6 folds among individual charr and was affected by body mass ($F_{(1,81)} = 9.161$, $p = 0.003$, $R^2_{adj} = 9.1\%$), but slopes did not vary significantly among enclosures ($F_{(5,71)} = 1.0703$, $p = 0.38$), and body mass was included in the further analyses involving consumption rate. Consumption rate differed significantly among enclosures (Table 2.1) and was affected by the density treatments, but did not differ between replicates (Table 2.2). Charr in the low (mean = 5.22

$kJ \cdot d^{-1}$) and medium (mean = 5.72 $kJ \cdot d^{-1}$) density enclosures consumed 23% (p = 0.037) and 34% (p = 5.07×10^{-5}) more food than the charr in the high density enclosures (4.26 $kJ \cdot d^{-1}$, p = 5.37×10^{-4}). Differences between the low and medium density enclosures (p = 0.26) were not statistically significant.

There were significant negative linear relationships (all model $p < 0.001$) between consumption, initial body mass and the three estimate of fish density, but all models improved (AIC improvement at 4.3, 8.6 and 6.0 for stocking, recapture and mean densities, respectively) by adding density squared as a third variable (Figure 2.2b). Both the comparisons of means and the regression analyses thus indicate a transitory increase in the consumption rate of Arctic charr from low to medium densities, followed by a decline at high densities.

Growth efficiency

The growth efficiency varied up to 91 folds among individual charr and was negatively affected by the initial body mass of Arctic charr ($F_{(1,81)}$ = 22.07, p = 1.06×10^{-5}, R^2_{adj} = 0.20). As for growth and consumption rate, the relationship between growth efficiency and the initial body mass of charr was similar among enclosures ($F_{(5,71)}$ = 0.4477, p = 0.81), and the initial body mass was included in the statistical analyses. Growth efficiency differed among enclosures (Table 2.1), among density treatments (Table 2.2), but not between treatment replicates. Charr reared in the low density enclosures (mean = 32.5%) had growth efficiencies 1.4 times higher than charr at medium densities (mean = 23.4%, p = 0.005) and 1.7 times higher than fish kept at high densities (mean = 18.7%, p = 3.66×10^{-5}). The growth efficiency of charr from the medium and high density enclosures did not differ significantly (p = 0.08). Growth efficiency decreased linearly with increasing density (Figure 2.2c), and quadratic models did not provide better fits (AIC improvement < 2). These results suggest that, as fish density increased, charr allocated an increasing proportion of their energy available from food consumption to expenses other than growth.

Activity rate

The water volume sampled by the video-cameras ranged from 0.18 to 4.8 m^3 (mean = 0.96 m^3) depending on conditions. Charr were observed swimming in 75 of the 96 recordings collected, and it was possible to estimate swimming speed from 71 of those recordings (74%). Median fish-second (FS) observed during one hour recording was 42.5 $fish \cdot s \cdot h^{-1}$, and the maximum value was 8253 $fish \cdot s \cdot h^{-1}$ (E3, zone B, 23 June, 10:00 AM). *Observed biomass density* ($B_{z,t}$) ranged 0-65.8 $g \cdot m^{-3}$ (mean = 3.28 $g \cdot m^{-3}$) among recordings and *Mean biomass density* ($B_{e,t}$) ranged from 1.43 to 6.42 $g \cdot m^{-3}$ among enclosures. Mean swimming speed varied up to nine folds among recordings and differed among enclosures (Table 2.1).

The activity rate of Arctic charr varied extensively among recordings (Table 2.1, Figure 2.3) and the most striking differences were observed between sampling zones. Charr were 16 times more active in zone B (mean = 5.68 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zone A (mean = 0.346 $kJ \cdot kg^{-1} \cdot h^{-1}$; $F_{(1,94)} = 42.104$, $p = 4.02 \times 10^{-9}$). Consequently, and in order to increase statistical power, this factor (*e.g.* sampling zone) was implicitly added to forthcoming statistical analyses involving activity rate. Hourly activity rate of charr did not follow any specific daily pattern ($F_{(3,88)} = 0.5141$, $p = 0.67$), and the manner charr activity distributed between sampling zones was not influenced by time of day (*e.g.* the zone x time of day interaction was not statistically significant: $F_{(3,88)} = 0.2668$, $p = 0.85$).

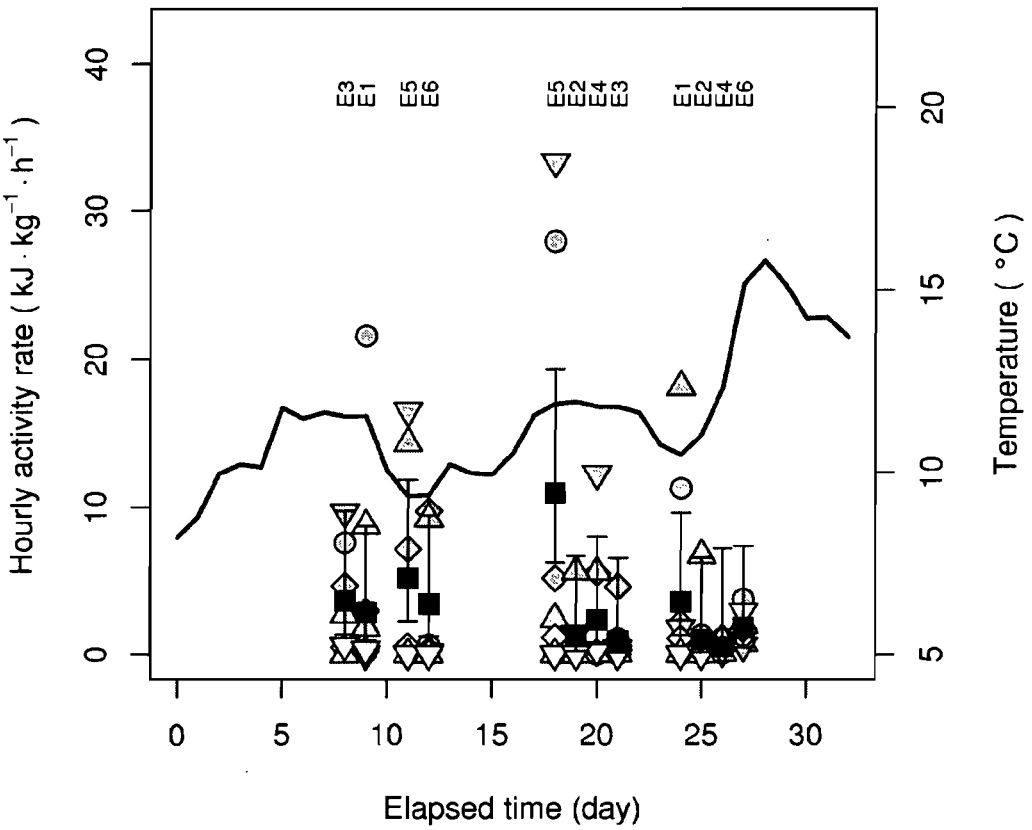

Figure 2.3 Hourly activity rate of Arctic charr swimming in zone A (white symbols) and zone B (grey symbols), at the different sample times of the schedule (4:00 AM: △, 10:00 AM: ▽, 4:00 PM: ○, and 10:00 PM: ◇), mean daily values (■, with their respective 95% confidence limits), and water temperature observed as a function of time elapsed from the beginning of the experiment.

Hourly activity rate differed among enclosures (Table 2.1), among density treatments, and between treatments replicates (Table 2.2). Charr in the high density treatment (mean = 5.35 kJ·kg^{-1}·h^{-1}) were 2.9 times and significantly (p = 0.04) more active than charr kept at medium density (mean = 1.84 kJ·kg^{-1}·h^{-1}), and marginally insignificantly (p = 0.07) more active than fish held at low densities (mean = 2.15 kJ·kg^{-1}·h^{-1}). Activity at low and medium densities did not differ significantly (p = 0.64). The activity rate of charr increased with density (Table 2.5, Figure 2.4). According to this model, the mean hourly activity rate of the charr increased by 25% as fish density doubled from 5 to 10 fish·100m^{-3}, and

by 56% as fish density doubled from 10 to 20 fish·100m^{-3}.

Table 2.5 Models (parameters ± 1 standard deviation) explaining hourly activity rate of Arctic charr as a function of fish density, or sampling zone (zone A: Z = 0 and zone B: Z = 1).

	Model	Parameter	value	Deviance	F	p
		b_0	-1.68 ± 0.67			
1.	$\lambda = b_0 + b_1 \cdot Z + b_2 \cdot D_S$	b_1	2.72 ± 0.62	269.7	45.856	$1.13 \cdot 10^{-9}$
		b_2	0.045 ± 0.019	34.2	5.8061	0.02
		b_0	-1.57 ± 0.65			
2.	$\lambda = b_0 + b_1 \cdot Z + b_2 \cdot D_R$	b_1	2.72 ± 0.62	269.7	46.047	$1.06 \cdot 10^{-9}$
		b_2	0.043 ± 0.018	33.0	5.6294	0.02
		b_0	-1.63 ± 0.66			
3.	$\lambda = b_0 + b_1 \cdot Z + b_2 \cdot D_M$	b_1	2.72 ± 0.62	269.7	45.977	$1.09 \cdot 10^{-9}$
		b_2	0.044 ± 0.019	33.7	5.7517	0.02

The linear predictor (λ) obtained from the latter models are converted to Hourly activity rate (kJ·kg^{-1}·h^{-1}) using the (natural) exponential function.

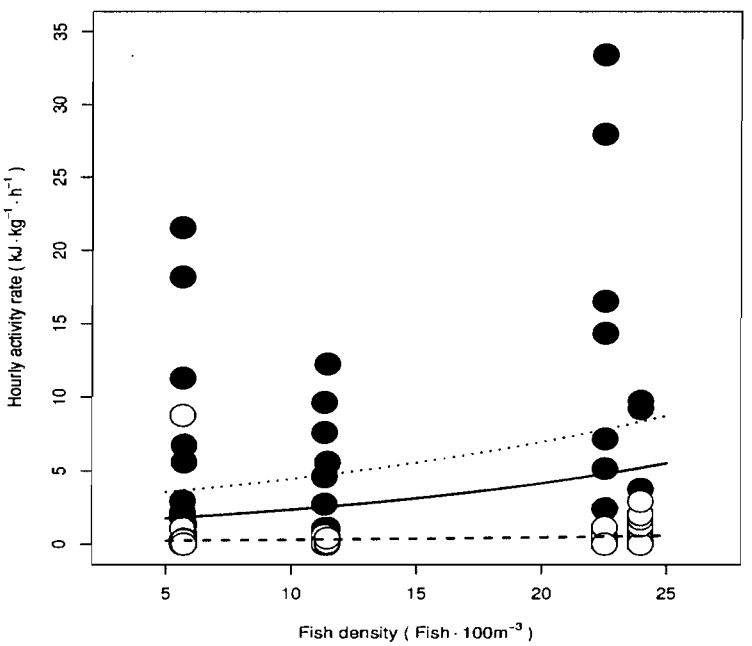

Figure 2.4 Estimates of the activity rate of Arctic charr obtained from SVC observations in zones A (○) and B (●) with respect to fish density and the global (solid line) and zone-specific (zone A: dashed line, zone B: dotted line) relationships between activity rate and fish density.

DISCUSSION

Linearly density-dependent growth was shown for Arctic charr within a range of fish densities typically observed in Scandinavian lakes. Charr reared in low density enclosures grew more than twice as fast as charr in high density enclosures, and growth declined linearly with increasing densities. Experimental densities (100 m^{-2}) ranged from 11.1 to 44.3 in numbers and 247 to 1040 in mass (g), which appear somewhat skewed towards high densities compared to reported natural densities (Table 2.6). However, enclosure and whole lake densities are not directly comparable, and we conclude that the applied densities are within the range of natural densities in lakes. We used three different estimates of densities (stocking, recapture and mean of the two) in the analyses, but results and conclusions were similar.

Table 2.6 Natural densities (number and biomass of Arctic charr per unit of surface) estimated on a whole lake basis in four lakes of the Scandinavian peninsula, and densities used in the present study.

Study	Lake / experiment	Fish density	
		fish·100m^{-2}	g (*fw*)·100m^{-2}
Langeland (1986)	ÿvre StavÂtj¯nna (62∞49'11" N. - 9∞45'58" E.)	11	710
	Vuorejaure (68∞11'38" N. - 19∞36'40" E.)	4.6	104
Bystr^m *et al.* (2004)	Ruozutjaure (68∞12'22" N. - 19∞34'15" E.)	5.8	131
	Suorujaure (68∞16'48" N. - 19∞06'00" E.)	6.8	207
	Low density	11.1	247
Present study	Medium density	20.2	455
	High density	44.3	1040

In contrast to recent studies on density-dependent growth in stream salmonids (Jenkins *et al.* 1999, Imre *et al.* 2005, Lobón-Cervia 2007) and a long term field study on Arctic charr (Amundsen *et al.* 2006), all showing negative power trajectories, the density relationship was best described by a linear model for the present Arctic charr. This may be due to the range of densities applied (we did not test performance at very low densities) as density effects appear more pronounced towards low densities (Jenkins *et al.* 1999). Moreover, significant fits to negative power models were obtain for the

present data, but fits were poorer. This may partly be due to that only three preset density levels were tested.

The present study, alongside previous studies, provides evidence that increased activity may be an important mechanism for reduced growth of fishes at high densities. The results from the present study on Arctic charr are very similar to the results from enclosure experiments on brook charr (Marchand and Boisclair 1998), in that they both show that increased activity at increased density is likely a major cause for decreased growth at high densities. Treatments were duplicated in the present study, and independent measures of activity, growth and food consumption were provided. The individual (among-recordings) variation in estimated activity levels was large, and significant differences were found between activity at high and medium densities only. However, there was a significant positive relationship between activity and charr density, and growth efficiency (estimated independently from the activity estimates) declined significantly with increasing densities. A likely cause for reduced growth efficiencies at similar diets (as found in terms of prey size in the present study) is increased activity costs. The importance of activity for density-dependent growth is also supported by field studies in which average food consumption of yellow perch appear to differ little among populations experiencing large differences in growth and fish densities (Boisclair and Leggett 1989a, Aubin-Horth *et al.* 1999).

A close link between variation in food consumption and growth was recently established in a long term field study on Arctic charr (Amundsen *et al.* 2006). Growth correlated negatively with density and positively with food consumption. This result does not, however, exclude variation in activity as an important mechanism of density-dependent growth in Arctic charr. Amundsen *et al.* (2006) correlated the mean annual growth, mean summer food consumption and fish densities (catch per unit effort in gill nets) from six years between 1980 and 1999. During this period, from 1984 to 1989, the charr population size was experimentally reduced by 75 %. It is likely that such population depletion have caused cascading ecological changes influencing feeding and growth conditions for fish,

beyond the density effect, which may influence the results. In our experiment, densities were experimentally manipulated within the same season, and enclosures were open for the main prey animals (zooplankton).

The potential complexity of the relationships between consumption, activity, growth and fish densities was illustrated by the apparent non-linearity of the relationship between consumption and density. Although care should be taken when interpreting the shape of density relationships based on three preset density levels only, both the regression analyses and the comparisons of means indicates that there was a transitory increase in consumption from low to medium densities followed by a significant decline at high densities. Thus, Arctic charr appear to increase both their activity and food consumption when densities increase from low to medium, likely to counter growth depletion, whereas consumption is reduced at higher densities. This pattern also indicate that the fish will have a greater *per capita* impact on their prey populations at medium than high and low densities, while the increased consumption rate may not translate into higher growth and higher production. This difference between low and high density may be one reason for differing results when growth effects of density increases have been tested. An increase from low to medium density can give reduced individual growth rate due to increased activity rate as found by Jenkins *et al.* (1999), with no similar density-dependent effect when the density is increased from medium to high (Elliott 1985), because of an activity decrease paralleled the individual consumption decrease of the fish.

If activity is an important part of the mechanism of density-dependent growth in fishes in general, as shown for three different species (Arctic charr, brook charr, and yellow perch) and indicated by the pattern of activity in Atlantic salmon (Orpwood *et al.* 2006), a new link is established between individual behavioural decisions, density relationships and population dynamics which may explain variable results in previous studies of density-dependent growth regulation in fishes. Since the reproductive success of fishes is strongly size related, density-dependent growth is also vital for the dynamics of fish populations.

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Chapitre 3 :

Experimental assessment of the morphological, bioenergetic and behavioural differences between two Arctic charr populations.

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ABSTRACT

Populations are presumed to adapt to different niches of their environment through ecological polymorphism. We assessed the magnitude of the responses, in terms of bioenergetics, associated with functional differences between Arctic charr originating from two Norwegian populations and reared under similar environmental conditions in a common garden experiment. The experimental framework encompassed four large (average volume: 146 m^3) enclosures stocked with charr from either of the two populations with duplicated treatments. The responses were defined as the growth, food consumption, activity cost, and spatial and temporal activity patterns. We quantified the morphology of charr, estimated their food consumption using caesium analysis, and estimated their activity cost and space-time activity patterns using video camera.

Charr populations were morphologically distinct and reacted differently in terms of growth (90% differences between populations), food consumption (three-fold difference), and spatial activity patterns (20-fold difference) to the conditions prevailing in the enclosures, indicating different ecotypes. The results of this study highlight that functional differences between charr ecotypes may drive important differences in their bioenergetic and behavioural responses when reared under similar environmental conditions. The functional differences between ecotypes should be incorporated when implementing habitat or trophic models.

Keywords: Arctic charr, ecotype, morphology, bioenergetics, behaviour.

RÉSUMÉ

Le polymorphisme écologique peut permettre aux populations de s'adapter aux différentes niches écologiques présentes dans leurs milieux. Nous avons quantifié la grandeur de la réponse, en termes de différentes variables bioénergétiques associées à leurs différences fonctionnelles, chez deux populations d'ombles chevaliers maintenues sous des conditions expérimentales semblables. Le cadre expérimental utilisé comprenait quatre enclos de grandes tailles (volume moyen: 146 m^3), chacun ensemencé avec des ombles provenant de l'une ou l'autre des populations (traitements dupliqués). Les réponses bioénergétiques ont été estimées en termes de taux de croissance, de consommation et d'activité et en terme des patrons spatiaux et temporels d'activité. Nous avons quantifié la morphologie des ombles, estimé leur taux de consommation à l'aide d'un traceur chimique (^{133}Cs) et estimé leur taux d'activité et leurs patrons d'activité à l'aide de vidéo-caméras.

Les deux populations d'omble chevalier sont morphologiquement distinctes et ont réagi différemment en termes de leurs taux de croissance (un différence de 90% entre populations), de consommation (différence de l'ordre de 3 fois) et de leurs patrons spatiaux d'activité (différence de l'ordre de 20 fois) aux conditions qui prévalaient dans les enclos expérimentaux. Ces résultats suggèrent que les différences fonctionnelles entre des écotypes d'ombles chevaliers peuvent engendrer des différences importantes dans la façon avec laquelle ils répondent, d'un point de vue bioénergétique et comportemental, à un ensemble de conditions environnementales semblables. Étant donné leurs grandeurs, ces différences devraient être considérées lors de la construction et de l'application de modèles de qualité d'habitat ou de modèles de cascade trophique.

INTRODUCTION

Polymorphism refers to the existence, within a species, of statistically discernible groups of individuals having different characteristics (*e.g.* morphological, physiological, behavioural; Skúlason and Smith 1995, Smith and Skúlason 1996, Losos 2000). Different such groups of individuals, or ecotypes, have been found for numerous species of fish (Jonsson *et al.* 1988, Robinson and Wilson 1994, Keeley *et al.* 2005), amphibians (Maerz *et al.* 2006, Pfennig *et al.* 2006), and reptiles (Hatase *et al.* 2007; birds: Galeotti *et al.* 2003). Polymorphism was diagnosed from within- and among-system comparisons of morphological characteristics of individuals. For instance, fish inhabiting different lakes and initially classified as different species because of their adult morphology have ultimately been defined as ecotypes of Arctic charr based on early life stages (*Salvelinus alpinus*; Behnke 1972, Nordeng 1983, Jonsson and Jonsson 2001). Likewise, individuals of the same species and inhabiting the same lake have been described, on the basis of their morphological differences, to belong to either littoral or pelagic ecotypes of Arctic charr (Hindar and Jonsson 1982, Jonsson *et al.* 1988) and Brook charr (*Salvelinus fontinalis*; Bourke *et al.* 1997; Dynes *et al.* 1999).

Polymorphism is presumed to represent an adaptive response of species to interactions such as competition and predation (Skúlason and Smith 1995, Robinson *et al.* 2000, Pfennig *et al.* 2007). Polymorphism has been the focus of numerous studies in the past two decades because of its potential importance in explaining evolutionary processes (*e.g.* sympatric speciation, adaptive radiation; Smith and Skúlason 1996) and, more recently, because of its potential impact on species-oriented wildlife conservation practices (Jonsson and Jonsson 2001, Adams *et al.* 2007). However, both the fundamental and the practical implications of polymorphism depend on the functional differences (in growth rates, reproduction rates, survival rates, feeding rates, distribution, behaviour, etc.) among ecotypes of a given species. Studies have shown that ecotypes of a species may differ functionally. Jonsson and Jonsson (2001) reported important variations in life history traits (*e.g.* asymptotic length, size at sexual

maturity, fecundity, etc.) between ecotypes of Arctic charr inhabiting post-glacial lakes and northern rivers. The time spent engaged in foraging activities and the rate of attack at specific depth have been shown to differ between pelagic and littoral ecotypes of Brook charr (Marchand *et al.* 2003). However, to our knowledge, no study has simultaneously examined the magnitude of the difference in a series of bioenergetic (growth, food consumption, activity cost) and behavioural variables (spatial and temporal patterns of habitat use) between ecotypes. These elements of the functional response of ecotypes may define the relative performance of ecotypes (fitness index) under specified environmental conditions and the different impacts ecotypes may have on the prey community.

The general objective of the present study was to assess the magnitude of the difference that may exist between ecotypes for a series of functional (*i.e.* bioenergetic and behavioural) variables. This general objective requires that ecotypes are identified and that functional variables are estimated under the same environmental conditions. Arctic charr may be particularly useful to attain such general objective. These fish have long been known to possess many ecotypes (Jonsson *et al.* 1988, Jonsson and Jonsson 2001, Snorrason *et al.* 1994). While many environmental factors may be involved in the process by which ecotypes of Arctic charr appear in different systems, one of the most common factor hypothesized to play a role in this process is the competitive pressure imposed on charr by their conspecifics or by brown trout (Salmo trutta; Nilsson 1963, Forseth *et al.* 1994). Arctic charr living in sympatry with brown trout feed predominantly on zooplankton while the diet of charr living in allopatry is composed mostly of zoobenthos (Nilsson 1963, Langeland *et al.* 1991, L'abbé-Lund *et al.* 1993). It may therefore be hypothesized that, in littoral habitats, Arctic charr originating from populations living in sympatry with brown trout may not perform as well as those originating from allopatric populations. In this context, the specific objectives of the present study were 1) to confirm that Arctic charr from two lakes, one containing and one lacking a population of brown trout, do represent different ecotypes of Arctic charr, and 2) to estimate and to compare the growth rate, the consumption rate, the activity rate, and the spatial-temporal patterns of habitat use of these fish under

similar environmental conditions.

METHODS

The magnitude of between-population variations in bioenergetic and behavioural variables were investigated by comparing estimates of growth, consumption, and activity rates and attributes of the spatial and temporal patterns of habitat use for Arctic charr originating from two contrasting ecosystems, and reared under similar environmental conditions in experimental enclosures. At the end of the experiment, we measured a set of morphological variables on every individual charr and established the morphological differences between the charr populations. Estimates of growth and consumption rates were performed at the individual level using a chemical tracer (caesium: Cs; Forseth *et al.* 1992) whereas activity rate and spatial-temporal patterns of habitat use were obtained using video observations.

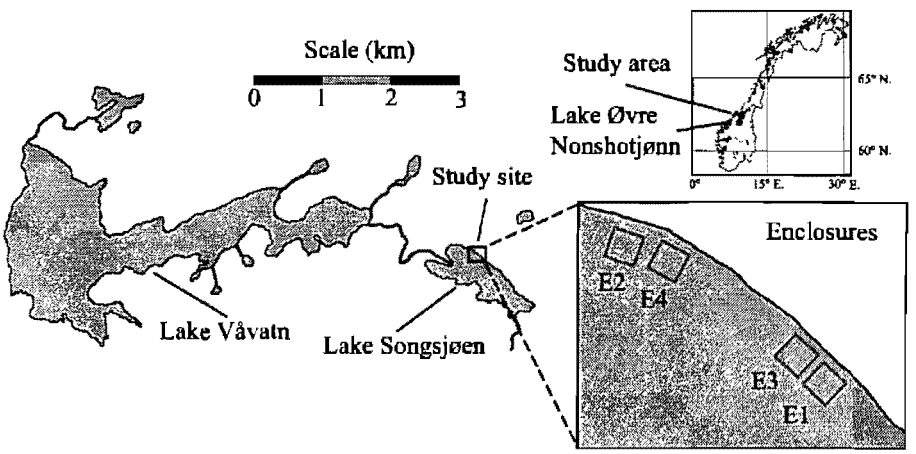

Figure 3.1 Study area, study site, and position of the experimental enclosures within the study site.

Site and enclosures

The experiment was conducted during summer 2001 in Lake Songsjøen, western Norway (Figure 3.1, 63°19'26"N. - 9°39'55"E., elevation: 262 m above sea level, area: 70 ha). Lake Songsjøen is

oligotrophic and supports populations of Arctic charr and brown trout (*Salmo trutta*). Lake Songsjøen was selected because 1) it contains suitable habitat for Arctic charr, 2) it is located near research facilities, and 3) charr from the populations under study had no previous experience with the conditions prevailing in this lake. During the period extending from 28 May – 3 June, four experimental enclosures (9.5 m x 9.5 m surface area, denoted E1 to E4) were deployed 3-5 m from the shoreline. Each enclosure consisted of a net (7 mm bar mesh size) attached to a frame and were positioned to minimize among-enclosure variation in average depth and water volume. Depth at the shallow end of the enclosures ranged from 75 cm (E4) to 101 cm (E1; average = 86 cm), and depth at the deep end of the enclosures ranged from 232 cm (E3) to 251 cm (E4; average = 238 cm). The volume of the enclosures ranged from 143 (E2) to 151 m^3 (E1, average = 146 m^3). To prevent fish escapement, the netting of the enclosures was sunk into the sediments or secured with gravel bags over hard substrate along the lake bottom and extended to 75 cm above the water surface. The absence of surface or bottom netting allowed the charr to feed on prey throughout the water column, at the water surface, along the lake bottom, and within the sediments.

Experimental Fish

Two charr populations were used during the experiments. The first population originated from Lake Våvatn (Figure 3.1, 63°19'41"N. - 9°34'29"E., elevation: 298 m above sea level). Lake Våvatn is located 1.2 km upstream of Lake Songsjøen, has an area of 425 ha, a maximum depth of 70 m, and is covered by ice from mid-November to mid-May. The charr inhabiting Lake Våvatn live in sympatry with brown trout and feed predominantly on zooplankton (L'Abée-Lund *et al.* 1993). The second population originated from Lake Øvre Nonshøtjønn (Figure 3.1, 62°43'05"N. - 9°32'03"E., 68 km south of Lake Songsjøen; elevation: 1004 m above sea level), a relatively small (area: 3.5 ha) and swallow (maximum depth: 17 m) lake covered by ice from the end of October to mid-June. The charr population inhabiting Lake Øvre Nonshøtjønn is allopatric, was introduced during 1905-1915, and feed predominantly on zoobenthos (Homme 2007).

During 25 May-15 June 2001, 41 juvenile charr (age II+ and III+; average size: 24.4 g, range: 13.0-55.5 g) were collected in Lake Våvatn whereas 42 juvenile charr (age II+ and III+; average size: 37.3 g, range: 10.2-93.5) were collected in Øvre Nonshøtjønn. Charr from both lakes were collected using baited minnow traps and kept in separate cages (one cage per population) located in a pool of a tributary of Lake Songsjøen until the onset of the experiment. On 20 June 2001, fish were anaesthetized using clove oil (25 $ml \cdot L^{-1}$), weighed (electronic balance, Mettler model BB1200, ±0.1 g), and marked individually using alcian blue dye (Sigma-Aldrich). Handling time was less than 90 s per fish and the fish were allowed to recover for at least 15 min. in aerated water. Charr were returned to the cages before being stocked in experimental enclosures.

Experimental procedure

The growth, consumption, activity rates, and the spatial-temporal patterns of habitat use of charr were estimated for duplicated treatments (*i.e.* charr from Lake Våvatn: enclosures E1-E2, or charr from Lake Øvre Nonshøtjønn: enclosures E3-E4). Baited hook lines (two lines with four hooks let 24 h) were installed and snorkel inspections were performed inside each enclosure to ensure that the enclosures were empty of fish prior to the experiment. On 20 June 2001, 60 charr (15 charr per enclosure) were distributed among the enclosures to ensure similar among-enclosure means and variances in body mass. The average density of charr in the enclosures was 10.3 $fish \cdot 100m^{-3}$ (range: 10.0-10.5 $fish \cdot 100m^{-3}$). The 21 charr not stocked into the enclosures (11 from Lake Våvatn and 12 from Lake Øvre Nonshøtjønn) were killed to obtain a baseline estimate of ^{133}Cs concentration in charr at the beginning of the experiment (see *Caesium analysis and computation of consumption rate*).

Zooplankton samples were taken on three occasions (13 June, 11 and 27 July) using a 5 L sampler and sieved through a 95 μm Nytex™ sieve. On each occasions, three samples, each obtained by combining four 5 L sub-samples (total volume = 20 L), were collected on different locations of the study site. Two of these samples were collected within pairs of adjacent enclosures (denoted E1-E3 and E2-E4; two 5 L sub-samples per enclosures x two enclosures), while a third sample (four 5 L sub-

samples) was collected outside the enclosures at mid-distance between enclosures E3 and E4 (denoted MID). Zoobenthos was sampled on two occasions, shortly before (18 June) and after (5 August) the experiments using an Ekman bottom sampler (surface area: 225 cm^2). On each occasions, ten samples were taken in each enclosures. Samples were sieved through a 0.5 mm net and kept in (95%) ethanol.

The experiment was terminated over two days because of the time required to recapture and process the fish (E1 and E3 terminated 2 August; E2 and terminated 3 August). Fish were recaptured by dragging a seine three times within each enclosure and killed immediately by an overdose of anaesthetic. They were identified individually, weighed, photographed (Fleming *et al.* 1994, Fleming and Einum 1997; camera: SONY™ DCR-VX 1000E), and dissected. The prey items in the stomach of the fish were identified to assess fish diet. The stomach contents of charr taken from a given enclosure were pooled to obtain sufficiently large samples for ^{133}Cs analysis. All tissues and stomach contents were kept frozen (-80°C) for ^{133}Cs analysis.

