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PAR
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CROISSANCE DE PERCHAUDES *(PERCA FLAVESCENS)* AU DÉBUT DE LEUR ONTOGÉNIE DANS UN LAC FLUVIAL DOMINÉ PAR UN VASTE LITTORAL

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AVANT-PROPOS

Ce mémoire comprend deux chapitres. Le premier consiste en une revue de littérature sur les divers sujets relatifs à l'ontogénie de la perchaude préalablement présentée dans le cadre du cours Séminaire I (ECL6005). Le second comprend l'article scientifique qui sera soumis pour publication et englobe l'ensemble des travaux réalisés au cours de ma maîtrise.

RÉSUMÉ

La présente étude vise à combler le manque d'information disponible sur les premières semaines de vie des larves de perchaudes afin de mieux comprendre les facteurs influençant leur recrutement annuel. Comme cette étude a été réalisée dans les marais du lac Saint-Pierre (fleuve Saint-Laurent), elle apporte aussi un éclairage particulier sur l'écologie des jeunes perchaudes dans un lac fluvial, dont la zone littorale est beaucoup plus vaste que celles des lacs typiques décrits dans la littérature. Les larves de perchaudes ont été échantillonnées juste après l'éclosion des œufs, tous les deux jours durant une période de cinq semaines consécutives, afin de capter les premiers changements ontogéniques des larves et de les mettre en relation avec leur croissance, leur alimentation et leur environnement. L'hétérogénéité naturelle du milieu physique au lac Saint-Pierre, nous a permis de choisir quatre sites d'échantillonnage peu profonds présentant des conditions environnementales contrastées, dont deux marais aménagés et deux marais naturels. Les résultats montrent que l'état d'avancement de la croissance différait d'un site à l'autre à cause des constrastes de température mesurés plus tôt en saison au cours de la fraye. Les différences de tailles entre les larves des différents sites ce sont vue conservées tout au long de la période étudiée, suggérant l'importance particulière de la température en début de croissance sur la taille atteinte à la fin de la saison et donc sur le potentiel de survie à la disette hivernale. Les relations de longueurs/poids montraient des bris de pente corroborant l'hypothèse de changements alimentaires chez les larves, mais qui n'étaient pas associés, au lac Saint-Pierre, à des migrations ontogéniques telles qu'habituellement décrites dans les lacs. À notre connaissance, cette étude est la première à tracer la croissance des larves de perchaudes sur une échelle de temps aussi fine dans un lac fluvial. De plus, elle est la première à suggérer qu'un changement de diète sans lien avec une migration ontogénique puisse survenir chez des larves de perchaudes en milieu naturel.

Mots clés : Perchaudes · Marais · Rapport ARN/ADN · Croissance · Jeunes de l'année · Ontogénie · Lac fluvial · Indices de croissance

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ANOVA	Analyse de variance; angl. « Analysis of variance »
CI	Intervalle de confiance; angl. « Confidence interval »
CV	Coefficient de variation; angl. « Coefficient of variation »
DNA	Acide désoxyribonucléique; angl. « Deoxyribonucleic acid »
DOC	Carbone organique dissous; angl. « Dissolved organic carbon »
EB	Solution d'extraction tampon; angl. « Extraction buffer »
FAC	Fer-à-Cheval
GLM	Modèle linéaire général; angl. « General linear model »
IDM	Ile-du-Moine
DOY	Jour de l'an; angl. « Day of year »
LSP	Lac Saint-Pierre; angl. « Lake Saint-Pierre »
MAS	Maskinongé
M	Mètres; angl. « Meters »
RNA	Acide ribonucléique; angl. « Ribonucleic acid »
SD	Écart type; angl. « Standard deviation »
STB	Saint-Barthélemy
TN	Azote total; angl. « Total nitrogen »
TOC	Carbone organique total; angl. « Total organic carbon »
TP	Phosphore total; angl. « Total phosphorus »
TE	Tris-HCL et EDTA
TL	Longueur totale; angl. « Total length »
YOY	Jeunes de l'année; angl. « Youngs-of-the-year »

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Problématique

1.1.1 État des stocks de perchaudes

En Amérique du Nord, la perchaude (*Perca flavescens*) représente un important enjeu économique tant au niveau commercial que récréatif (Langlois et al. 1992, Shroyer et McComish. 1998). Les fortes baisses des débarquements commerciaux au cours des deux dernières décennies (Magnan 2002, Trumper et Lauer 2005, Wilberg et al. 2005) et les enjeux socio-économiques qui leur sont associés soulignent l'importance d'étudier cette pêcherie et d'en assurer le maintien. Parmi les variables clés, le recrutement des larves de perchaudes, c'est-à-dire leur capacité à survivre à la première année et ainsi contribuer aux classes d'âge supérieur, a été suggéré comme jouant un rôle majeur sur les stocks de poissons adultes disponibles (Shroyer et McComish 1998, Magnan 2002, Makauskas et Clapp 2008).

1.1.2 Succès du recrutement

Dans les climats tempérés, l'un des facteurs ayant le plus d'impact sur le recrutement des jeunes larves de perchaudes est sans doute la masse corporelle atteinte à la fin de leur première saison de croissance (Post et Evans 1989, Post et al. 1998, Huss et al. 2008b). D'une part, une masse importante permet de mieux résister à l'hiver grâce à d'abondantes ressources lipidiques (Post et Evans. 1989, Post et al. 1998, Huss et al. 2008b). D'autre part, une masse volumineuse offre une meilleure protection contre les prédateurs, rendant les larves plus difficiles à ingérer. L'accroissement en longueur est en fait relié à la capacité natatoire des larves et donc à une propension à échapper aux prédateurs (Fuiman et al. 2005, Fulford et al. 2006). Une croissance rapide semblerait donc avantager nettement la survie des jeunes larves.

1.2 Croissance de la perchaude

1.2.1 Facteurs morphologiques liés à l'alimentation

Tout au long de leur ontogénie, les perchaudes subissent des changements morphologiques affectant leur alimentation. Ces effets sont d'autant plus marqués au cours des premiers stades larvaires.

Au début de l'alimentation exogène, soit juste à la suite ou peu avant la résorption complète du sac vitellin, les yeux des larves ne sont pas totalement développés (Wahl et al. 1993 dans Fulford et al. 2006). Ceci limite donc les larves dans leur quête alimentaire en affectant la taille des proies qu'elles peuvent percevoir et leur efficacité à la capture en général (Graeb et al. 2004). Le développement des facultés natatoires influence également l'alimentation chez les jeunes larves de perchaudes. En effet, en bas âge, la capacité de déplacement des larves est très limitée (Fulford et al. 2006). Elles consomment alors préférentiellement des rotifères, dont le déplacement est lent et ce, même si les bénéfices énergétiques sont faibles comparativement à d'autres proies telles que des copépodes (Fulford et al. 2006). Toutefois, cette stratégie n'est que temporaire, car les larves se tournent plus tard vers un régime énergétiquement plus rentable (Fulford et al. 2006). Des études en laboratoire suggèrent que des larves continuant à se nourrir de rotifères parviendraient à survivre, mais avec un taux de croissance nettement inférieur à celui de larves se nourrissant de copépodes (Graeb et al. 2004). La conséquence en milieu naturel serait que leur croissance plus faible les désignerait comme des proies faciles et expliquerait qu'elles ne soient pas recrutées (Fulford et al. 2006).

La taille des larves joue également un rôle prédominant dans l'alimentation en déterminant la taille de l'ouverture de la bouche (Schael et al. 1991). Une embouchure large permet la capture de proies plus grosses, augmentant de ce fait la diversité des particules alimentaires disponibles. La consommation de rotifères en jeune âge est donc en grande partie reliée à une embouchure étroite, puisque les perchaudes n'ont pas encore la capacité d'ingérer de plus grosses particules (Whiteside et al. 1985).

Cependant, Schael et al. (1991) suggèrent que l'alimentation des larves ne soit pas seulement contrôlée par l'embouchure. Effectivement, l'observation des contenus stomacaux indique que la taille de la plupart des proies ingérées était inférieure à la taille maximale de proies ingérables par l'animal. Cette stratégie viserait à maximiser le nombre de particules alimentaires dans l'estomac, car de plus petites proies peuvent être entassées plus facilement que des grosses et constitueraient ainsi un volume de nourriture plus important (Wong et Ward 1972 dans Schael et al. 1991, Mills et al. 1986).

1.2.2 Sélection des proies

L'abondance du zooplancton est l'un des facteurs pouvant influencer la sélection alimentaire. En effet, la perchaude, qui est surtout opportuniste (Truemper et Lauer 2005), sélectionne principalement ses proies non pas en fonction d'une espèce particulière, mais selon la disponibilité des particules alimentaires. Donc, l'espèce de zooplancton la plus disponible (abondante) serait l'une des proies les plus consommées des larves de perchaudes (Truemper et Lauer 2005). De plus, Graeb et al. (2004) soulignent que la disponibilité des proies est un facteur important dans la détermination de la croissance et de la survie des larves de perchaudes. Toutefois, cet effet serait contrebalancé par la qualité de la nourriture en question. Effectivement, outre la diminution du temps de recherche d'une proie, attribuable à une grande abondance de cette dernière, l'apport énergétique de la proie y est pour beaucoup dans la sélection alimentaire. Par exemple, bien que les cladocères renferment de fortes concentrations de nutriments et soient facile à capturer, leur exosquelette rend leur digestion difficile, ce qui réduit leur apport énergétique total. Les copépodes, quant à eux, sont plus difficiles à capturer et renferment moins de nutriments que les cladocères. Toutefois, leur digestion est facile. De plus, l'ingestion de copépodes gravides, portant leurs œufs sur eux, représente une source d'énergie importante pour les larves de perchaudes. Compte tenu de ces facteurs, il est plutôt difficile d'établir les proies représentant le plus grand avantage énergétique. Il est probable que la préférence pour certaines proies varie aussi selon les variables environnementales. La luminosité, par exemple, limite la perception

oculaire de la larve et donc, influence la taille des proies sélectionnées par la perchaude. Mills et al. (1986) ont déterminés expérimentalement que la taille médiane des proies dans l'estomac de larves de perchaudes tendait à diminuer avec la hausse de l'intensité lumineuse. De plus, la diminution de l'intensité lumineuse ainsi que la turbidité du milieu réduisent la distance de réaction des larves vis-à-vis leur proies (Vinyard et O'brien 1976, Confer et al. 1978 dans Mills et al. 1986). L'intensité lumineuse a donc deux effets distincts sur la croissance des perchaudes. Premièrement, en limitant la visibilité des individus perçus, une faible luminosité peut occasionner un changement dans la taille, et donc les espèces, de proies sélectionnées et ainsi affecter la croissance (Mills et al. 1986, Richmond et al. 2004). Le second effet est d'avantage relié à la distance de réaction (Richmond et al. 2004). Utne (1997) indique que le temps de recherche diminue avec une augmentation de l'intensité lumineuse et qu'il y a une relation linéaire entre la distance de réaction et le temps de recherche pour les proies d'une certaine taille (l'effet étant plus important pour des proies plus petites). En augmentant la distance de réaction, le temps de recherche consacré à la quête de nourriture est donc plus long et de l'énergie pouvant être consacré à la croissance est ainsi perdue.