Video sampling

The activity rate of charr was estimated from their swimming behaviour according to Boisclair (1992). Fish swimming behaviour was recorded using Stereo-Video-Cameras (SVC), which consisted of a pair of cameras (either Panasonic™ WV-BL602 or Panasonic™ WV-BP312) enclosed side-by-side in a water-resistant (Plexiglas®) case, 10 cm from one another. Two SVC were used, allowing simultaneous observation at two locations of the enclosure. The four images produced by the two SVC were assembled into a single image using a Quad image processor (Panasonic™ WJ-410). A time-date generator (Panasonic™ WJ-810) was used to add the time of filming to the images (± 0.001 s). The resulting video sequences were recorded using a VHS videocassette recorder (Panasonic™ AG-1330).

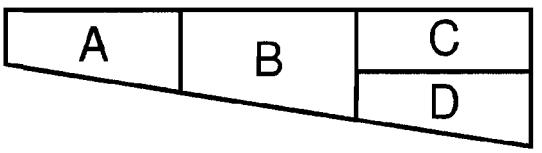

Figure 3.2 Lateral cut-out view of the enclosure with the sampled zones.

The spatial distribution of fish was quantified by defining four sampling zones (denoted A, B, C, and D; Figure 3.2). Zones A and B included the entire water column within the shallowest two thirds of the enclosure surface. Zone A included the first, shallowest, third whereas zone B included the second, deeper, third. Zones C and D included the remaining deepest third of the enclosure. Zone C included the volume comprised below the surface to a depth of 110 cm whereas zone D included the remaining volume from a depth of 110 cm to the bottom. The average volumes of zones A, B, C, and D were respectively 31, 50, 33, and 33 m^3. SVC were positioned such that zones A or B were filmed simultaneously with zones C or D. The SVC filming zones A and B were positioned 50 cm from the perpendicular sides of the enclosures (perpendicular to shore), 75 cm below water surface (35 to 75 cm above the bottom), and 3.15 m offshore the shallowest enclosure side (between zone A and B). This SVC was oriented parallel to water surface, and its yaw angle (relative to the enclosure wall) was changed to film zone A (45° to 60° toward shore) or zone B (75° to 85° toward deep). The SVC sampling zone B was positioned 50 cm from the middle of the deepest side of the enclosures, 110 cm below the surface (120 to 140 cm above the bottom), and with its yaw angle oriented perpendicular with the wall. The pitch angle of the cameras (relative to the surface) was set 20-30° upward when sampling zone C, and 10° downward when sampling zone D. The total duration of a filming session was 1 h: two zones were filmed for 30 min. (A and C for example), then the orientation of the SVC was changed and the remaining zones (B and D in this example) were filmed for 30 min. SVC took 10-20 min. to reposition, and an additional 5 min. was allowed before recording was resumed.

Fish behaviour in each enclosure was quantified during two days. On any given sampling day, filming was organized into four sessions beginning at 4:00 AM, 10:00 AM, 4:00 PM, and 10:00 PM, and denoted 04h (early morning), 10h (late morning), 16h (late afternoon), and 22h (evening), respectively. However, to obtain good recordings as day length decreased, beginning of the filming sessions were progressively shifted to 6:30 AM, 10:30 AM, 3:30 AM, and 8:30 PM from 23 July and onward. Following this schedule, a total of 32 h of filming were obtained (4 sampling sessions x 2 sampling sessions per enclosure x 4 enclosures). As four sampling zones were filmed, the total number of zone-specific estimates of activity rate was 128.

Zooplankton and zoobenthos analyses

Zooplankton from the samples collected before, during, and after the experiment were identified to genera (cladocerans: *Holopedium*, *Bosmina*, *Sida*, *Diaphanasoma*, *Polyphemus*, and *Leptodora*; copepods, adults and copepodites: *Cyclops*, *Diaptomus*, and *Heterocope*), counted, and measured under a dissecting microscope. Body length was measured on whole animals and was converted to dry mass using length-mass regressions (Breistein and Nøst 1997). Volumetric biomass data (g $dw \cdot m^{-3}$) were log(x+1) transformed before statistical analysis.

Zoobenthos sampled at the beginning and at the end of the experiment were identified and counted under a dissecting microscope, and grouped into four classes: benthic insects (larvae of Ephemeroptera, Plecoptera, Trichoptera, Odonata, Zygoptera, and Coleoptera and adults of aquatic Coleoptera), dipterans larvae (families Chironomidae and Ceratopogonidae), mollusks (snails and mussels), and others (Nematoda, Hirudinea and Oligochaeta). Zoobenthos data were expressed in terms of number of animals per square meters.

Morphological analysis

Fish morphology was quantified using the photographs (numerical bitmaps; resolution: 720 x 576 pixels) taken at the end of the experiment. Morphological measurements involved three steps. First,

a set of 23 landmarks (Figure 3.3) were plotted on each image and their coordinates (***x***, ***y***; in pixels) were measured using an image analysis software (ImageJ version 1.25I). Second, a total of 29 morphological characters, each represented by virtual distances (in pixels) between two given landmarks were calculated. Among these variables, five were used to describe the shape of the head (HEAD1-5), fifteen for the shape of the trunk (BODY01-15), eight for the shape of the fins (FIN1-8), and one for the diameter of the eye (EYE, Table 3.1). Third, the real values of the characters (mm) was calculated by multiplying their virtual values by a pixel conversion factor ($mm \cdot pixel^{-1}$), obtained for each pictures using the image of a ruler (graduated to mm) that was photographed with the fish.

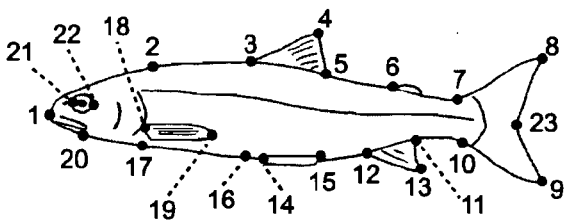

Figure 3.3 Landmarks used for morphological analysis.

Table 3.1 Morphological variables associated with their respective landmarks, the allometry coefficients and R^2_{adj} (with respect of fork length) used to standardized them, and their means and ranges estimated on individual charr.

Variable	Landmarks		Allometry			Mean (mm)	Range (mm)
	a	b	a_j	b_j	R^2_{adj}		
L_F	1	23	—	—	—	150.04	122.2 - 191.8
HEAD1	1	2	-0.858	0.817	0.798	25.44	19.9 - 33.8
HEAD2	1	20	-1.880	0.882	0.679	12.65	9.3 - 16.2
HEAD3	17	20	-1.662	0.911	0.833	18.26	14.8 - 23.8
HEAD4	2	20	-1.081	0.843	0.809	23.14	17.9 - 30.0
HEAD5	2	17	-1.039	0.836	0.937	23.38	19.1 - 29.1
BODY01	2	3	-1.910	1.117	0.933	39.99	32.5 - 52.0
BODY02	14	17	-1.539	1.045	0.941	40.42	31.6 - 52.5
BODY03*	3	6	-1.067	0.992	0.916	49.68	39.4 - 66.4
BODY04	12	14	-1.747	1.038	0.905	31.66	25.5 - 41.5
BODY05	6	7	-2.130	1.002	0.757	18.03	13.8 - 23.4

Variable	Landmarks		Allometry			Mean (mm)	Range (mm)
	a	b	a_j	b_j	R^2_{adj}		
BODY06	10	12	-1.698	1.010	0.833	28.93	22.6 - 40.2
BODY07	2	14	-1.133	1.018	0.975	52.89	43.1 - 67.7
BODY08	3	17	-1.553	1.059	0.963	42.59	33.5 - 55.2
BODY09	3	16	-1.530	0.980	0.907	29.34	23.5 - 38.0
BODY10	3	12	-1.475	1.059	0.966	46.15	36.4 - 60.4
BODY11	6	14	-1.124	1.000	0.955	48.86	39.5 - 61.9
BODY12	6	12	-2.212	1.073	0.921	23.69	18.1 - 31.6
BODY13	6	10	-1.799	0.979	0.821	22.33	17.8 - 29.6
BODY14	7	12	-1.615	1.029	0.938	34.45	27.8 - 45.4
BODY15	7	10	-2.274	0.952	0.871	12.14	9.8 - 16.0
FIN1	18	19	-1.716	0.968	0.892	22.93	18.8 - 31.7
FIN2	3	4	-2.099	1.047	0.878	23.27	18.3 - 32.2
FIN3*	12	13	-2.764	1.132	0.781	18.29	14.2 - 25.9
FIN4	7	8	-1.985	1.082	0.854	31.13	23.6 - 42.8
FIN5	9	10	-1.460	0.991	0.821	33.32	26.0 - 44.7
FIN6	3	5	-1.844	0.947	0.538	18.24	13.1 - 26.5
FIN7	11	12	-3.197	1.173	0.733	14.58	10.6 - 21.6
FIN8	14	15	-2.205	1.023	0.856	18.56	14.5 - 24.4
EYE*	21	22	-1.366	0.692	0.412	8.16	6.2 - 10.3

* Variables that significantly discriminated between populations

Diet analysis

The diet of charr was assessed by analyzing their stomach contents at the end of the experiment. Prey animals in the stomach contents were identified, counted, and measured under a dissecting microscope. Crustaceans were identified to species whereas other animals were identified to family or order. For larger animals, all individuals were counted and measured, whereas for crustaceans, representative sub-samples were counted and measured. Body length was measured on whole animals or specific body parts. In the latter case, regression equations were used to estimate body length, which was converted to dry mass using the same length-mass regressions as for zooplankton analysis. The diet of each fish was expressed as proportion of dry mass by prey type, and the average mass of the prey animals in the diet of each fish was calculated.

For analyses, the prey animals were grouped into seven categories: surface insects (terrestrial

insects and adults of the aquatic Ephemeroptera, Trichoptera and Diptera), benthic insects (see Zooplankton and zoobenthos analysis), mollusks (snails and mussels), aquatic dipterans (larvae and pupae of the families Chironomidae and Ceratopogonidae), planktonic cladocerans (species of genera *Daphnia*, *Bosmina*, *Holopedium*, *Polyphemus*, and *Bythotrephes*), planktonic copepods (*Heterocope* and *Cyclops*), and benthic crustaceans (*Eurycercus lamellatus* and *Sida crystallina*). Diet composition data were arcsine-square-root transformed before statistical analysis.

Caesium analysis

Caesium concentration ($ng \cdot g^{-1}$ dry weight: *dw*) was estimated for individual charr recaptured an the end of the experiment. Each fish was weighed (g *fw*), and dried until mass stabilized (60°C for 24-48h) to determine its dry mass (g dry weight: g *dw*) and the proportion of dry matter. Dry fish tissues were then ground and a 300 mg sub-sample taken and digested with HNO_3. Stable caesium (^{133}Cs) concentration ($ng \cdot g^{-1}$ dw) were measured on the digested sub-sample using a high resolution Inductively Coupled Plasma Mass Spectrometer (ICP-MS, Thermo Electron Corp. model Finnigan™ Element1). Cs burden in charr (ng *fw*) was obtained by multiplying the ^{133}Cs concentration per gram of dry tissues by the proportion of dry matter and original fresh mass of the fish (g *fw*).

Video analysis

VHS recordings were converted to numeric format using a computer interface (ATI video acquisition interface, resolution: 640x480 pixels), and image analysis was performed with software developed by the first author using XBasic Program Development Environment (2002, version 6.2.3). For every second of recording, all moving charr (velocity > 1 $cm \cdot s^{-1}$) that were observed simultaneously in both cameras of a given SVC were counted and summed over the duration of a recording (30 min.) to provide a measure of the total moving fish second (*FS*, fish·s). Positioning of the head and tail of fish (in raw pixel coordinates) were done manually in both images rendered by the SVC (see Boisclair 1992a for details). Swimming speeds of charr were estimated on a single one second interval, randomly

selected over the complete displacement of a given fish in the volume sampled by the SVC.

Computations

Growth rate

We calculated the growth rate (G, kJ·d^{-1}) as:

$$G = \frac{(w_F - w_0) \cdot ED}{n} \quad (3.1)$$

where w_0 and w_F are the body mass of the fish (g fw) at the beginning and the end of the experiment, respectively; n is the duration of the experiment (day), and ED is fish energy density (kJ·g^{-1} *fw*) predicted by the model of Hartman and Brandt (1995, their equation #13, developed for Salmonids) using the proportion of dry matter.

Morphology

Morphological analysis was performed on size-corrected values of traits in order to compare fish on the basis of their shape, rather than with respect of their actual size. The values (c_j) of any given morphological character j were size-corrected (the fork length was taken as an index of fish size) using the following equation:

$$c_j' = c_j \cdot \left(\frac{L_{STD}}{L_T} \right)^{b_j} \quad (3.2)$$

where c_j' is the size-corrected value of the character, L_{STD} is the fork length used to standardize the characters (*i.e.* the mean length of all fish at the end of the experiment; mm), L_F is the fork length of the fish at the end of the experiment (mm), and b_j is the allometry coefficient between character j and the fork length of the fish (*i.e.* the slope of the relationship between log c_j and log L_T estimated for all fish, Table 3.1).

Consumption rate

Initial ^{133}Cs burden of the fish was estimated from the ^{133}Cs concentration of the 23 charr sampled at the beginning of the experiments (Lake Våvatn: average body mass = 28.18 g *fw*, range: 16.25-43.87 g *fw*; Lake Øvre Nonshøtjønn: average body mass = 63.91 g *fw*, range: 46.50-93.53 g *fw*). No statistically significant relationship was found between ^{133}Cs concentration ($\log_{10}$-transformed) and the fresh body mass of charr (Lake Våvatn: $t_{(9)}$ = -0.427, p = 0.68, R^2_{adj} = -0.089; Lake Øvre Nonshøtjønn: $t_{(10)}$ = 0.641, p = 0.5357, R^2_{adj} = -0.057). As a consequence, the initial ^{133}Cs burden (ng) of charr was estimated by multiplying the mean initial ^{133}Cs concentration (Lake Våvatn: 19.56 ng·g^{-1} *fw*, Lake Øvre Nonshøtjønn: 28.57 ng·g^{-1} *fw*) by their fresh body mass at the start of the experiments (g *fw*). ^{133}Cs concentration in the food consumed by charr (pooled stomach contents) was evaluated using the same procedure as for body tissues and reported as the dry weight concentration (ng·g^{-1} *dw*).

Consumption rate was calculated for individual charr following the method proposed by Forseth *et al.* (1992). For any given day i, we calculated the linearly interpolated body mass w_i (g *fw*) and ^{133}Cs burden Q_i (ng) of the fish, and the ^{133}Cs elimination rate (k_i, d^{-1}) was estimated from w_i and mean daily temperature (°C) using the model of Ugedal *et al.* (1992). Daily ^{133}Cs intake (I_i, ng·d^{-1}) was calculated as proposed by Forseth *et al.* (1992, their equation 3b), and mean daily consumption rate (C, kJ·d^{-1}) was calculated as:

$$C = \frac{\sum_{i=1}^{n} I_i \cdot \sum_{j=1}^{m} (p_j \cdot S_j)}{[Cs]_f \cdot Eff \cdot n} \qquad (3.3)$$

where $[Cs]_f$ (ng·g^{-1} *dw*) is the concentration of ^{133}Cs in the diet of charr from each enclosure, Eff the ^{133}Cs absorption coefficient (the proportion of the ^{133}Cs found in the diet that is assimilated by the fish), n the duration of the experiment (day), p_j the proportion (calculated dry mass percentage) of prey item j in fish diet, and S_j (kJ·g^{-1} *dw*) the energy density of prey item j (kJ·g^{-1} *dw*). The energy densities of prey items were obtained from Cummin and Wuycheck (1971). Where species-specific energy density

were unavailable, generic values to the nearest taxonomic group were substituted. Because stomach contents were pooled, the energy density of the diet was estimated once for each enclosure.

Calibration of the SVC

Calibration of the SVC was done underwater using a target consisting of a board with lines spaced apart by 10, 20 and 30 cm. This target was placed at distances ranging from 40 cm to 240 cm from the SVC (increments of 40 cm). Calibration was done before the first filming day, and was repeated each four filming days. A non-linear function was used to estimate real lengths (L, cm) from virtual lengths (l, pixels) and parallax (*i.e.* the offset between images from the cameras in abscissa: Δx, pixels):

$$L = \frac{l}{\frac{c_1}{\Delta x + c_2} + c_3} \tag{3.4}$$

where c_1 is a scale parameter, and c_2 and c_3 are offset parameters. Parameters c_1, c_2, and c_3 were estimated by least-squares non-linear regression of known distances between pairs of landmarks on the calibration target against values of Δx and l obtained from image analysis. The quotient of real and virtual length (L / l) was used to evaluate the distance between the target and the SVC (z, cm):

$$z = c_4 \cdot \frac{L}{l} + c_5 \tag{3.5}$$

where parameters c_4 and c_5 were estimated using linear regression of known values of distance of the calibration target and known values of L / l. Coefficients of determination associated with these relationships (Equations 3.4 and 3.5) ranged from 92% and 99%.

Volume sampled by the SVC

The volume filmed by a video-camera has the shape of a rectangle-based pyramid with a volume increasing with the distance from the camera. This volume crossed the bottom of the littoral

zone or the surface of the lake at an angle. Hence, the volume sampled by the SVC was calculated as the volume of a truncated rectangle-based pyramid. This volume began at 25 cm from the objective of the cameras (minimum distance to perceive a fish simultaneously in two cameras of the same SVC) and extended to a maximum distance of fish detection determined using the coordinates of the head and tail of the fish observed during filming. The volume sampled by the SVC for different recordings were grouped according filming conditions defined by the zone sampled, the position and the orientation of the cameras, and the characteristics of the images (pixel brightness and their frequency distribution). The volume sampled by a SVC for recordings during which no fish were observed was used as the average volume sampled by SVC when fish were observed under similar filming conditions.

Activity rate

Calculation of activity rate from swimming behaviour involved three steps. First, the biomass density ($B_{z,t}$, g·m^{-3} fw) of actively swimming charr observed in a zone z and at time t in the volume sampled by the SVC ($V_{z,t}$, m^3) was calculated as:

$$B_{z,t} = \frac{FS_{z,t} \cdot w_t}{T_{z,t} \cdot V_{z,t}} \quad (3.6)$$

where $FS_{z,t}$ is the total number of moving fish-second (fish·s), is the mean body mass of fish inside the enclosure (g *fw*: linearly interpolated at the time of sampling), and $T_{z,t}$ is the duration of the recording (s). Second, the Mean swimming cost (MSC: kJ·kg^{-1}·h^{-1}) in a zone z and at time t was calculated using mean body mass, and mean swimming speed ($\bar{v}_{z,t}$, cm·s^{-1}):

$$MSC_{z,t} = 13.54 \cdot 10^{b_0} \cdot \bar{w}_t^{(b_{MASS}-1)} \cdot \bar{v}_{z,t}^{b_{SPEED}} \quad (3.7)$$

where 13.54 is the oxy-caloric coefficient (J·mgO$_2^{-1}$, Elliott and Davison 1975), and parameters b_0, b_{MASS}, and b_{SPEED} (b ± 1 standard deviation) are respectively –1.411 ± 0.092, 0.915 ± 0.039, and 0.886 ± 0.096. The parameters b_0, b_{MASS}, and b_{SPEED} were obtained from the swimming cost model developed

by Guénard *et al.* (In press). Third, activity rate ($A_{z,t}$, kJ·kg^{-1}·h^{-1}) in zone z and at time t was calculated as:

$$A_{z,t} = \frac{B_{z,t} \cdot MSC_{z,t}}{B_{e,t}} \quad (3.8)$$

where $B_{e,t}$ (g·m^{-3} *fw*) is the mean biomass density of fish in the enclosure per unit of volume (*e.g.* the sum of the interpolated body masses at time t divided by the volume of the enclosure).

Statistical analysis

Computations and statistical analyses were performed using R language and environment (version 2.4.1; R Development Core Team 2007). Statistical significance of among-enclosures differences and differences between charr populations were examined by analysis of variance (ANOVA) or multiple analysis of variance (MANOVA). Where post-hoc comparisons were applicable, between-enclosure differences were tested using Scheffé tests (Scheffé 1953). Normality of the residuals was tested by the Shapiro-Wilk's test of normality (Shapiro and Wilk 1965). When residuals were found to be non-normally distributed, the explanatory variable was transformed using the Box and Cox (1964) method prior to analysis. Homogeneity of within-group or residual variance was tested using Bartlett's test (Snedecor and Cochran, 1989), or by examining the plots of residual (y) and predicted values (x). The presence of morphological differences between was assessed using forward-stepwise multiple logistic regressions. Analyses of activity rate and active biomass density were done using Generalized Linear Model (McCullagh and Nelder 1989; Quasi-Poisson likelihood model using logarithmic link function: Hastie and Pregibon 1992). Statistical significance of the resulting deviance tables were calculated using an F test. For all statistical analyses, a significance threshold of 5% was used for type I (α) error. Type I error rates associated with multiple statistical inferences (*e.g.* forward-stepwise selection of morphological variables, contrasts obtained from GLM) were corrected sequentially using the Šidák inegality (Šidák 1967, Wright 1992). The corrected p-values are reported as p'.

RESULTS

Conditions in the enclosures

The water temperature varied between 13.5°C and 19.6°C over the course of the experiment (average: 16.3°C), and decreased at a mean rate of 0.042°C·d^{-1} ($F_{(1,43)}$ = 6.666, p = 0.01). Superimposed to this trend, three fluctuations (±3-4°C) of 10-15 day periods were also observed.

The total zooplankton biomass ranged 12.4-51.2 g *dw*·m^{-3} (Table 3.2a, mean = 18.8 g *dw*·m^{-3}), and did not differ among the three sampling sites ($F_{(2,6)}$ = 1.5171, p = 0.29) and sampling times ($F_{(2,6)}$ = 3.0915, p = 0.12). No among-sites difference in the composition of the zooplankton community were found using a multiple analysis of variance performed on the five most abundant genera (*i.e. Holopedium*, *Bosmina*, *Sida*, *Leptodora*, and *Heterocope*; Wilk's $\lambda_{(2,6)}$ = 0.02926, p = 0.27). Among the zoobenthos samples taken at the end of the experiment, six were lost before counting the invertebrates, leaving seven replicates for enclosures E1 and E3. Mollusks and dipterans larvae (mainly chironomids) were the most abundant groups of benthic animals, accounting for 83% of the total density (Table 3.2b). The composition of the bottom fauna in the experimental enclosures were similar at the onset of the experiment ($\lambda_{(3,36)}$ = 0.789, p = 0.76), but differed at the end ($\lambda_{(3,30)}$ = 0.296, p = 4.38x10^{-4}). The composition was affected by the charr population ($\lambda_{(1,30)}$ = 0.592, p = 0.006) and differences were also detectable among treatment replicates ($\lambda_{(2,30)}$ = 0.439, p = 0.003). Taken together, these results indicate that the taxonomic composition and the abundance of prey were relatively uniform among the enclosures at the beginning of the experiment.

Table 3.2 (a) Biomass (g *dw*·m^{-3}) of the zooplankton genera found in the nine mixed samples performed on the study site, and (b) bottom animals density (number·m^{-2}; format: mean [-SE, +SE]) in the experimental enclosures at the beginning and end of the experiment. See main text for details on grouping of bottom animals.

(a)

Order	Genus	13 June			11 July			27 July		
		E1-E3	MID	E2-E4	E1-E3	MID	E2-E4	E1-E3	MID	E2-E4
Cladocerans	*Holopedium*	0.04	0.00	0.00	2.51	2.77	7.01	0.00	0.00	0.10
	Bosmina	9.98	10.15	13.07	7.08	4.16	11.51	14.39	10.81	16.72
	Sida	0.00	1.85	1.33	0.00	0.00	1.02	0.06	0.21	0.88
	Diaphanasoma	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
	Polyphemus	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Leptodora	0.00	0.00	0.00	0.00	0.00	25.0	0.00	0.21	0.00
Copepods	*Cyclops*	0.06	0.00	0.06	0.00	0.03	0.03	0.32	0.07	0.08
	Diaptomus	0.00	0.00	0.00	0.00	0.00	0.49	0.20	0.35	1.59
	Heterocope	4.90	0.44	0.88	20.8	8.75	6.17	0.81	0.70	0.08
Total		16.0	12.4	15.3	30.4	15.7	51.2	16.0	12.4	19.4

(b)

Time	Enclosures and lake of origin		N	Groups				Total
				Insects	Dipterans larvae	Mollusks	Other	
18 June	Våvatn	E1	10	8.9 [4.3, 18.3]	80.0 [56.4, 113]	97.8 [72.3, 132]	8.9 [3.6, 22.2]	187 [145, 241]
		E2	10	22.2 [14.1, 35.1]	66.7 [45.5, 97.8]	31.1 [18.2, 53.1]	17.8 [9.3, 34.0]	120 [87.4, 165]
	Øvre Non-shøtjønn	E3	10	22.2 [14.1, 35.1]	102 [75.0, 139]	107 [79.9, 142]	4.4 [1.2, 16.2]	231 [184, 290]
		E4	10	26.7 [17.6, 40.4]	142 [109, 185]	40.0 [25.0, 64.1]	26.7 [15.7, 45.2]	209 [164, 266]
5 August	Våvatn	E1	7	50.8 [35.4, 72.9]	0.0 [--, --]	114 [81.9, 159]	76.2 [52.4, 111]	165 [120, 228]
		E2	10	31.1 [21.2, 45.7]	107 [78.8, 144]	244 [202, 296]	4.4 [1.2, 16.2]	382 [320, 457]
	Øvre Non-shøtjønn	E3	7	6.4 [2.3, 17.6]	108 [75.3, 155]	95.2 [66.1, 137]	25.4 [13.3, 48.5]	210 [157, 279]
		E4	10	31.1 [21.2, 45.7]	129 [97.9, 170]	169 [134, 212]	0.0 [--, --]	329 [272, 398]
Grand mean			74	24.6 [20.8, 29.2]	94.9 [83.4, 108]	113 [100, 127]	18.0 [12.8, 25.3]	232 [213, 254]

Fish mass and growth rate

At the beginning of the experiment, the body mass of the charr and the densities at which they were stocked were similar among enclosures (Table 3.3). On average, 82% of the charr were recaptured at the end of the experiment (range: 73% in E2 to 87% in E3-E4). Among-enclosure differences in mean charr body mass were 4.1 times larger at the end than at the beginning of the experiment (Table 3.3), but these differences were not statistically significant. The differences in fish density observed among the experimental enclosures at the end of the experiment were 2.9 larger than at the beginning, as a consequence of fish loss. The growth rate of individual charr was positively influenced by the body mass of charr at the beginning of the experiment (b = 0.016 kJ·d^{-1}·g^{-1} *fw*, $F_{(1,43)}$ = 6.4441, p = 0.015, R^2_{adj} = 0.070), but the slope of the relationship between growth rate and initial body mass was similar among enclosures ($F_{(3,40)}$ = 1.7954, p = 0.16). Once corrected for body mass, growth rate differed significantly among enclosures, between populations, but not between treatment replicates (Table 3.3, 3.4; Fig. 3.4a). Charr originating from Lake Øvre Nonshøtjønn (mean = 1.28 kJ·g^{-1}) achieved 90% higher growth than charr from Lake Våvatn (mean = 0.67 kJ·d^{-1}).

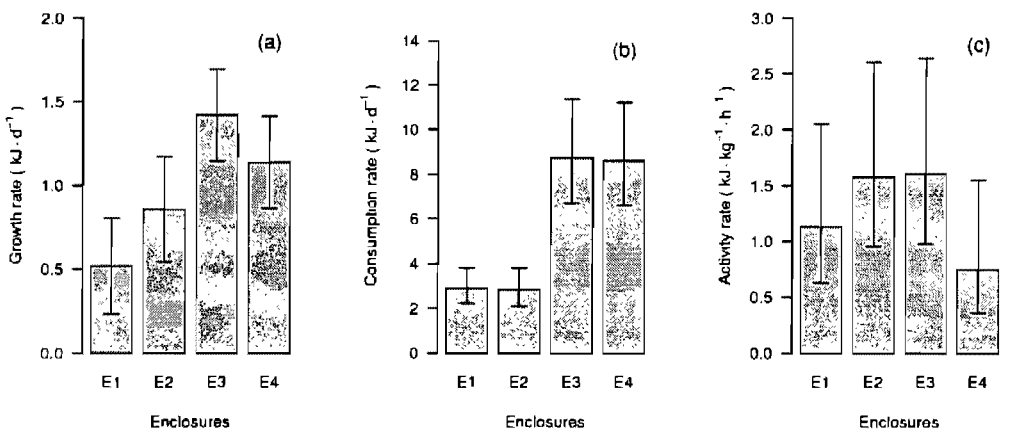

Figure 3.4 Mean (± 95 % CL) growth rate (a), consumption rate (b), and activity rate (c) of charr from Lake Våvatn (E1-E2) and Lake Øvre Nonshøtjønn (E3-E4) in experimental enclosures.

Table 3.3 Variables estimated in the experimental enclosures and results of statistical tests of among-enclosure differences.

Variable		Units	Mean	Range	Enclosure				Among-enclosures differences		
					E1	E2	E3	E4	$F_{3,\nu}$	ν	p
Mass	Initial	g *fw*	22.45 [21.18, 23.79]	10.2, 55.2	21.43 [19.04, 24.12]	21.24 [18.87, 23.91]	24.02 [21.34, 27.04]	23.21 [20.62, 26.12]	0.2597	56	0.85
	Final		32.50 ± 1.90	15.2, 65.0	24.85 ± 3.65	30.41 ± 3.81	37.73 ± 3.51	36.11 ± 3.51	2.656	45	0.06
Number of fish recaptured		Fish	12	11, 13	12	11	13	13	---	---	---
Fish density	Initial	Fish ·100m^{-3}	10.26	9.95, 10.52	9.95	10.52	10.39	10.20	---	---	---
	Final		8.38	7.71, 9.00	7.96	7.71	9.00	8.84	---	---	---
Biomass density	Initial	g·m^{-3}	2.30	2.13, 2.50	2.13	2.23	2.50	2.37	---	---	---
	Final		2.73	1.98, 3.40	1.98	2.35	3.40	3.19	---	---	---
Growth rate		kJ·d^{-1}	1.00 ± 0.08	-0.32, 2.44	0.52^{a} ±0.14	0.86^{ab} ± 0.16	1.42^{b} ± 0.14	1.14^{b} ± 0.14	6.167*	43	0.001
Cs Burden	Initial	ng	519 [482, 559]	253, 1440	385 [341, 435]	369 [323,4 22]	681 [606,7 66]	675 [600,75 9]	---	---	---
	Final		964 [864, 1075]	311, 4129	496^{a} [439, 560]	478^{a} [418, 547]	1710^{b} [1520, 1924]	1722^{b} [1530, 1937]	34.923	44	1.05x10^{-11}
Consumption rate		kJ·d^{-1}	5.22 [4.70, 5.79]	1.47, 21.52	2.90^{a} [2.53, 3.33]	2.82^{a} [2.43, 3.28]	8.73^{b} [7.66, 9.95]	8.60^{b} [7.55, 9.81]	21.825*	43	9.61x10^{-9}
Swimming speed		cm·s^{-1}	13.59 ± 0.51	3.6, 25.0	10.76^{a} ± 0.90	10.72^{a} ± 0.82	15.46^{b} ± 0.72	16.92^{b} ± 0.90	14.197	72	2.31x10^{-7}
Activity rate		kJ·kg^{-1}·h^{-1}	1.27 [1.09, 1.47]	0, 13.68	1.13^{ab} [0.84, 1.53]	1.58^{ab} [1.22, 2.03]	1.61^{a} [1.25, 2.06]	0.75^{b} [0.52, 1.08]	3.2028**	100	0.03

Mean values of the variables are presented with their standard error (± 1 SE), or in the form: "mean [mean - 1 SE, mean + 1 SE]" for asymetric intervals.

Enclosures of equal means are labelled using superscript a and b. Enclosures labelled as "ab" are not statistically different from both a and b.

* After correcting the effect of body mass.

** After correcting the effect of sampling zone and time-of-day.

Table 3.4 Statistical tests of the differences among charr populations and between replicates of the population treatments.

Variables		Difference among populations treatments and treatments replicates			
		$F_{v1,v2}$	v_1	v_2	p
Growth rate*	Population	12.6326	1	43	9.36×10^{-4}
	Replicates	2.4494	2		0.10
Consumption rate*	Population	65.1057	1	43	3.79×10^{-10}
	Replicates	0.0067	2		0.99
Swimming speed	Population	42.309	1	72	8.94×10^{-9}
	Replicates	0.815	2		0.45
Activity rate**	Population	0.0005	1	106	0.98
	Replicates	3.9237	2		0.023
	Population x zone	5.7055	3		0.001

* After correcting the effect of body mass.
** Models including the sampling zone and time-of-day.

Morphology

The mean fork length of the charr used for the experiment was 151.2 mm. Hence, a rounded-up value of 150 mm was taken as the standard value of fork length (L_{STD}) used for size-correction. The coefficients of determination (R^2_{adj}) of the relationships between the morphological traits and fork length (both transformed to log-natural) ranged from 0.412 to 0.975 and the allometry coefficient (b) ranged from 0.692 to 1.134 (Table 3.1). The charr from the two populations differed in terms of eye diameter (EYE; $X^2_{(1)} = 14.259$, $p = 1.59 \times 10^{-4}$, $p' = 0.005$), anal fin length (FIN3; $X^2_{(1)} = 11.026$, $p = 0.001$, $p' = 0.03$), and distance between the anterior insertions of the main and adipose dorsal fins (BODY03; $X^2_{(1)} = 12.398$, $p = 2.52 \times 10^{-4}$, $p' = 0.007$; see Table 3.1 and Figure 3.3 for morphological traits). The model including these three variables ($X^2_{(3)} = 38.683$, $p = 2.03 \times 10^{-8}$) could correctly classify 87.5% of the individual charr to their original population (81.8% of charr from Lake Øvre Nonshøtjønn and 92.3% of charr from Lake Våvatn; Figure 3.5). The linear estimator (λ) of the logistic model is:

$$\lambda = -44.98 + 2.922 \cdot EYE' - 1.919 \cdot FIN3' + 1.118 \cdot BODY03' \quad (3.9)$$

where quoted variable names represent size-corrected traits values (mm). The linear predictor (λ) represents the degree of similarity with charr from Lake Våvatn. Consequently, individual charr having

negative values of λ are predicted to origin from Lake Øvre Nonshøtjønn, and those having positive values are predicted to origin from Lake Vågvatn. Charr from Lake Vågvatn were found to have 11% larger eye diameter (mean = 8.62 mm), 3.7% longer distance between the dorsal fins (mean = 50.7 mm), and 6.1% shorter anal fin (mean = 17.7 mm) than charr from Lake Øvre Nonshøtjønn (means: 7.79, 48.9, and 18.8 mm, respectively).

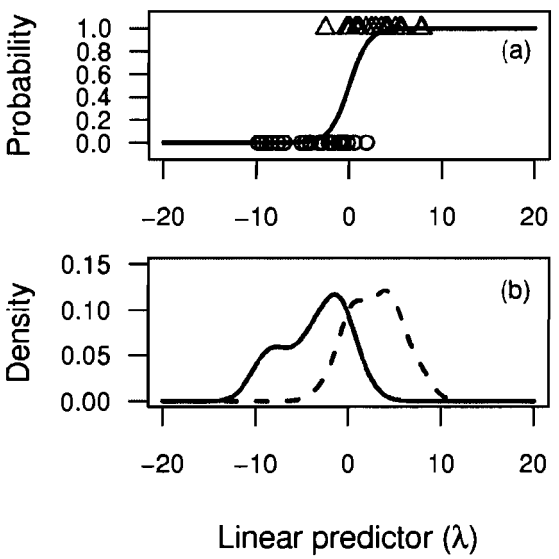

Figure 3.5 Predicted probabilities for charr from Lake Øvre Nonshøtjønn (O) and Vågvatn (△) to origin from Lake Vågvatn as a function of a linear predictor incorporating three morphological traits (a; see Equation 8), and the kernel density curves for both populations (b; Lake Øvre Nonshøtjønn: solid, Lake Vågvatn: dashed).

Table 3.5 Diet composition (mean dry weight %) and prey size (geometric mean mg dry weight) in the experimental enclosures. See main text for details on grouping of prey animals.

Group	Lake Våvatn		Øvre Nonshøtjønn		Mean
	E1	E2	E3	E4	
Surface insects	0.3 [0.1, 0.6]	0.8 [0.4, 1.2]	0.0 [0.0, 0.0]	0.8 [0.4, 1.2]	0.3 [0.2, 0.4]
Benthic insects	0.0 [0.0, 0.1]	0.0 [0.0, 0.1]	0.5 [0.2, 0.8]	0.0 [0.0, 0.1]	0.1 [0.0, 0.1]
Mollusks	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]
Aquatic dipterans	9.0 [6.0, 12.6]	19.9 [15.0, 25.2]	6.7 [4.2, 9.8]	5.1 [2.7, 8.1]	9.2 [7.5, 11.1]
Planktonic cladocerans	84.6 [76.1, 91.5]	65.0 [53.4, 75.8]	10.4 [4.9, 17.5]	35.4 [25.1, 46.5]	46.8 [39.7, 54.0]
Planktonic copepods	0.0 [0.0, 1.7]	1.9 [0.0, 7.0]	65.3 [54.1, 75.7]	47.7 [35.4, 60.0]	21.4 [14.9, 28.6]
Benthic crustaceans	2.4 [1.1, 4.2]	2.1 [0.8, 3.9]	2.0 [0.9, 3.6]	0.5 [0.0, 1.5]	1.6 [1.1, 2.4]
Mean prey size (mg)	0.010 [0.009, 0.012]	0.015 [0.012, 0.017]	0.037 [0.032, 0.043]	0.023 [0.020, 0.027]	0.019 [0.017, 0.021]

Diet composition

Crustacean zooplankton (cladocerans and copepods) accounted for 85% of the diet of charr, followed by aquatic dipterans (mean = 9.2%; Table 3.5). Diet composition differed among enclosures ($\lambda_{(3,42)}$ = 0.2347, p = 4.73x10^{-6}), between charr treatments ($\lambda_{(1,42)}$ = 0.4, p = 5.18x10^{-6}), and between treatment replicates ($\lambda_{(1,42)}$ = 0.6, p = 0.03). Hence, the charr from Lake Våvatn (mean = 76.4%) incorporated a 3.7 times greater proportion of planktonic cladocerans in their diet than the charr from Lake Øvre Nonshøtjønn (mean = 20.5%). Moreover, charr from Lake Øvre Nonshøtjønn ate mostly planktonic copepods (mean = 57.3%) while this prey type only accounted for a small fraction (mean = 0.5%) of the diet of charr from Lake Våvatn. Charr from Lake Våvatn incorporated a 2.3 times larger proportion of aquatic dipterans to their diet (mean = 13.5%) than charr from Lake Øvre Nonshøtjønn (mean = 5.6%; $F_{(1,44)}$ = 4.619, p = 0.04). No differences were found among enclosures, between charr treatments, and between treatment replicates when planktonic cladocerans, planktonic copepods, and aquatic dipterans were not included in the diet composition analysis, indicating that variation in diet composition was mostly associated with these three prey types. The mean prey size varied 8.7-fold among individual fish (range: 0.008-0.070 mg), differed among enclosures ($F_{(3,42)}$ = 13.070, p =

3.63×10^{-6}), between charr treatments ($F_{(1,42)} = 29.806$, $p = 2.37 \times 10^{-6}$), and between treatment replicates ($F_{(2,42)} = 3.3415$, $p = 0.045$). The preys consumed by charr from Lake Øvre Nonshøtjønn (mean = 0.030 mg) were on average 2.5 times larger that the preys consumed by charr from Lake Våvatn (mean = 0.012 mg). These results suggest that the charr from the two populations under study have specific behavioural traits about prey selection. Given the lack of difference of the prey communities in the enclosures particularly at the beginning of the experiment (see *Conditions in the enclosures*), these results also suggest that the charr from the different populations may have had different impacts on the structure of the zoobenthos communities possibly from differences in their prey selection.

Consumption rate

On average, the ^{133}Cs body burden of charr doubled during the course of the experiment, and differed significantly among-enclosures at the end of the experiment (Table 3.3). Charr from Lake Øvre Nonshøtjønn (mean = 1716 ng), at the end of the experiment, contained 3.5 times more ^{133}Cs than charr from Lake Våvatn (mean = 488 ng). Energy densities used to transform consumption rate from a dry mass to energy were 21.93 $kJ \cdot g^{-1}$ *dw* for cladocerans, 24.22 $kJ \cdot g^{-1}$ *dw* for copepods, 22.69 $kJ \cdot g^{-1}$ *dw* (chironomids) for aquatic dipterans, 20.18 $kJ \cdot g^{-1}$ *dw* for surface insects, and 19.77 $kJ \cdot g^{-1}$ *dw* (mean value of arthropods) for all other prey items (Cummin and Wuycheck 1971). The estimated energy density of food ranged from 22.00 (E1) to 23.36 (E3) $kJ \cdot g^{-1}$ *dw* (mean ± SD = 22.7 ± 0.67 $kJ \cdot g^{-1}$ *dw*). The mean (± SD) ^{133}Cs concentration in the diet of charr from Lake Våvatn was 55.3 ± 12.2 $ng \cdot g^{-1}$ *dw*, and 105.0 ± 5.3 $ng \cdot g^{-1}$ *dw* for charr from Lake Øvre Nonshøtjønn. Because zooplankton dominated the diet, consumption rate were calculated using the ^{133}Cs absorption coefficient (0.816 ± 0.044) for zooplankton in Forseth *et al.* (1992).

Consumption rate varied 15-fold among individual charr, was positively influenced by their initial body mass (b = 0.31 $kJ \cdot d^{-1} \cdot g^{-1}$ *fw*, $F_{(1,46)} = 39.832$, $p = 9.874 \times 10^{-8}$, $R^2_{adj} = 0.45$), and the relationship between consumption rate and the initial body mass did not differ among enclosures ($F_{(3,40)} = 0.3732$, $p = 0.77$). When corrected for body mass, the consumption rate of charr differed significantly

among enclosures and between charr populations, but did not differ between treatment replicates (Table 3.3, 3.4; Figure 3.4b). Charr from Lake Øvre Nonshøtjønn (mean = 8.67 $kJ \cdot d^{-1}$) consumed three times more food than the charr from Lake Våvatn (mean = 2.87 $kJ \cdot d^{-1}$).

Activity rate and spatial-temporal patterns of habitat use

The water volume sampled by the SVC ranged from 0.099 to 1.13 m^3 (mean = 0.49 m^3) depending on filming conditions. Among the 128 recordings collected, charr were observed swimming in 91 recordings (76 %), and it was possible to estimate swimming speed on 76 (59 %) of them. Median fish-seconds observed during a 30 min. recording was 14.0 fish·s, and the maximum value was 411 fish·s (E2, zone C, 10 July, 4:00 AM). Observed biomass density ($B_{z,t}$) ranged 0-9.14 g·m-3 (mean = 1.14 $g \cdot m^{-3}$) among recordings and *Mean biomass density* ($B_{e,t}$) ranged from 2.26 to 3.69 $g \cdot m^{-3}$ among enclosures. Mean swimming speed varied up to seven-fold among recordings, differed among enclosures, among charr populations, but not between treatment replicates (Table 3.3, 3.4). Charr from Lake Øvre Nonshøtjønn (mean = 16.0 $cm \cdot s^{-1}$) swam, on average, 50% faster than charr from Lake Våvatn (mean = 10.7 $cm \cdot s^{-1}$).

Values of fish-second (FS; fish·s) and activity rate ($kJ \cdot kg^{-1} \cdot h^{-1}$) were estimated for each zone of the enclosures and for each time of day. While FS corrected for the volume and the time spent filming ($FS \cdot m^{-3} \cdot h^{-1}$) represents the time spent by fish in any given zone (notwithstanding their swimming speed during this time), activity rate represents the energy spent swimming by fish in these zones. In our study, both variables provided exactly the same perspective about the way fish utilized the different zones of the enclosures. This may be related to the use of FS to estimate activity rate for each combinations of zones and time of day and to the dominant role of this variable during the estimation of fish activity rate (Trudel and Boisclair 1996). Hence, for practical reasons, only activity rates are presented in details to describe the spatial-temporal patterns of habitat use by fish. The use by charr of the different zones of the enclosures varied significantly ($F_{(3,124)} = 8.9071$, $p = 2.17 \times 10^{-5}$). Charr were

3.9 times more active in zones C and D (mean = 2.16 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A and B (mean = 0.56 $kJ \cdot kg^{-1} \cdot h^{-1}$). However, differences between zones A and B and between zones C and D were small and not statistically significant (p = 0.83 and 0.74, respectively). Activity rate did not differ among time of day ($F_{(3,112)}$ = 2.3950, p = 0.07), but the interaction between the sampling zone and time of day was statistically significant (*i.e.* the spatial distribution of fish changed with time of day; $F_{(9,112)}$ = 2.1485, p = 0.03). During early and late morning (04h and 10h), charr were 4.0 and 6.8 times more active in zone C (means: 3.69 and 2.44 $kJ \cdot kg^{-1} \cdot h^{-1}$, respectively) than in the remaining zones (A, B, and D; means: 0.55 – 0.61 $kJ \cdot kg^{-1} \cdot h^{-1}$), respectively, whereas during the evening (22h), charr were only 75% more active in zone C (mean = 1.05 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A, B, and D (mean = 0.60 $kJ \cdot kg^{-1} \cdot h^{-1}$). During the afternoon (16h), charr were 6.2 times more active in zone D (mean = 5.35 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in the remaining zones (A-C; mean = 0.86 $kJ \cdot kg^{-1} \cdot h^{-1}$). Because these mean spatial and temporal patterns of activity encompass a significant fraction of fish activity, and in order to increase statistical power, the factor sampling zone, and the interaction between sampling zone and time of day, was added to the analyses involving activity rate (*e.g.* among-enclosure, between charr treatments, and between treatment replicates differences in hourly activity rate). Hourly activity rate differed among enclosures (Table 3.3, Figure 3.4c), and manner by which charr distributed their activity across space (*i.e.* the interaction of factors enclosure and sampling zone) also differed among enclosures ($F_{(9,100)}$ = 2.6526, p = 0.008), indicating that the charr reared in different enclosures also had different spatial patterns of activity (Figure 3.6). These differences in spatial patterns were associated with differences between charr populations (Table 3.4). The tendency of charr from Lake Våvatn to be more active in zones C and D than in zones A and B was 20 times more pronounced than that of charr from Lake Øvre Nonshøtjønn. Charr from Lake Våvatn were 35 times more active in zones C and D (mean = 2.60 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A and B (mean = 0.074 $kJ \cdot kg^{-1} \cdot h^{-1}$) whereas charr from Lake Øvre Nonshøtjønn were only 1.74 times more active in zones C and D (mean = 1.59 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A and B (mean = 0.91 $kJ \cdot kg^{-1} \cdot h^{-1}$). Differences of spatial activity patterns between treatment replicates were not statistically significant ($F_{(6,88)}$ = 1.0558, p = 0.40). Moreover, activity rate was similar between

charr populations, but differed between treatment replicates (Table 3.4), with charr from Lake Øvre Nonshøtjønn in enclosure E3 being 2.1 times more active than in enclosure E4 (Table 3.3). These results suggest that the charr used in the present study had population-specific strategies of modulating their activity within the experimental enclosures (*i.e.* among sampling zones). Moreover, the results highlighted that, although environmental conditions in these enclosures were similar, the differences in mean activity rate between treatment replicates could be high, as observed between the enclosures containing charr from Lake Øvre Nonshøtjønn.

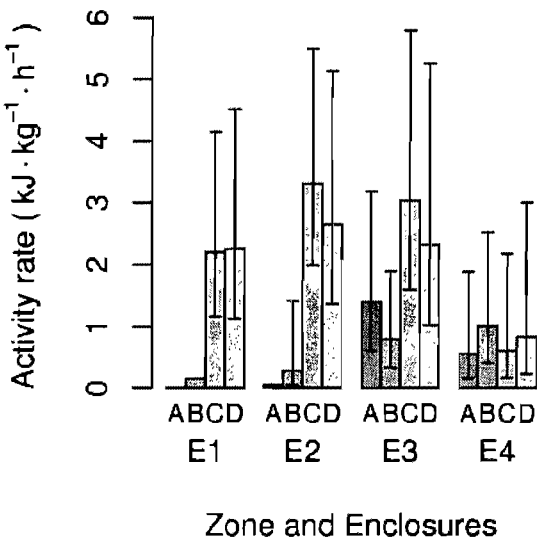

Figure 3.6 Mean (± 95 % CL) hourly activity rate of charr from Lake Våvatn (E1-E2) and Lake Øvre Nonshøtjønn (E3-E4) in the sampling zones (see Fig. 3.2) of the experimental enclosures.

DISCUSSION

Charr from the two populations under study were morphologically distinct with respects of three traits, and behaviourally distinct in terms of average swimming speed and spatial activity patterns (*i.e.* how much they were active in the different zones of the enclosures). Charr from the populations under study were different with respect of their eye diameter, the length of their dorsal-posterior area,

and the length of the leading edge of the anal fin. Eye diameter may be related with a better ability of the fish to detect small preys within a larger volume of water. This may, in turn, improve the ability of the fish to feed profitably on such preys by decreasing their search time (*i.e.* Holling 1959). On average, charr from Lake Vâvatn had 11% larger eye diameter and fed on 2.5-fold smaller preys than charr from Lake Øvre Nonshøtjønn thereby supporting the functional significance of this trait. Charr from Lake Vâvatn were also found to have a shorter anal fin, and a longer posterior-dorsal trunk than the charr from Lake Øvre Nonshøtjønn. These traits may be related with reduced hydraulic drag and could allow the charr from Lake Vâvatn to reduce their swimming cost. However, the absence of swimming cost models specific for ecotypes of Arctic charr precludes further assessment of the functional significance of these traits with regards to swimming cost. In this respect, it should be noted that the use in the present study of a single swimming cost model (Guénard *et al.* In press; based on four fish species) may represent a simplification of the inherent complexity associated with the estimation of swimming cost of different ecotypes. However, it have been shown by Trudel and Boisclair (1996) and Guénard *et al.* (In press) that estimates of activity rate obtained using video-cameras are primarily driven by the number of fish-second observed, accounting for 87% of the variation in activity rate, while body mass and swimming speed account for modest fractions (3.2% and 0.2%, respectively). It is unlikely that morphological variations of the magnitude observed for these traits (3.7 and 6.1%, respectively) between the populations of charr under study would increase or decrease Mean swimming cost associated with variations in swimming speed by 2-3 folds. These variations are expected to have a limited impact (< 13%) on the estimates of activity rate provided by the video-cameras method. Because the differences in activity rate found in the present study had a magnitude of 74% or higher, it is reasonable to assert that the error associated with morphologically-related differences in swimming cost may not affect the conclusions of the present study regarding activity rate. Beside morphology, charr from the two populations under study also showed marked differences in their spatial distribution and spatial activity patterns within the enclosures. Compared to charr from Lake Øvre Nonshøtjønn, charr from Lake Vâvatn used more prominently zones C and D of the enclosures, and made fewer (*i.e.*

20 times less) incursions toward zones A and B. Thus, charr from Lake Øvre Nonshøtjønn make an apparently more exhaustive usage of the habitats available in the enclosures. Because brown trout also use littoral habitats, the difference in spatial distribution between populations may be interpreted as an adaptive consequence of the presence of brown trout in Lake Vâvatn. Therefore, the avoidance of zones A and B by charr from Lake Vâvatn could be interpreted as the avoidance of the habitats were the probability of encountering brown trout is the highest, would trout be present in the enclosures. Alternatively, the differences in the structure of the habitats used by the charr in their respective ecosystems may also explain these differences in behaviour. Lake Øvre Nonshøtjønn is an alpine lake 121 times smaller (in terms of surface area) and four times shallower than Lake Vâvatn and has a high water transparency (Secchi depth > 10 m), as a consequence of its location at higher altitude than the upper limit of forest growth (*i.e.* it does not contain substantial concentrations of humic acids). Fish habitats available in Lake Øvre Nonshøtjønn are thus mostly, if not entirely littoral (depth < 2 x Secchi depth, and thus suitable for macrophyte growth). However, it may be hypothesized that the pelagic zone of Lake Vâvatn may provide better feeding opportunities for Arctic charr than its littoral zone which is inhabited by brown trout. Likewise, charr from Lake Vâvatn showed a behaviour oriented toward the conditions found in the ecosystem where they originated (*i.e.* they were most active in the most pelagic sections of the enclosures: zones C and D) rather than to the conditions found in the complete enclosures. Because charr from the populations under study showed marked phenotypic differences and since these differences could be interpreted as being the result of adaptation to their respective habitats, we assert that they represent distinct ecotypes of Arctic charr. However, it is impossible to assess the relative importance of inter-specific competition and other environmental conditions as factors contributing to the appearance of different ecotypes. In the present study, the phenotypic differences observed between ecotypes were associated with significant differences in growth and consumption rates of charr reared under similar experimental conditions (*i.e.* same time, similar size of enclosures, similar zooplankton and zoobenthos at the beginning of the experiment). The charr from Lake Øvre Nonshøtjønn had 90% higher growth rate than charr from Lake Vâvatn and their consumption rate was

thrice as high. The lower growth realized by the charr from Lake Vâvatn compared to those from Lake Øvre Nonshøtjønn was apparently associated with their lower consumption rate. Insights about the mechanisms underlying these contrasting responses could by provided by the results obtained from the analysis of spatial activity (*i.e.* distribution) patterns. Charr from Lake Vâvatn barely used zones A and B although they represented two-thirds of the surface, and 56% of the volume of the enclosures. The spatial patterns of habitat use and the shape of the enclosures suggest that the fish density actually experienced by charr from Lake Vâvatn was roughly twice that calculated simply by dividing the number of fish in the enclosure by its volume (which assumes an homogeneous spatial distribution of fish). Because charr from Lake Øvre Nonshøtjønn made a more even use of the different zones of the enclosure, dividing their number by the volume of the enclosure may adequately represent the density experienced by fish. These observations suggest that density-dependent processes may be invoked to explain the lower growth and consumption rates achieved by the charr from Lake Vâvatn. Hence, charr from Lake Øvre Nonshøtjønn made a more extensive usage of the habitat located within the enclosures than charr from Lake Vâvatn, resulting in higher growth and food consumption. These results support the hypothesis that charr from Lake Øvre Nonshøtjønn show a better ability to use the littoral zone of lakes (where experimental enclosures were located) than charr from Lake Vâvatn.

In the present study, we found important contrasts in the relative performance, in terms of growth, of Arctic charr ecotypes under specified environmental conditions. Such differences in the performance of ecotypes may have profound impacts on the implementation of numerical habitat models (NHM). The main purpose of these models is to predict the value of habitats, in terms of their ability to sustain growth, survival, and reproduction (Boisclair 2001). The results of the present study show that, in a same habitat, the growth and consumption rates achieved by members of a given ecotype may differ from those belonging to another ecotype. Hence, the predictions of growth or consumption rates obtained using models developed for one ecotype may not adequately represent the potential performance of another ecotype under the same environmental conditions. In our study,

growth and consumption rates varied two- to three-fold among ecotypes held under similar environmental conditions. The present study is, to our knowledge, the first to provide an assessment of the magnitude of the discrepancies that may arise by using a single NHM for different ecotypes.

The present study outlines that the quantity of food consumed by ecotypes may differ three-fold. Similarly, the diet of one ecotype could be dominated either by cladoderans (76% of diet for charr from Lake Vålvatn) or by copepods (57% for charr from Øvre Nonshøtjønn). This may affect the way trophic cascade models (van Leeuven *et al.* 2000, Christensen *et al.* 2005) are developed and implemented. Trophic cascade models are often used to describe or predict the flow of matter or energy from on trophic level to another (Paine 1980, Pace *et al.* 1999). The large differences in consumption rate and prey selection highlighted in the present study between two Arctic charr ecotypes suggest that trophic models may provide biased predictions if they assume that all ecotypes of a given species are equivalent from a trophic-dynamic perspective. Because Arctic charr typically live in allopatry or in sympatry with few fish species (*e.g.* brown trout, threespines stickleback: *Gasterosteus acculeatus*), and may thereby represent a correspondingly large component of the trophic network, polymorphism may have profound impacts on the implementation of trophic models. The magnitude of the difference in growth rates, consumption rates, and spatial-temporal patterns of habitat use noted for two ecotypes of charr suggest that a better understanding of the functional implications of morphological variations within species may improve the quality of the predictions made by habitat and trophic models.

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Chapitre 4 :

Effect of brown trout (*Salmo trutta*) on growth, consumption and activity rates of two ecotypes of Arctic charr (*Salvelinus alpinus*)

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ABSTRACT

We assessed the magnitude of the responses in terms of growth, food consumption, activity costs, and spatial and temporal activity patterns of two ecotypes of Arctic charr to inter-specific competition by brown trout. These charr ecotypes are known to differ, in terms of morphology and behaviour, and originated from different lakes, particularly with respect to the presence of brown trout. We used an experimental framework consisting in eight enclosures (average volume: 143m^3) stocked with either of the two charr ecotypes in the absence or presence of brown trout, with duplicated treatments. We estimated the growth rate of Arctic charr, their consumption rate using stable caesium (^{133}Cs), and their activity rate and activity patterns in space and time using video cameras.

The presence of brown trout affected the growth, food consumption, and activity costs of Arctic charr. Moreover, both charr ecotypes reacted similarly to the presence of trout in terms of growth, food consumption, and activity patterns, but differently in terms of swimming speed and activity costs. These results are consistent with previous findings about the bioenergetic mechanism of competition, but does not support the hypothesis that competition by brown trout was the major driver of the morphological divergence of these two particular charr ecotypes.

Keywords: Arctic charr, brown trout, ecotype, bioenergetics, behaviour.

RÉSUMÉ

Nous avons quantifié la grandeur des réponses, en termes de croissance, de consommation de nourriture, de taux d'activité et de patrons spatiaux et temporels d'activité, chez deux écotypes d'omble chevalier à la compétition inter-spécifique par la truite brune. Il a déjà été rapporté que ces écotypes diffèrent par leur morphologie et leur comportement et proviennent de lacs différents, notamment par l'absence ou à la présence de truites brunes. Nous avons utilisé un cadre expérimental comprenant huit enclos de grandes tailles (volume moyen: 143 m^3) ensemencés avec des ombles de l'un ou l'autre écotype et maintenues seules ou en présence de truites. Nous avons estimé la croissance des ombles, leur consommation à partir de l'analyse du leur contenu en césium stable (^{133}Cs) et leur taux d'activité et leurs patrons spatiaux et temporels d'activité à l'aide d'une méthode basée sur l'échantillonnage par vidéo-caméras.

La présence de truite a affecté négativement la croissance, la consommation de nourriture et les coûts d'activité des ombles. De plus, les différents écotypes ont réagi de façons semblables à la présence de la truite brune en termes de leurs taux de croissance et de consommation et patrons d'activité, mais différemment en termes de leur vitesse moyenne de nage et taux d'activité. Ces résultats obtenus lors de cette étude concordent avec les résultats d'études antérieures sur les mécanismes bioénergétiques de la compétition. Cependant, ils n'appuient pas l'hypothèse selon laquelle la compétition par la truite brune est un facteur clé ayant conduit à la divergence morphologique et comportementale observée entre les écotypes d'omble chevalier étudiés.

INTRODUCTION

Competition, and its consequences on distribution (Kennedy and Strange 1986b), resource use (Svanback and Bolnick 2007), populations dynamics (survival and growth rates: Kennedy and Strange 1986a, Lorenzen and Enberg 2002, Matthews *et al.* 2001), and natural selection (Bolnick 2001, Schluter 2003, Pfennig *et al.* 2007) is a topic central to community and evolutionary ecology (Roughgarden 1983, Schoener 1983, Law and Watkinson 1989). The role of competition in regulating population size and structuring communities has been the subject of debates (Strong 1986, Murdoch 1994) but its importance has been supported by observational and experimental studies (Jenkins *et al.* 1999, Lorenzen and Enberg 2002, Blanchet *et al.* 2007).

Competition has recently been studied from two different and yet interdependent perspectives. One relates to the mechanism by which competition operates (Hanson and Leggett 1986, Marchand and Boisclair 1998, Guénard *et al.* Chapitre 3) and the other to the consequences of competition either for individuals or communities (niche shift: Werner and Hall 1976, 1977, Hindar *et al.* 1988; character displacement and release: Robinson and Wilson 1994, Gray and Robinson 2002, Dayan and Simberloff 2005).

From a mechanistic perspective, competition has long been known to have a negative effect on growth and its correlates (*e.g.* survival and reproductive success; Schoener 1983, Reiman and Myers Mazur *et al.* 1993). The decrease of average individual growth as population density increases have long been thought to operate strictly by decreasing consumption rate (Henderson and Brown 1985, Henderson 1985, Amundsen *et al.* 2007). However, the few studies that have tested this hypothesis confirmed that increase population density may cause both a decrease in consumption rate and an increase in activity rate (Marchand and Boisclair 1998, Guénard *et al.* Chapitre 2). Hence, the relationship between consumption rate and density may be affected by the extent to which organisms react to changes of density by means of their behaviour and activity rate. Because the impact of a

population on its prey depends on the product of individual consumption and population density, any compensatory (decreased activity rate as density increases) or decompensatory (increased activity rate as density increases) mechanism involving activity rate may affect the anticipated effect of the increase of the density of a population on its prey and hence, the understanding of the interactions that exist among different trophic levels of a community. To date, the effects of competition on growth, consumption, and activity rates have been explored in the context of intra-specific competition but it may be hypothesized that inter-specific competition may also affect energy partitioning of organisms.