1.2.3 Facteurs comportementaux liés à la prédation

Chez les perchaudes, la compétition intra-spécifique pour la nourriture est surtout passive (exploitative) et dépend donc principalement de la densité d'individus (Staffan et al. 2002). Une grande densité de perchaudes entraînerait donc un taux de croissance plus faible, puisque la compétition pour la nourriture serait plus forte. Toutefois, le taux de croissance des jeunes larves de perchaudes peut ne pas être pas affecté par la densité. En effet, même si leur densité est importante, il est possible que les larves de perchaudes ne consomment pas suffisamment de proies pour avoir un impact sur la population de zooplancton (Romare 2000). Autrement dit, l'effet de la densité sur le taux de croissance ne devient effectif que lorsque les prédateurs exercent un certain contrôle sur la population de proies ou que la nourriture devient autrement limitée.

D'autre part, les larves de perchaudes effectuent plusieurs migrations au cours de leur ontogénie (Figure 1.1).

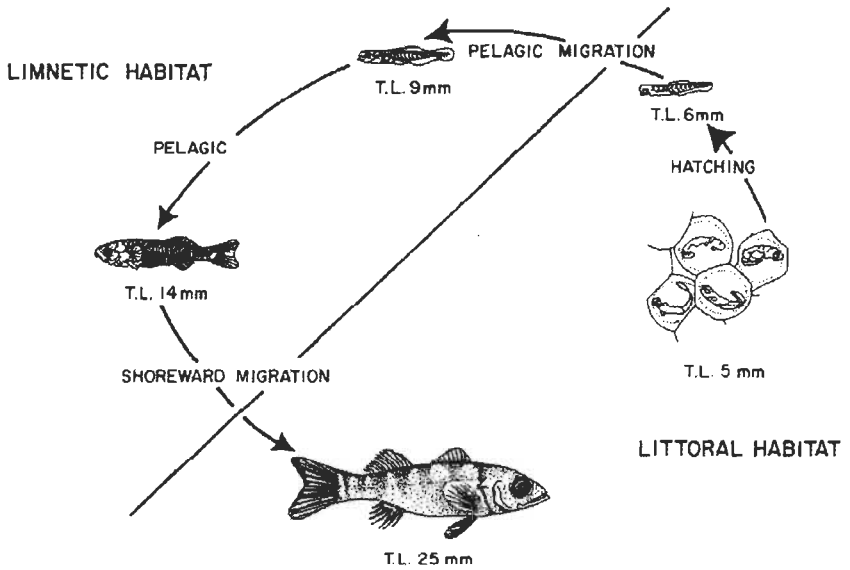

Figure 1.1 : Historique de vie des jeunes perchaudes (*Perca flavescens*) au Lac Itasca, Minnesota. Tiré de Whiteside et al. 1985.

Ces migrations, surtout considérées comme étant un moyen de réduire la pression de prédation (Whiteside et al. 1985), ont également un rôle important dans les choix alimentaires des larves. Tout d'abord, peu après l'éclosion, lorsque la température de l'eau atteint 15°C, les larves migrent du littoral vers le milieu pélagique, où, une fois capables de s'alimenter de façon exogène (longueur totale ~9 mm), elles se nourrissent principalement de petits copépodes et, occasionnellement, de rotifères (Whiteside et al. 1985). Rapidement, les larves s'orientent vers les cladocères (~12 mm) (Graeb et al. 2004). Leur régime reste ensuite assez constant jusqu'au moment où elles atteignent une longueur d'environ 25 mm. C'est alors quelles retournent vers le littoral. Leur régime reste d'abord sensiblement le même qu'en milieu pélagique (copépodes, cladocères), quoique les proies soient plus grosses. Graduellement, leur alimentation évoluera vers des proies telles que des amphipodes et/ou des insectes aquatiques (Whiteside et al. 1985). Toutefois, la densité de perchaudes peut également influencer les migrations. Post et al. (1997) ont notés que lorsque la densité de perchaude est élevée, une même cohorte peut se séparer en deux groupes distincts. En effet, lors de la seconde migration (retour vers le littoral), l'un des groupes peut migrer vers le littoral, alors que l'autre peut

rester en milieu pélagique. Un article de Nakano et Furukawa-Tanaka (1994) (dans Post et al. (1997)) suggère qu'il serait possible que le phénomène soit dû à la présence d'un gène chez certains poissons causant un comportement dominant lorsqu'une certaine densité d'individus serait atteinte. Les individus dominants forceraient donc les autres à rester en milieu pélagique, là ou la qualité de la nourriture est inférieure. Cette compétition par interférence, qui a également été observée dans des milieux où la nourriture est limitante ou lorsque la compétition intra spécifique est élevée (Huss 2008a), a généralement pour effet la création d'un vide entre les classes de tailles des larves de perchaudes. Les plus grosses perchaudes, contrôlant l'accès à la nourriture de meilleure qualité, deviennent encore plus grosses, alors que les petites perchaudes conservent une taille réduite. Il est à noter que ces patrons de migrations ont été observés dans des lacs clairement stratifiés (où les zones littorale et pélagique sont bien délimitées) et qu'il n'y a aucune évidence quant à leur existence dans les marais du lac Saint-Pierre, dont la plaine inondable est extrêmement étendue comparativement à l'image classique d'un lac telle que décrite dans Whiteside et al. (1985).

Un dernier aspect comportemental, le plus souvent négligé, est la tendance au cannibalisme des perchaudes. En effet, il est courant qu'une perchaude juvénile ou adulte se nourrisse de jeunes larves de perchaudes, ce qui accroît la pression de prédation (Brabrand 1995). De surcroît, certaines perchaudes au stade larvaire s'adonnent également au cannibalisme sur des perchaudes de leur propre cohorte. Ceci leur octroie donc un avantage au niveau de la croissance et peut être favorisé lorsqu'une large gamme de taille est disponible dans le même milieu. Ce comportement contribue également à un meilleur recrutement, puisque les plus petites perchaudes, qui n'auraient sans doute pas survécu, fournissent une meilleure chance de survie aux perchaudes présentant déjà un potentiel de recrutement plus élevé (Brabrand 1995).

1.2.4 Effets de la température

La température de l'eau joue un rôle primordial sur la croissance. Les perchaudes étant des organismes poïkilothermes, une température élevée de l'eau accélère leur taux

métabolique, ce qui influence de nombreux facteurs tel que le taux de croissance, la vitesse des réactions chimiques et le temps de digestion (Buckley et al. 1999). Autrement dit, la température n'influence pas seulement la croissance d'une façon directe en accélérant la production cellulaire, mais également de façon indirecte en influençant l'alimentation par la digestion plus rapide des proies, favorisant ainsi une quête de nourriture plus active, rendue elle-même possible par l'énergie supplémentaire découlant de cette même hausse de température. De plus, selon Power et Heuvel (1999) les perchaudes nécessitent une température supérieure à 13,5 degré-jours pour croître, ce qui supporte d'avantage le fait que la température soit un facteur primordial durant toute la saison de croissance.

1.2.5 Effet maternel

La variation en taille à l'éclosion joue un rôle primordial chez les jeunes perchaudes, puisqu'une importante variation en taille faciliterait le cannibalisme au sein d'une même cohorte (Brabrand 1995) ou encore le contrôle des ressources alimentaires par les plus gros individus (Huss 2008a), entraînant une compétition par interférence. Le facteur initial influençant la variation en taille des perchaudes est dû à un effet maternel. En effet, l'âge et la taille des femelles influencent diverses caractéristiques chez leur progéniture, tel que leur taille, leur condition et leur viabilité (Solemdal 1997). Plus précisément, les géniteurs les plus gros et âgés produisent des rejetons trapus munis de gros sacs vitellins, alors que les rejetons de géniteurs plus jeunes sont longs, fins et munis de sacs vitellins plus modestes (Heyer et al. 2001). Les rejetons des plus grosses femelles sont donc mieux adaptés pour faire face à un manque de nourriture peu après l'éclosion, puisqu'ils disposent de réserves énergétiques plus importantes. Par contre, les larves des jeunes géniteurs disposent d'une mobilité accrue, leur permettant un engagement plus actif dans la quête de nourriture et favorisant l'évitement de prédateurs potentiels. Donc, tout dépendant de la condition du milieu après l'éclosion, l'une ou l'autre des portées démontrera un avantage de croissance, menant à une divergence de taille plus ou moins importante selon le cas.

1.3 Caractéristiques du lac Saint-Pierre

1.3.1 Physiographie et hydrologie

Le lac Saint-Pierre (LSP), situé entre Montréal et Québec, est le plus grand élargissement du fleuve Saint-Laurent (superficie d'environ 400 km^2). Il comprend une large plaine inondable d'une profondeur maximale d'environ trois mètres traversée par un chenal de navigation d'une profondeur garantie de 11,3 m. Compte tenu de sa bathymétrie relativement uniforme, le LSP ne possède pas de zones littorales et pélagiques bien distinctes, comme c'est le cas par exemple dans les lacs typiques du bouclier Canadien. Par contre, le lac est composé de plusieurs masses d'eau qui se mélangent très peu latéralement et qui courent les unes à côtés des autres en créant des conditions physicochimiques très contrastées (Morin et Bouchard 2000, Frenette et al. 2003). Les masses d'eau proviennent des apports de plusieurs tributaires qui varient par leur débit et leur concentration en particules organiques dissoutes et en matières en suspension (Frenette et Vincent 2003). Les caractéristiques photiques des masses d'eau sont déterminées par les propriétés physico-chimiques des tributaires (Frenette et al. 2003). Le LSP est dominé en été par la masse d'eau provenant du lac Ontario (~80 % de la décharge du lac), qui est restreinte au chenal de navigation et dont le courant est orienté de l'ouest vers l'est (Morin et Bouchard 2000). Les masses d'eau de la rive nord, qui proviennent principalement de la rivière des Outaouais, sont les plus turbides et sont caractérisées par une couleur brune riche en particules en suspension, une forte concentration en phosphore et une concentration relativement élevée en carbone organique dissous (COD) (Frenette et al. 2003). Il est à noter qu'une forte concentration en COD pourrait avoir un effet protecteur sur les œufs de perchaudes ainsi que sur leurs larves en les protégeant des rayonnements ultraviolets (Bertolo et Magnan, 2007). Les tributaires qui drainent les terres agricoles sur la rive sud du fleuve Saint-Laurent apportent une eau chargée en éléments nutritifs tout au long de la rive (Vis et al. 2003), ce qui lui confère une plus grande productivité que la rive nord et se reflète à plusieurs niveaux trophiques : production primaire (Vis et al. 2007), zooplancton (Basu et al. 2000) et benthos (Huggins et al. 2004).

1.3.2 Habitat des larves de perchaude

Les marais peu profonds aux abords du lac Saint-Pierre sont des lieux de prédilection pour la reproduction des perchaudes, car leurs eaux stables se réchauffent rapidement au printemps. Les marais sont donc des habitats utilisés par la perchaude pour la fraye (Brodeur et al. 2004), mais également pour l'élevage, la croissance et l'alimentation, car ils favorisent aussi la production de zooplancton (Langlois et al. 1992), principale source de nourriture des jeunes larves. Depuis plusieurs années, les marais aménagés le long du Saint-Laurent font l'objet d'études pour déterminer leurs contributions à la production de perchaude du fleuve. L'étude de Tardif et al. (2005) met en évidence que la croissance des perchaudes était plus élevée dans les marais aménagés au printemps (i.e. en mai), mais qu'au début de l'été (i.e. juin) la tendance s'inversait en faveur des marais naturels. Les auteurs ont alors émis l'hypothèse que la température particulièrement élevée au printemps dans les marais aménagés avait favorisé le développement des jeunes larves, mais que les ressources alimentaires des milieux aménagés pouvaient se tarir avec le temps jusqu'à devenir limitante.