Competition has also been hypothesized to promote the adaptive divergence of ecological niches among intra- and inter-specific competitors resulting in polymorphisms within and among populations (Forseth *et al.* 2003, Pfennig *et al.* 2007, Robinson and Wilson 1994). For instance, Arctic charr (*Salvelinus alpinus*), for which populations ranging from lake dwelling dwarfs and large anadromous ecotypes have been described (Nordeng 1983, Jonsson *et al.* 1988, Jonsson and Jonsson 2001), have been known to be affected by the presence of brown trout (*Salmo trutta*; Nilsson 1963). While allopatric populations of Arctic charr feed on zoobenthos (a diet similar to brown trout), the diet of sympatric populations of Arctic charr shifts toward pelagic zooplankton. This shift in diet and habitat has been hypothesized as an expression of the effect of inter-specific competition on both the growth and the life-history of Arctic charr (Langeland *et al.* 1991, L'Abée-Lund *et al.* 1993, Forseth *et al.* 1994). However, the ecosystems sustaining different ecotypes may differ in many attributes beside the presence of competitors (*e.g.* physical structure of habitats, types of resources available, presence and identity of predators), it has been difficult to identify the drivers of the ecological force (competition *vs* habitat) responsible for the adaptive divergence. One solution to resolve this situation and better assess the role played by inter-specific competition on adaptive divergence may be to study the effect of the presence of competitors on naive and experienced ecotypes. Naive ecotypes are here defined as ecotypes that have not been subjected to the competitive pressure imposed by the presence of a presumed competitor while experienced ecotypes are ecotypes that have been subjected to such

pressure for numerous generations.

The first objective of the present study is to test the hypothesis that inter-specific competition may affect energy allocation patterns between growth, consumption, and activity rates, and this, for a naive and an experienced ecotype. The second objective of this study is to assess the role of inter-specific competition as the driving force of adaptive divergence among ecotypes. This is achieved by testing the hypotheses that, under similar environmental conditions, *i*) the absence of a competitor for an experienced ecotype should cause a niche expansion and enhance fitness relative to the situation observed when this ecotype is maintained with a competitor, *ii*) the presence of a competitor for the naive ecotype should cause a niche contraction and decreased fitness relative to the situation observed when this ecotype is held in absence of a competitor, and *iii*) the niche and the fitness of experienced ecotype should be less affected by the presence of a competitor than naive ecotype relative to the situation observed when these respective ecotypes are held in absence of a competitor.

METHODS

We achieved our objectives by performing an experiment in which Arctic charr belonging to two ecotypes (one naive to the presence of brown trout and the other subjected to the presence of brown trout for at least 90 years) were held in enclosures in the absence of, or together with, brown trout. This configuration was selected because brown trout have been described as competitor that affect the ecological niche, and the fitness Arctic charr (Langeland *et al.* 1991, L'Abée-Lund *et al.* 1993, Forseth *et al.* 1994). In the present study, niche shifts (expansion or contraction) are described using fish diet and spatio-temporal descriptors of habitat use and fitness indices are described using growth, consumption and activity rates. The Arctic charr ecotypes inhabit two Norwegian lakes that differ with respects of their size, depth, altitude, temperature regimes (*i.e.* the duration of ice cover, mean and maximum water temperature during summer), and the presence of other fish species (brown trout). The differences between these ecotypes in terms of morphology, growth, consumption, activity

rates, and spatial-temporal patterns of habitat use were quantified under similar environmental conditions in the absence of trout (Guénard *et al.* Chapitre 3). In the present study, these same variables were estimated and compared for ecotypes of Arctic charr held without and with brown trout. We estimated growth rate and consumption rate (using sable caesium: ^{133}Cs) at the level of individual fish, and average activity rate and spatio-temporal distribution patterns using under-water video-cameras. This experimental design allowed us to quantify the effect of brown trout on 1) the growth, 2) the food consumption, 3) the activity rates, and 4) the spatial-temporal patterns of habitat use of two ecotypes of Arctic charr.

Site and enclosures

The experiment was conducted during summer 2001, in Lake Songsjøen, western Norway (Figure 4.1; 63°19'26" N. - 9°39'55" E.; 262 m above sea level; area = 70 ha), an oligotrophic lake supporting populations of brown trout and Arctic charr. Experiments were conducted in Lake Songsjøen because the Arctic charr from the two populations under study had no experience with the conditions prevailing in this lake. During 28 May – 3 June, eight square enclosures (9.5 m x 9.5 m surface area, denoted E1 to E8) were deployed 3-5 m from the shoreline. Each enclosure consisted of a net (7mm bar mesh size) attached to a frame and was positioned to minimize among-enclosure variation in average depth and water volume. Depth at the shallow end of the enclosures ranged from 75 cm (E4) to 101 cm (E1, average = 89 cm), whereas depth at the deep end of the enclosures ranged from 231 cm (E7) to 260 cm (E8, average = 243 cm). The volume of the enclosures ranged from 143 m^3 (E2) to 157 m^3 (E7, average = 150 m^3). To prevent the fish from escaping the enclosures, the netting was sunk into the sediments or secured with gravel bags over hard substrate along the lake bottom and extended to 75 cm above the water surface. The absence of surface or bottom netting was designed to allow the charr to feed on prey throughout the water column, at the water surface, along the lake bottom, and within the sediments.

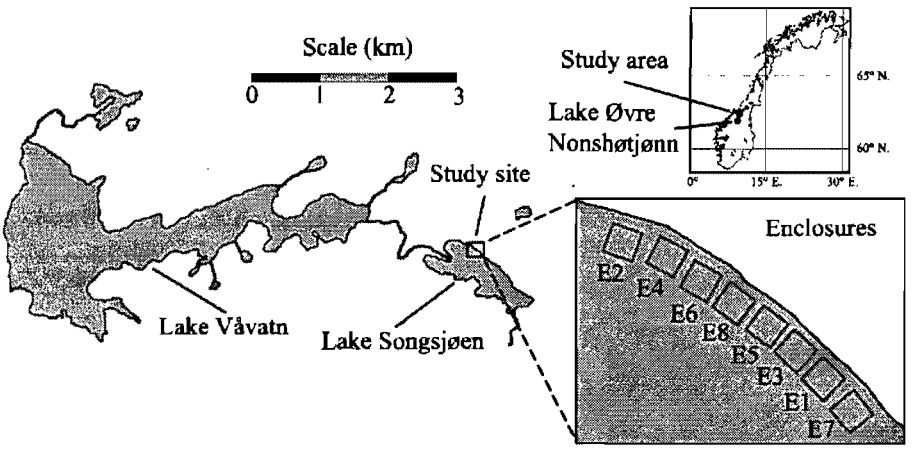

Figure 4.1 Study area, study site, and position of the experimental enclosures within the study site.

Experimental Fish

The Arctic charr specimens used in the present study originated from two lakes and were captured using baited minnow traps. Lake Øvre Nonshøtjønn (Figure 4.1, 62°43'05"N. - 9°32'03"E., elevation: 1004 m above sea level) is located 68 km south of Lake Songsjøen. This lake has an area of 3.5 ha, a maximum depth of 17 m, and is covered by ice from the end of October to mid-June. Lake Øvre Nonshøtjønn does not support a population of brown trout and consequently, Arctic charr from this lake are here defined as the 'naive ecotype'. During 25 May-15 June 2001, 72 juvenile Arctic charr (age II+ and III+; average size: 33.13 g *fw*, range: 10.0-93.5 g *fw*) were collected in Øvre Nonshøtjønn. Lake Våvatn (Figure 4.1, 63°19'41"N. - 9°34'29"E., elevation: 298 m above sea level) is located 1.2 km upstream of Lake Songsjøen, has an area of 425 ha, a maximum depth of 70 m, and is covered by ice from mid-November to mid-May. Lake Våvatn supports a population of brown trout. Arctic charr from this lake are therefore defined as the 'experienced ecotype'. During 3-12 June 2001, 71 juvenile Arctic charr (age II+ and III+; average size: 23.75 g fresh weight: *fw*; range: 13.0-55.5 g *fw*) were collected in Lake Våvatn. On 12 June 2001 36 brown trouts (average size: 34.19 g *fw*, range: 18.2-54.7 g *fw*) were captured in the main inlet of Lake Songsjøen (Figure 4.1) using an electro-fisher (Geomega FA-4, 50

Hz Pulsed 700 VDC with 25% duty cycle). On 20 June 2001, Arctic charr and brown trouts were anaesthetized using clove oil (25 $ml \cdot L^{-1}$), weighed (electronic balance, Mettler model BB1200, ± 0.1 g), and marked individually using alcian blue dye (Sigma-Aldrich). Handling time was less than 90 s and the fish were allowed to recover for 15 min. in aerated water.

Experimental procedure

The growth, consumption, and activity rate of charr were estimated under a factorial design encompassing two factors with duplicated treatments. The first factor was the charr ecotype (naive ecotype from Lake Øvre Nonshøtjønn: enclosures E3, E4, E7, and E8; experienced ecotype from Lake Våvatn: enclosures E1, E2, E5, and E6) and the second factor was the absence (allopatric enclosures; E1-E4) or the presence (sympatric enclosures; E5-E8) of trout. Baited hook lines (two lines with four hooks set for 24 h) were installed and snorkel inspections performed inside each enclosure to ensure that the enclosures were empty of fish prior to the experiment. On 20 June 2001, 120 charr (15 charr / enclosure) and 36 trouts (9 trouts / enclosure E5-E8) were distributed among the enclosures to ensure similar among-enclosure means and variances in body mass. The average fish density in the enclosure was 10.0 $fish \cdot 100m^{-3}$ for charr and 5.9 $fish \cdot 100m^{-3}$ for trout. The remaining 21 charr (11 from Lake Våvatn and 12 from Lake Øvre Nonshøtjønn) were killed to obtain a baseline estimate of ^{133}Cs concentration in charr at the beginning of the experiment (see *Caesium analysis and computation of consumption rate*).

Zooplankton samples were taken on three occasions (13 June, 11 and 27 July) using a 5 L sampler and sieved through a 95 μm Nytex™ sieve. On each occasions, three samples, each obtained by combining four 5 L sub-samples (total volume = 20 L), were collected within pairs of adjacent enclosures located at the south-eastern end (denoted E1-E7), in the middle (E5-E8), and at the north-western end (E2-E4) of the study site (2 samples per enclosures x 2 enclosures x 5 L per sample = 20 L). Zoobenthos were sampled on two occasions, shortly before (18 June) and after (5 August) the experiments using an Ekman bottom sampler (surface area: 225 cm^2). On each occasion, ten samples

were taken in each enclosure. Samples were sieved through a 0.5 mm net and kept in (95%) ethanol.

The experiment was terminated over two days because of the time required to recapture and process the fish (2 August: E1, E3, E5, and E7; 3 August: E2, E4, E6, and E8). Fish were recaptured by dragging a seine three times within each enclosure and killed immediately by an overdose of anaesthetic. Each fish was then identified individually, weighed, photographed using a standardized procedure (Fleming *et al.* 1994, Fleming and Einum 1997; camera: SONY™ Digital Handycam®, model DCR-VX 1000E), and dissected. The prey items in the stomach of the fish were identified to assess fish diet. The stomach contents of charr taken from a given enclosure were pooled to obtain sufficiently large samples for ^{133}Cs analysis. All tissues and stomach contents were kept frozen (-80°C) for ^{133}Cs analysis.

Video sampling

The activity rate of fish was estimated from their swimming behaviour according to Boisclair (1992a). Fish swimming behaviour was recorded using Stereo-Video-Cameras (SVC), which consisted of a pair of cameras (either Panasonic™ WV-BL602 or Panasonic™ WV-BP312) enclosed side-by-side in a water-resistant (Plexiglas®) case, 10 cm from one another. Two SVC were used, allowing simultaneous observations at two locations of the enclosure. The four images produced by the two SVC were assembled into a single image using a Quad image processor (Panasonic™ WJ-410). Time of filming was added to the images using a time-date generator (Panasonic™ WJ-810 ± 0.001 s) and the resulting video sequences were recorded using a VHS videocassette recorder (Panasonic™ AG-1330).

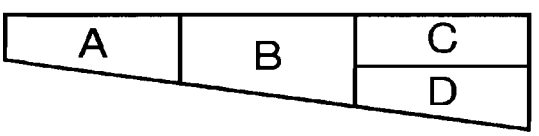

Figure 4.2 Lateral cut-out view of the enclosure with the sampled zones.

The spatial distribution of fish was quantified by defining four sampling zones (denoted A, B, C, and D; Figure 4.2). Zones A and B included the entire water column within the shallowest two thirds of the enclosure surface (zone A: first, shallowest, third; zone B: second third). Zones C and D included the remaining deepest third of the enclosure. Zone C included the volume comprised below the surface to a depth of 110 cm whereas zone D included the remaining volume from a depth of 110 cm to the bottom. The average volumes of Zones A, B, C, and D were 34, 50, 33, and 33 m^3, respectively. SVC were positioned such that zone A or B were filmed simultaneously with Zone C or D. The SVC filming zones A and B were positioned 50 cm from the perpendicular sides of the enclosures (perpendicular to shore), 75 cm below water surface (35 to 75 cm above the bottom), and 3.15 m offshore the shallowest enclosure side (between zone A and B). This SVC was oriented parallel to water surface, and its yaw angle (relative to the enclosure wall) was changed so to film Zone A (45° to 60° toward shore) or Zone B (75° to 85° toward deep). The SVC sampling Zone B was positioned 50 cm from the middle of the deepest side of the enclosures, 110 cm bellow the surface (120 to 140 cm above the bottom), and with its yaw angle oriented perpendicular with the wall. The pitch angle of the cameras (relative to the surface) was set 20-30° upward when sampling Zone C, and 10° downward when sampling Zone D. The total duration of a filming session was 1 h: two zones were filmed for 30 min. (A and C for example), then the orientation of the SVC was changed and the remaining zones (B and D in this example) were filmed for 30 min. SVC took 10-20 min. to reposition, and an additional 5 min. was allowed before recording was resumed.

Fish behaviour in each enclosure was quantified during two days. On any given sampling day, filming was organized into four sessions beginning at 4:00 AM, 10:00 AM, 4:00 PM, and 10:00 PM, and denoted 04h (early morning), 10h (late morning), 16h (late afternoon), and 22h (evening), respectively. However, to obtain good recordings as day length decreased, beginning of the filming sessions were progressively shifted to 6:30 AM, 10:30 AM, 3:30 AM, and 8:30 PM from 23 July and onward. Following this schedule, a total of 64 h of filming were obtained (4 sampling sessions x 2

sampling sessions per enclosure x 8 enclosures). As four sampling zones were filmed, the total number zone-specific estimate of activity rate was 256.

Zooplankton and zoobenthos analyses

Zooplankton from the samples collected before, during, and after the experiment were identified to genera (cladocerans: *Holopedium*, *Bosmina*, *Sida*, *Diaphanasoma*, *Polyphemus*, and *Leptodora*; copepods, adults and copepodites: *Cyclops*, *Diaptomus*, and *Heterocope*), counted, and measured (body length) under a dissecting microscope. Body lengths were converted to dry mass using length-mass regressions (Breistein and Nøst 1997). Biomass data (g *dw*·m^{-3}) were log(x+1) transformed before statistical analysis.

Zoobenthos sampled at the beginning and at the end of the experiment were identified and counted under a dissecting microscope, and grouped into four classes: benthic insects (see *Diet analysis*), dipterans larvae (families Chironomidae and Ceratopogonidae), mollusks (snails and mussels), and other (Nematoda, Hirudinea and Oligochaeta). Zoobenthos data were expressed in terms of number of animals per square meters.

Caesium analysis

Cs concentration was estimated for individual charr. Each fish was weighed, and then dried until mass stabilized (60°C for 24-48 h) to determine its dry mass (g dry weight; g *dw*) and the proportion of dry matter. Dry fish tissues were ground into a powder and a 300 mg sub-sample was digested with HNO_3. Measurements of Cs concentration (ng·g^{-1} *dw*) were made on the digested sub-sample using a high resolution Inductively Coupled Plasma Mass Spectrometer (ICP-MS, Thermo Electron Corp. model Finnigan™ Element1).

Diet analyses

The diet of charr was examined by analyzing their stomach contents at the end of the

experiment. Prey animals found in the stomach contents of each fish were identified, counted and measured under a dissecting microscope. Crustaceans were identified to species whereas other animals were identified to family or order. For larger animals, all individuals were counted and measured, whereas for crustaceans representative sub-samples were counted and measured. Body length was measured on whole animals or specific body parts. In the latter case, regression equations were used to estimate body length (Breistein and Nøst 1997). Body length was converted to dry mass using the same relationships as for zooplankton analysis. Data were expressed as proportion of dry mass by prey type, and the average mass of the animals in each sample was calculated.

For analyses, the prey animals were grouped into seven categories: surface insects (terrestrial insects and adults of the aquatic Ephemeroptera, Trichoptera and Diptera), benthic insects (larvae of Ephemeroptera, Plecoptera, Trichoptera, Odonata, Zygoptera, and Coleoptera and adults of aquatic Coleoptera), mollusks (snails and mussels), aquatic dipterans (larvae and pupae of the families Chironomidae and Ceratopogonidae), planktonic cladocerans (species of genera *Daphnia*, *Bosmina*, *Holopedium*, *Polyphemus*, and *Bythotrephes*), planktonic copepods (*Heterocope* and *Cyclops*), and benthic crustaceans (*Eurycercus lamellatus* and *Sida crystallina*). Diet composition data were arcsine-square-root transformed before statistical analysis.

Video analysis

VHS recordings were converted to numeric format using a PC-based interface (ATI video acquisition interface, resolution: 640x480 pixels) to ease computer-based image analysis. We did not estimate behaviour and activity rate of trout because they were rarely observed (*i.e.* on approximately 20% of the recordings) and rarely performed measurable movements (*i.e.* they remained immobile 95% of the time they were observed). For every second of recording, all fish moving $\geq$ 1 cm·s^{-1}, and observed simultaneously in both cameras of a given SVC were counted and summed over the duration of a recording (30 min.) to provide a measure of the total moving fish second (*FS*, fish·s). Image analysis was done with a software developed by the first author using XBasic Program Development

Environment (2002, version 6.2.3). The analysis involved positioning (in pixel coordinates) the head and tail of fish (see Boisclair 1992a for details) through time. Swimming characteristics were estimated on a single second interval, randomly selected over the complete displacement of a given fish in the volume sampled by the SVC. This sub-sampling strategy was adopted to minimize the effects of pseudo-replication. A maximum of 100 measurements were taken per recording. Random sub-sampling was thus conducted when more than 100 fish passages where available per 30 min. of filming.

Computations

Growth rate

We calculated the growth rate of charr (G, kJ·d^{-1}) as:

$$G = \frac{(w_F - w_0) \cdot ED}{n} \tag{4.1}$$

where w_0 and w_F are, respectively, the body mass of the fish (g *fw*) at the beginning and the end of the experiment; n is the duration of the experiment (day), and ED is the energy density (kJ·g^{-1} *fw*) predicted by the model of Hartman and Brandt (1995, Equation #13, developed for Salmonids) using the proportion of dry matter.

Consumption rate

Initial Cs burden of the charr was estimated from the Cs concentration of the 23 charr sampled at the beginning of the experiment (Lake Øvre Nonshøtjønn: average body mass = 63.91 g *fw*, range: 46.50-93.53 g *fw*; Lake Våvatn: average body mass = 28.18 g *fw*, range: 16.25-43.87 g *fw*). No statistically significant relationship was found between the Cs concentration ($\log_{10}$-transformed) and the fresh body mass of charr (Lake Øvre Nonshøtjønn: $t_{(10)} = 0.641$, $p = 0.5357$, $R^2_{adj} = -0.057$; Lake Våvatn: $t_{(9)} = -0.427$, $p = 0.68$, $R^2_{adj} = -0.089$). As a consequence, the initial Cs burden (ng) of charr

was estimated by multiplying the mean initial Cs concentration (Lake Øvre Nonshøtjønn: 28.57 $ng \cdot g^{-1}$ *fw*; Lake Våvatn: 19.56 $ng \cdot g^{-1}$ *fw*) by their fresh body mass at the beginning of the experiment (g *fw*). Cs concentration in the food consumed by charr (pooled stomach contents) was evaluated using the same procedure as for body tissues and reported as the dry weight concentration ($ng \cdot g^{-1}$ *dw*). Caesium analyses were not performed on trout.

Consumption rate was calculated for individual charr following the method proposed by Forseth *et al.* (1992). For any given day i, we calculated the (linearly) interpolated body mass w_i (g *fw*) and Cs burden Q_i (ng) of the fish, and the Cs elimination rate (k_i, d^{-1}) was estimated from w_i and mean daily temperature (°C) using the model of Ugedal *et al.* (1992). Daily Cs intake (I_i, $ng \cdot d^{-1}$) was calculated as proposed by Forseth *et al.* (1992, their equation 3b), and mean daily consumption rate (C, $kJ \cdot d^{-1}$) was calculated as:

$$C = \frac{\sum_{i=1}^{n} I_i \cdot \sum_{j=1}^{m} (p_j \cdot S_j)}{[Cs]_f \cdot Eff \cdot n} \tag{4.2}$$

where $[Cs]_f$ ($ng \cdot g^{-1}$ *dw*) is the concentration of Cs in the diet of charr from each enclosure, Eff the Cs absorption coefficient (the proportion of the Cs found in the diet that is assimilated by the fish), n the duration of the experiment (day), p_j the proportion (calculated dry mass percentage) of prey item j in fish diet, and S_j ($kJ \cdot g^{-1}$ *dw*) the energy density of prey item j ($kJ \cdot g^{-1}$ *dw*). The energy densities of prey items were obtained from Cummin and Wuycheck (1971). When species-specific energy density were unavailable, generic values to the nearest taxonomic group were substituted. Because stomach contents were pooled, the energy density of the diet was estimated once for each enclosure.

Calibration of the SVC

Calibration of the SVC was done underwater using a target consisting of a board with lines spaced apart by 10, 20 and 30 cm. This target was placed at distances ranging from 40 cm to 240 cm from the SVC (40 cm increments). Calibration was done before the first filming day, and was repeated

each four filming days. A non-linear function was used to estimate real lengths (L, cm) from virtual lengths (l, pixels) and parallax (*i.e.* the offset between images from the cameras in abscissa: Δx, pixels):

$$L = \frac{l}{\frac{c_1}{\Delta x + c_2} + c_3} \tag{4.3}$$

where c_1 is a scale parameter, and c_2 and c_3 are offset parameters estimated by least-squares non-linear regression of known distances between pairs of landmarks on the calibration target against values of Δx and l obtained from image analysis. The quotient of real and virtual length (L / l) was used to evaluate the distance between the target and the SVC (z, cm):

$$z = c_4 \cdot \frac{L}{l} + c_5 \tag{4.4}$$

where parameters c_4 and c_5 were estimated using linear regression of known values of distance of the calibration target and known values of L / l. The coefficients of determination (R^2) of these relationships (Equations 4.3 and 4.4) ranged from 92% and 99%.

Volume sampled by the SVC

The volume sampled by a video-camera has the shape of a rectangle-based pyramid with a volume increasing with the distance from the camera. This volume crossed the bottom of the littoral zone or the surface of the lake at an angle. Hence, the volume sampled by the SVC was calculated as the volume of a truncated rectangle-based pyramid. This volume began at 25 cm from the objective of the cameras (minimum distance to perceive a fish simultaneously in two cameras of the same SVC) and extended to a maximum distance of fish detection determined using the coordinates of the head and tail of the fish observed during filming. The volume sampled by the SVC for different recordings were grouped according filming conditions defined by the zone sampled, the position and the orientation of the cameras, and the characteristics of the images (pixel brightness and their frequency

distribution). The volume sampled by a SVC for recordings during which no fish were observed was used as the volume sampled by SVC when fish were observed under similar filming conditions.

Activity rate

Activity rate was calculated from swimming behaviour following three steps. First, the biomass density ($B_{z,t}$, g·m^{-3} *fw*) of actively swimming charr observed in a zone z and at time t in the volume sampled by the SVC ($V_{z,t}$, m^3) was calculated as:

$$B_{z,t} = \frac{FS_{z,t}\bar{w}_t}{T_{z,t}\cdot V_{z,t}} \quad (4.5)$$

where $FS_{z,t}$ is the total number of moving fish per second (fish·s), $\bar{w}_t$ is the mean body mass of fish inside the enclosure (g *fw*: linearly interpolated at the time of sampling), and $T_{z,t}$ is the duration of the recording (s). Second, the mean swimming cost (MSC: kJ·kg^{-1}·h^{-1}) in a zone z and at time t was calculated using mean body mass, and mean swimming speed ($\bar{v}_{z,t}$, cm·s^{-1}):

$$MSC_{z,t} = 13.54\cdot 10^{b_0}\cdot \bar{w}_t^{(b_{MASS}-1)}\cdot \bar{v}_{z,t}^{b_{SPEED}} \quad (4.6)$$

where 13.54 is the oxy-caloric coefficient (J·mgO$_2^{-1}$, Elliott and Davison 1975), and parameters b_0, b_{MASS}, and b_{SPEED} (b ± 1 standard deviation) are respectively –1.411 ± 0.092, 0.915 ± 0.039, and 0.886 ± 0.096. The parameters b_0, b_{MASS}, and b_{SPEED} were obtained from the swimming cost model developed by Guénard *et al.* (In Press). Third, activity rate ($A_{z,t}$, kJ·kg^{-1}·h^{-1}) in zone z and at time t was calculated as:

$$A_{z,t} = \frac{B_{z,t}\cdot MSC_{z,t}}{B_{e,t}} \quad (4.7)$$

where $B_{e,t}$ (g·m^{-3} *fw*) is the *mean biomass density* of fish in the enclosure per unit of volume (*e.g.* the sum of the interpolated body masses at time t divided by the volume of the enclosure).

Statistical analysis

Computations and statistical analyses were performed using R language and environment (version 2.4.1; R Development Core Team 2007). Statistical significance of among-enclosures differences and differences between charr populations were examined by analysis of variance (ANOVA) or multiple analysis of variance (MANOVA). Where post-hoc comparisons were applicable, between-enclosure differences were tested using Scheffé tests (Scheffé 1953). Normality of the residuals was tested by the Shapiro-Wilk's test of normality (Shapiro and Wilk 1965). When residuals were found to be non-normally distributed, the explanatory variable was transformed using the Box and Cox (1964) method prior to analysis. Homogeneity of within-group or residual variance was tested using Bartlett's test (Snedecor and Cochran, 1989), or by examining the plots of residual (y) and predicted values (x). Analyses of activity rate and active biomass density were done using Generalized Linear Model (McCullagh and Nelder 1989; Quasi-Poisson likelihood model using logarithmic link function: Hastie and Pregibon 1992). Statistical significance of the resulting deviance tables were calculated using an F test. For all statistical analyses, a significance threshold of 5% was used for type I (α) error. Type I error rates associated with multiple statistical inferences (*e.g.* contrasts obtained from GLM) were corrected sequentially using the Šidák inequality (Šidák 1967, Wright 1992).

RESULTS

The body mass of charr and the densities at which they were stocked into the allopatric and sympatric enclosures were similar at the beginning of the experiment (Table 4.1). The initial body mass and stocking density of trout were also similar among the sympatric enclosures. During the experiment, the water temperature varied between 13.5°C and 19.6°C (average: 16.3°C), and decreased at a mean rate of $0.042°C \cdot d^{-1}$ ($F_{(1,43)} = 6.666$, $p = 0.01$). Superimposed to this trend, three fluctuations of 3-4°C over periods 10-15 days were also observed.

Table 4.1 Variables estimated in the experimental enclosures and results of statistical tests of among-enclosure differences.