1.4 Indices de croissances

1.4.1 Rapport ARN/ADN

L'utilisation du rapport ARN/ADN comme indice de croissance est basée sur la stabilité relative de la quantité d'ADN d'un organisme comparativement à son poids et à la variation de son ARN (Ferron et Leggett 1993). En effet, lorsqu'un organisme croît, la synthèse protéique augmente, entraînant une augmentation du nombre de ribosomes pour soutenir cette demande. L'augmentation d'ARNr est donc la principale source de la variation de l'ARN d'un organisme. Il en découle qu'un organisme ayant une forte croissance aura un rapport ARN/ADN élevé, alors qu'un individu présentant une croissance plus faible aura un rapport moins important.

La valeur du rapport ARN/ADN change au cours de l'ontogénie du poisson. Elle diminue avec l'âge compte tenu du ralentissement naturel du métabolisme et de la

croissance. Selon Buckley et al. (1999), le rapport ARN/ADN varie également selon le cycle circadien des larves. Autrement dit, il y aurait une variation journalière de l'indice qui serait relié à l'activité du poisson. Ces changements pourraient être expliqués par des différences dans le taux métabolique, les exigences alimentaires et le temps de digestion (Buckley et al. 1999). Toutefois, ce patron apparaît surtout chez les espèces d'eau chaude et semble être faible, voire absent, chez les espèces de milieux froids (Buckley et al. 1999). Il est donc important d'échantillonner durant la même période de la journée pour toute la durée de l'échantillonnage afin de minimiser la variation de l'indice.

Un autre facteur ayant un effet important sur la variation du rapport ARN/ADN des perchaudes est la température de l'eau. Tout d'abord, tel que mentionné précédemment, la température influence la croissance des perchaudes. En effet, pour un même âge, une température plus élevée produira de plus grosses larves (Malzahn et al. 2003). Il en découle donc que plus la température est élevée, plus le rapport ARN/ADN des larves devrait augmenter (jusqu'à un seuil critique de température). Cependant, Buckley et al. (1999) soulignent que la quantité d'ARN et le rapport ARN/ADN diminuent avec une augmentation de la température même si le taux de croissance augmente. Goolish et al. (1984) ont suggéré que des rapports élevés à faible température faisaient partie d'un mécanisme compensatoire pour l'activité réduite de l'ARN à basse température. La stratégie consiste à augmenter la quantité d'ARN dans l'organisme pour compenser sa perte d'efficacité. Buckley et al. (1999) suggèrent de ne comparer les données de rapport ARN/ADN que pour des données provenant de milieux où l'écart de température est inférieur à 2°C. Effectivement, au-delà de cette limite, il deviendrait impératif d'appliquer une correction pour la température avant de comparer les rapports puisque pour un même rapport ARN/ADN, la croissance augmente de 1 $\%\cdot j^{-1}$ pour chaque augmentation de 1°C de la température de l'eau (Buckley et al. 1999). Afin d'appliquer ces corrections, la croissance devrait être exprimée en taux de croissance protéique en $\%\cdot j^{-1}$ suivant l'équation proposée par Buckley (1984). Toutefois, il faut prendre en compte que cette équation a été mise au point pour des espèces marines et qu'elle pourrait devoir être adaptée pour décrire la croissance d'espèces d'eau douce.

Le rapport ARN/ADN indique la croissance « instantanée » d'un individu, c'est-à-dire qu'il fournit une indication sur la croissance actuelle du poisson, sans tenir compte de son historique de croissance. La nature même du rapport ARN/ADN en fait donc un indice ponctuel à faible inertie temporelle. Le rapport ARN/ADN étant un indice biochimique, il répond de façon rapide aux changements environnementaux. Buckley (1984) a évalué que le rapport ARN/ADN reflète la croissance sur les 2 à 4 jours précédant la capture lorsque mis en relation avec la température. Toutefois, selon Tardif et al. (2005), l'indice ARN/ADN refléterait la croissance au septième jour précédant la capture dans un milieu où la faible température de l'eau est un facteur limitant la croissance.

1.4.2 Longueur totale

La longueur totale ne constitue pas un indice de croissance en soi. Cependant, des mesures répétées de la longueur peuvent être utilisées à cette fin pour mesurer des accroissements de longueur et établir un taux de croissance. Ces mesures constituent un indice intégrateur et englobe l'ensemble de l'historique de croissance. Le temps de réponse de l'indice de longueur est relativement long compte tenu de la nature morphologique de l'indice et du délai nécessaire avant de détecter un accroissement en longueur significatif. De plus, la longueur seule ne tient pas compte des stratégies de croissance adoptées par les poissons. Par exemple, la stratégie de croissance des larves de perchaudes est de tout d'abord croître en longueur, et ensuite, en poids (Whiteside et al. 1985).

1.4.3 Poids

Bien qu'il soit, comme la longueur, un indice morphométrique, les données de poids peuvent nous renseigner sur certaines caractéristiques autrement ignorées par la longueur totale. Par exemple, le poids indique la condition dans laquelle se trouvent les larves de perchaudes en indiquant leur corpulence, un reflet des réserves énergétiques accumulées. De plus, compte tenu du changement progressif de stratégie de croissance

des larves de perchaudes de la longueur vers le poids (Whiteside et al. 1985), les effets d'un ralentissement ou d'une accélération de croissance seront éventuellement d'avantage perçus par les mesures de poids que de longueur.

1.5 Références

Basu, B.K., Kalff, J., et Pinel-Alloul, B. 2000. Midsummer plankton development along a large temperate river: the St. Lawrence River. Can. J. Fish. Aquat. Sci. **57**(S1): 7-15. doi: 10.1139/f99-249.

Bertolo, A., et Magnan, P. 2007. Logging-induced variations in dissolved organic carbon affect yellow perch *(Perca flacescens)* recruitment in Canadian Shield lakes. Can. J. Fish. Aquat. Sci. **64**(2): 181-186. doi: 10.1139/f07-004.

Brabrand, Å. 1995. Intra-cohort cannibalism among larval stages of perch (*Perca fluviatilis*). Ecol. Freshw. Fish **4**(2): 70-76. doi: 10.1111/j.1600-0633.1995.tb00119.x.

Brodeur, P., Mingelbier, M., et Morin, J. 2004. Impact des variations hydrologiques sur les poissons des marais aménagés du Saint-Laurent fluvial. Nat. Can. **128**(2): 66-77. Disponible à : http://www.provancher.qc.ca/upload/file/128_2%20p%2066-77.pdf. [cité 21 Mars 2012].

Buckley, L.J. 1984. RNA-DNA ratio: an index of larval fish growth in the sea. Mar. Biol. **80**(3): 291-298. doi: 10.1007/BF00392824.

Buckley, L., Caldarone, E., et Ong, T.-L. 1999. RNA–DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. Hydrobiologia **401**(0): 265–277. doi: 10.1023/A:1003798613241.

Confer, J.L., Howich G.L., Corzette, M.H., Kramer, S.L., Fitzgibbon, S., et Landesberg, R. 1978. Visual predation by planktivores. Oikos **31**(1): 27-37. Disponible à : http://www.jstor.org/stable/3543380. [cité 13 Mars 2012].

Ferron, A., et Leggett, W.C. 1993. An appraisal of condition measures for marine fish larvae. Adv. Mar. Biol. **30**: 217-303. doi: 10.1016/j.bbr.2011.03.031.

Frenette, J.J., Arts, M.T., et Morin, J. 2003. Spectral gradients of downwelling light in a fluvial lake (Lake Saint-Pierre, St. Lawrence River). Aquat. Ecol. **37**(1): 77-85. doi: 10.1023/A:1022133530244.

Frenette, J.J., et Vincent, W.F. 2003. Bio-optical variability in the littoral zone: Local heterogeneity and implications for water quality monitoring. *In* Freshwater Management: Global versus local perspectives. Edited by M. Kumagai and W.F. Vincent. Springer-Verlag, Tokyo, Japan. pp. 41-59.

Fuiman, L.A., Cowan, J.H., Smith, M.E. Jr., et O'Neal, J.P. Behavior and recruitment success in fish larvae: variation with growth rate and the batch effect. Can. J. Fish. Aquat. Sci. **62**(6): 1337–1349. doi: 10.1139/f05-053.

Fulford, R.S., Rice, J.A., Miller, T.J., Binkowski, F.P., Dettmers, J.M., et Belonger, B. 2006. Foraging selectivity by larval yellow perch (*Perca flavescens*): implications for understanding recruitment in small and large lakes. Can. J. Fish. Aquat. Sci. **63**(1): 28-42. doi: 10.1139/f05-196.

Goolish, E.M., Barron, M.G., et Adelman, I.R. 1984. Thermoclimatory response of nucleic acid and protein content of carp muscle tissue: influence of growth rate and relationship to glycine uptake by scales. Can. J. Zool. **62**(11): 2164–2170. doi: 10.1139/z84-314.

Graeb, B.D.S., Dettmers, J.M., Wahl, D.H., et Cáceres, C.E. 2004. Fish size and prey availability affect growth, survival, prey selection and foraging behavior of larval yellow perch. T. Am. Fish. Soc. **133**(3): 504-514. doi: 10.1577/T03-050.1.

Heyer, C.J., Miller, T.J., Binkowski, F.P., Caldarone, E.M., et Rice, J.A. 2001. Maternal effects as a recruitment mechanism in Lake Michigan yellow perch (*Perca flavescens*). Can. J. Fish. Aquat. Sci. **58**(7): 1477–1487. doi: 10.1139/f01-090.

Huggins, K., Frenette, J.J., et Arts, M.T. 2004. Nutritional quality of biofilms with respect to light regime in Lake Saint-Pierre (Québec, Canada). Freshwater Biol. **49**(7): 945-959. doi: 10.1111/j.1365-2427.2004.01236.x.

Huss, M., Byström, P., et Persson, L. 2008a. Resource heterogeneity, diet shifts and intra-cohort competition: effects on size divergence in YOY fish. Oecologia **158**(2): 249–257. doi: 10.1007/s00442-008-1140-9.

Huss, M., Byström, P., Strand, A., Eriksson L.-O., et Persson, L. 2008b. Influence of growth history on the accumulation of energy reserves and winter mortality in young fish. Can. J. Fish. Aquat. Sci. **65**(10): 2149-2156. doi: 10.1139/F08-115.

Langlois, C., Lapierre, L., Léveillé, M., Turgeon, P., et Ménard, C. 1992. Synthèse des connaissances sur les communautés biologiques du lac Saint-Pierre. Rapport technique. Zone d'intérêt prioritaire 11. Centre Saint-Laurent, Conservation et Protection, Environnement Canada, Québec.

Magnan, P. 2002. Avis scientifique sur l'état du stock de perchaudes au lac Saint-Pierre, les indicateurs biologiques utilisés pour effectuer son suivi et la pertinence de protéger la période de fraye de façon partielle ou totale. Chaire de recherche du Canada en écologie des eaux douces. Université du Québec à Trois-Rivières, Québec.

Makauskas, D., et Clapp, D. 2008. Status of yellow perch in Lake Michigan and Yellow Perch Task Group Progress Report. Report to the Lake Michigan committee. Niagara Falls, Ontario.

Malzahn, A. M., Clemmesen, C., et Rosenthal, H. 2003. Temperature effects on growth and nucleic acids in laboratory-reared larval coregonid fish. Mar. Ecol. Prog. Ser. **259**: 285-293. Disponible à: http://epic.awi.de/9335/1/Mal2003a.pdf. [cité 13 Mars 2012].

Mills, E.L., Confer, J.L., et Kretchmer, D.W. 1986. Zooplankton selection by young yellow perch: the influence of light, prey density, and predator size. T. Am. Fish. Soc. **115**(5): 716-725. doi: 10.1577/1548-8659(1986)115<716:ZSBYYP>2.0.CO;2.

Morin, J. et Bouchard, A. 2000. Les bases de la modélisation du tronçon Montréal/Trois-Rivières. Rapport scientifique SMC-Hydrométrie RS-100. Environnement Canada, Sainte-Foy, Québec.

Nakano, S., et Furukawa-Tanaka, T. 1994. Intra- and interspecific dominance hierarchies and variation in foraging tactics of two species of stream-dwelling chars. Ecol. Res. **9**(1): 9-20. doi: 10.1007/BF02347237.

Post, D.M., Kitchell, J.F., et Hodgson, J.R. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. Can. J. Fish. Aquat. Sci. **55**(12): 2588–2600. doi: 10.1139/f98-139.

Post, J.R., et Evans, D.O. 1989. Size-Dependent Overwinter Mortality of Young-of-the-Year Yellow Perch (*Perca* flavescens): Laboratory, In Situ Enclosure, and Field Experiments. Can. J. Fish. Aquat. Sci. **46**(11): 1958-1968. doi: 10.1139/f89-246.

Post, J.R., Johannes, M.R.S., et McQueen D.J. 1997. Evidence of density-dependent cohort splitting in age-0 yellow perch (*Perca flavescens*): potential behavioural mechanisms and population-level consequences. Can. J. Fish. Aquat. Sci. **54**(4): 867-875. doi: 10.1139/f96-335.

Power, M., et Van Den Heuvel, M.R. 1999. Age-0 yellow perch growth and its relationship to temperature. T. Am. Fish. Soc. **128**(4): 687-700. doi: 10.1577/1548-8659(1999)128<0687:AYPGAI>2.0.CO;2.

Richmond, H.E., Hrabik, T.R., et Mensinger, A.F. 2004. Light intensity, prey detection and foraging mechanisms of age 0 year yellow perch. J. Fish. Biol. **65**(1): 195-205. doi: 10.1111/j.0022-1112.2004.00444.x.

Romare, P. 2000. Growth of larval and juvenile perch: the importance of diet and fish density. J. Fish. Biol. **56**(4): 876-889. doi: 10.1111/j.1095-8649.2000.tb00878.x.

Schael, D.M., Rudstam, L.G., et Post, J.R. 1991. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (*Aplodinotus grunniens*), and black crappie (*Pomoxis nigromaculatus*). Can. J. Fish. Aquat. Sci. **48**(10): 1919-1925. doi: 10.1139/f91-228.

Shroyer, S.M., et McComish, T.S. 1998. Forecasting abundance of quality-size yellow perch in Indiana waters of Lake Michigan. N. Am. J. Fish. Manage. **18**(1): 19-24. doi: 10.1577/1548-8675(1998)018<0019:FAOQSY>2.0.CO;2.

Solemdal, P. 1997. Maternal effects - a link between the past and the future. J. Sea Res. **37**(3-4): 213-227. doi: 10.1016/S1385-1101(97)00029-4.

Staffan, F., Magnhagen, C., et Alanärä, A. 2002. Variation in food intake within groups of juvenile perch. J. Fish. Biol. **60**(3): 771-774. doi: 10.1111/j.1095-8649.2002.tb01702.x.

Tardif, D., Glémet, H., Brodeur, P., et Mingelbier, M. 2005. RNA/DNA ratio and total length of yellow perch (*Perca flavescens)* in managed and natural wetlands of a large fluvial lake. Can. J. Fish. Aquat. Sci. **62**(10): 2211-2218. doi: 10.1139/f05-137.

Truemper, H.A., et Lauer, T.E. 2005. Gape limitation and piscine prey size-selection by yellow perch in the extreme southern area of Lake Michigan, with emphasis on two exotic prey items. J. Fish. Biol. **66**(1): 135–149. doi: 10.1111/j.0022-1112.2005.00588.x.

Utne, A.C.W. 1997. The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. J. Fish. Biol. **50**(5): 926–938. doi: 10.1111/j.1095-8649.1997.tb01619.x.

Vinyard, G.L., et O'Brien W.J. 1976. Effects of light and turbidity on the reactive distance of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. **33**(12): 2845-2849. doi: 10.1139/f76-342.

Vis, C., Hudon, C., et Carignan, R. 2003. An evaluation of approaches used to determine the distribution and biomass of emergent and submerged aquatic macrophytes over large spatial scales. Aquat. Bot. **77**(3): 187–201. doi : 10.1016/S0304-3770(03)00105-0.

Vis, C., Hudon, C., Carignan, R., et Gagnon, P. 2007. Spatial analysis of production by macrophytes, phytoplankton and epiphyton in a large river system under different water-level conditions. Ecosystems **10**(2): 293-310. doi: 10.1007/s10021-007-9021-3.

Wahl, C.M., Mills, E.L., McFarland, W.N., et DeGisi, J.S. 1993. Ontogenetic changes in prey selection and visual acuity of the yellow perch, *Perca flavescens*. Can. J. Fish. Aquat. Sci. **50**(4): 743–749. doi: 10.1139/f93-085.

Whiteside, M.C., Swindoll, C.M., et Doolittle, W.L. 1985. Factors affecting the early life history of yellow perch, *Perca flavescens*. Environ. Biol. Fish. **12**(1): 47-56. doi: 10.1007/BF00007709.

Wilberg, M.J., Bence, J.R., Eggold, B.T., Makauskas, D., et Clapp, D.F. 2005. Yellow perch dynamics in southwestern Lake Michigan during 1986–2002. N. Am. J. Fish. Manage. **25**(3): 1130-1152. doi: 10.1577/M04-193.1.

Wong, B., et Ward, F.J. 1972. Size selection of Daphnia pulicaria by yellow perch (*Perca* flavescens) fry in West Blue Lake, Manitoba. J. Fish. Res. Board Can. **29**(12): 1761-1764. doi: 10.1139/f72-277.

CHAPITRE II

YELLOW PERCH (*PERCA FLAVESCENS*) GROWTH DURING EARLY ONTOGENY IN A FLUVIAL LAKE DOMINATED BY A VAST LITTORAL

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Yellow perch (*Perca flavescens*) growth during early ontogeny in a fluvial lake dominated by a vast littoral

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Early growth of larval yellow perch

Keywords Yellow perch · Wetlands · RNA/DNA ratio · Growth · Young of the year Ontogeny · Fluvial lake · Littoral · Growth indices

2.1 Abstract

Yellow perch (*Perca flavescens*) young-of-the-year (YOY) growth was evaluated for a consecutive 5-week period following hatching. YOY were sampled in four contrasting wetlands of Lake Saint-Pierre, the largest fluvial lake of the St. Lawrence River, to capture habitat heterogeneity. Cumulated degree days over 13.5°C followed YOY body size ranking between sites during the entire 5 weeks. Ranking conservation throughout the studied period suggests that early temperature conditions may modulate YOY total lengths reached by the end of the growth season and ultimately influence winter survival. Breaks in growth rate were observed on length/weight growth trajectories and were seemingly linked to diet switches and unrelated to ontogenic migrations. This is contrary to observations made in lakes where diet changes follow migrations between well-defined littoral/pelagic zones. Our results suggest that YOY growth rates can be modulated by diet changes occurring in the absence of ontogenic migrations. Repercussions on YOY survival and recruitment need to be further investigated in fluvial systems where the littoral zone is particularly extensive.

2.2 Introduction

In temperate climates, survival through the first winter constitutes an important bottleneck for fish recruitement and fisheries (Post and Evans 1989, Post et al. 1998, Huss et al. 2008). Since young-of-the-year (YOY) fish need to reach a minimum size threshold and a given level of energetic reserves by the end of their first growth season in order to withstand winter starvation, their survival largely depends on their growth rate (Post and Evans 1989, Huss et al. 2007, Huss et al. 2008). Among the factors known to influence growth rate, temperature and diet are considered the most important (Buckley et al. 1982, Whiteside et al. 1985, Romare 2000). It thus becomes important to measure these factors as it could lead to a better understanding of fish recruitement and fisheries sustainability.

The study of fish growth and recruitement is particularly relevant in Lake Saint-Pierre (LSP), where historically important commercial and sport fisheries for yellow perch (*Perca flavescens*) were supported until the mid-1990's (Guénette et al. 1994). High exploitation rates combined with poor recruitment during the 1988-1998 period led to a 70% decline in yellow perch abundance (Mailhot and Dumont 2003). In spite of a major reduction of the fishing effort in recent years, the yellow perch stock did not recover (Magnan et al. 2008). This decline in yellow perch abundance over the last two decades has been observed in numerous systems (Truemper and Lauer 2005, Wilberg et al. 2005). While it is generally accepted that increased fishing pressure was the primary cause of decline, poor recruitment, and thus failure to reinforce fish stocks, has been suggested as playing a major role in fisheries collapse (Shroyer and McComish 1998, Magnan et al. 2008, Makauskas and Clapp 2008).

Numerous studies have attempted to characterize YOY yellow perch growth (Whiteside et al. 1985, Post et al. 1997, Fitzgerald 2000). One common downfall of many of these studies is the large time interval between sampling periods. Studies were conducted on a monthly or seasonal basis, and may fail to capture the complexity of yellow perch growth during early ontogeny occuring on a daily or weekly scale (Post et al. 1997, Fitzgerald 2000, Tardif et al. 2005). In addition, these studies took place in

relatively deep lake systems with well defined littoral and pelagic zones (henceforth referred to as: "typical" lakes). This habitat structure has an impact on early larval growth since two migrations occur within a few weeks between the littoral and pelagic zones in order to maximize energetic gain through changes in diet and reduce predation risk (Whiteside et al. 1985, Urho 1997). Fluvial lakes, like LSP, differ from typical ones by their shallow and uniform topography, which results in a particularly extented littoral zone. In particular, no information is currently available on the seemingly absence of migrations between well defined littoral and pelagic zones and the potential effects this may have on yellow perch early growth history. In addition, distinct water masses from different tributaries, flowing side by side with reduced lateral mixing (Frenette et al. 2006), are affecting yellow perch growth and ontogeny by contrasting the physicochemical composition of this wide open fish nursery.

This paper aims at filling the current gaps in our knowledge on early growth of YOY yellow perch at the onset of ontogeny in lakes dominated by a vast shallow littoral. Specifically, we examined how varying environmental conditions impact larval growth and eventually recruitment success by monitoring growth in newly hatched larvae throughout a five-week period using several growth indices. Environmental conditions contrasting spatially and changing temporally in fluvial Lake Saint-Pierre (Frenette et al. 2003, Frenette et al. 2006) are expected to offer yellow perch larvae distinctive site-specific growth conditions.