Variable		Units	Mean	Range	Enclosures								Among-enclosures differences		
					E1	E2	E3	E4	E5	E6	E7	E8	$F_{\nu1,\nu2}$	ν_1,ν_2	p
Mass (charr)	Initial	g fw	22.63 [21.75, 23.56]	10.0-57.0	21.4 [19.1, 24.1]	21.2 [18.9, 23.8]	24.0 [21.4, 27.0]	23.2 [20.7, 26.1]	21.6 [19.2, 24.2]	21.5 [19.1, 24.1]	24.7 [22.0, 27.7]	23.8 [21.2, 26.7]	0.2813	7, 112	0.96
	Final		31.63 ±1.21	14.6-65.0	24.8[a] ±3.4	30.4[a] ±3.5	37.7[a] ±3.3	36.11[a] ±3.26	26.5[a] ±3.1	27.6[a] ±3.1	38.5[a] ±3.1	30.9[a] ±3.1	2.6649	7, 98	0.01
Mass (trout)	Initial	g fw	34.19 ±1.71	18.2-54.7	---	---	---	---	34.2 ±3.6	34.3 ±3.6	34.0 ±3.6	34.2 ±3.6	0.0013	3, 32	1
	Final		42.22 ±1.71	24.8-68.0	---	---	---	---	41.2 ±3.6	45.5 ± 3.4	38.2 ± 3.4	43.9 ±3.4	0.8955	3, 31	0.45
Fish recaptured		Charr	13.1	11-14	12	11	13	13	14	14	14	14	---	---	---
		Trout	8.8	8-9	---	---	---	---	8	9	9	9	---	---	---
Fish density (charr)	Initial	Fish ·100m^{-3}	10.03	9.52-10.52	10.0	10.5	10.4	10.20	10.2	9.7	9.5	9.8	---	---	---
	Final		8.76	7.71-9.49	8.0	7.7	9.0	8.84	9.5	9.0	8.9	9.2	---	---	---
Fish density (trout)	Initial	Fish ·100m^{-3}	5.88	5.71-6.10	---	---	---	---	6.1	5.8	5.7	5.9	---	---	---
	Final		5.71	5.71-5.90	---	---	---	---	5.4	5.8	5.7	5.9	---	---	---
Biomass density (charr)	Initial	g·m^{-3}	2.27	2.07-2.50	2.1	2.2	2.5	2.37	2.2	2.1	2.4	2.3	---	---	---
	Final		3.69	3.28-4.10	3.3	3.5	3.4	3.88	3.9	4.1	3.4	4.0	---	---	---
Biomass density (trout)	Initial	g·m^{-3}	1.92	1.84-2.01	---	---	---	---	2.0	1.9	1.8	1.9	---	---	---
	Final		2.48	2.18-2.63	---	---	---	---	2.5	2.6	2.2	2.6	---	---	---
Growth rate		kJ·d^{-1}	0.86 ±0.06	-0.47-2.44	0.5[a] ±0.1	0.9[ab] ±0.1	1.4[b] ±0.1	1.14[ab] ±0.12	0.4[a] ±0.1	0.5[a] ±0.1	1.3[b] ±0.1	0.7[ab] ±0.1	10.615	7, 96	7.92x10^{-10}
Cs Burden	Initial	ng	517 [520, 552]	253-1440	385 [342, 435]	369 [323, 421]	681 [607, 765]	675 [601, 758]	423 [378, 473]	426 [381, 476]	728 [651, 814]	620 [554, 693]	---	---	---
	Final		913 [850, 981]	287-4129	496[a] [437, 563]	478[a] [416, 549]	1710[b] [1515, 1931]	1722[b] [1525 1944]	510[a] [453, 573]	499[a] [443, 560]	1743[b] [1551 1960]	1302[b] [1158 1464]	27.162	7, 96	< 2.2x10^{-16}
Consumption rate *		kJ·d^{-1}	4.68 [4.35, 5.03]	0.91-21.52	2.9[a] [2.5, 3.4]	2.8[a] [2.4, 3.3]	8.7[b] [7.6, 10.1]	8.60[b] [7.45, 9.94]	2.7[a] [2.4, 3.1]	2.4[a] [2.1, 2.8]	8.4[b] [7.3, 9.6]	6.0[ab] [5.2, 6.9]	16.877	7, 95	2.61x10^{-14}
Swimming speed		cm·s^{-1}	12.7 [12.4, 13.1]	3.6-37.7	10.5[ab] [9.6, 11.5]	10.2[a] [9.4, 11.1]	14.7[ab] [13.7, 15.8]	16.5[b] [15.1, 18.0]	11.7[ab] [10.9, 12.5]	12.0[ab] [11.1, 12.9]	13.5[ab] [12.6, 14.6]	13.4[ab] [12.5, 14.4]	4.1569	7, 163	3.10x10^{-4}
Activity rate **		kJ·kg^{-1}·h^{-1}	1.39 [1.26, 1.54]	0-16.1	1.1[ab] [0.8, 1.5]	1.6[ab] [1.2, 2.0]	1.61[ab] [1.3, 2.1]	0.75[a] [0.52, 1.08]	1.8[ab] [1.4, 2.2]	2.3[b] [1.9, 2.9]	1.1[ab] [0.8, 1.5]	0.9[a] [0.6, 1.3]	4.8315	7, 212	4.53x10^{-5}

* The model includes the body mass of charr at the beginning of the experiment (1 degree-of-freedom: df).

** The analytical model (GLM) includes the effects of sampling zone (3 df), time of day (3 df), the interaction between sampling zone and time of day (9 df), and the interaction between the sampling zone and enclosures (21 df).

The total zooplankton biomass ranged 12.4-51.2 g *dw*·m^{-3} (Table 4.2a, mean = 18.8 g *dw*·m^{-3}), and did not differ among the three sampling sites ($F_{(2,6)}$ = 1.5171, p = 0.29) and sampling times ($F_{(2,6)}$ = 3.0915, p = 0.12). No among-site differences in the composition of the zooplankton community were found using a MANOVA performed on the five most abundant genera (*i.e. Holopedium*, *Bosmina*,

Sida, *Leptodora*, and *Heterocope*; Wilk's $\lambda_{(2,6)} = 0.02926$, $p = 0.27$). Among the zoobenthos samples taken at the end of the experiment, 12 were lost before counting the invertebrates, leaving 7 replicates for enclosures E1, E3, E5, and E7. Mollusk and dipterans larvae (mainly chironomids) were the most abundant groups of zoobenthic animals, accounting for 88% of the total density (Table 4.2b). The initial composition of the zoobenthos in the enclosures was similar ($\lambda_{(7,72)} = 0.6810$, $p = 0.46$), but differed at the end of the experiment ($\lambda_{(7,60)} = 0.330$, $p = 4.15 \times 10^{-5}$). Zoobenthos composition at the end of the experiment differed following the charr ecotype reared in the enclosures ($\lambda_{(1,60)} = 0.784$, $p = 0.007$), but was not related to the presence of trout ($\lambda_{(1,60)} = 0.912$, $p = 0.25$). Specific zoobenthic invertebrates in enclosures containing the naive ecotype were 68% lower (mollusks; 87.7 ind·m^{-2}) and 65% higher (dipterans larvae; 74.6 ind·m^{-2}) than in enclosures containing the experienced ecotype (means: 147.6 and 45.2 ind·m^{-2}), respectively. The interaction between the experimental factors (*i.e.* charr population and absence / presence of trout) was not statistically significant ($\lambda_{(1,60)} = 0.884$, $p = 0.13$), but the differences between treatment replicates were significant ($\lambda_{(4,60)} = 0.488$, $p = 3.16 \times 10^{-4}$). These results indicate that, at the onset of the experiment, the density of prey animals was similar among the enclosures. Moreover, the results suggest that the structure of the benthic community in the enclosures was affected by the identity of the ecotype of charr they contained but not by the absence / presence of trout.

On average, 88% of the charr (range: 73% in E2 to 93% in E5-E8) and 97% of trout (range: 89% in E5 to 100% in E6-E8) were recaptured at the end of the experiment. The density of charr was similar among enclosures and the density of trout among sympatric enclosures E5-E8 were also similar (Table 4.1). The body mass of charr differed among enclosures, but differences between pairs of enclosures were too small to be detected using *a posteriori* tests. The final average body mass of trout were similar among enclosures.

Table 4.2 (a) Biomass (g *dw*·m^{-3}) of the zooplankton genera found in the nine mixed samples performed on the study site, and (b) bottom animals density (number·m^{-2}; format: mean [-SE, +SE]) in the experimental enclosures at the beginning and end of the experiment. See main text for details on grouping of bottom animals.

(a)

Order	Genera	13 June			11 July			27 July		
		E1-E7	E5-E8	E2-E4	E1-E7	E5-E8	E2-E4	E1-E7	E5-E8	E2-E4
Cladocerans	*Holopedium*	0.04	0.00	0.00	2.51	2.77	7.01	0.00	0.00	0.10
	Bosmina	9.98	10.15	13.07	7.08	4.16	11.51	14.39	10.81	16.72
	Sida	0.00	1.85	1.33	0.00	0.00	1.02	0.06	0.21	0.88
	Diaphanasoma	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00
	Polyphemus	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Leptodora	0.00	0.00	0.00	0.00	0.00	25.0	0.00	0.21	0.00
Copepods	*Cyclops*	0.06	0.00	0.06	0.00	0.03	0.03	0.32	0.07	0.08
	Diaptomus	0.00	0.00	0.00	0.00	0.00	0.49	0.20	0.35	1.59
	Heterocope	4.90	0.44	0.88	20.8	8.75	6.17	0.81	0.70	0.08
	Total	16.0	12.4	15.3	30.4	15.7	51.2	16.0	12.4	19.4

(b)

Time	Enclosures	N	Groups				Total
			Insects	Dipteran larvae	Mollusks	Other	
18 June	E1	10	8.9 [4.1, 19.5]	80.0 [57.3, 112]	97.8 [71.0, 135]	8.9 [2.7, 28.9]	187 [144, 243]
	E2	10	22.2 [13.5, 36.5]	66.7 [46.3, 96.1]	31.1 [17.6, 54.9]	17.8 [7.7, 40.9]	120 [86.6, 166]
	E3	10	22.2 [13.5, 36.5]	102 [76.1, 137]	107 [78.5, 145]	4.4 [0.84, 23.6]	231 [183, 292]
	E4	10	26.7 [17.0, 41.9]	142 [111, 183]	40.0 [24.3, 66.0]	26.7 [13.5, 52.7]	209 [163, 268]
	E5	10	17.8 [10.2, 31.0]	57.8 [39.0, 85.5]	111 [82.3, 150]	17.8 [7.7, 40.9]	187 [144, 243]
	E6	10	17.8 [10.2, 31.0]	111 [83.7, 147]	66.7 [45.2, 98.2]	97.8 [68.5, 140]	196 [151, 253]
	E7	10	31.1 [20.5, 47.3]	191 [154, 237]	97.8 [71.0, 135]	71.1 [46.9, 108]	320 [262, 391]
	E8	10	13.3 [7.0, 25.3]	116 [87.6, 152]	102 [74.7, 140]	35.6 [19.7, 64.1]	231 [183, 292]
5 August	E1	7	50.8 [34.3, 75.2]	0.0 [---, ---]	114 [80.2, 163]	76.2 [47.1, 123]	165 [118, 230]
	E2	10	31.1 [20.5, 47.3]	107 [79.9, 142]	244 [200, 299]	4.4 [0.84, 23.6]	382 [318, 459]
	E3	7	6.3 [2.1, 19.3]	108 [76.6 ,152]	95.2 [64.6, 140]	25.4 [11.0, 58.5]	210 [156, 282]
	E4	10	31.1 [20.5, 47.3]	129 [99.1, 168]	169 [132, 215]	0.0 [---, ---]	329 [270, 401]
	E5	7	57.1 [39.5, 82.7]	57.1 [35.7, 91.6]	152 [112, 207]	12.7 [3.9, 41.3]	267 [205, 347]
	E6	10	31.1 [20.5, 47.3]	71.1 [49.9, 101]	178 [140, 225]	8.9 [2.7, 28.9]	280 [226, 347]
	E7	7	25.4 [14.6, 44.2]	108 [76.6, 152]	121 [85.5, 170]	76.2 [47.1, 123]	254 [194, 332]
	E8	10	80.0 [61.6, 104]	62.2 [42.6, 90.8]	71.1 [48.9, 103]	0.0 [---, ---]	213 [167, 273]
Grand mean		148	29.1 [25.8, 32.9]	96.4 [88.6, 105]	112 [103, 121]	28.8 [22.4, 37.0]	237 [223, 252]

Growth rate

The growth rate of charr was not influenced by their body mass ($F_{(1,102)} = 3.189$, $p = 0.08$, $R^2_{adj} = 0.021$) and differed among enclosures (Table 4.1). Growth rate differed between charr ecotypes; the naive ecotype (mean = 1.15 $kJ \cdot d^{-1}$) grew twice as fast as the experienced ecotype (mean = 0.54 $kJ \cdot d^{-1}$, Table 4.3, Figure 4.3). Growth rate was also influenced by the presence of trout, with charr growing 36% faster in the absence of trout (mean = 1.00 $kJ \cdot d^{-1}$) than in their presence (mean = 0.74 $kJ \cdot d^{-1}$; Figure 4.3a,b). The effect of trout on the growth rate of charr was similar between the two ecotypes and differences between treatment replicates were statistically significant. These results suggest that competition occurred between charr and trout. However, both charr ecotypes were similarly affected by this interaction.

Table 4.3 Statistical significance of the experimental factors (charr ecotype and absence / presence of trout) and of the difference between treatment replicates.

Variable and factor		Test results			
		$F_{\nu 1,\nu 2}$	ν_1	ν_2	p
Growth rate	Ecotype	45.410	1	96	1.18×10^{-9}
	Trout	7.6772	1		0.007
	Pop. x trout	0.0014	1		0.97
	Replicates	4.6179	4		0.002
Consumption rate *	Ecotype	107.20	1	95	$< 2.2 \times 10^{-16}$
	Trout	4.7982	1		0.03094
	Pop. x trout	0.0001	1		0.99
	Replicates	0.6521	4		0.63
Swimming speed	Ecotype	25.498	1	163	1.17×10^{-6}
	Trout	0.0443	1		0.83
	Pop. x trout	4.4382	1		0.04
	Replicates	0.2530	4		0.91
Activity rate **	Ecotype	9.8422	1	230	0.002
	Trout	1.2981	1		0.26
	Pop. x Trout	8.0680	1		0.005
	Pop. x Zone	6.6739	3		2.44×10^{-4}
	Replicates	2.2187	4		0.07

* The ANOVA model includes the effect of body mass (1 df) at the beginning of the experiment.
** The analytical model (GLM) also includes the effects of sampling zone (3 df), time of day (3 df) and the interaction between sampling zone and time of day (9 df).

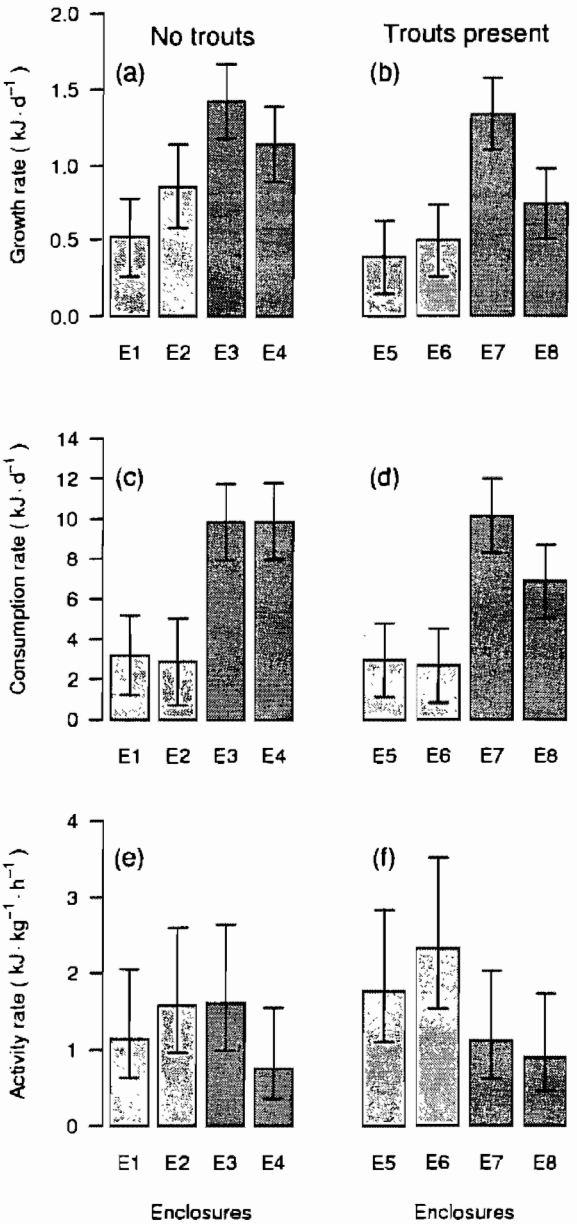

Figure 4.3 Mean (±95% CL) growth (a and b), consumption (c and d), and activity (e and f) rates of experienced (light grey) and naive (dark grey) Arctic charr reared alone (a, c, and e) or in presence of brown trout (b, d, and f) in the experimental enclosures.

Consumption rate

On average the Cs body burden of the naive ecotype increased 238% whereas the Cs body burden of the experienced ecotype increased by 23% during the course of the experiment. Among-enclosure differences in final Cs body burden were statistically significant (Table 4.1), with the naive ecotype (mean = 1604 ng) having 323% higher Cs body burden than the experienced ecotype (mean = 497 ng).

Table 4.4 Diet composition (mean dry weight %) and prey size (geometric mean mg dry weight) of Arctic charr (a) and brown trout (b) in the experimental enclosures. See main text for details on grouping of prey animals.

a) Arctic charr

Group	Trout absent				Trout present				Mean
	Lake Våvatn		Lake Øvre Nonshøtjønn		Lake Våvatn		Lake Øvre Nonshøtjønn		
	E1	E2	E3	E4	E5	E6	E7	E7	
Surface insects	0.3 [0.1, 0.5]	0.8 [0.4, 1.2]	0.0 [0.0, 0.0]	0.8 [0.4, 1.2]	0.0 [0.0, 0.1]	0.1 [0.0, 0.2]	0.2 [0.0, 0.3]	0.3 [0.1, 0.5]	0.2 [0.1, 0.2]
Benthic insects	0.0 [0.0, 0.1]	0.0 [0.0, 0.1]	0.5 [0.2, 0.8]	0.0 [0.0, 0.0]	0.2 [0.1, 0.4]	0.0 [0.0, 0.1]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.1]
Mollusks	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]	0.0 [0.0, 0.0]
Aquatic dipterans	9.0 [5.1, 13.9]	19.9 [13.5, 27.1]	6.7 [3.5, 10.9]	5.1 [2.1, 9.2]	8.5 [4.9, 12.9]	10.1 [6.2, 14.8]	10.3 [6.4, 15.1]	6.4 [3.4, 10.4]	9.0 [7.5, 10.5]
Planktonic cladocerans	84.6 [75.6, 91.8]	65.0 [52.8, 76.3]	10.4 [4.7, 17.9]	35.4 [24.6, 47.1]	80.3 [71.4, 88.0]	85.4 [77.2, 92.0]	30.7 [21.5, 40.8]	28.8 [19.8, 38.7]	52.7 [47.9, 57.5]
Planktonic copepods	0.0 [0.0, 2.0]	1.9 [0.0, 7.6]	65.3 [53.0, 76.5]	47.7 [34.4, 61.1]	0.8 [0.1, 4.3]	0.0 [0.0, 1.4]	42.4 [30.9, 54.4]	42.7 [31.2, 54.7]	16.9 [12.9, 21.4]
Benthic crustaceans	2.4 [1.3, 3.8]	2.1 [1.0, 3.5]	2.0 [1.1, 3.2]	0.5 [0.1, 1.2]	2.2 [1.3, 3.4]	3.3 [2.1, 4.7]	0.0 [0.0, 0.2]	3.2 [2.0, 4.6]	1.6 [1.3, 2.0]
Mean prey size (mg)	0.010 [0.008, 0.011]	0.014 [0.012, 0.016]	0.033 [0.027, 0.041]	0.021 [0.018, 0.026]	0.011 [0.010, 0.012]	0.010 [0.009, 0.011]	0.022 [0.019, 0.026]	0.022 [0.019, 0.026]	0.015 [0.015, 0.017]

b) Brown trout

Group	Lake Våvatn		Lake Øvre Nonshøtjønn		Mean
	E5	E6	E7	E8	
Surface insects	18.1 [7.2, 32.4]	7.8 [1.6, 18.1]	22.9 [11.3, 37.3]	44.5 [29.4, 60.2]	22.1 [15.7, 29.2]
Benthic insects	14.0 [4.8, 26.9]	10.5 [3.1, 21.6]	26.9 [14.6, 41.3]	7.1 [1.4, 16.8]	13.9 [9.1, 19.6]
Mollusks	0.2 [0.1, 0.5]	0.1 [0.0, 0.3]	0.5 [0.2, 0.8]	0.0 [0.0, 0.1]	0.1 [0.1, 0.2]
Aquatic dipterans	19.0 [12.4, 26.5]	19.9 [13.5, 27.1]	16.9 [11.0, 23.7]	6.8 [3.2, 11.8]	15.1 [12.1, 18.3]
Planktonic cladocerans	0.0 [0.0, 0.0]	0.0 [0.0, 0.1]	0.0 [0.0, 0.1]	0.3 [0.1, 0.5]	0.0 [0.0, 0.1]
Planktonic copepods	3.7 [0.8, 8.8]	1.1 [0.0, 4.2]	0.0 [0.0, 1.4]	3.3 [0.7, 7.8]	1.5 [0.5, 3.0]
Benthic crustaceans	14.8 [8.4, 22.6]	38.2 [29.3, 47.6]	3.7 [1.0, 8.1]	11.3 [6.0, 17.9]	15.1 [11.4, 19.2]
Mean prey size (mg)	0.221 [0.155, 0.340]	0.096 [0.077, 0.125]	0.551 [0.332, 1.092]	0.166 [0.124, 0.234]	0.190 [0.158, 0.233]

Crustacean zooplankton dominated the diet of the charr, followed by aquatic dipterans (Table 4.4a). Diet of charr at the end of the experiment differed among enclosures (Wilk's $\lambda_{(7,94)} = 0.3151$, $p = 8.83 \times 10^{-8}$), between populations ($\lambda_{(1,94)} = 0.6$, $p = 7.9 \times 10^{-10}$), between treatment replicates ($\lambda_{(4,94)} = 0.7$, $p = 0.03$), but the effect of the presence of trout ($\lambda_{(1,94)} = 0.09$, $p = 0.57$), and the interaction between the experimental factors (i.e. charr ecotypes and the absence / presence of trout; $\lambda_{(1,94)} = 0.9$, $p = 0.09$) were not statistically significant. The diet of the naive ecotype comprised a higher proportion of planktonic copepods (mean = 52%, against 4% for the experienced ecotype) whereas the experienced ecotype consumed mostly cladocerans (mean = 78%, against 31% for the naive ecotype). The diet of trout was composed of surface insects, aquatic dipterans, benthic crustaceans, and benthic insects (Table 4.4b). Aquatic dipteran was the only type of prey consumed to a substantial extent (contribution > 5% to the diet) by both charr and trout. The diet of trout differed among enclosures ($\lambda_{(3,31)} = 0.3002$, $p = 0.036$), but did not vary between the charr ecotype in the enclosures ($\lambda_{(1,31)} = 0.61$, $p = 0.064$) or between treatment replicates ($\lambda_{(2,31)} = 0.48$, $p = 0.11$). The mean size of preys consumed by charr differed among enclosures ($F_{(7,94)} = 9.2789$, $p = 1.09 \times 10^{-8}$) and between ecotypes ($F_{(1,94)} = 51.973$, $p = 1.40 \times 10^{-10}$), with

the naive ecotype (mean = 0.020 mg *dw*) eating preys twice as large as those consumed by the experienced ecotype (mean = 0.010 mg *dw*). The mean prey size consumed by charr was not affected by the presence of trout ($F_{(1,94)}$ = 3.2960, p = 0.073) and the interaction between the experimental factors ($F_{(1,94)}$ = 0.0353, p = 0.85) and the differences between treatment replicates ($F_{(4,94)}$ = 0.3327, p = 0.20) were not statistically significant. On average, trout ate 27% larger preys than charr. The mean size of prey items consumed by trout differed among enclosures ($F_{(3,31)}$ = 4.361, p = 0.011), but was not affected by the identity of the charr ecotype ($F_{1,31}$ = 4.1402, p = 0.051). Large and statistically significant differences in the mean prey size were found between treatment replicates ($F_{2,31}$ = 4.3225, p = 0.022), with trout reared with the naive ecotype in enclosure E7 eating preys 3.3 times larger than trout in enclosure E8 and with trout reared with the experienced ecotype in enclosure E5 eating preys, on average, 2.3 times larger than trout in enclosure E6.

The energy density of the diet ranged from 22.00 (E1) to 23.36 (E3) kJ·g^{-1} *dw* (mean ± *SD* = 22.64 ± 0.59 kJ·g^{-1} *dw*). The mean (± *SD*) Cs concentration in the diet were, respectively, 105.0 (± 5.3) and 55.3 (± 12.2) ng·g^{-1} *dw* for the naive and the experienced charr ecotypes. Because the diet of charr was dominated by zooplankton, their consumption rate was calculated using the Cs absorption coefficient (0.816 ± 0.044) suggested for zooplankton by Forseth *et al.* (1992).

Consumption rate varied up to 24-fold among individual charr and was positively influenced by body mass (b = 0.037 kJ·d^{-1}·g^{-1} *fw*, $F_{(1,102)}$ = 6.329, p = 6.69x10^{-9}, R^2_{adj} = 0.27). The slope of the relationships between consumption rate and body mass did not differ among enclosures ($F_{(7,88)}$ = 0.3243, p = 0.94). Consequently, body mass was included in the analyses involving consumption rate. Consumption rate differed among enclosures, between ecotypes, and was negatively affected by the presence of trout (Table 4.1, 4.3; Figure 4.3c,d). The naive ecotype (mean = 7.80 kJ·d^{-1}) consumed 2.9 times more food than the experienced ecotype (mean = 2.69 kJ·d^{-1}). Charr in sympatric enclosures (mean = 4.26 kJ·d^{-1}) had consumption rate 23% lower than in allopatric enclosures (mean = 5.22 kJ·d^{-1}). The consumption rate of charr from both ecotypes were affected similarly by the presence of

trout and differences between replicates were not statistically significant. These results suggest that the naive ecotype has a better ability than the experienced ecotype to forage under the environmental conditions found in the experimental enclosures. Furthermore, the respective abilities of the two ecotypes of charr to feed under these conditions were similarly affected by the presence of trout. The effect of these factors on the food consumption of charr may thus be imparted as a possible factor explaining the differences in growth rate observed between the charr ecotypes.

Activity rate

The water volume sampled by the SVC ranged from 0.093 to 1.13 m^3 (mean = 0.52 m^3) depending on the filming conditions. Among the 256 recordings, charr were observed swimming in 206 (81 %), and swimming speed could be estimated for 171 (67 %) recordings. Median fish-seconds (FS) observed during a 30 min. recording was 14.0 fish·s, and the maximum value was 823 fish·s (E6, zone D, 13 July, 10:00 AM). Biomass density ($B_{z,t}$) ranged 0-15.15 $g \cdot m^{-3}$ (mean = 1.25 $g \cdot m^{-3}$) among recordings and mean biomass density ($B_{e,t}$) ranged from 2.26 to 3.69 $g \cdot m^{-3}$ among enclosures. No intra-specific or inter-specific aggressive interactions were observed. Mean swimming speed varied 10-fold among recordings and differed among enclosures (Table 4.1). While the absence/presence of trout did not, on its own, affect the swimming speed of charr, the interaction term between ecotype and trout was significant (Table 4.3). On average, the naive ecotype (mean = 15.4 $cm \cdot s^{-1}$) swam 48% faster than the experienced ecotype (mean = 10.3 $cm \cdot s^{-1}$) in the absence of trout whereas this difference decreased to 14% (means: 13.5 and 11.8 $cm \cdot s^{-1}$, respectively) in the presence of trout. Differences between treatment replicates were not statistically significant.

The activity rate of charr varied widely among recordings (Table 4.1), and differed most between sampling zones ($F_{(3,252)} = 15.448$, $p = 2.96 \times 10^{-9}$). On average, activity rate in zones C and D (mean = 2.27 $kJ \cdot kg^{-1} \cdot h^{-1}$) were 3.5 times higher than in zones A and B (mean = 0.64 $kJ \cdot kg^{-1} \cdot h^{-1}$). Activity rate was also influenced by the time of day ($F_{(3,240)} = 3.7889$, $p = 0.01$). The interaction between time of day and the sampling zone was statistically significant (*i.e.* the spatial pattern of charr

activity in the enclosures were influenced by the time of day; $F_{(9,240)} = 3.4142$, $p = 5.70 \times 10^{-4}$). On average, charr were 77% more active during the late morning and the afternoon (mean = 1.77 $kJ \cdot kg^{-1} \cdot h^{-1}$) than during the evening and early morning (mean = 1.00 $kJ \cdot kg^{-1} \cdot h^{-1}$). During the late morning and evening, charr were respectively 4.1 and two times more active in zones C and D (late morning: mean = 2.73 $kJ \cdot kg^{-1} \cdot h^{-1}$; evening: mean = 1.27 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A and B (late morning: mean = 0.66 $kJ \cdot kg^{-1} \cdot h^{-1}$; evening: mean = 0.65 $kJ \cdot kg^{-1} \cdot h^{-1}$), respectively. Moreover, charr were 5.3 times more active in zone C (mean = 2.73 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A, B, and D (mean = 0.51 $kJ \cdot kg^{-1} \cdot h^{-1}$) during the early morning, and 5.8 times more active in zone D (mean = 4.83 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A, B, and C (mean = 0.83 $kJ \cdot kg^{-1} \cdot h^{-1}$) during the afternoon. As a consequence, and in order to increase statistical power, the factors 'sampling zone', 'sampling time of day', and their interaction were added to statistical analyses involving activity rate (*e.g.* among-enclosures, between-treatments and between treatment replicates differences in activity rates and activity patterns).

Hourly activity rate differed among enclosures (table 4.1) and the interaction between enclosure and sampling zone was statistically significant ($F_{(21,212)} = 2.6974$, $p = 1.68 \times 10^{-4}$), indicating that the charr had different spatial patterns of activity among enclosures (Figure 4.4). Hourly activity rate differed significantly between the naive and the experienced charr ecotypes (Table 4.3). The naive ecotype (mean = 1.09 $kJ \cdot kg^{-1} \cdot h^{-1}$) had activity rate 56% lower than the experienced ecotype (mean = 1.70 $kJ \cdot kg^{-1} \cdot h^{-1}$). On average, charr were not more active in the presence of trout, but the effect of the presence of trout on charr activity differed between ecotypes. The presence of trout decreased the activity rate of the naive ecotype by 18% (means: from 1.18 to 1.00 $kJ \cdot kg^{-1} \cdot h^{-1}$) and increased the activity rate of the experienced ecotype by 51% (means: from 1.36 to 2.04 $kJ \cdot kg^{-1} \cdot h^{-1}$). Spatial patterns of activity differed between the two ecotypes. The naive ecotype was only 66% more active in zones C and D (mean = 1.39 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A and B (mean = 0.84 $kJ \cdot kg^{-1} \cdot h^{-1}$) while the experienced ecotype was, on average, 7.3 times more active in zones C and D (mean = 3.14 $kJ \cdot kg^{-1} \cdot h^{-1}$) than in zones A and B (mean: 0.43 $kJ \cdot kg^{-1} \cdot h^{-1}$). Spatial patterns of charr activity were not affected by the presence of

trout ($F_{(3,209)}$ = 1.3107, p = 0.27). Differences between treatment replicates were not statistically significant (Table 4.3). The results highlighted that the charr from the two ecotypes compared in the present study differed in swimming speed, hourly activity rate, and spatio-temporal patterns of habitat use, and that their swimming speed and hourly activity rate was affected differently by the absence or the presence of trout.