2.3 Methods

2.3.1 Study site

Lake St. Pierre (LSP) is the largest (~400 km^2) fluvial lake of the St. Lawrence River. LSP encompasses a large (30 x 15 km), shallow floodplain (mean depth ~3 m). It is relatively slow-flowing (<0.5 $m \cdot s^{-1}$) with the exception of a man-made navigation channel (width ~300 m; depth ≥11.3 m) that delimits the north and south shores. The shallow depth, gentle slope, slow current, and high nutrient content that prevail in the littoral zone of LSP favour the development of large beds of submerged aquatic vegetation dominated by *Vallisneria americana*. Several tributaries, flow into LSP and contribute to the formation of distinct water masses flowing side by side with low lateral mixing (Frenette et al. 2006). While the main water mass originating from Lake Ontario (clear water and nutrient depleted) occupies the central, fast-flowing navigation channel, slow-flowing areas along the south shore are largely under the influence of tributaries that drain extensive farmlands and constitute major sources of nutrients to LSP. The north shore water mass is turbid and rich in suspended matter, phosphorus and dissolved organic carbon (DOC) (Frenette et al. 2003). The south shore of LSP is a high productivity area for primary producers (Vis et al. 2007), zooplankton (Basu et al. 2000), and benthic invertebrates (Tourville Poirier et al. 2010). The south shore also supports higher yellow perch growth (Glémet and Rodriguez 2007) and higher relative fish biomass and productivity (La Violette et al. 2003) than the north shore of LSP, which are attributed to the extensive wetland area and the enrichment by tributaries.

2.3.2 Sampling

To take into account the spatial heterogeneity of LSP and its potential impact on larval yellow perch growth, four contrasting sites were sampled (Figure 2.1): the natural marsh of the Maskinongé bay (MAS; 46°12'N, 72°58'W) and the managed marsh of Saint-Barthélemy (STB; 46°10'N, 73°00'W) on the north shore and the natural marsh of Anse du Fer-à-Cheval (FAC; 46°11'N, 72°45'W) and the managed marsh of Ile-du-Moine (IDM; 45°11'N, 73°00'W) on the south shore. By spring time, fish can

access the managed and natural wetlands located in the floodplain to spawn. After the spring flood, the contact is interrupted between the managed wetlands and the surrounding water masses and for several weeks, fish remain captive in the managed wetlands while the water level is stabilized. Annual drawdown operations in June and in October evacuate fish production before ice cover to prevent high fish predation in summer and to avoid winterkill during ice cover (Lepage and Lalumière 2003). Stable water level in managed wetlands generally favors rapid warming of water in spring and can thus maximize larval growth at these sites (Tardif et al. 2005). Conversely, the water level of the natural marshes varies daily with changing river flow.

YOY yellow perch (length <30 mm) were sampled simultaneously in the four sites every two days starting on May 27th up to June 28th, 2005. A push net (500 µm mesh size) was used until June 16th (larvae size between 12.95 and 29.25 mm) at which point a beach seine (3.2 mm mesh size) was used afterwards to account for the increase in fish swimming capacity and ability to avoid the push net (see Paradis et al. 2008 for a complete description of the sampling method). During each visit, a varying number of 50 m push net transects or beach seine stations, generally up to three, were sampled until at least 30 larvae were captured at each site. It is noteworthy that because of low larval abundance, no larvae could be captured at the STB site after June 6th. Yellow perch larvae were immediately placed on dry ice to avoid tissue degradation and later transferred to a -80°C freezer.

Water was sampled at each site at the same frequency as larvae starting on May 29th. Two thermographs (Minilog-T™ VEMCO; ± 0.1°C) were used to obtain hourly water temperature measures at each of the four sites between April 22nd and June 28th, 2005. Each thermograph was placed 0.2 m from the bottom and protected from direct sunlight by a white screen. Air temperature, precipitation and LSP water level data were measured at the Sorel station (Environment Canada and Fisheries and Oceans Canada).

2.3.3 Laboratory analyses

Yellow perch larvae were identified, weighed (± 0.001 g) and measured for their total length using a caliper (± 0.01 mm) before their heads were removed by cutting behind the operculum to preserve otoliths for further analysis. RNA/DNA ratio was determined for each larvea using a modification of the microfluorometric method developed by Kyle et al. (2003). The headless larvea were homogenized (Powergen 125, PolyScience X-120) in an extraction buffer (EB) solution composed of N-lauroylsarcosine sodium (1%) using a dilution factor of 91.25 ml/g. A 25 µl subsample was further diluted (7.5 dilution factor) within a solution composed of EB and Tris-HCL and EDTA (TE buffer). All further steps were done as described in Kyle et al. (2003).

Water samples were analysed for chlorophyll *a*, total organic carbon, total nitrogen, and total phosphorus (Centre d'expertise en analyse environnementale du Québec). Chlorophyll *a* concentrations were determined by fluorometry. Total organic carbon was quantified by infrared detection, while total nitrogen and phosphorus concentrations were obtained by an automated colorimetric method with UV digestion.

2.3.4 Data analysis

Twenty-one randomly selected larvae from each site and for each sampling day were used in statistical tests. To get a better understanding of the growth trajectory of yellow perch larvae for each marsh, data were split equally into three periods (each period containing a similar number of sampling days). Period one (I) corresponds to May 26th to June 6th (Day of Year, DOY 146-157), period two (II) to June 8th to June 16th (DOY 159-167) and period three (III) to June 20th to June 28th (DOY 171-179).

Analyses of variance (ANOVAs) followed by a post-hoc Bonferroni test were performed on both log-transformed total length and RNA/DNA values to test for growth differences between sites for each given time period. Since a negative relationship exists between RNA/DNA ratios and water temperature, high RNA/DNA ratios at low

temperatures may be a RNA compensation mechanism (Goolish et al. 1984, Buckley et al. 1999). Since general linear models (GLM) revealed interactions between RNA/DNA ratio and temperature for period I, we could not perform an ANCOVA to remove temperature effects. Instead, an ANOVA followed by a Bonferroni test was perfomed for period I using only data covering a similar temperature range across sites. Analyses of covariance (ANCOVAs) were used for testing inter-site comparisons of log-transformed weight data to correct for any length effect. Mean daily length and weight increments were calculated for each site by period and compared between sites using ANOVAs and ANCOVAs on log transformed values respectively. Unimodality in length-frequency plots suggest that a single cohort of larvae was present throughout the observed growth period. Consequently, no hatch date correction on the total length was necessary at a given site.

Log-transformed mean values of total length and weight were plotted as a function of sampling day (DOY) and used to estimate breakpoints in the growth trajectory using Davies tests (Davies 1987). Piecewise regressions were also run to compare slopes before and after each breakpoint. Davies (Davies, 1987) and piecewise regression tests were conducted using R 2.10.1 (R Development Core Team, 2009) with the Segmented package (Muggeo, 2008).

In order to determine any site differences in environmental conditions, daily means of environmental variables (temperature, chlorophyll *a*, pheophytin, total organic carbon (TOC), total nitrogen (TN) and total phosphorus (TP)) were compared for each period using ANOVAs. Furthermore, a constrained redundancy analysis (RDA) was performed (R 2.10.1, R Development Core Team, 2009) on each time period to determine how environmental variables influenced larval growth. RDAs were performed on three time periods rather than a single one over 5 weeks in order to maximize the chances of detecting environmental effects which were otherwise completely masked. Daily log-transformed mean values of length, weight and RNA/DNA ratio were used as dependent variables, while daily means of water temperature, cholophyll *a*, TOC, TN and log-transformed values of pheophytin and TP were used as independent variables.

The water level effect was excluded since managed sites presented stable water levels throughout the sampling period. The site effect was removed by including sites as a dummy variable. TP values were removed from the test for period II and III because of numerous missing values. Given the relatively fast response time of RNA/DNA ratio (Ferron and Leggett. 1994) we explored the time scale at which the index responded to environmental changes occurring up to 10 days before the fish were sampled. To this end, we explored the correlations between the RNA/DNA ratio and environmental variables including temperature, water level, chlorophyll a, pheophytin, TOC, TN and PT. All sites and periods were included in the tests to provide a more general portrait. Data anomalies, such as important peaks in environmental variables and/or RNA/DNA ratio, were at first removed from the test to avoid any possible bias. However since results remained consistent, all data were incorporated in the final tests.

All statistical tests were conducted using Systat 10.2 (© Systat software Inc. 2002) except where otherwise noted.

Yellow perch spawning date was estimated from air temperature (Mingelbier et al. 2005) whereas hatching dates were estimated from the relationship between incubation period and water temperature (Guma'a 1978). Water temperature was the mean measured during the 20 days following the simulated spawning date.

2.4 Results

2.4.1 Total length and weight

The length frequency distributions of yellow perch larvae were unimodal at each of the study sites and for each time period and were generally normally distributed except at the Maskinongé (MAS) site (Figure 2.2). At the MAS site, the distribution was slightly skewed to the left during periods II and III indicated there was a high frequency of small fish and few large ones. This contrast with other sites where intermediate length classes were the most represented. For the Saint-Barthélemy (STB) site, period II and III were excluded from the analyses since larvae were not captured then.

Significant differences in mean total length of yellow perch larvae were observed between sites for each time period (Figure 2.2). The relative ranking of body size with regard to both total length and weight between sites was somewhat maintained throughout the sampled 5-week period. Yellow perch larvae from Ile-du-Moine (IDM) were always longer followed by those from FAC and MAS sites ($F > 69.48$; $p < 0.001$) and those from STB (for Period I only) (Figure 2.2; Table 2.1). Compared to TL, some differences in the ranking between sites were observed for body weight. Notably during period II, FAC larvae were of similar weight to IDM ($F = 0.34$; $p = 0.56$) (Table 2.1) and during period III, MAS larvae were of similar weight to FAC ($F = 0.07$; $p = 0.79$) (Table 2.1). These results suggest that accelerated growth is occuring at some sites enabling larvae to catch up to those other larvae with regards to their weight. However, mean daily growth increment differences in body size, total length and weight between sites were not significant for any time period ($F < 0.40$; $p > 0.67$).

Breakpoints for both the length and weight growth trajectories were estimated using Davies tests (Figure 2.3). A breakpoint in the total length-time relationship was estimated at the MAS site on Day of Year (DOY) 160.5 ($p < 0.01$; with confidence interval (CI) between DOY 154.6 and 166.4) at a mean total length value of 12.4 mm. The growth rate increased following this break with the slope value changing from 0.024 to 0.042 before and after the breakpoint respectively. A similar breakpoint in total length

was estimated at IDM on DOY 166.3 ($p < 0.001$; with CI between DOY 163.4 and 169.1), and corresponded to a nearly simultaneous breakpoint in the weight-time relationship on DOY 165.9 ($p < 0.001$; with CI between DOY 162.6 and 169.1). Breaks in length and weight trajectories corresponded to a mean larval length value of 24.3 mm and 23.9 mm respectively. In this case, growth rates decreased following the breaks, with slope values of 0.035 to 0.014 for length and from 0.134 to 0.039 for weight. A breakpoint in weight at the FAC site was estimated on DOY 165.7 ($p < 0.001$; CI between DOY 160.6 and 170.9) corresponding to a mean larval length of 18.4 mm. Growth rate decreased after the breakpoint with the slope value of 0.187 to 0.050. Intrestingly this breakpoint occurred on the same date as the one observed at the IDM site. The Davies test failed to detect a breakpoint for length at FAC ($p = 0.145$). It is noteworthy that the dates at which breakpoints were observed at IDM and FAC coincide with a change in sampling methods from push net to beach seine (June 16th = DOY 167). It is be possible that the beach seine could have favored the capture of larger individuals thus influencing the length/weight growth trajectories. However, this is unlikely since no similar breakpoints were observed at the MAS site where a similar sampling procedure was applied.

2.4.2 Short term growth index (RNA/DNA ratio)

During the study period, RNA/DNA ratios varied similarily between sites with the exception that at the FAC site an important RNA/DNA peak occured at DOY 163 (Figure 2.4).

When RNA/DNA ratios were compared among sites at the beginning of the 5-week period, the short-term growth index in managed sites was not always higher than that of natural sites (Table 2.1) as was expected (Tardif et al. 2005). In fact, in only one case was this observed when RNA/DNA ratios at the managed site IDM, was higher than at the natural site FAC ($F = 18.55$; $p < 0.001$). RNA/DNA ratios at the other managed site (STB) were actually identical to that of the natural site FAC ($F = 2.40$; $p = 0.124$) and lower than that of MAS ($F = 8.59$; $p = 0.004$).

2.4.3 Environmental influence on growth

The presence of multiple water masses, heterogenous water temperature and nutrients, all contribute to creating contrasting conditions for fish development in LSP. Effectively, while the simulated onset of spawning was similar among sites, the simulated hatching dates varied between sites because of water temperature differences (Table 2.2). Larvae at the IDM site hatched nearly one week earlier than at the other sites. Degree days cumulated over 13.5°C between hatching and May 26th (day corresponding to the first sampling) ranged from 3-10 fold higher at IDM compared to the other sites (Table 2.2). Similarily for the period between hatching to the end of sampling, cumulated degree days over 13.5°C at IDM were higher than at other sites but this time only by 1.1-1.5 fold higher. The amount of degree days over 13.5°C cumulated at FAC was second highest while MAS and STB ranked third and fourth respectively (Table 2.2). The same ranking held true for the period between hatching and the first day of sampling. Despite observed site differences in cumulated degree days over 13.5°C it is interesting to note that no significant differences in mean daily water temperature were found during the 5-week study period ($F = 2.87$; $p > 0.180$) except between the IDM and STB sites ($F = 2.87$; $p < 0.039$).

Water nutrient concentrations (total organic carbon TOC, total nitrogen TN and total phosphorus TP) were similar between all sites (Table 2.1). It is noteworthy that peaks occurred in water nutrients and chlorophyll *a* at the FAC site on DOY 157 and coincided with mild precipitations received that day (not shown).

Environmental variables only affected growth during period I ($F = 5.02$; $p = 0.02$) and III ($F = 3.48$; $p = 0.04$) as revealed by the redundancy analysis (RDA) (Table 2.3). Environmental variables accounted for 47 and 37% of the variation for period I and III respectively. For period I, 62% of the variation was represented on the first axis by environmental variables (chlorophyll *a*, pheophytin, temperature, TOC, TN, TP) which were negatively positioned (Table 2.3a). The second axis explained 19% of the variation and was positively related with chlorophyll *a* and TP, and negatively with temperature and pheophytin (Table 2.3a). The RNA/DNA ratio was positively related with axis one

and two, while total length and weight were both negatively related with axis one and positively related with axis two (Table 2.3a). For period III, the first axis explained 50% of the variation and was, like for period I, negatively related with all environmental variables (chlorophyll *a*, pheophytin, temperature, TOC, TN) (Table 2.3b), while the second axis explained 27% of the variation and was positively related with temperature, and negatively with the remaining environmental variables (Table 2.3b). The position of the growth indices relative to the axes was similar to those of period I (Table 2.3b), with the RNA/DNA being positively related with axis one and two, and total length and weight being negatively related with axis one and positively related with axis two (Table 2.3b).

2.4.4 Response time of short-term growth index (RNA/DNA ratio)

Correlations between RNA/DNA ratio and environmental variables revealed significant regression coefficients ($R^2 = 0.17$-0.26) for water temperature and nutrient concentrations. Water temperature measured the same day as when fish were sampled were the most determinant for the short-term growth index of YOY ($R^2 = 0.17$; $F = 8.71$; $p = 0.01$, data not shown). For example, the water temperature on the day of capture had an immediate impact on the RNA/DNA ratio by causing it to decrease. In contrast, water nutrient parameters TOC ($R^2 = 0.17$; $F = 4.84$; $p = 0.04$), PT ($R^2 = 0.21$; $F = 6.28$; $p = 0.02$) and chlorophyll *a* ($R^2 = 0.26$; $F = 8.22$; $p = 0.01$) measured 6 days before sampling were most determinant on the short-term growth index. No significant correlations were established between the RNA/DNA ratio and TN and pheophytin.

2.5 Discussion

2.5.1 Larval growth in relation to lake heterogeneity

The particularly extended littoral zone in the fluvial Lake St. Pierre (LSP) offered contrasting environmental conditions, particularly with regards to temperature, for newly hatched young-of-the-year (YOY) yellow perch. Water temperature influenced YOY growth as revealed by three growth indices, total length, weight and RNA/DNA ratio. The body size of YOY yellow perch during the 5-week study period was significantly different among LSP sites. Throughout the study period, from May 26th to June 28th YOY from Ile-du-Moine (IDM) were significantly longer than larvae from Fer-à-Cheval (FAC), which in turn were longer than those at Maskinongé (MAS). Water temperature is likely responsible since the ranking of cumulative degree days >13.5°C between sites was similar to that of the body-size ranking: IDM had the most degree days followed by FAC, and MAS had the least. This suggest that water temperature is highly determinant for YOY growth as is expected since degree days cumulated over 13.5°C are important for growth in length (Power and Heuvel 1999). It is interesting that although ranking differences existed between sites for TL, no differences in incremental growth were detected. This suggests that body size differences between sites are established early in YOY ontogeny and thereafter relatively conserved. It is also interesting that no larvae were captured at the STB site after the second week of sampling. Lower temperatures at that site may have played an adverse role on larvae survival and or prey availability however these assumptions remain to be validated.

In LSP, some of the littoral wetland habitats have been managed by the erection of dikes isolating them from the main water course so that their water level is stable. Maintenance of low water levels in managed wetlands leads to faster warming in spring comparatively to natural wetlands and favors early yellow perch spawning and hatching and presumably increased body size. In two-year study by Tardif et al. (2005) where YOY yellow perch growth was compared between managed and natural sites in LSP, total length was highest in managed sites early in the growth season, but by the onset of summer, a switch occurred where the longest YOY were present in natural sites. This is

contrary to our observations since the longest YOY are continuously observed at the managed site, IDM, throughout the five-week study period. In fact, at the time corresponding to summer sampling in Tardif et al. (2005), larvae at IDM in our study were still 11% to 27% longer than those at both of the natural sites. This suggests that the conditions responsible for such a switch-over in favor of natural sites later in the season are not met every year. In addition, in our study, the comparison with managed marshes is limited to one site, IDM. In Tardif et al. (2005), however, several managed sites were pooled which may have masked inter-site heterogeneity such that an overall lower TL was observed.

2.5.2 Larval growth history in relation to fish ontogeny

Within the five-week period over which YOY were sampled, important changes occurred in larvae length/weight relationships, revealed as breakpoints where presumably a significant change in YOY growth rate occurs. Both at IDM and FAC such breakpoints were detected in total length or weight growth trajectories at an approximate mean larval total length value of 24 mm and 18 mm respectively. In addition, lower slope value after the breakpoints were observed which indicates a growth rate decrease. The mean total length values at which the previously mentioned breaks occur approaches the 19-25 mm total length range where YOY yellow perch are known to undergo their second ontogenic migration in a typical lake (Whiteside et al. 1985). The TL values at which migrations occur, however, seem to vary from year to year and from one lake to another (Urho 1997), and may depend on the prey community composition (Fulford et al. 2006). Thus, previously observed TL thresholds are used here more as guidelines than as definitive values. In a typical lake, this migration entails movement from the pelagic to the littoral zone, coupled with an initial diet change from small to large copepods and cladocerans, and followed by another, progressive, diet change to benthic preys (Whiteside et al. 1985, Urho 1997). We believe the previous breaks in growth trajectories at IDM and FAC correspond to the beginning of the benthic diet switch, as yellow perch larvae in LSP begin feeding on substrate-dwelling preys in June (Hudon et al. 2011) (breaks correspond approximately to June 15th).

Following a diet change towards bigger prey types, the growth rate is usually expected to increase (Jones et al. 1994). However, the contrary is observed at the IDM and FAC sites where a decrease in growth rate occurs. Heath and Roff (1996) note that: "Fish with ontogenetic diet shifts similar to those in perch have exhibited reduced growth at the size at which the fish would normally switch to a limited prey type". What we observe at the IDM and FAC sites could thus reflect a limited availability of benthic preys, which could translate to a reduced YOY growth rate. Further support for this idea is a study by Hudon et al. (2011) which explores the effects of wetlands epuration from a mesotrophic to a nearly oligotrophic state along the south shore of LSP. The low levels of nitrogen and phosphorus in these epurated zones cause a decrease in submerged aquatic vegetation and epiphytes which have negative impacts on the feeding and habitat of benthic invertebrates leading to a decrease in their biomass. YOY of IDM and FAC, which are both located on LSP south shore, could thus be faced with a benthic bottleneck, effectively stunting their growth until they eventually change towards a piscivorous diet (Heath and Roff 1996). This stunt in growth may have important repercussions on recruitment levels as it could interfere with YOY capacity to reach the minimal size threshold, so as to accumulate enough energetic reserves to withstand winter starvation (Post and Evans 1989, Huss et al. 2008, Hudon et al. 2011).

The total length trajectory of the MAS site did not present breaks at similar mean total length as IDM and FAC. This might indicate that MAS YOY have not yet engaged in their second ontogenic stage, which would be coherent with the smaller YOY TL observed at this site compared to IDM and FAC. However, a break does occur in the MAS length trajectory at a smaller TL value of ~12 mm, followed by an increase in slope indicating a higher growth rate.

The total length value corresponding to the MAS break coincides with the 6-10 mm TL range where YOY yellow perch from typical lakes undergo their first ontogenic migration from the littoral to the pelagic zone (Whiteside et al. 1985, Urho 1997). This migration is accompanied by a switch from a rotifer to a copepod diet (Fulford et al. 2006). The increase in growth rate following the break in MAS length

trajectory is consistent with a diet switch (Jones et al. 1994) and suggests a shift in prey from rotifers to copepods might be occurring within this site. A study by Théberge et al. (2008) adds further support to the possibility that YOY were first feeding on rotifers since YOY from the MAS site were observed feeding on rotifers during the period preceding the breakpoint. The absence of breakpoints in the weight trajectory is not unusual since at that time in their ontogeny, yellow perch growth is primarily in length; not in weight (Whiteside et al. 1985). No similar breakpoints were observed at the other sites in LSP. It is possible that at the time at which larvae were sampled, a diet shift from rotifers to copepods had already occurred at those sites since those YOY were already longer than 11 mm on the first sampling day.