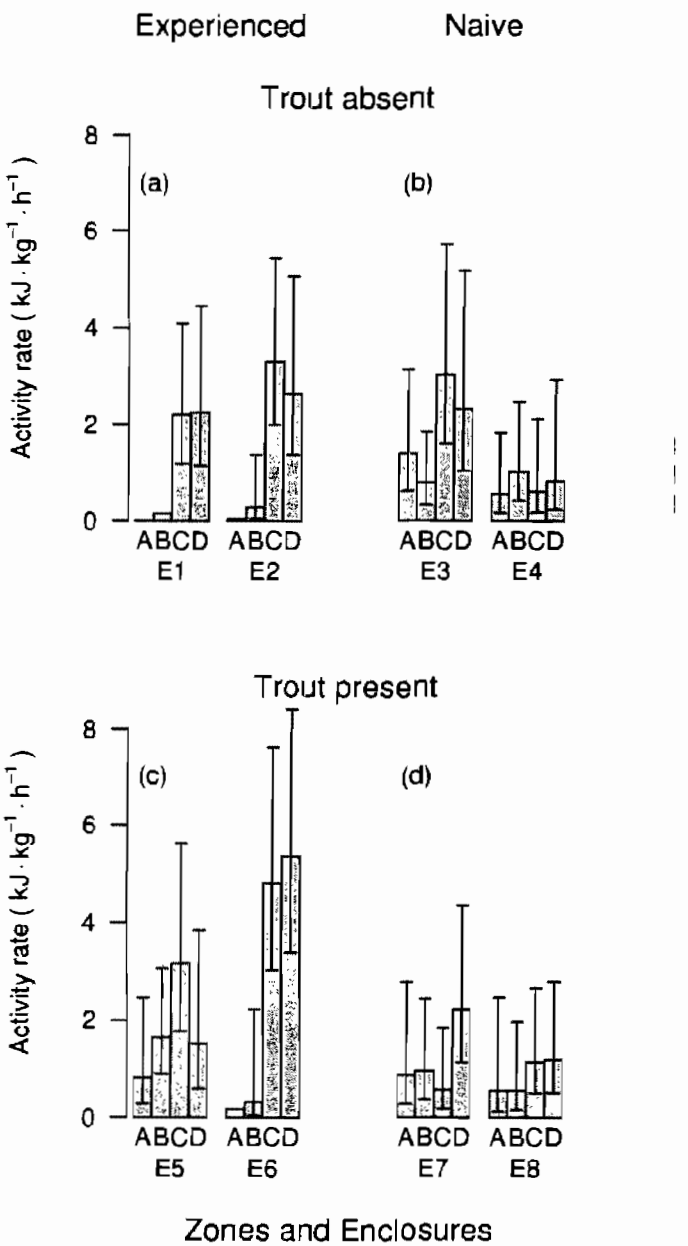

Figure 4.4 Mean hourly activity rate (±95% CL) in the four sampling zones (A, B, C, and D; see Figure 4.2) for experienced and naive Arctic charr in the absence and in the presence of brown trout.

DISCUSSION

The effect of inter-specific competition by trout was detected for the naive and the experienced charr ecotypes. The growth rate of naive and experienced ecotypes was, on average, 36% lower in allopatric than in sympatric enclosures. Similarly, the consumption rate of naive and experienced ecotypes was, on average, 23% higher in allopatric than in sympatric enclosures. Although, the relative magnitude and the direction of the effect of inter-specific competition on growth and consumption rates were similar for the two ecotypes, the effect of trout on the activity rate of charr differed between the two ecotypes. The activity rate of the naive ecotype was 18% higher (not statistically significant; represented similar fractions of the energy budget in allopatry and sympatry: 9.2% and 8.7%, respectively) in allopatric than in sympatric enclosures. However, the activity rate of the experienced ecotype was 51% lower (statistically significant; increase from 24.6% of the energy budget in allopatry to 44.0% of the energy budget in sympatry) in allopatric than in sympatric enclosures. These findings support the hypothesis that at least one element, and namely the activity component, of the energy budget of the two ecotypes of charr may be affected differently by the presence of trout. The results also indicate that the relative magnitude of the effect of trout on activity rate is larger for the experienced than for the naive ecotype. In the case of the naive ecotype, the decrease of growth rate from the allopatric to the sympatric enclosures may be best explained by a simple decrease in consumption rate in the presence of an inter-specific competitor (no statistically significant difference in activity rate). This mechanism is consistent with the classical view regarding the mode of operation of density-dependent processes (competition for food implies decreases in consumption rate; Henderson and Brown 1985, Henderson 1985, Amundsen *et al.* 2007). In contrast, the presence of trout significantly affected both consumption and activity rates of the experienced ecotype. The response of the experienced ecotype to inter-specific competition (*i.e.* decreased growth associated with concomitant decrease of consumption rate and increase of activity rate) is thus similar to that reported in previous studies on the bioenergetic mechanism by which intra-specific competition affects fish

growth (density-dependence; Marchand and Boisclair 1998, Guénard *et al.* In press). The present study therefore suggest that the mechanism by which competition affects fish growth may be similar for intra- and inter-specific competition and that it may vary among ecotypes of a same species.

The results of the present study do not support the hypothesis that inter-specific competition (*i.e.* the presence of brown trout) is the key driving force behind the presumed adaptive divergence between the two charr ecotypes studied. For instance, the absence of trout did not cause a niche expansion of the experienced ecotype. The diet of experienced charr, whether in allopatric or sympatric enclosures, was dominated by planktonic cladocerans (65% to 85% of the diet) despite the fact that zoobenthos, which were available in the enclosures, have been described as more profitable preys (Nilson 1963, Langeland *et al.* 1991). Although it must be recognized that the data on fish diet was taken only at the end of the experiment, it is useful to note that zooplankton did not vary through the experimental period and that zoobenthos was different between allopatric and sympatric enclosures only at the end of the experiment. Hence, diet differences are expected to be particularly evident, if ever, at the end of the experiment. The experienced ecotype was most commonly observed in zones C and D (75% to 98% of fish seconds) whether in the allopatric or the sympatric enclosures. Experienced charr therefore made the same use of the habitats available in the allopatric and the sympatric enclosures and, in absence of trout, did not make a more intense use of the more profitable (*i.e.* containing larger preys) bottom section of the littoral zone. Conversely, the presence of trout did not cause a niche contraction of the naive ecotype. The diet of these charr was always dominated by planktonic copepods (42% to 65 % of the diet) in both the allopatric and the sympatric enclosures. Naive ecotype made a relatively even usage of all zones of the enclosures and this choice was not affected by the absence or presence of trout. However, as anticipated, the fitness of both ecotypes was negatively affected by the presence of trout. The negative effect of trout on the fitness of charr was expressed by a decrease in growth rate (23% decrease for naive ecotype; 53% decrease for the experienced ecotype), a decrease in consumption rate (23% decrease for naive ecotype; 12% decrease

for the experienced ecotype), and, in the case of the experienced ecotype, by a 51% increase in activity rate in sympatric relative to allopatric enclosures. One key objective of the present study was to test the hypothesis that fitness indices of an experienced (and presumably adapted) ecotype may be less affected by the presence of a competitor than a naive (and presumably not-adapted) ecotype. The results of the present study indicate that the naive ecotype more evenly exploits all habitats available in the enclosures, feeds on larger and presumably more profitable preys, has higher growth (190% to 236% difference) and consumption (276% to 302% difference) rates, and lower activity rate (15% to 204% difference) than the experienced ecotype. This situation persisted whether the naive ecotype was held in allopatry or in sympatry. In fact, the naive ecotype held in sympatric enclosures performed better than the experienced ecotype held in allopatric enclosures regardless of the fitness index considered (Table 4.3). Finally, the activity rate of the naive ecotype was not significantly affected by the presence of trout but the activity rate of the experienced charr was 51% higher in sympatric than in allopatric enclosures. The increase of activity rate by experienced charr in the presence of trout may act as a decompensatory mechanism resulting in a lower growth in the presence of a competitor. As a consequence, the naive ecotype always performed better than the experienced ecotype under similar environmental conditions, and this, irrespective of the presence of an inter-specific competitor.

The two ecotypes used for study originated from lakes that differ in several respects beside the absence or presence of trout. Lake Øvre Nonshøtjønn (origin of the naive ecotype) is 121 times smaller and four times shallower (in terms of maximum depth) than Lake Vålvatn (origin of the experienced ecotype). Lake Øvre Nonshøtjønn comprises a proportionally more important littoral zone than Lake Vålvatn (Guénard *et al.* Chapitre 3). Given that the naive ecotype had a wider niche and higher fitness values than the experienced ecotype, and this, irrespective of the presence or absence of trout, it may be hypothesized that the prevalence of littoral habitats in Lake Øvre Nonshøtjønn relative to the situation found in Lake Vålvatn may have been a more potent determinant of the ecological divergence between the two specific ecotypes studied than the presence or absence of trout. The generality of this

observation is impossible to establish until and unless other similar studies are realized. However, the hypothesized role of the physical structure of habitats is consistent with many other studies which identified this type of variable as the driving force of the adaptive divergence of ecotypes inhabiting different ecosystem (Robinson *et al.* 1996, Imre *et al.* 2002, Peres-Neto and Magnan 2004).

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Conclusion

Les résultats détaillés dans les chapitres de la présente thèse illustrent la puissance des méthodes bioénergétiques qui, lorsque appliquées avec rigueur, constituent un source fiable et utile d'informations pour l'étude de divers aspects de l'écologie, des processus adaptatifs, et des sciences environnementales en général. Les contributions présentées dans cette thèse, combinées aux nombreux accomplissements réalisés au cours des quelques cinquante années ayant suivies les travaux de pionniers comme Winberg (1956) témoignent du grand potentiel de ce cadre méthodologique.

SYNTHÈSE

Le premier chapitre de cette thèse a mis en évidence que les méthodes bioénergétique et comportementale d'estimation des taux d'activité peuvent produire des résultats différents. La méthode bioénergétique s'appuie sur plusieurs de prémisses que la méthode comportementale. En plus de nécessiter des estimations précises du taux de consommation, cette méthode requière que l'on dispose de modèles adéquats pour estimer les pertes fécales (F) et d'excrétion (E), le métabolisme standard (SMR) et le métabolisme de digestion (SDA). Les taux d'activité représentent une fraction du taux de consommation et les erreurs d'estimations associées aux modèles précédemment mentionnés peuvent s'accumuler. La méthode bioénergétique implémentée dans le premier chapitre peut donc souffrir de l'inadéquation des prémisses inhérentes à son application. Les erreurs liées à l'estimation du taux de consommation, en particulier celles associées à la stabilité de la quantité et de l'absorption de traceur chimique dans la nourriture, sont particulièrement susceptibles d'affecter les résultats de la méthode bioénergétique. Les résultats du premier chapitre de cette thèse suggèrent qu'il est nécessaire de vérifier ces prémisses (*i.e.* précision des estimations de taux de consommation et adéquation des modèles prédictifs de F, E, SMR et SDA) afin de disposer d'estimations fiables du taux d'activité produites par la méthode bioénergétique. Comme peu de prémisses sont associées à la méthode comportementale, il

est proposé d'utiliser celle-ci, lorsqu'elle est applicable. La méthode comportementale a aussi l'avantage de produire des estimations spécifiques à un endroit et à un temps donné. Dans les travaux subséquents (*i.e.* chapitres 2-4), la méthode comportementale est la seule utilisée pour estimer les taux d'activité. La nature spatialement et temporellement spécifique des estimés d'activité rendus par la méthode comportementale est exploitée dans le troisième chapitre afin de mettre en évidence les différences comportementales entre deux écotypes d'omble chevalier.

Les estimations indépendantes des taux de croissance, de consommation et d'activité pratiquées lors des travaux de cette thèse ont permis d'explorer les mécanismes par lesquels la compétition intra-spécifique (densité: 2^{ième} chapitre) et inter-spécifique (présence de truite brune: 4^{ième} chapitre) affecte la croissance chez l'omble chevalier. Dans ces deux situations, nous avons observé une diminution du taux de croissance liée à une diminution du taux de consommation. En situation de compétition intra-spécifique, la diminution de la consommation ne semble pas opérer de façons semblables à différents niveaux de densité. De plus, une augmentation du taux d'activité, concomitante à la diminution du taux de croissance a aussi été observée dans des traitements de densité croissante. En situation de compétition inter-spécifique, une telle augmentation du taux d'activité n'a été détectée que chez un des écotypes d'omble chevalier étudiés. Ces résultats suggèrent que la croissance est affectée à la fois par la compétition intra-spécifique et la compétition inter-spécifique par le truite brune. Il apparaît cependant que les mécanismes bioénergétiques par lesquels ces facteurs opèrent puissent varier au sein d'une même espèce, illustrant la complexité des conséquences bioénergétiques associées aux interactions entre compétiteurs.

Les outils bioénergétiques utilisés dans la présente thèse ont permis à la fois d'explorer les différences comportementales entre deux écotypes d'une espèce polymorphe et de quantifier leurs aptitudes respectives à utiliser la zone littorale des lacs (3^{ième} chapitre). En plus d'être distincts sur le plan morphologique et comportemental, ces écotypes ont démontré des aptitudes différentes à exploiter les ressources de la zone littorale des lacs. Les résultats d'une autre étude (4^{ième} chapitre) suggèrent que

la compétition inter-spécifique par la truite brune dans la zone littoral des lacs n'est pas le principal facteur expliquant la différentiation des écotypes d'omble chevalier. Nous suggérons que d'autre facteurs, en particulier la structure des habitats disponibles au sein des écosystèmes pour lesquels ces écotypes se sont adaptés, peuvent agir de façons simultanées.

PERSPECTIVES

Les travaux effectués au cours de la présente thèse ont permis de produire des apports substantiels à l'avancement de nos connaissances, notamment en ce qui concerne les mécanismes de la compétition, la quantification des différences fonctionnelles associées à la diversité intra-spécifique (*i.e.* inter-ecotypes) et l'importance de la compétition comme facteur de diversification. Ces travaux ont aussi permis de mettre en évidence certains besoins. Dans cette perspective, citons trois avenues de recherche qui devraient retenir l'attention : 1) augmenter la fiabilité des méthodes utilisant des marqueurs chimiques estimer de la consommation, 2) augmenter l'efficacité opérationnelle des outils bioénergétiques et 3) estimer la transférabilité des outils bioénergétiques entre espèces et entre écotypes d'une même espèce.

Marqueurs chimiques et consommation

Les méthodes d'estimation de la consommation utilisant des marqueurs chimiques (*e.g.* Cs, Hg total, Me-Hg, BPC, DDE) requièrent la connaissance de quatre quantités fondamentales, soit 1) la charge de marqueur mesurable (Q_M), 2) la charge de marqueur éliminée (Q_E), 3) la concentration de marqueur présente dans la nourriture ($[Q]$) et 4) la proportion de marqueur ingéré qui est assimilé (α), afin de pouvoir calculer la quantité de nourriture ingérée (Équations I.6-I.8). Lors des calculs, on pose souvent comme prémisse que la variation de Q_M dans le temps est décrite par une fonction linéaire. Bien qu'il est probable cette prémisse soit adéquate à petite échelle de temps (*e.g.* un mois), il est envisageable qu'elle ne le soit pas à une plus grande échelle (*e.g.* un an, la durée de vie de l'organisme).

Dans ce cas, le calcul de la charge de traceur ingérée (Q_I) dans l'intervalle de temps et, de ce fait, le taux de consommation, pourraient être biaisés de différentes façons. Ce phénomène devrait, par conséquent, faire l'objet d'une attention particulière lorsque des estimés de consommation à long terme seront requis. Une attention semblable devrait aussi être portée en ce qui concerne la stabilité temporelle de la concentration du marqueur dans la nourriture et la proportion de marqueur assimilée. Le choix d'un marqueur chimique adéquat apparaît donc comme crucial pour les utilisateurs de telles méthodes.

Efficacité opérationnelle des outils bioénergétiques

Dans l'avenir, des efforts devront être déployés afin d'augmenter l'efficacité opérationnelle des outils bioénergétiques. Plus particulièrement, il serait souhaitable de revoir l'implémentation mathématique des modèles de bilan énergétique. L'approche actuellement employée consiste à estimer chacun des compartiments du bilan énergétique (Equation I.1) à l'aide de sous-modèles. Ces sous-modèles sont eux-mêmes construits à partir de données provenant d'expériences dédiées à leur estimation respective. Ce mode de construction néglige cependant les interactions possibles entre les différents compartiments (*e.g.* $A - SDA$; Beamish 1974) et implique un découplage entre les observations (*i.e.* les observations ne sont pas effectuées sur les mêmes individus d'un sous-modèle à un autre). Cette situation représente une source d'erreur substantielle (*i.e.* cas où l'équation I.1 n'est pas balancée) et pourrait être corrigée. Dans un premier temps, un protocole expérimental doit être créé et des moyens techniques développés afin de générer des jeux de données exhaustifs de l'ensemble des compartiments du bilan énergétique des mêmes individus (*e.g.* par respirométrie ou electro-physiologie). Disposant de telles données, des modèles prédictifs de l'intégralité des flux énergétiques et s'appuyant sur des variables explicatives (*e.g.* masse, température, vitesse de nage) pourraient être construits. Des méthodes de modélisation issue de la recherche sur l'intelligence artificielle (*e.g.* réseaux de neurones artificiels) pourraient être utilisées à cet escient. De cette manière, il serait possible d'appliquer le principe thermodynamique de conservation de l'énergie d'une manière explicite,

dès la construction des modèles, plutôt que de simplement l'utiliser comme prémisse lors de leur utilisation. Un modèle de ce type pourrait être qualifié de « modèle énergétique intégré » (MEI; *anglais* : Integrated Energetic Model, IEM).

Transférabilité des outils bioénergétiques

À l'heure actuelle, la bioénergétique souffre principalement du manque de données sur un ensemble plus vaste d'espèces et de groupes taxonomiques. Bien que des sous-modèles aient été construits pour un certain nombre d'espèces de poissons (Hanson *et al.* 1997), nous ne disposons pas encore de telles informations pour un grand nombre d'entre elles. Cette situation incite à l'emprunt de paramètres d'une espèce à une autre et ce, malgré qu'il ait été rapporté qu'une telle pratique puisse représenter une source substantiel de bias d'estimation (*i.e.* Trudel and Welsh 2005). De plus, il est possible que les différences morphologiques observées au sein d'une même espèce (*e.g.* inter-écotypes) soient aussi couplées à des différences physiologiques substantielles. Il est donc nécessaire que des moyens de recherche (financiers et logistiques) plus adéquats soient rendus disponibles afin de quantifier adéquatement de quelles manières les paramètres associés aux compartiments du bilan énergétique fluctuent, à différentes échelles, dans l'espace phylogénétique. Dans ce contexte, les modèles énergétiques intégrés (MEI), une fois rendus disponibles, pourraient constituer une base opérationnelle solide pour l'analyse de ces fluctuations.

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Annexes

ANNEXE 1

Tableau A1.1 Conditions rencontrées dans les enclos lors des travaux réalisés à Songli, Norvège au cours des étés 2000 et 2001.

Année	Enclos	Nom attribués dans les chapitres				Nombre de poissons (début ; fin)		Origine des ombles**	Volume [zone*] (m^3)					Durée	Numéros des Poissons
		1	2	3	4	Omble	Truite		A	B	C	D	Total		
2000	1	E1	E3			20 ; 19	0	V	129	47			177	31	1 - 20
	2		E1			10 ; 8	0	V	130	47			177	31	21 - 30
	3		E5			40 ; 36	0	V	130	47			178	30	31 - 70
	4	E2	E4			20 ; 12	0	V	129	46			175	29	71 - 90
	5		E2			10 ; 7	0	V	130	45			175	30	91 - 100
	6		E6			40 ; 38	0	V	122	45			167	30	101 - 140
2001	1				E7	15 ; 14	9 ; 9	ØN	41	53	32	31	158	43	1-5; 21-25; 56-60 Truites: 130-138
	2	E3		E1	E1	15 ; 12	0	V	37	50	32	31	151	43	61-65; 96-113; 116; 120
	3	E5		E3	E3	15 ; 13	0	ØN	32	48	33	29	144	43	6-10; 26-30; 51-55
	4				E5	15 ; 14	9 ; 8	V	32	49	34	33	148	43	66-71; 91-95; 102; 106-109 Truites: 121-129
	5				E8	15 ; 14	9 ; 9	ØN	33	51	32	37	153	44	11-15; 31-35; 46-50 Truites: 148-156
	6				E6	15 ; 14	9 ; 9	V	35	52	32	36	156	44	69; 72; 74-76; 86-90; 114-115; 117-119 Truites: 139-147
	7	E6		E4	E4	15 ; 13	0	ØN	31	49	33	34	147	44	16-20; 36-45
	8	E4		E2	E2	15 ; 11	0	V	32	48	33	30	143	44	73; 77-85; 101; 103-105; 110

* Dans l'article rapporté au premier chapitre de la présente thèse, les zones A-D des enclos E3-E6 sont représentés par les lettres C-F

** V : lac Våvatn, ØN : lac Øvre Nonshøtjønn

Tableau A1.2 Masses initiale et finale, pourcentage de masse sèche / masse humide et concentration de césium mesurées dans les ombles chevaliers utilisés lors de l'expérience réalisée à l'été 2000 à Songli, Norvège.

#	Masse		Pourcentage de masse sèche / humide	[Cs] ($ng \cdot g^{-1}$)
	Initiale	Finale		
1	19.6	24.9	22.0	12.97
2	21.4	28.8	23.2	24.37
3	22.7	31.4	23.9	23.45
4	15.2	24.4	23.2	22.98
5	18.1	24.6	22.6	23.24
6	30.7	33.5	22.6	24.87
7	23.9	31.1	23.2	22.94
8	31.3	37.5	23.3	26.36
9	23.8	32.4	22.9	22.93
10	26.3	33.8	23.7	22.04
11	27.8	37.2	24.0	21.40
12	28.2	35.4	22.8	25.36
13	23.2	30.6	23.1	24.25
14	25	33.9	23.3	24.27
15	26.9	35.1	24.0	29.33
16	15.4	21.8	24.1	25.30
17	18	NA	NA	NA
18	19	31.9	24.2	19.57
19	15.8	23.9	23.6	19.12
20	18.3	25.4	23.3	20.97
21	24.3	34.1	23.1	31.43
22	27.3	34.7	23.6	20.78
23	19.3	32.9	24.3	17.95
24	15.3	23.3	22.6	21.69
25	27	35.1	22.2	23.29
26	28.7	42.2	24.4	20.50
27	23.1	NA	NA	NA
28	20.9	25.9	22.5	19.57
29	18.1	NA	NA	NA
30	18.5	26.4	22.4	19.27
31	17.5	24.2	22.6	17.88
32	18.8	23.6	NA	NA
33	22.9	28	23.0	12.86
34	32.9	38.4	22.4	22.80
35	33.3	36.4	22.3	19.87
36	13.4	17.2	22.8	19.60
37	19.7	31.9	24.3	20.91
38	27.6	31.8	22.7	17.46
39	28.8	32.4	NA	NA

#	Masse		Pourcentage de masse sèche / humide	[Cs] ($ng \cdot g^{-1}$)
	Initiale	Finale		
71	21.4	31.3	24.6	18.45
72	15.3	22.3	22.7	24.95
73	28	NA	NA	NA
74	19.8	24.7	25.5	22.73
75	28.3	35	22.4	20.64
76	22	NA	NA	NA
77	19.2	24.6	18.8	16.56
78	15.2	19.1	22.3	23.88
79	16.9	NA	NA	NA
80	29.5	NA	NA	NA
81	19.5	NA	NA	NA
82	16.9	24	23.0	23.00
83	15.6	27.3	22.5	22.98
84	25.6	NA	NA	NA
85	24.8	30.7	21.2	23.97
86	29.4	33.3	21.5	21.91
87	32.7	38.4	22.9	22.40
88	21.3	NA	NA	NA
89	16.9	25.5	23.4	19.68
90	21.4	NA	NA	NA
91	19.8	27.8	23.3	23.08
92	14.4	NA	NA	NA
93	15.7	26.9	22.6	18.33
94	22.3	33.8	23.5	22.33
95	29.7	38.3	23.1	17.81
96	26	37.6	22.7	20.87
97	24	34	22.7	18.61
98	32.8	NA	NA	NA
99	21.6	32.3	22.9	20.83
100	17.4	NA	NA	NA
101	28	30.5	NA	NA
102	31.2	35.6	23.2	27.83
103	17.7	21.5	NA	NA
104	15.5	21.2	21.7	22.59
105	31.1	33.7	21.9	19.31
106	17.7	21.5	NA	NA
107	33.6	36.1	21.4	24.39
108	15	19.2	22.0	20.49
109	24.8	NA	NA	NA

#	Masse		Pourcentage de masse sèche / humide	[Cs] ($ng \cdot g^{-1}$)
	Initiale	Finale		
40	23.2	NA	NA	NA
41	18.3	23.4	NA	NA
42	22.8	27.3	NA	NA
43	28.3	37	NA	NA
44	20.9	25.3	22.4	24.46
45	28.8	38.8	23.7	21.13
46	22.6	NA	NA	NA
47	26.3	26.5	21.5	27.48
48	19.3	23.3	22.5	21.12
49	26.5	30.5	23.1	24.25
50	32.2	34.8	22.7	25.84
51	25.1	28.4	NA	NA
52	30.3	34.4	NA	NA
53	23.2	26.5	NA	NA
54	30.4	35.3	NA	NA
55	27.9	32	22.4	22.60
56	19.3	21.3	NA	NA
57	16.8	NA	NA	NA
58	15.2	20.3	23.3	24.44
59	17.6	20.2	21.1	22.84
60	32.9	37.6	21.7	18.44
61	29.4	34.2	NA	NA
62	16.7	23.7	NA	NA
63	15.9	21.5	22.0	17.13
64	19.5	26.5	24.2	23.20
65	22.1	25	NA	NA
66	23.3	28.1	NA	NA
67	17.4	21.1	NA	NA
68	16.2	24.1	23.3	24.96
69	17.8	NA	NA	NA
70	18.8	24.8	NA	NA

#	Masse		Pourcentage de masse sèche / humide	[Cs] ($ng \cdot g^{-1}$)
	Initiale	Finale		
110	21.5	26.2	NA	NA
111	27.7	31.7	NA	NA
112	15.5	20.7	22.0	20.67
113	21.2	24.3	21.6	20.05
114	19.5	22.9	NA	NA
115	15.7	21.9	23.2	23.01
116	20	22.3	22.1	22.72
117	17.4	21.3	22.4	21.98
118	31.5	34.7	NA	NA
119	32.5	35.2	NA	NA
120	22.4	27.7	22.1	22.28
121	23.8	27.7	21.8	24.18
122	26.2	28.9	NA	NA
123	25.6	29.5	NA	NA
124	18.3	23.1	NA	NA
125	31.2	32.7	22.4	22.87
126	25.9	29.4	22.1	21.40
127	19.5	24.5	NA	NA
128	20.6	25.7	NA	NA
129	21.3	25.4	NA	NA
130	18.8	22.4	NA	NA
131	30.9	36.4	22.9	18.54
132	14.7	18.5	NA	NA
133	23.9	27.2	22.7	21.59
134	27.3	32.1	NA	NA
135	23	26.6	NA	NA
136	33	34.6	23.1	21.24
137	19.7	23.1	21.9	16.23
138	25.1	28.3	22.7	22.93
139	19.6	23.5	22.8	20.04
140	26.1	NA	NA	NA

Tableau A1.3 Masses initiale et finale, pourcentage de masse sèche / masse humide et concentration de césium mesurées dans les ombles chevaliers utilisés lors de l'expérience réalisée à l'été 2001 à Songli, Norvège.

#	Masse		Pourcentage de Masse sèche / humide	[Cs] ($ng \cdot g^{-1}$)	#	Masse		Pourcentage de Masse sèche / humide	[Cs] ($ng \cdot g^{-1}$)
	Initiale	Finale				Initiale	Finale		
1	17.9	29.7	23.5	56.69	61	20.6	25.5	24.1	15.96
2	13.3	25.3	23.4	48.73	62	27.2	NA	NA	NA
3	16.5	21.4	22.5	44.46	63	30.9	32.4	21.5	27.96
4	12.1	14.6	20.2	31.87	64	54.6	NA	NA	NA
5	10.9	NA	NA	NA	65	38.0	34.9	20.9	26.13
6	14.7	22.8	23.2	46.63	66	28.9	33.1	22.1	19.06
7	10.2	NA	NA	NA	67	26.6	29.9	21.8	17.95
8	11.3	22.9	22.4	62.25	68	52.5	48.3	20.4	22.12
9	10.8	15.2	24.4	37.39	69	45.7	47.0	21.3	18.98
10	17.8	27.0	24.6	40.27	70	30.7	32.7	22.3	21.96
11	13.7	16.5	20.4	34.02	71	28.3	33.5	22.3	29.04
12	16.6	27.7	24.6	51.20	72	26.3	29.9	22.1	18.87
13	10.0	15.7	22.3	56.95	73	55.5	64.7	23.0	43.86
14	17.3	20.4	22.5	47.79	74	24.2	32.2	22.8	17.80
15	12.4	16.3	22.0	37.00	75	39.2	43.7	21.2	16.08
16	17.3	20.0	21.3	44.35	76	28.9	28.5	20.5	21.62
17	12.4	19.1	23.7	73.34	77	22.8	31.0	23.4	19.26
18	11.5	NA	NA	NA	78	36.8	47.5	23.5	16.92
19	17.5	24.4	23.2	51.28	79	28.9	NA	NA	NA
20	11.8	21.0	23.3	55.62	80	22.1	NA	NA	NA
21	28.5	41.3	24.3	51.43	81	13.0	17.4	21.0	22.58
22	28.2	35.2	24.9	44.89	82	16.1	NA	NA	NA
23	24.9	38.0	25.5	56.57	83	17.0	26.7	24.1	15.08
24	19.1	34.7	24.3	55.20	84	15.3	22.2	22.8	17.48
25	34.0	48.2	25.3	60.34	85	18.6	24.6	22.6	21.11
26	25.0	40.7	25.8	53.44	86	20.7	28.9	23.1	20.74
27	25.3	44.3	23.7	57.37	87	17.2	20.5	22.9	20.70
28	32.0	41.9	25.0	65.20	88	15.0	17.3	21.3	21.28
29	27.7	41.3	25.7	48.22	89	18.8	24	22.7	14.39
30	20.9	24.3	23.2	39.24	90	15.8	20.2	22.5	17.90
31	24.3	30.7	24.7	53.44	91	16.5	21.9	22.0	20.88
32	28.3	37.4	23.3	49.21	92	17.5	23.8	23.5	16.63
33	18.5	21.5	22.4	31.09	93	15.8	19.2	22.2	18.80
34	16.6	26.5	23.2	62.45	94	20.6	24.0	22.7	17.20
35	25.5	32.4	24.8	50.34	95	20.0	24.8	22.2	18.29

#	Masse		Pourcentage de Masse sèche / humide	[Cs] ($ng \cdot g^{-1}$)
	Initiale	Finale		
36	26.0	NA	NA	NA
37	21.2	36.6	24.6	60.37
38	20.8	27.3	22.5	41.96
39	13.3	23.5	25.2	37.69
40	32.7	43.4	24.2	46.39
41	36.5	48.2	24.8	57.73
42	41.9	43.6	24.1	34.93
43	41.5	52.9	24.8	53.90
44	51.8	65.0	24.2	63.53
45	36.6	44.4	24.5	64.26
46	49.6	55.9	24.1	54.92
47	37.7	42.4	23.9	36.42
48	57.0	NA	NA	NA
49	37.2	41.0	23.2	51.69
50	41.3	48.3	23.2	36.32
51	40.4	51.8	24.9	47.16
52	47.3	57.6	24.5	55.57
53	35.5	44.2	24.0	49.19
54	43.4	NA	NA	NA
55	45.5	56.5	24.9	41.52
56	50.7	58.6	25.4	52.33
57	44.1	55.6	25.1	49.03
58	34.1	39.4	24.6	24.58
59	38.6	52.5	25.0	69.08
60	39.1	44.2	25.2	49.91

#	Masse		Pourcentage de Masse sèche / humide	[Cs] ($ng \cdot g^{-1}$)
	Initiale	Finale		
96	17.5	21.3	22.4	28.32
97	17.2	20.0	22.3	19.23
98	15.1	15.9	21.4	19.56
99	20.2	28.2	23.3	18.68
100	14.2	21.5	23.3	18.15
101	20.0	27.7	22.8	17.08
102	17.1	20.9	22.2	20.59
103	21.2	29.9	24.2	17.83
104	16.5	21.6	22.6	19.27
105	23.0	NA	NA	NA
106	18.6	23.2	21.9	18.05
107	17.3	20.0	21.9	19.38
108	18.8	NA	NA	NA
109	14.8	15.7	21.9	23.52
110	16.7	21.2	19.5	18.33
111	19.2	25.9	23.5	20.04
112	15.1	22.2	23.2	17.74
113	16.7	NA	NA	NA
114	20.6	25.8	23.2	21.99
115	15.7	21.2	21.4	16.69
116	16.9	19.4	23.3	19.39
117	16.1	NA	NA	NA
118	21.6	28.4	22.4	24.56
119	16.2	18.7	21.7	15.32
120	24.1	31.0	24.0	18.57

Tableau A1.4 Masses initiale et finale des truites brunes utilisées lors de l'expérience réalisée à l'été 2001 à Songli, Norvège.