2.5.3 Response of growth to environmental conditions

Water temperature and nutrients in LSP were both important environmental determinants of larval growth, in general during the 5-week study period. For the short-term growth index, the time frame over which the index responded to changes in temperature and nutrient concentrations was different. The RNA/DNA ratio responded relatively rapidly to changes in temperature occuring the same day as fish were sampled. This implies that the time lapse between a temperature change and the RNA/DNA ratio response was likely within 24 hours. Such a rapid response contradicts that previously reported in Tardif et al. (2005) for YOY yellow perch in LSP where temperature response time was 7 days. In that 2-year study (2002-2003), a response time for temperature was only detected for one of the years (2002) when overall temperatures were considerably cold. Presumably when water temperatures were warmer during 2003, temperature became non-limiting for short-term growth. Intrestingly the mean water temperature at LSP for our 2005 study was situated intermediate to theirs. The detection of a response time, albeit a fast one, implies that water temperatures in LSP were still determinant for short-term growth. A response time may have been more rapid than previously observed through an overall influence of water temperature on fish metabolism. It is likely that once water temperatures rise beyond that threshold other factors such as diet become determinant for short-term growth in YOY yellow perch.

The response of the RNA/DNA ratio to changes in nutrient concentration was estimated to occur six days after the said changes. It is plausible that a punctual rise in nutrient concentrations could indirectly cause an increase in larval growth via the trophic chain. Effectively, nutrient concentrations can influence production throughout trophic levels from phytoplankton to zoobenthos or zooplankton (Basu et al. 2000, Huggins et al. 2004, Vis et al. 2007). In addition Buckley et. al. (1999), estimated a RNA/DNA response time in marine fish to changes in feeding conditions in a laboratory setting of around 1-3 days. A longer response time of 6 days under natural conditions may be required before the effect of water nutrients is conveyed throughout the trophic chain and a RNA/DNA ratio response is induced in YOY yellow perch. Laboratory studies on the combined influence of temperature and diet should be conducted to better understand how the short-term growth index in YOY responds under heterogenous natural conditions as such are present in LSP.

2.6 Conclusion

Growth of young-of-the-year (YOY) yellow perch was greatly influenced by habitat heterogeneity in Lake St. Pierre (LSP) wetlands mainly through spatial variation in temperature during the spawning period. Throughout the five-week study period, YOY body-size ranking between sites followed the amount of cumulated degree days over 13.5°C from time of hatching to sampling. Hatching dates were earlier where the amount of cumulated degree days over 13.5°C was higher and presumably allowed YOY yellow perch to grow faster. It is likely the body-size ranking, established early in the study period, and thereafter maintained, would eventually be reflected on the YOY body lengths reached at the end of the growing season. This suggest that early temperature conditions, particularly the amount of cumulated degree days over 13.5°C may be key for modulating YOY yellow perch growth and determing the potential for winter survival and recruitement in a heterogenous fluvial lake.

This study, where larvae were sampled continuously over a 5-week period, allowed us to follow the evolution of YOY growth and to pinpoint the moments at which important changes in growth occurred. In LSP, changes in YOY growth rate occurred at the same total lengths as those observed in standard lakes where diet changes are associated with ontogenic migrations between pelagic and littoral habitats. Given the nature of both managed and natural habitat structure in LSP, where distinct pelagic and littoral zones are absent, it is unlikely that such ontogenic migrations can occur. This implies that in lakes with vast littoral zone, YOY growth rates may be modulated by diet changes occurring in the absence of ontogenic migrations. Repercussions on YOY yellow perch survival and recruitment need to be investigated in fluvial systems.

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2.8 References

Basu, B.K., Kalff, J., and Pinel-Alloul, B. 2000. Midsummer plankton development along a large temperate river: the St. Lawrence River. Can. J. Fish. Aquat. Sci. **57**(S1): 7-15. doi: 10.1139/f99-249.

Buckley, L., Caldarone, E., and Ong, T.-L. 1999. RNA–DNA ratio and other nucleic acid-based indicators for growth and condition of marine fishes. Hydrobiologia. **401**(0): 265-277. doi : 10.1023/A:1003798613241.

Centre d'expertise en analyse environnementale du Québec. Méthodes d'analyses en usage au CEAEQ (analyses chimie inorganique). Available from http://www.ceaeq.gouv.qc.ca/methodes/chimie_inorg.htm. [accessed 25 November 2011].

Davies, R.B. 1987. Hypothesis testing when a nuisance parameter is present only under the alternative. Biometrika. **74**(1): 33-43. doi: 10.1093/biomet/74.1.33.

Environment Canada. National Climate Data and Information Archive. Available from http://climate.weatheroffice.gc.ca/climateData/canada_e.html. [accessed 21 July 2011].

Ferron, A., and Leggett, W.C. 1994. An appraisal of condition measures for marine fish larvae. Adv. Mar. Biol. **30**: 217-303. doi: 10.1016/j.bbr.2011.03.031.

Fisheries and Oceans Canada. Canadian Station Inventory and Data Download. Available from http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/twl-mne/inventory-inventaire/list-liste-eng.asp?user=isdm-gdsi&region=LAU&tst=1. [accessed 21 July 2011].

Fitzgerald, D.G. 2000. Comparative hatching, growth, and overwinter survival of age-0 yellow perch (*Perca flavescens* Mitchill) in temperate lakes of the Great Lakes basin. Doctorate's Thesis, Department of Biological Sciences, University of Windsor, Windsor (Ontario). Available from http://www.collectionscanada.ca/obj/s4/f2/dsk1/tape2/PQDD_0035/NQ62316.pdf [accessed 31 January 2012].

Frenette, J.J., Arts, M.T., and Morin, J. 2003. Spectral gradients of downwelling light in a fluvial lake (Lake Saint-Pierre, St. Lawrence River). Aquat. Ecol. **37**(1): 77-85. doi: 10.1023/A:1022133530244.

Frenette, J.J, Arts, M.T, Morin, J., Gratton, D. and Martin, C. 2006. Hydrodynamic control of the underwater light climate in fluvial Lac Saint-Pierre. Limnol. Oceanogr. **51**(6): 2632-2645. Available from http://www.jstor.org/stable/4499644 [accessed 1 February 2012].

Fulford, R.S., Rice, J.A., Miller, T.J., Binkowski, F.P., Dettmers, J.M., and Belonger, B. 2006. Foraging selectivity by larval yellow perch (*Perca flavescens*): implications for understanding recruitment in small and large lakes. Can. J. Fish. Aquat. Sci. **63**(1): 28-42. doi: 10.1139/f05-196.

Glémet, H., and Rodriguez, M. 2007. Short-term growth (RNA/DNA ratio) of yellow perch (*Perca flavescens*) in relation to environmental influences and spatio-temporal variation in a shallow fluvial lake. Can. J. Fish. Aquat. Sci. **64**(12): 1646-1655. doi: 10.1139/f07-126.

Goolish, E.M., Barron, M.G., and Adelman, I.R. 1984. Thermoclimatory response of nucleic acid and protein content of carp muscle tissue: influence of growth rate and relationship to glycine uptake by scales. Can. J. Zool. **62**(11): 2164–2170. doi: 10.1139/z84-314.

Graeb, B.D.S., Dettmers, J.M., Wahl, D.H., and Caceres, C.E. 2004. Fish size and prey availability affect growth, survival, prey selection, and foraging behavior of larval yellow perch. T. Am. Fish. Soc. **133**(3): 504-514. doi: 10.1577/T03-050.1.

Guénette, S., Mailhot, Y., McQuinn, I., Lamoureux, P., and Fortin, R. 1994. Paramètres biologiques, exploitation commerciale et modélisation de la population de perchaudes (*Perca flavescens*) du lac Saint-Pierre. Ministère de l'Environnement et de la Faune, Université du Québec à Montréal, Québec.

Guma'a, S. A. 1978. The effects of temperature on the development and mortality of eggs of perch, *Perca fluviatilis*. Freshwater Biol. **8**(3): 221-227. doi: 10.1111/j.1365-2427.1978.tb01443.x.

Heath, D.D, and Roff, D.A. 1996. The role of trophic bottlenecks in stunting: a field test of an allocation model of growth and reproduction in yellow perch, *Perca flavescens*. Environ. Biol. Fishes. **45**(1): 53-63. doi: 10.1007/BF00000627.

Hudon, C., Cattaneo, A., Tourville Poirier, A.M., Brodeur, P., Dumont, P., Mailhot, Y., Amyot, J.P., Despatie, P., and Lafontaine, Y. 2011. Oligotrophication from wetland epuration alters the riverine trophic network carrying capacity for fish. Aquat. Sci. **73**(1): 1-17. doi: 10.1007/s00027-011-0243-2.

Huggins, K., Frenette, J.J., and Arts, M.T. 2004. Nutritional quality of biofilms with respect to light regime in Lake Saint-Pierre (Québec, Canada). Freshwater Biol. **49**(7): 945-959. doi: 10.1111/j.1365-2427.2004.01236.x.

Huss, M., Persson, L., and Byström, P. 2007. The origin and development of individual size variation in early pelagic stages of fish. Oecologia. **153**(1): 57-67. doi: 10.1007/s00442-007-0719-x.

Huss, M., Byström, P., Strand, A., Eriksson L.-O., and Persson, L. 2008. Influence of growth history on the accumulation of energy reserves and winter mortality in young fish. Can. J. Fish. Aquat. Sci. **65**(10): 2149-2156. doi: 10.1139/F08-115.

Jones, M.S., Goettl, J.P., Jr., and Flickinger S.A. 1994. Changes in walleye food habits and growth following a rainbow smelt introduction. N. Am. J. Fish. Manage. **14**(2): 409-414. doi: 10.1577/1548-8675(1994)014<0409:CIWFHA>2.3.CO;2.

Kyle, M., Watts, T., Schade, J., and Elser, J.J. 2003. A microfluorometric method for quantifying RNA and DNA in terrestrial insects. J. Insect. Sci. **3**(1): 7pp. Available from http://www.ncbi.nlm.nih.gov/pmc/articles/PMC524641/. [accessed 17 March 2012].

Langlois, C., Lapierre, L., Léveillé, M., Turgeon, P., and Ménard, C. 1992. Synthèse des connaissances sur les communautés biologiques du lac Saint-Pierre. Rapport technique. Zone d'intérêt prioritaire 11. Centre Saint-Laurent, Conservation et Protection, Environnement Canada, Québec.

La Violette N., Fournier D., Dumont P., and Mailhot Y. 2003. Caractérisation des communautés de poissons et développement d'un indice d'intégrité biotique pour le fleuve Saint-Laurent, 1995–1997. Société de la faune et des parcs du Québec, Direction de la recherche sur la faune, Québec.

Lepage, S., and Lalumière, R. 2003. Modalités de gestion du poisson dans les aménagements fauniques en plaine inondable. Société de la faune et des parcs du Québec, Direction du développement de la faune et Groupe conseil GENVIVAR inc., Québec.

Magnan, P., Mailhot, Y., and Dumont, P. 2008. État du stock de perchaude du lac Saint-Pierre en 2007 et efficacité du plan de gestion de 2005. Comité aviseur scientifique sur la gestion de la perchaude du lac Saint-Pierre, Université du Québec à Trois-Rivières et ministère des Ressources naturelles et de la Faune du Québec, Québec.