#	Masse		#	Masse		#	Masse	
	Initiale	Finale		Initiale	Finale		Initiale	Finale
121	48.3	44.9	133	41.8	42.7	145	28.0	42.3
122	37.2	52.9	134	27.7	29.7	146	25.1	41.1
123	36.6	42.4	135	35.3	46.1	147	22.9	40.8
124	35.1	NA	136	44.2	44.6	148	49.4	63.0
125	37.8	43.0	137	20.8	24.8	149	36.3	46.2
126	33.2	40.8	138	22.3	27.4	150	42.2	47.9
127	39.7	44.2	139	43.3	48.4	151	18.7	36.5
128	20.9	29.5	140	32.4	29.9	152	35.8	44.3
129	19.3	31.5	141	33.5	37.7	153	43.8	44.5
130	36.5	39.2	142	38.2	57.3	154	44.9	54.8
131	22.7	34.9	143	53.3	68.0	155	18.8	27.4
132	54.7	54.5	144	31.9	43.8	156	18.2	30.8

Tableau A1.5 Mesures morphologiques (mm) réalisées sur les ombles chevaliers utilisées lors de l'expérience réalisée à l'été 2001 à Songli, Norvège.

a) Variables HEAD1 à BODY09

#	L_F	HEAD 1	HEAD 2	HEAD 3	HEAD 4	HEAD 5	BODY 01	BODY 02	BODY 03	BODY 04	BODY 05	BODY 06	BODY 07	BODY 08	BODY 09
1	144.3	25.5	12.2	17.9	23.7	23.8	39.8	37.0	46.3	30.5	19.1	29.0	50.6	42.1	29.5
2	138.4	24.0	10.7	16.2	21.8	21.7	36.3	35.9	44.8	30.1	19.0	25.5	47.8	39.5	28.1
3	132.1	19.6	11.7	15.7	18.2	20.0	37.5	37.0	40.8	27.6	16.0	26.3	49.4	37.3	25.8
4	122.3	19.8	10.2	15.3	17.6	18.6	35.0	33.4	37.0	25.2	15.0	20.9	44.8	33.8	21.7
5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	138.8	22.4	12.3	16.0	19.9	21.3	36.5	36.7	45.0	30.2	16.5	27.0	48.6	37.6	26.0
7	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	137.1	23.6	12.2	15.8	21.8	21.6	35.0	35.1	46.5	28.6	18.2	26.5	46.7	37.9	26.9
9	122.2	19.9	10.7	16.1	17.9	20.1	32.4	31.6	40.1	25.5	15.1	22.9	43.4	33.5	24.0
10	145.8	22.2	12.6	17.2	19.5	22.6	42.6	39.4	46.9	31.3	18.2	28.1	53.5	41.7	28.1
11	126.4	21.8	10.5	17.0	19.7	19.4	32.2	32.2	40.2	25.7	16.6	24.1	43.0	33.7	22.8
12	142.8	22.7	10.6	17.8	21.0	21.9	39.9	41.5	45.7	28.6	17.9	27.9	53.6	41.6	28.5
13	116.2	20.8	10.6	12.9	18.7	18.9	31.3	31.8	35.8	22.6	14.4	22.2	41.8	34.3	23.9
14	132.0	20.8	12.3	15.5	19.4	20.3	38.3	37.7	40.8	28.1	16.7	23.4	49.1	38.6	24.5
15	122.8	20.9	11.2	14.1	18.7	19.2	31.1	31.4	39.0	26.3	17.6	23.0	41.7	33.6	23.5
16	131.9	21.8	12.9	15.8	19.4	20.6	36.1	35.1	40.6	26.3	15.8	24.8	46.8	36.9	25.2
17	126.8	21.3	12.1	14.8	19.3	19.1	34.4	33.0	39.4	28.4	17.7	23.1	44.5	35.9	26.0
18	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
19	131.1	23.7	12.5	17.6	21.8	21.6	34.3	34.2	41.0	25.5	15.1	24.6	46.2	37.4	27.6

#	L_F	HEAD 1	HEAD 2	HEAD 3	HEAD 4	HEAD 5	BODY 01	BODY 02	BODY 03	BODY 04	BODY 05	BODY 06	BODY 07	BODY 08	BODY 09
20	131.8	21.9	9.3	17.6	20.6	20.8	35.7	35.7	44.3	27.0	15.4	24.6	47.2	37.7	26.9
21	169.3	28.5	13.5	18.6	26.0	25.3	44.6	43.6	57.3	37.8	22.0	31.9	56.0	48.3	31.6
22	153.2	26.3	14.5	17.4	23.0	24.2	40.0	38.3	49.4	34.2	17.1	28.9	52.1	42.6	31.0
23	159.8	26.1	12.3	18.2	24.1	24.3	43.6	43.6	52.3	33.0	19.4	30.9	56.6	46.4	32.2
24	158.8	26.4	13.3	17.6	24.0	24.0	43.5	42.4	52.1	34.1	22.3	29.4	55.3	45.7	30.4
25	171.5	27.9	13.7	18.0	25.2	25.4	46.2	48.7	57.6	36.5	20.9	33.2	61.6	49.6	34.2
26	160.0	25.8	15.4	20.1	23.3	26.3	43.9	40.9	51.0	32.0	19.7	33.3	57.2	45.7	34.3
27	173.8	27.0	15.4	18.9	24.6	26.7	47.8	46.9	60.7	36.5	19.5	33.5	61.8	49.4	32.9
28	170.0	27.4	14.2	21.0	25.1	25.2	48.5	44.7	53.5	36.7	22.5	32.3	59.3	49.6	33.2
29	169.8	26.6	13.5	19.3	25.2	24.9	46.4	47.2	56.8	37.2	20.8	33.1	60.6	48.6	32.2
30	145.5	24.3	12.0	19.1	22.4	21.8	39.0	38.9	49.6	30.2	16.0	26.9	50.8	40.7	27.0
31	150.3	25.4	13.6	15.3	22.0	22.3	40.7	41.5	50.4	30.6	17.6	27.7	52.8	43.9	29.6
32	163.4	22.2	13.4	19.7	22.4	24.9	49.5	44.8	52.1	33.6	21.0	30.9	60.5	47.9	30.9
33	137.1	22.8	12.2	17.2	21.0	21.1	38.3	36.6	43.3	27.6	17.6	26.2	48.1	39.4	25.6
34	142.3	23.3	13.2	16.6	21.0	22.2	39.6	37.7	46.9	28.6	17.8	27.3	51.2	40.8	29.4
35	153.2	23.0	13.1	18.0	21.6	23.4	44.0	41.0	48.9	34.0	18.6	27.9	55.1	44.1	29.7
36	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
37	156.2	24.7	11.2	20.0	23.7	24.0	44.2	44.0	52.0	32.6	19.8	29.8	56.6	46.2	30.5
38	145.2	25.5	11.3	18.9	23.4	22.7	40.0	38.7	45.0	33.7	19.0	26.9	51.0	41.8	27.1
39	136.6	24.0	11.1	16.5	21.4	21.4	34.8	37.7	44.0	28.7	16.2	26.2	48.4	38.6	27.8
40	165.1	26.9	12.8	19.3	24.9	24.9	45.6	45.1	52.8	34.6	22.0	34.6	58.7	48.7	34.3
41	173.3	26.5	15.1	20.4	26.2	26.6	48.7	49.9	55.4	39.1	22.5	30.3	64.1	50.1	32.5
42	170.0	29.2	14.1	20.3	25.0	25.2	45.3	47.1	53.8	36.6	21.7	32.8	59.2	49.0	32.5
43	185.0	29.8	16.0	22.2	27.0	27.6	48.3	49.5	64.7	38.7	21.5	36.1	64.3	51.0	36.0
44	191.7	33.8	15.3	23.8	30.0	28.7	52.0	50.5	59.7	41.5	23.2	35.8	66.4	55.2	38.0
45	170.1	28.3	13.5	20.8	25.0	25.5	45.9	45.7	55.5	37.9	23.4	29.7	59.5	49.0	33.7
46	188.2	31.9	16.2	22.5	29.3	28.0	50.2	53.7	61.2	39.1	23.2	34.5	66.9	54.2	35.6
47	166.9	28.1	12.7	19.7	26.5	25.6	47.5	45.2	51.7	36.5	21.9	32.5	58.0	50.3	31.7
48	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
49	166.6	28.0	13.6	21.6	26.0	24.8	45.7	43.4	52.6	36.7	21.4	31.9	57.0	47.5	31.1
50	175.5	30.0	14.6	21.1	27.6	26.7	44.9	46.6	57.3	34.4	22.5	36.6	60.4	48.5	33.8
51	180.4	30.2	16.2	22.3	27.1	27.3	47.8	48.3	59.2	34.4	21.6	36.4	64.3	50.0	36.0
52	190.4	30.0	16.1	22.4	28.1	29.1	49.9	52.5	66.4	39.9	22.1	35.6	67.7	52.8	35.2
53	173.0	28.7	14.4	21.4	26.5	26.6	50.0	46.4	54.9	37.5	20.6	32.3	61.3	51.3	33.1
54	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
55	185.8	30.5	15.8	22.5	28.0	27.5	51.6	47.7	61.3	37.5	21.9	40.2	63.8	53.8	37.3
56	187.7	31.1	16.9	21.6	26.9	28.0	48.7	51.0	62.4	40.1	23.3	37.0	66.5	50.7	34.8
57	178.4	29.0	14.8	20.6	26.9	27.2	49.2	49.4	61.1	36.0	21.5	33.4	63.3	52.8	36.0
58	163.3	26.6	15.1	18.7	22.6	24.3	45.6	42.7	50.7	33.8	21.1	31.8	56.4	47.2	31.7
59	176.0	29.6	14.5	18.2	25.9	25.3	47.4	48.8	57.8	38.7	21.7	34.1	62.5	50.3	35.7
60	172.4	29.7	15.6	16.0	26.1	26.1	45.5	47.9	56.3	35.9	20.4	35.9	59.1	50.8	32.8
61	141.1	25.5	11.4	17.4	23.4	22.5	36.0	37.4	46.9	29.7	16.6	27.3	49.2	40.0	29.6
62	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

#	L_F	HEAD 1	HEAD 2	HEAD 3	HEAD 4	HEAD 5	BODY 01	BODY 02	BODY 03	BODY 04	BODY 05	BODY 06	BODY 07	BODY 08	BODY 09
63	160.2	29.6	14.4	20.7	26.5	25.5	39.6	42.2	53.9	32.8	20.2	27.7	55.2	44.0	32.4
64	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
65	164.6	28.6	13.7	19.1	26.0	26.0	44.9	45.8	54.3	35.6	18.1	33.9	59.1	47.2	30.5
66	156.3	26.7	12.0	19.1	24.5	23.1	42.0	40.6	53.4	36.4	18.4	29.4	53.8	43.4	29.3
67	150.5	23.8	13.0	16.3	21.2	22.2	36.7	44.2	52.6	32.2	18.2	29.8	53.6	40.9	28.6
68	183.6	33.0	18.0	21.3	30.1	29.3	48.9	48.1	59.0	39.5	21.8	36.3	64.3	51.0	34.3
69	177.8	28.3	14.9	20.9	24.6	26.7	46.9	48.9	59.1	38.7	21.0	35.3	63.4	48.8	34.5
70	154.3	27.7	13.3	19.0	24.2	24.1	38.6	41.3	49.8	31.6	18.3	30.4	53.4	42.4	30.3
71	153.8	26.0	12.5	20.2	24.0	24.6	43.0	40.5	49.5	32.1	18.3	31.2	54.3	45.4	30.9
72	153.2	25.7	12.7	18.5	23.1	22.9	38.5	41.8	53.0	30.5	20.2	29.9	53.6	41.4	29.7
73	188.3	28.1	14.1	21.5	28.3	30.3	51.1	54.7	65.5	41.2	20.8	36.9	70.2	54.9	38.0
74	152.0	25.3	13.4	17.5	21.7	23.8	40.0	41.6	52.0	31.7	17.5	28.5	54.7	42.2	30.9
75	172.0	31.2	16.5	18.6	28.4	27.7	44.9	48.0	57.8	35.4	20.4	34.3	61.2	49.5	33.0
76	150.4	24.7	13.6	18.4	22.2	24.1	38.9	40.2	48.7	33.5	19.0	28.3	53.3	42.0	30.6
77	149.2	24.5	12.0	17.4	22.6	23.8	41.0	41.8	50.2	31.5	17.6	27.5	54.3	43.8	30.0
78	171.8	29.3	12.5	21.2	27.0	26.2	46.8	48.5	58.0	38.2	19.6	32.0	61.5	50.8	34.5
79	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
80	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
81	126.2	22.5	11.2	15.1	20.0	20.1	33.5	35.3	41.4	26.3	16.1	22.6	45.0	35.9	23.5
82	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
83	143.4	23.2	12.8	15.2	20.6	21.7	40.8	40.0	47.8	30.3	15.0	27.9	50.8	43.0	26.8
84	135.3	23.1	11.7	16.8	21.6	21.3	35.2	37.0	43.9	28.5	18.3	28.1	48.0	37.6	26.1
85	140.2	26.2	11.4	17.0	23.1	21.9	34.8	38.4	48.6	29.1	13.8	27.5	48.2	39.0	26.5
86	143.9	25.6	11.6	17.2	23.5	23.6	36.8	38.0	48.5	32.0	18.0	27.0	48.8	42.1	29.0
87	134.4	23.1	10.5	16.9	20.6	20.0	33.9	36.3	45.3	26.9	18.5	26.3	46.6	36.3	25.5
88	127.8	22.5	11.9	15.1	19.7	19.8	32.7	33.0	42.5	27.5	18.2	24.9	44.1	34.3	24.5
89	136.2	24.9	11.7	17.1	22.1	22.0	34.1	35.4	45.1	28.5	18.0	26.5	47.0	37.5	27.6
90	132.8	23.3	12.0	16.6	20.6	21.4	34.2	34.8	44.3	28.3	15.8	27.0	46.4	36.6	25.6
91	135.7	22.3	11.3	17.8	20.2	21.2	34.9	37.5	46.4	26.5	15.3	25.9	48.6	37.2	25.6
92	138.2	23.8	12.9	16.3	19.7	21.8	36.2	36.7	47.4	30.1	14.6	24.7	48.7	38.7	28.2
93	130.5	25.0	11.7	16.3	22.2	21.0	32.0	33.7	43.3	27.6	16.7	24.6	44.4	36.1	25.8
94	138.4	23.0	11.7	17.9	21.4	22.0	36.9	38.2	45.9	28.2	15.0	27.2	50.6	38.5	27.1
95	136.8	23.3	10.2	17.6	21.6	22.1	36.3	38.2	44.4	29.1	18.1	25.8	50.0	38.8	27.4
96	136.6	23.1	11.7	17.1	20.4	21.2	34.7	37.9	47.2	27.9	15.1	28.3	49.1	36.8	26.9
97	140.6	24.2	12.5	16.9	21.5	21.3	36.3	35.9	47.6	28.7	16.4	29.3	47.4	38.3	26.0
98	125.7	23.7	10.9	16.2	21.5	20.7	32.7	31.6	42.8	26.2	15.8	22.7	43.1	34.7	23.6
99	150.4	24.1	11.8	17.5	22.1	23.1	38.5	41.0	52.0	32.7	17.2	32.0	53.2	41.1	29.5
100	136.8	25.1	11.7	16.5	22.9	22.2	36.2	38.3	43.8	29.1	16.7	25.3	49.6	39.2	27.2
101	149.4	26.0	11.5	19.9	24.2	23.9	38.7	39.2	49.9	31.3	17.8	29.5	51.9	41.3	28.7
102	132.2	22.9	10.8	16.7	21.8	21.0	35.3	34.8	44.6	27.6	17.0	26.7	46.3	37.4	26.3
103	146.5	26.0	12.3	17.5	23.4	23.9	37.8	39.7	50.1	33.9	16.8	28.4	51.9	41.4	29.1
104	135.4	23.2	11.2	16.3	21.8	21.1	35.4	35.2	45.3	30.0	16.0	28.5	46.1	38.2	26.1
105	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

#	L	HEAD 1	HEAD 2	HEAD 3	HEAD 4	HEAD 5	BODY 01	BODY 02	BODY 03	BODY 04	BODY 05	BODY 06	BODY 07	BODY 08	BODY 09
106	139.0	23.6	11.6	17.2	20.8	20.9	36.0	37.9	49.3	28.5	14.8	27.3	48.7	38.4	26.7
107	129.9	23.8	11.1	17.2	22.0	21.9	33.8	33.8	43.4	27.5	14.3	26.1	44.9	37.8	26.8
108	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
109	125.0	22.6	10.8	15.8	20.7	19.7	32.4	33.8	40.7	24.7	15.6	24.8	43.3	35.5	24.1
110	132.3	23.4	10.8	16.4	22.2	21.5	34.1	37.1	45.9	27.6	14.9	26.8	46.8	38.5	27.0
111	140.0	24.8	12.9	16.8	23.6	23.1	36.1	38.9	47.6	28.0	16.2	28.3	49.1	41.7	28.8
112	141.2	25.4	13.3	16.1	21.0	22.1	37.2	39.1	48.9	27.6	17.2	26.3	49.9	40.1	26.5
113	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
114	142.7	24.7	11.7	17.9	22.9	22.8	38.3	38.7	48.7	31.0	15.8	28.1	50.4	41.4	28.5
115	131.6	23.3	11.0	15.8	21.0	20.6	34.6	34.9	43.1	27.2	16.8	26.0	45.5	38.2	27.1
116	131.8	23.1	9.9	17.0	20.9	21.1	33.5	33.6	45.8	28.4	15.8	26.9	44.7	36.5	26.2
117	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
118	146.8	24.7	12.2	18.0	23.5	23.7	38.7	40.8	49.2	32.5	18.7	26.2	52.3	42.5	29.6
119	128.9	24.1	10.9	16.9	21.4	20.7	33.2	31.6	42.6	28.0	15.9	26.1	43.4	34.9	24.3
120	150.8	28.3	13.1	19.1	24.6	24.8	38.9	40.9	51.9	31.1	16.9	26.8	52.9	43.3	30.0

b) Variables BODY10 à EYE

#	BODY 10	BODY 11	BODY 12	BODY 13	BODY 14	BODY 15	FIN 1	FIN 2	FIN 3	FIN 4	FIN 5	FIN 6	FIN 7	FIN 8	EYE
1	44.5	47.1	23.8	24.5	34.0	12.7	20.9	22.8	18.1	30.6	31.0	19.9	14.9	18.1	7.7
2	43.4	45.4	22.2	20.7	33.0	11.4	21.0	20.2	16.2	29.2	32.4	17.8	13.6	17.3	6.9
3	39.9	41.6	20.5	21.4	29.4	10.6	20.7	20.8	17.1	30.4	30.3	15.5	14.0	17.3	6.4
4	36.4	36.2	17.7	18.0	25.6	9.3	19.5	19.4	14.3	28.3	29.6	14.1	11.1	15.6	6.5
5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
6	42.1	45.5	22.1	20.3	32.0	10.8	20.0	20.6	17.3	30.0	31.3	14.7	13.7	17.7	6.4
7	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
8	42.6	45.1	22.3	20.2	33.1	10.8	20.4	22.7	19.1	27.7	31.4	18.1	14.4	18.3	6.2
9	36.4	40.0	18.8	18.1	27.8	9.8	18.8	20.0	16.0	25.6	27.2	16.3	12.0	15.9	7.1
10	43.6	48.2	23.6	21.0	34.6	11.5	20.4	21.6	17.1	28.0	33.1	18.5	14.3	17.0	8.1
11	36.9	38.9	17.7	18.4	28.9	9.5	19.0	20.1	16.2	28.0	30.1	13.1	12.0	16.4	6.3
12	44.5	44.3	22.7	23.1	32.5	12.1	21.2	21.9	15.9	30.5	30.3	14.5	13.6	16.4	8.5
13	34.8	36.5	19.2	17.9	27.0	9.8	19.2	18.8	16.3	25.5	28.0	12.7	11.9	14.5	7.0
14	39.5	40.9	19.1	20.2	28.3	10.4	18.1	18.1	15.9	27.4	28.9	14.2	11.1	15.8	6.6
15	38.1	37.8	17.4	19.3	28.3	9.9	19.1	18.5	15.6	26.5	29.1	14.1	12.2	15.9	6.3
16	38.3	40.8	20.3	19.6	29.1	9.9	21.7	19.7	16.5	29.9	32.0	13.4	12.0	16.1	6.8
17	40.5	40.4	19.7	21.0	28.9	11.1	19.9	18.7	14.4	26.3	28.5	14.5	11.8	14.5	6.4
18	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
19	40.8	40.1	21.6	21.0	28.5	10.9	21.6	21.8	17.0	29.5	31.0	15.3	12.8	16.7	7.2
20	40.4	42.9	20.9	20.1	29.1	10.7	19.0	20.9	15.6	28.3	28.6	16.3	12.2	15.7	6.8
21	52.3	56.3	25.8	25.4	38.9	13.4	24.2	26.7	21.4	35.9	39.6	19.5	17.6	22.2	7.1
22	48.2	50.7	25.2	22.9	34.8	13.3	24.0	24.7	22.6	35.1	35.7	21.5	17.4	20.4	7.2

#	BODY 10	BODY 11	BODY 12	BODY 13	BODY 14	BODY 15	FIN 1	FIN 2	FIN 3	FIN 4	FIN 5	FIN 6	FIN 7	FIN 8	EYE
23	47.9	53.1	26.6	23.5	38.0	13.4	26.2	25.7	24.3	33.6	37.5	20.0	19.7	20.5	8.0
24	48.5	51.6	24.5	24.8	37.1	13.0	23.7	25.2	19.7	32.9	35.5	21.9	16.8	20.2	7.2
25	54.8	55.8	28.0	26.2	40.1	14.5	26.3	26.3	22.3	35.5	37.4	23.6	18.3	22.7	7.4
26	48.9	51.2	26.1	25.5	38.5	14.0	25.8	25.2	22.1	33.2	35.1	22.8	16.1	21.0	10.0
27	53.4	58.5	28.2	22.5	40.8	12.7	25.0	27.8	23.0	36.4	32.7	23.4	18.8	20.9	9.7
28	52.8	53.6	26.4	26.7	39.0	13.6	25.7	26.5	21.4	33.7	37.7	23.6	15.5	21.2	8.8
29	52.1	56.8	26.6	24.5	39.3	12.6	24.0	24.6	23.5	35.2	36.8	18.2	15.3	20.1	7.8
30	45.0	46.6	21.9	19.6	31.9	10.7	21.7	21.8	18.1	32.0	34.3	14.9	14.1	17.8	8.1
31	46.8	48.5	24.4	20.9	35.0	12.5	24.2	23.7	19.6	31.9	35.4	17.4	15.5	18.2	7.3
32	49.4	50.3	24.2	24.7	36.7	12.4	25.5	24.5	21.2	36.1	38.6	17.3	17.0	20.9	8.1
33	39.9	43.1	21.2	20.8	31.8	11.2	21.0	20.8	17.3	28.7	30.9	15.1	13.7	16.8	6.8
34	44.3	45.5	23.2	20.7	33.6	11.2	20.8	21.8	17.8	29.4	32.6	16.7	14.7	18.2	6.5
35	46.8	51.0	25.3	21.8	35.5	12.5	23.9	23.5	19.6	33.5	36.0	14.0	14.5	19.5	10.2
36	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
37	48.5	50.4	25.3	23.2	36.7	12.5	23.1	24.3	19.2	30.8	34.8	19.6	14.9	18.2	7.6
38	44.4	47.0	21.2	23.8	31.7	12.2	23.1	23.4	16.9	29.7	31.1	18.5	14.9	18.2	7.6
39	42.3	44.5	22.4	20.4	31.3	10.8	21.0	22.5	18.3	30.2	31.5	17.9	13.4	17.0	6.5
40	52.1	52.7	27.0	27.3	40.0	13.7	25.9	26.6	23.5	33.5	35.8	19.0	17.4	21.2	8.4
41	55.0	55.6	26.8	27.2	38.0	14.5	26.4	25.3	19.8	35.2	37.6	19.7	16.2	20.7	8.7
42	52.8	52.6	24.8	26.6	37.8	13.1	25.2	25.1	18.0	36.6	36.7	18.4	14.2	19.4	7.7
43	58.1	60.8	29.5	26.5	43.2	15.2	28.8	29.8	25.1	38.9	43.8	19.3	21.1	21.6	9.4
44	58.9	61.4	30.0	29.6	42.7	16.0	31.7	30.2	23.0	42.8	44.6	23.2	21.6	24.3	10.3
45	55.8	53.8	26.1	26.4	37.2	12.7	26.2	25.5	18.8	37.1	40.1	18.1	15.4	19.3	7.3
46	58.7	58.1	28.5	27.8	41.4	14.1	28.4	28.7	23.2	41.6	43.9	19.6	17.9	23.4	9.0
47	51.1	53.0	26.6	26.3	39.6	14.4	24.8	25.9	20.8	35.8	37.9	18.8	18.1	20.2	7.2
48	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
49	51.4	53.3	26.3	26.4	38.3	14.0	25.0	25.2	20.2	34.7	36.2	20.2	15.4	20.5	10.1
50	53.2	56.0	30.0	25.5	44.5	14.0	28.3	28.1	25.2	37.9	41.4	22.9	19.4	21.8	8.9
51	54.9	57.6	31.0	27.2	43.3	14.6	26.8	29.2	23.2	40.4	44.2	22.2	18.8	22.3	9.8
52	60.4	61.9	30.1	26.2	43.5	14.7	29.4	32.1	25.9	40.0	44.7	20.2	18.8	24.1	8.9
53	51.4	57.3	27.7	25.4	39.3	14.0	26.2	27.2	21.8	36.3	39.0	22.3	18.4	22.2	10.3
54	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
55	55.8	61.8	31.6	28.8	45.4	15.4	27.9	29.4	24.6	38.5	40.5	20.3	19.4	24.4	9.3
56	60.5	59.5	30.7	29.2	44.2	15.9	30.7	32.0	25.8	40.6	42.9	29.0	19.9	23.2	8.3
57	54.9	58.2	28.9	26.4	41.3	15.2	26.9	26.7	23.4	37.1	41.5	23.4	18.6	21.7	8.5
58	48.7	51.2	25.4	25.1	37.9	12.9	24.8	25.0	21.5	35.1	36.4	17.2	15.1	18.6	7.4
59	55.8	58.5	29.2	27.6	40.5	14.2	27.7	27.5	22.0	39.2	39.6	23.2	18.9	22.3	8.6
60	52.5	55.6	27.8	26.7	40.3	13.7	28.0	28.3	22.6	38.0	38.9	24.9	18.6	24.2	9.2
61	43.6	47.2	23.5	20.6	33.6	12.2	22.3	23.3	17.4	31.1	32.8	20.4	14.6	18.6	7.4
62	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
63	49.2	51.6	24.5	23.0	36.3	14.0	23.9	26.8	20.3	32.9	37.6	26.5	17.5	21.8	8.8
64	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
65	52.2	52.1	25.6	25.2	37.2	13.7	25.7	27.6	18.6	36.9	31.1	19.2	14.9	22.9	10.0

#	BODY 10	BODY 11	BODY 12	BODY 13	BODY 14	BODY 15	FIN 1	FIN 2	FIN 3	FIN 4	FIN 5	FIN 6	FIN 7	FIN 8	EYE
66	50.3	52.4	23.6	22.9	35.3	13.2	24.6	24.4	17.7	31.3	34.1	19.7	14.4	20.1	8.9
67	45.4	52.1	24.8	22.7	35.6	12.4	24.1	23.6	17.6	32.1	35.0	19.5	14.1	19.2	7.6
68	56.7	58.7	29.0	27.1	43.0	15.3	31.4	28.5	22.4	38.4	39.9	22.9	19.0	24.0	10.3
69	54.7	59.1	28.6	26.8	40.9	14.0	28.6	26.3	21.3	39.1	41.4	20.0	19.5	24.1	7.9
70	46.9	48.5	23.5	24.1	34.7	12.9	24.9	23.6	18.8	35.8	36.0	20.9	16.8	19.3	8.8
71	47.7	49.1	24.4	23.9	35.4	12.4	23.6	23.3	17.1	35.4	34.2	19.6	16.0	18.4	7.5
72	47.7	48.7	24.0	23.3	36.8	13.2	23.4	24.0	18.8	31.9	34.3	19.3	14.5	19.0	7.9
73	60.9	63.2	30.4	27.8	42.7	15.3	29.3	26.1	22.3	41.9	42.3	24.7	17.8	23.4	9.4
74	46.7	50.2	24.0	21.7	34.5	12.3	22.8	22.3	17.8	31.7	33.8	17.9	15.3	19.5	9.7
75	54.0	54.8	27.0	26.0	40.0	14.5	27.9	26.4	20.9	34.2	33.6	20.0	17.9	22.7	8.8
76	46.9	49.4	22.8	22.8	34.6	13.0	24.2	23.1	17.4	34.1	36.2	15.8	13.2	20.0	8.5
77	46.9	49.0	24.0	22.3	34.0	13.1	23.7	22.7	18.1	31.3	35.6	19.1	11.8	20.3	9.9
78	54.3	57.9	27.4	24.5	38.7	13.7	25.7	25.4	18.5	36.0	36.8	21.1	15.4	21.6	8.5
79	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
80	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
81	38.2	39.5	18.1	18.7	28.1	10.6	19.5	20.3	14.8	23.6	26.0	15.0	11.9	15.2	7.4
82	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
83	43.0	47.8	23.2	20.2	32.6	11.8	21.2	21.5	16.4	28.0	31.3	16.7	13.0	17.1	8.3
84	41.0	43.0	20.2	22.4	31.9	11.1	20.6	21.0	15.9	25.7	27.8	16.9	11.3	16.9	8.5
85	42.7	46.4	22.1	19.4	30.6	10.6	20.4	21.9	15.5	31.5	31.7	16.0	11.8	15.8	8.8
86	44.2	49.0	22.5	21.2	33.8	12.7	22.7	22.2	17.2	30.1	33.1	15.6	14.5	19.7	9.0
87	40.4	43.3	21.3	19.0	33.6	11.0	20.4	20.4	16.3	24.6	30.3	14.9	14.2	15.2	7.5
88	38.2	41.5	18.0	19.7	30.1	9.9	19.4	17.6	14.9	23.1	28.5	13.6	11.6	14.6	7.0
89	41.8	44.2	21.1	21.1	32.7	12.2	21.2	21.7	16.8	29.9	31.4	15.4	13.3	16.9	7.9
90	40.1	44.1	20.8	20.3	31.2	11.5	22.2	20.8	17.1	28.2	30.0	15.4	12.0	16.6	6.7
91	40.6	43.7	21.5	19.5	31.1	11.5	21.1	22.1	14.5	28.6	29.0	17.9	13.5	17.1	8.2
92	42.3	47.2	21.7	17.8	31.1	11.4	21.2	21.6	15.4	31.1	32.4	17.1	14.7	18.2	8.4
93	39.8	42.9	20.2	20.1	30.1	11.3	20.2	21.6	14.6	28.1	27.8	18.2	12.6	16.5	8.2
94	41.9	44.9	21.8	20.3	31.4	11.9	22.3	21.6	17.3	31.7	31.3	17.3	13.9	18.0	7.0
95	41.2	44.9	21.0	21.6	31.7	12.0	21.9	21.4	17.2	30.8	31.7	16.5	13.8	18.7	8.7
96	42.5	44.5	22.1	20.5	31.7	11.2	21.5	21.1	16.4	30.4	29.1	16.5	14.3	16.3	7.4
97	40.5	46.6	21.6	20.1	33.4	11.0	19.8	19.2	16.1	28.3	29.6	16.9	14.0	16.0	8.3
98	38.2	40.4	18.4	17.8	28.6	10.5	19.2	18.3	14.2	24.3	30.1	13.1	10.6	15.7	7.2
99	46.2	52.0	25.1	22.3	36.3	12.1	23.0	21.9	17.7	32.0	31.6	20.3	16.1	17.9	8.3
100	41.6	44.2	20.8	20.4	30.6	11.2	20.9	20.4	16.4	27.0	31.0	18.6	13.7	16.8	8.3
101	45.3	48.9	23.5	21.6	35.3	12.4	23.0	23.2	17.4	28.4	31.3	20.2	13.4	18.7	7.9
102	39.9	43.4	20.2	20.1	31.8	11.2	21.2	21.1	16.8	27.9	30.2	17.0	14.0	16.2	8.2
103	47.7	49.5	22.9	22.3	32.8	12.1	22.9	23.3	15.8	27.4	31.1	20.4	13.4	18.8	8.0
104	41.6	45.2	21.1	21.2	31.5	11.1	20.9	22.0	16.9	25.8	29.3	15.4	11.5	17.6	8.0
105	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
106	43.0	46.2	22.5	18.2	32.6	10.9	22.5	20.8	17.1	28.8	32.3	16.3	15.3	18.3	8.4
107	40.5	42.8	20.9	19.3	30.1	11.3	21.3	20.8	14.7	30.0	28.9	16.7	11.2	17.6	8.7
108	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

#	BODY 10	BODY 11	BODY 12	BODY 13	BODY 14	BODY 15	FIN 1	FIN 2	FIN 3	FIN 4	FIN 5	FIN 6	FIN 7	FIN 8	EYE
109	35.7	40.4	19.5	18.3	29.9	10.4	20.0	20.3	14.8	27.5	27.3	15.3	13.1	16.5	8.8
110	41.2	44.2	21.5	19.8	30.7	10.8	21.0	20.2	14.9	25.8	28.6	17.2	12.5	15.8	8.7
111	43.0	46.1	23.1	21.4	32.6	11.5	22.7	20.4	17.6	29.8	30.6	16.4	15.2	18.0	8.2
112	41.8	45.5	21.7	18.7	33.1	11.0	21.3	21.2	15.7	27.5	33.2	15.4	14.8	17.1	8.1
113	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
114	43.1	49.1	23.0	19.9	33.2	11.4	22.3	21.5	17.0	29.4	31.2	15.0	13.5	19.1	8.7
115	39.7	42.7	20.0	19.8	30.6	10.2	21.0	21.3	15.7	25.1	29.9	14.3	13.1	17.4	8.5
116	40.0	45.3	21.3	19.3	31.7	10.8	20.4	20.6	16.4	29.0	29.7	15.7	14.4	16.2	8.5
117	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
118	46.8	47.7	21.9	22.9	32.3	12.6	23.3	20.6	16.0	31.8	32.2	15.5	12.4	18.7	9.0
119	39.5	42.3	20.2	20.3	30.1	11.0	21.0	21.4	15.6	27.7	28.3	14.3	12.9	16.5	8.6
120	46.3	49.8	23.8	20.7	33.7	12.4	24.6	22.8	18.8	30.9	33.8	20.9	15.9	19.4	9.4

Tableau A1.6 Masses et concentrations de césium mesurées dans les poissons sélectionnés au début des expériences.

Våvatn 2000			Våvatn 2001			Øvre Nonshøtjønn 2001		
#	Masse (g *fw*)	[Cs] ($ng \cdot g^{-1}$)	#	Masse (g *fw*)	[Cs] ($ng \cdot g^{-1}$)	#	Masse (g *fw*)	[Cs] ($ng \cdot g^{-1}$)
1	12.9	16.52	1	25.03	21.77	1	47.25	20.13
2	19.4	18.02	2	23.08	23.46	2	52.69	19.11
3	19.7	16.03	3	25.33	18.12	3	50.11	39.65
4	19.9	17.24	4	16.25	22.3	4	61.67	21.61
5	27.1	14.23	5	27.98	16.92	5	68.15	36.48
6	35.9	18.83	6	24.89	20.33	6	68.93	31.03
7	12.4	14.49	7	43.87	21.46	7	46.50	22.95
8	27.4	14.11	8	38.57	18.91	8	59.84	30.25
9	12.5	17.97	9	37.11	17.59	9	60.90	32.61
10	14.5	19.99	10	22.62	16.25	10	93.53	25.62
11	23.1	17.36	11	24.52	18.03	11	76.57	36.58
12	22.2	20.85				12	80.78	26.83
13	24.7	21.49						
14	34.8	19.65						
15	27.2	20.37						
16	23.7	20.11						
17	20.1	20.74						
18	25.8	16.64						

Tableau A1.7 Longueur moyenne des proies et composition de la diète des poissons (%) pour les expériences des étés 2000 et 2001.

a) Été 2000

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Crustaceans	Benthic Crustaceans
1	0.0106	0.0	0.0	0.0	6.2	86.8	7.0
2	0.0130	0.0	0.0	0.0	11.1	67.2	21.7
3	0.0108	0.0	0.0	0.0	7.5	85.2	7.4
4	0.0150	0.0	0.0	0.0	30.5	62.2	7.3
5	0.0112	0.0	0.0	0.0	12.4	81.9	5.7
6	0.0119	0.0	0.0	0.0	11.1	74.9	14.0
7	0.0124	0.0	0.0	0.0	6.5	93.5	0.0
8	0.0110	0.0	0.0	0.0	8.4	84.3	7.3
9	0.0164	0.0	0.0	0.0	13.7	53.3	33.0
10	0.0102	0.0	0.0	0.0	6.1	91.8	2.1
11	0.0116	0.0	0.0	0.0	2.6	88.9	8.5
12	0.0116	0.0	0.0	0.0	11.7	79.0	9.3
13	0.0114	0.0	0.0	0.0	8.5	83.2	8.2
14	0.0119	0.0	0.0	0.0	7.6	78.0	14.4
15	0.0793	0.0	0.0	0.0	5.8	92.3	1.8
16	0.0159	0.0	0.0	0.0	20.0	55.6	24.4
17	NA	NA	NA	NA	NA	NA	NA
18	0.0124	0.0	0.5	0.0	0.9	66.2	32.4
19	0.0118	0.0	0.0	0.0	17.9	78.1	4.0
20	0.0129	0.0	0.0	0.0	3.6	63.3	33.2
21	0.0132	0.0	0.0	0.0	0.0	44.1	55.9
22	0.0179	0.0	0.0	0.0	27.0	32.3	40.7
23	0.0196	0.0	0.0	0.0	12.0	19.3	68.7
24	0.0197	0.0	0.0	0.0	16.6	18.3	65.1
25	0.0110	0.0	0.0	0.0	4.8	76.3	18.9
26	0.0118	0.0	0.0	0.0	1.1	58.1	40.8
27	NA	NA	NA	NA	NA	NA	NA
28	0.0117	0.0	4.7	0.0	10.4	79.3	5.7
29	NA	NA	NA	NA	NA	NA	NA
30	0.0117	0.0	0.0	0.0	8.2	67.0	24.8
31	0.0228	0.0	0.0	0.0	25.7	15.8	58.5
32	0.0133	0.0	1.3	0.0	16.3	56.8	25.6
33	0.0248	2.1	0.0	0.0	58.3	32.3	7.2
34	0.0143	0.0	0.0	0.0	15.5	48.8	35.8
35	0.0124	0.0	0.0	0.0	11.2	70.2	18.6
36	0.0131	3.3	0.0	0.0	16.3	74.0	6.3
37	0.0236	1.7	0.0	0.0	7.4	15.0	75.9
38	0.0130	1.0	0.0	0.0	12.9	74.3	11.8
39	0.0161	0.6	0.0	0.0	19.4	41.5	38.5

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Crustaceans	Benthic Crustaceans
40	NA	NA	NA	NA	NA	NA	NA
41	0.0769	0.3	0.0	0.0	3.8	94.7	1.2
42	0.1340	0.0	0.0	0.0	0.4	99.5	0.1
43	0.1436	0.1	0.0	0.0	0.2	99.5	0.1
44	0.0166	0.0	0.0	0.0	23.4	38.4	38.2
45	0.0181	0.0	0.0	2.2	13.1	23.1	61.6
46	NA	NA	NA	NA	NA	NA	NA
47	0.0097	0.0	0.0	0.0	2.3	91.8	5.9
48	0.0117	1.7	0.0	0.0	14.1	71.6	12.7
49	0.0379	0.5	0.3	0.0	73.5	19.9	5.9
50	0.0105	0.0	0.0	0.0	4.9	82.9	12.3
51	0.0113	0.9	0.0	0.0	11.5	76.4	11.3
52	0.0106	1.0	0.0	0.0	7.1	87.1	4.8
53	0.0104	0.0	0.0	0.0	7.5	85.5	6.9
54	0.0156	0.0	0.0	0.0	11.4	33.3	55.3
55	0.0123	0.0	0.0	0.0	16.2	68.1	15.7
56	0.0431	0.6	0.0	0.0	78.7	18.7	2.0
57	NA	NA	NA	NA	NA	NA	NA
58	0.0100	0.0	0.0	0.0	8.0	90.1	1.9
59	0.0098	0.0	0.0	0.0	5.0	92.5	2.6
60	0.1094	0.4	0.1	0.0	91.7	5.6	2.1
61	0.0094	0.0	0.0	0.0	0.7	94.6	4.7
62	0.0137	1.1	0.0	0.0	11.8	49.7	37.4
63	0.0105	0.0	0.0	0.0	6.0	82.4	11.7
64	0.0192	0.0	0.0	0.0	6.5	18.1	75.4
65	0.0196	2.9	0.0	0.0	38.6	35.8	22.7
66	0.0106	0.0	0.0	0.0	6.4	88.8	4.7
67	0.0136	2.5	0.0	0.0	26.0	67.2	4.3
68	0.1331	0.0	0.0	0.0	0.2	99.7	0.1
69	NA	NA	NA	NA	NA	NA	NA
70	0.0115	0.0	0.0	0.0	4.4	90.8	4.8
71	0.0286	4.3	0.0	7.7	3.7	44.8	39.4
72	0.0098	0.0	0.0	0.0	3.7	95.5	0.8
73	NA	NA	NA	NA	NA	NA	NA
74	0.0180	0.0	0.0	0.0	32.9	54.3	12.8
75	0.0267	0.0	7.1	0.0	26.1	37.0	29.8
76	NA	NA	NA	NA	NA	NA	NA
77	0.0187	2.9	0.0	0.0	7.5	83.4	6.2
78	0.0137	0.0	0.0	0.0	1.9	97.1	1.0
79	NA	NA	NA	NA	NA	NA	NA
80	NA	NA	NA	NA	NA	NA	NA
81	NA	NA	NA	NA	NA	NA	NA
82	0.0105	0.0	0.0	0.0	3.5	90.7	5.8

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Crustaceans	Benthic Crustaceans
83	0.0126	0.0	0.0	0.0	5.3	89.3	5.4
84	NA	NA	NA	NA	NA	NA	NA
85	0.0261	0.0	0.0	0.0	16.9	52.7	30.4
86	0.0192	4.9	0.0	0.0	24.1	57.2	13.8
87	0.0344	0.0	0.0	0.0	53.9	14.2	32.0
88	NA	NA	NA	NA	NA	NA	NA
89	0.0217	0.0	0.0	0.0	16.8	36.6	46.6
90	NA	NA	NA	NA	NA	NA	NA
91	0.0107	0.0	0.8	0.0	8.0	82.4	8.8
92	NA	NA	NA	NA	NA	NA	NA
93	0.0171	0.0	0.0	0.0	26.8	45.3	27.9
94	0.0127	0.0	0.0	0.0	17.2	65.0	17.8
95	0.0113	1.2	0.0	0.0	10.9	76.4	11.5
96	0.0180	0.0	0.0	0.0	22.5	33.2	44.2
97	0.0241	0.8	12.1	0.0	41.6	31.9	13.7
98	NA	NA	NA	NA	NA	NA	NA
99	0.0103	0.0	0.0	0.0	5.8	87.0	7.2
100	NA	NA	NA	NA	NA	NA	NA
101	0.0123	0.0	0.0	0.0	3.9	52.7	43.4
102	0.0711	0.0	0.0	0.0	1.6	98.4	0.0
103	0.0103	0.0	0.0	0.0	0.6	93.5	5.9
104	0.0103	0.0	0.0	0.0	0.0	93.0	7.0
105	0.0108	0.0	0.0	0.0	1.8	84.0	14.3
106	0.0102	0.0	0.0	0.0	1.0	96.7	2.4
107	0.0108	1.0	0.0	0.0	1.9	86.4	10.7
108	0.0104	0.0	0.0	0.0	1.0	92.8	6.2
109	NA	NA	NA	NA	NA	NA	NA
110	0.0106	0.0	3.0	0.0	1.0	93.6	2.4
111	0.0107	0.0	0.0	0.0	3.9	90.0	6.2
112	0.0105	0.0	0.0	0.0	1.6	91.2	7.3
113	0.0102	0.0	0.0	0.0	0.2	95.9	3.8
114	0.0105	0.0	0.0	0.0	1.3	90.7	8.0
115	0.0108	0.0	0.0	0.0	2.6	91.2	6.2
116	0.0104	0.0	0.0	0.0	0.3	93.2	6.5
117	0.0104	0.0	0.0	0.0	0.2	90.3	9.6
118	0.0105	0.0	0.0	0.0	1.2	93.1	5.7
119	0.0108	0.0	0.0	0.0	4.1	91.1	4.8
120	0.0105	0.0	0.0	0.0	1.6	92.9	5.5
121	0.0108	0.9	0.0	0.0	4.1	92.5	2.4
122	0.0105	0.0	3.7	0.0	0.1	94.4	1.9
123	0.0110	1.0	0.0	0.0	0.8	80.9	17.3
124	0.0104	0.0	0.0	0.0	2.3	92.9	4.8
125	0.0108	0.0	0.0	0.0	0.6	82.3	17.1

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Crustaceans	Benthic Crustaceans
126	0.0103	0.0	0.0	0.0	0.8	94.1	5.1
127	0.0105	0.0	0.0	0.0	0.9	93.5	5.6
128	0.0102	0.0	0.0	0.0	0.4	95.2	4.4
129	0.0104	0.0	0.0	0.0	0.3	92.7	7.0
130	0.0110	0.0	0.0	0.0	0.5	76.8	22.6
131	0.0142	0.0	26.5	0.9	1.0	68.7	3.0
132	0.0104	0.0	0.0	0.0	0.7	91.8	7.5
133	0.0108	0.0	0.0	0.0	0.6	82.1	17.3
134	0.0104	0.0	1.3	0.0	0.2	92.9	5.6
135	0.0106	0.0	0.0	0.0	2.1	89.4	8.5
136	0.0107	0.0	0.0	0.0	2.1	85.3	12.6
137	0.0108	0.0	0.0	0.0	3.8	87.9	8.3
138	0.0103	0.0	0.0	0.0	0.2	94.7	5.1
139	0.0104	0.0	0.0	0.0	0.9	94.1	5.0
140	NA	NA	NA	NA	NA	NA	NA

b) Été 2001

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Copepods	Planktonic Cladocerans	Benthic Crustaceans
1	0.0112	0.0	0.0	0.0	8.8	22.5	68.4	0.3
2	0.0437	0.0	0.0	0.0	0.0	95.8	4.2	0.0
3	0.0081	0.0	0.0	0.0	0.0	0.0	100.0	0.0
4	0.0149	0.0	0.0	0.0	45.9	0.0	54.1	0.0
5	NA	NA	NA	NA	NA	NA	NA	NA
6	0.0656	0.0	21.0	0.0	29.6	12.2	0.0	37.3
7	NA	NA	NA	NA	NA	NA	NA	NA
8	0.0703	0.0	0.0	0.0	50.1	46.1	3.8	0.0
9	0.0126	0.0	0.0	0.0	19.1	14.2	66.6	0.0
10	0.0436	0.0	0.0	0.0	0.8	94.3	2.4	2.5
11	0.0097	0.0	0.0	0.0	3.5	0.3	80.7	15.5
12	0.0145	1.0	0.0	0.0	0.9	44.1	48.5	5.6
13	0.0524	0.0	0.0	0.0	0.0	99.8	0.2	0.0
14	0.0095	0.0	0.0	0.0	7.3	0.0	84.4	8.3
15	0.0088	0.0	0.0	0.0	3.8	0.3	92.5	3.4
16	0.0085	0.0	0.0	0.0	0.0	0.0	100.0	0.0
17	0.0227	9.3	0.0	0.0	11.0	49.1	28.7	2.0
18	NA	NA	NA	NA	NA	NA	NA	NA
19	0.0435	0.0	0.0	0.0	0.0	95.4	3.4	1.3
20	0.0417	1.8	0.0	0.0	8.3	82.9	6.4	0.6
21	0.0467	3.5	0.0	0.0	1.3	90.5	4.7	0.0
22	0.0193	0.0	0.0	0.0	5.7	62.6	31.8	0.0

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Copepods	Planktonic Cladocerans	Benthic Crustaceans
23	0.0130	2.7	0.0	0.0	6.2	34.7	56.4	0.0
24	0.1190	0.0	0.0	0.0	90.4	4.3	5.3	0.0
25	0.0437	0.0	0.0	0.0	0.0	97.3	2.7	0.0
26	0.0476	0.0	0.0	0.0	0.0	99.3	0.6	0.2
27	0.0364	0.0	0.0	0.0	2.8	88.6	7.9	0.7
28	0.0476	0.0	0.0	0.0	18.5	74.9	4.3	2.2
29	0.0485	0.0	0.0	0.0	0.0	99.8	0.2	0.0
30	0.0095	0.0	5.3	0.0	2.9	0.0	91.7	0.0
31	0.0493	0.0	0.0	0.0	1.2	96.8	1.4	0.5
32	0.0403	0.0	0.0	0.0	3.4	86.9	5.8	3.9
33	0.0106	0.0	0.0	0.0	8.8	0.0	73.8	17.4
34	0.0486	0.6	0.0	0.0	0.4	94.5	1.4	3.0
35	0.0335	11.8	0.0	0.0	12.5	57.6	13.7	4.4
36	NA	NA	NA	NA	NA	NA	NA	NA
37	0.0474	4.4	0.0	0.0	14.1	76.2	5.2	0.0
38	NA	NA	NA	NA	NA	NA	NA	NA
39	0.0259	0.0	0.0	0.0	23.3	47.6	22.8	6.3
40	NA	NA	NA	NA	NA	NA	NA	NA
41	0.0276	0.0	0.0	0.0	0.0	82.8	17.2	0.0
42	0.0086	0.0	0.0	0.0	0.0	0.0	99.0	1.0
43	0.0194	1.2	0.0	0.0	8.1	56.1	34.7	0.0
44	0.0109	3.9	0.0	0.0	18.2	0.0	77.9	0.0
45	0.0515	0.0	0.0	0.0	6.0	92.5	1.0	0.4
46	0.0087	0.8	0.0	0.0	2.3	0.8	93.9	2.2
47	0.0411	0.8	0.0	0.0	0.8	92.7	5.6	0.2
48	NA	NA	NA	NA	NA	NA	NA	NA
49	0.0504	0.0	0.0	0.0	0.0	98.2	0.8	1.0
50	0.2900	0.0	0.0	0.0	100.0	0.0	0.0	0.0
51	0.0155	0.0	0.0	0.0	26.8	21.0	52.2	0.0
52	0.0675	0.0	0.0	0.0	3.1	61.7	0.2	35.0
53	0.0434	0.0	0.0	0.0	0.0	97.3	2.7	0.0
54	NA	NA	NA	NA	NA	NA	NA	NA
55	0.0506	0.0	3.6	0.0	0.0	94.6	0.2	1.6
56	0.1595	0.0	0.0	0.0	75.7	23.4	0.8	0.0
57	0.0496	0.0	0.0	0.0	0.0	99.9	0.1	0.0
58	0.0087	0.0	0.0	0.0	7.1	0.2	92.6	0.0
59	0.0498	0.0	0.0	0.0	0.0	100.0	0.0	0.0
60	0.0096	3.8	0.0	0.0	11.6	0.0	84.6	0.0
61	0.0086	0.0	0.0	0.0	0.8	0.0	99.2	0.0
62	NA	NA	NA	NA	NA	NA	NA	NA
63	0.0108	1.8	0.0	0.0	20.0	0.0	76.0	2.2
64	NA	NA	NA	NA	NA	NA	NA	NA
65	0.0092	0.0	0.0	0.0	9.3	0.0	90.7	0.0

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Copepods	Planktonic Cladocerans	Benthic Crustaceans
66	0.0112	0.0	16.9	0.0	1.4	0.0	70.8	10.9
67	0.0116	0.0	0.0	0.0	27.6	0.0	70.4	2.0
68	0.0087	0.0	0.0	0.0	4.3	0.0	94.6	1.1
69	0.0096	0.8	0.0	0.0	13.9	0.0	84.0	1.3
70	0.0097	0.0	0.0	0.0	14.1	0.0	85.6	0.3
71	0.0368	0.0	0.0	0.0	0.2	89.6	7.6	2.6
72	0.0091	0.0	0.0	0.0	7.2	0.0	89.9	2.9
73	0.0496	0.0	0.0	0.0	8.2	88.4	3.0	0.4
74	0.0085	0.0	0.0	0.0	2.8	0.0	94.2	3.0
75	0.0092	0.9	1.6	0.0	8.5	0.0	87.4	1.5
76	0.0093	0.0	0.0	0.0	9.7	0.0	85.4	4.9
77	0.0102	1.5	0.0	0.0	13.6	0.0	84.9	0.0
78	0.0155	0.9	0.0	0.0	24.5	0.0	50.0	24.6
79	NA	NA	NA	NA	NA	NA	NA	NA
80	NA	NA	NA	NA	NA	NA	NA	NA
81	0.0108	0.0	0.0	0.0	18.7	0.0	79.9	1.4
82	NA	NA	NA	NA	NA	NA	NA	NA
83	0.0103	0.0	0.0	0.0	14.6	0.0	83.5	1.9
84	0.0112	4.4	0.0	0.0	17.3	0.0	77.1	1.1
85	0.0098	0.9	0.0	0.0	10.3	0.0	88.8	0.0
86	0.0085	0.3	0.0	0.0	3.3	0.0	94.7	1.7
87	0.0087	0.0	0.0	0.0	6.0	0.0	91.7	2.3
88	0.0086	0.0	0.0	0.0	2.3	0.0	92.3	5.4
89	0.0089	0.0	0.0	0.0	8.8	0.0	90.6	0.6
90	0.0232	0.0	0.0	0.0	61.8	0.0	34.2	4.0
91	0.0094	0.4	1.2	0.0	9.1	0.0	88.1	1.2
92	0.0105	0.0	0.0	0.0	20.6	0.0	78.8	0.6
93	0.0084	0.0	0.0	0.0	0.0	0.0	98.9	1.1
94	0.0093	0.0	0.2	0.0	8.9	0.0	88.1	2.9
95	0.0086	0.0	0.0	0.0	3.3	0.0	96.7	0.0
96	0.0148	4.2	0.0	0.0	38.5	0.0	55.5	1.8
97	0.0113	2.9	0.0	0.0	23.9	0.0	73.1	0.0
98	0.0094	0.0	0.0	0.0	11.4	0.0	86.6	2.0
99	0.0097	0.0	0.0	0.0	3.5	0.0	82.2	14.2
100	0.0088	0.0	0.0	0.0	3.2	1.9	93.7	1.1
101	0.0154	3.5	0.7	0.0	35.8	0.0	54.8	5.2
102	0.0091	0.0	0.0	0.0	8.5	0.0	91.5	0.0
103	0.0119	2.4	0.0	0.0	24.3	0.0	72.5	0.8
104	0.0252	0.0	0.0	0.0	39.8	2.1	54.9	3.2
105	NA	NA	NA	NA	NA	NA	NA	NA
106	0.0090	0.5	0.0	0.0	4.0	0.0	91.8	3.7
107	0.0107	0.0	0.0	0.0	21.0	0.0	76.2	2.8
108	NA	NA	NA	NA	NA	NA	NA	NA

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Copepods	Planktonic Cladocerans	Benthic Crustaceans
109	0.0158	0.0	0.0	0.0	31.4	0.0	48.0	20.7
110	NA	NA	NA	NA	NA	NA	NA	NA
111	0.0092	1.6	0.0	0.0	8.7	0.0	89.7	0.0
112	0.0097	0.0	0.0	0.0	9.6	0.0	83.7	6.7
113	NA	NA	NA	NA	NA	NA	NA	NA
114	0.0103	1.8	0.0	0.0	18.3	0.0	77.8	2.2
115	0.0087	0.0	0.0	0.0	3.3	0.0	91.7	5.0
116	0.0123	0.0	0.4	0.0	0.6	0.0	65.9	33.1
117	NA	NA	NA	NA	NA	NA	NA	NA
118	0.0089	0.0	0.0	0.0	4.1	0.0	88.5	7.5
119	0.0110	0.0	0.0	0.0	20.9	0.0	71.0	8.1
120	0.0087	0.0	0.0	0.0	4.3	0.0	95.2	0.5
121	0.4704	55.9	0.0	0.0	42.4	0.0	0.0	1.7
122	0.1487	1.7	0.0	0.0	6.4	91.0	0.0	0.8
123	1.0332	48.6	20.1	1.2	27.9	0.4	0.0	1.7
124	NA	NA	NA	NA	NA	NA	NA	NA
125	0.0527	0.0	0.0	4.1	3.3	0.0	0.0	92.6
126	0.1592	30.2	49.4	0.0	2.7	0.8	0.0	17.0
127	0.1267	22.2	27.5	0.0	26.7	1.7	0.0	21.9
128	0.8185	40.9	12.7	0.6	42.4	0.0	0.0	3.4
129	0.6841	0.0	62.2	0.0	21.5	0.0	0.0	16.3
130	0.9248	0.0	86.6	4.8	0.0	0.0	0.0	8.6
131	0.0758	0.0	15.9	0.0	49.6	2.8	0.2	31.5
132	1.4491	0.0	93.6	2.0	2.1	0.0	0.0	2.3
133	0.3546	3.1	37.7	2.6	46.5	0.0	0.0	10.2
134	1.0500	100.0	0.0	0.0	0.0	0.0	0.0	0.0
135	1.8225	0.0	94.0	0.7	3.6	0.0	0.0	1.7
136	0.7475	35.1	0.0	0.0	63.7	0.0	0.0	1.2
137	0.9375	37.3	0.0	0.0	61.9	0.0	0.0	0.8
138	0.9390	98.7	0.0	0.0	1.2	0.0	0.0	0.2
139	0.1290	39.0	0.0	0.0	25.9	30.7	0.0	4.4
140	0.2446	0.0	38.6	0.0	23.3	0.0	0.0	38.1
141	0.9581	25.8	49.8	0.0	9.7	0.0	0.0	14.8
142	0.2479	23.0	40.9	5.6	9.6	0.0	0.0	21.0
143	0.0810	0.0	17.1	0.0	46.0	12.2	0.0	24.6
144	0.0388	0.0	0.0	0.0	13.9	0.0	0.2	85.9
145	0.0320	0.0	0.0	0.0	17.8	0.0	0.0	82.2
146	0.1176	54.7	15.2	0.0	6.7	0.0	0.0	23.4
147	0.0612	0.0	0.0	0.0	38.0	0.0	0.0	62.0
148	3.0524	0.8	97.2	0.0	0.0	0.0	0.0	2.0
149	0.0853	52.8	0.0	0.0	21.1	0.0	0.3	25.8
150	0.2225	8.0	28.0	0.6	3.8	40.2	0.4	19.0
151	0.0753	52.4	0.0	0.0	16.5	0.0	0.4	30.7

#	Longueur moyenne (mm)	Surface Insects	Benthic Insects	Mollusks	Aquatic Dipterans	Planktonic Copepods	Planktonic Cladocerans	Benthic Crustaceans
152	0.1297	76.9	0.0	0.0	4.8	0.0	0.0	18.3
153	0.3630	91.3	0.0	0.0	5.2	0.0	0.0	3.5
154	0.1722	0.0	20.4	0.0	5.1	68.0	0.0	6.5
155	0.0743	70.6	0.0	0.0	13.5	0.0	9.8	6.1
156	0.2996	89.3	0.0	0.0	5.4	0.0	0.0	5.3