Mailhot, Y., and Dumont, P. 2003. Another Yellow Perch Population Decline in the 1990s: The Lake St. Pierre Case Study, St. Lawrence River, Quebec. *In* Proceedings of Percis III: The Third International Percid Fish Symposium (Barry, T.P., and J.A. Malison, Eds.), Madison, WI, 20-24 July 2003, University of Wisconsin Sea Grant Institute, Madison, WI. pp. 135-136.

Makauskas, D., and Clapp, D. 2008. Status of yellow perch in Lake Michigan and Yellow Perch Task Group Progress Report. Report to the Lake Michigan committee. Niagara Falls, Ontario.

Mingelbier, M., Brodeur, P., and Morin J. 2005. Recommandations concernant les poissons et leurs habitats dans le Saint-Laurent fluvial et évaluation des critères de régularisation du système lac Ontario – Saint-Laurent. Rapport soumis à la Commission Mixte Internationale. Ministère des Ressources naturelles et de la faune, Direction de la recherche sur la faune, Québec.

Muggeo, V.M.R. 2008. Segmented relationships in regression models. R package version 0.2-6. Available from http://CRAN.R-project.org/package=segmented. [accessed 17 March 2012].

Paradis, Y., Mingelbier, M., Brodeur, P., and Magnan, P. 2008. Comparisons of catch and precision of popnets, push-nets and seines for sampling larval and juvenile yellow perch. N. Am. J. Fish. Manage. **28**(5): 1554-1562. doi: 10.1577/M07-122.1.

Poirier, A.M.T., Cattaneo, A., and Hudon, C. 2010. Benthic cyanobacteria and filamentous chlorophytes affect macroinvertebrate assemblages in a large fluvial lake. J. North. Am. Benthol. Soc. **29**(2): 737-749. doi: 10.1899/09-110.1.

Post, J.R., and Evans, D.O. 1989. Size-Dependent Overwinter Mortality of Young-of-the-Year Yellow Perch (*Perca flavescens*): Laboratory, In Situ Enclosure, and Field Experiments. Can. J. Fish. Aquat. Sci. **46**(11): 1958-1968. doi: 10.1139/f89-246.

Post, J.R., Johannes, M.R.S., and McQueen, D.J. 1997. Evidence of density-dependent cohort splitting in age-0 yellow perch (*Perca flavescens*): potential behavioural mechanisms and population-level consequences. Can. J. Fish. Aquat. Sci. **54**(4): 867-875. doi: 10.1139/f96-335.

Post, D.M., Kitchell, J.F., and Hodgson, J.R. 1998. Interactions among adult demography, spawning date, growth rate, predation, overwinter mortality, and the recruitment of largemouth bass in a northern lake. Can. J. Fish. Aquat. Sci. **55**(12): 2588-2600. doi: 10.1139/f98-139.

Power, M., and Van Den Heuvel, M.R. 1999. Age-0 yellow perch growth and its relationship to temperature. T. Am. Fish. Soc. **128**(4): 687-700. doi: 10.1577/1548-8659(1999)128<0687:AYPGAI>2.0.CO;2.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available from http://www.R-project.org. [accessed 17 March 2012].

Romare, P. 2000. Growth of larval and juvenile perch: the importance of diet and fish density. J. Fish. Biol. **56**(4): 876-889. doi: 10.1111/j.1095-8649.2000.tb00878.x.

Shroyer, S.M., and McComish, T.S. 1998. Forecasting abundance of quality-size yellow perch in Indiana waters of Lake Michigan. N. Am. J. Fish. Manage. **18**(1): 19-24. doi: 10.1577/1548-8675(1998)018<0019:FAOQSY>2.0.CO;2.

Tardif, D., Glémet, H., Brodeur, P., and Mingelbier, M. 2005. RNA/DNA ratio and total length of yellow perch (*Perca flavescens*) in managed and natural wetlands of a large fluvial lake. Can. J. Fish. Aquat. Sci. **62**(10): 2211-2218. doi: 10.1139/f05-137.

Théberge, M. 2008. Variation de la croissance, de l'alimentation et de la composition spécifique des jeunes perchaudes de l'année (*Perca flavescens*) dans un lac fluvial, fleuve Saint-Laurent (Québec, Canada). Master's Thesis. Department of Biology, Université du Québec à Trois-Rivières, Trois-Rivières, Québec.

Truemper, H.A., and Lauer, T.E. 2005. Gape limitation and piscine prey size-selection by yellow perch in the extreme southern area of Lake Michigan, with emphasis on two exotic prey items. J. Fish. Biol. **66**(1): 135–149. doi: 10.1111/j.0022-1112.2005.00588.x.

Urho, L. 1996. Habitat shifts of perch larvae as survival strategy. Ann. Zool. Fennici. **33**: 329-340. Available from http://www.annzool.net/PDF/anzf33/anzf33-329p.pdf. [accessed 17 March 2012].

Vis, C., Hudon, C., Carignan, R., and Gagnon, P. 2007. Spatial analysis of production by macrophytes, phytoplankton and epiphyton in a large river system under different water-level conditions. Ecosystems. **10**(2): 293-310. doi: 10.1007/s10021-007-9021-3.

Whiteside, M.C., Swindoll, C.M., and Doolittle, W.L. 1985. Factors affecting the early life history of yellow perch, *Perca flavescens*. Environ. Biol. Fish. **12**(1): 47-56. doi: 10.1007/BF00007709.

Wilberg, M.J., Bence, J.R, Eggold, B.T., Makauskas, D., and Clapp, D. 2005. Yellow perch dynamics in southwestern Lake Michigan during 1986–2002. N. Am. J. Fish. Manage. **25**(3): 1130-1152. doi: 10.1577/M04-193.1.

2.9 Tables

Table 2.1 Growth indices for larval yellow perch (*flavescens*) and environmental variables over 5 weeks in four wetland sites in Lake Saint-Pierre; Fer-à-Cheval (FAC), Maskinongé (MAS), Ile-du-Moine (IDM), Saint-Barthélemy (STB). Period I corresponds to DOY 146-157, period II to DOY 159-167 and period III to DOY 171-179. Values are presented as means ± SD (in parenthesis). Different letters indicate a significant intra-site difference ($p < 0.05$; ANOVA).

Time period (Julian days)	Site	Total length (mm)	Weight (mg)	RNA/DNA ratio	Temperature (degree Celsius)	Chlorophyll *a* (mg/m3)	Pheophytin (mg/m3)	Total Organic Carbon (mg/L)	Total Nitrogen (mg/L)	Total Phosphorus (mg/L)	Water level (m)
I	FAC	12.43^{a} (2.3)	15.93^{a} (10.82)	1.91^{a} (0.74)	22.6^{a} (1.64)	7.83^{a} (2.99)	2.40^{a} (0.90)	9.03^{ab} (2.72)	0.50^{ab} (0.26)	0.07^{a} (0.09)	4.60 (0.09)
	MAS	10.12^{b} (1.48)	7.62^{b} (3.19)	2.21^{ab} (1.02)	18.67^{a} (4.54)	4.66^{a} (1.70)	2.46^{a} (1.37)	7.38^{a} (1.96)	0.37^{a} (0.16)	0.05^{a} (0.06)	4.75 (0.26)
	IDM	14.95^{c} (2.56)	32.01^{c} (18.49)	2.55^{b} (1.13)	21.06^{a} (4.39)	8.23^{a} (3.00)	2.30^{a} (0.22)	10.48^{ab} (0.43)	0.63^{ab} (0.06)	0.07^{a} (0.02)	5.40 (0.00)
	STB	11.81^{a} (2.36)	13.76^{ab} (10.12)	1.70^{a} (0.65)	16.71^{a} (3.95)	5.40^{a} (2.56)	3.30^{a} (1.04)	12.40^{b} (1.73)	0.76^{b} (0.11)	0.14^{a} (0.04)	5.80 (0.00)
II	FAC	17.09^{a} (4.04)	61.4^{a} (43.84)	2.78^{a} (1.56)	21.46^{a} (4.32)	5.20^{a} (4.14)	2.60^{a} (1.34)	5.95^{ab} (0.53)	0.36^{ab} (0.09)	-	4.52 (0.16)
	MAS	13.83^{b} (2.19)	25.73^{b} (15.72)	1.97^{b} (0.75)	21.04^{a} (3.87)	5.40^{a} (2.70)	2.26^{a} (0.77)	4.60^{a} (0.88)	0.29^{a} (0.08)	0.01^{a} (0.01)	4.50 (0.15)
	IDM	21.61^{c} (3.44)	109.77^{a} (50.03)	1.96^{b} (0.73)	21.32^{a} (3.39)	8.58^{a} (4.15)	3.20^{a} (1.05)	9.05^{b} (2.70)	0.61^{b} (0.28)	0.08^{b} (0.06)	5.40 (0.00)
III	FAC	25.45^{a} (3.34)	183.13^{a} (74.89)	1.95^{a} (0.72)	21.78^{a} (3.16)	6.20^{a} (2.26)	2.50^{a} (0.78)	7.50^{a} (1.04)	0.51^{a} (0.24)	-	4.86 (0.28)
	MAS	22.16^{b} (4.44)	130.53^{a} (98.69)	2.29^{b} (0.69)	19.87^{a} (1.92)	7.70^{a} (2.88)	2.48^{a} (0.32)	5.98^{a} (0.32)	0.52^{a} (0.17)	0.02^{a} (0.02)	4.97 (0.23)
	IDM	28.18^{c} (2.87)	242.05^{b} (59.45)	2.19^{b} (0.52)	22.48^{a} (1.87)	7.48^{a} (3.46)	3.88^{a} (1.25)	9.70^{b} (0.94)	0.60^{a} (0.05)	0.08^{b} (0.01)	5.40 (0.00)

Table 2.2 Spawning and hatching dates and cumulative degree-days between hatching and the beginning, and until the end, of sampling of yellow perch (*flavescens*) for four studied marshes of Lake Saint-Pierre; Maskinongé (MAS), Fer-à-Cheval (FAC), Saint-Barthélemy (STB) and Ile-du-Moine (IDM).

Site	Spawning date[1]	Hatching date [2]	Cumulative degree-days[3] (degree days >13.5°C)	
			from hatching until first sampling day	from hatching until end of sampling
MAS	April 21	May 19	1.78	211.98
FAC	April 21	May 20	3.73	237.24
STB	April 21	May 18	1.10	167.65
IDM	April 21	May 13	11.02	258.90

[1] Estimated from air temperature (Mingelbier et al. 2005).
[2] Estimated from the relationship between incubation period and water temperature (Guma'a 1978).
[3] Only temperatures >13.5°C were used, corresponding to those required to produce growth in length for yellow perch (Power and Heuvel 1999).

Table 2.3 Constrained redundancy analyses of growth indices and environmental variables for period I (DOY 146-157) (a) and III (DOY 171-179) (b).

(a)

Variable	Axis 1	Axis 2
Ordination statistics for each axis		
Eigenvalue	0.28	0.09
Growth indices score on each axis		
Length	-0.21	0.09
Weight	-0.89	0.33
RNA/DNA ratio	0.61	0.51
Biplot score of constraining variables on each axis		
Temperature	-0.51	-0.14
Chlorophyll a	-0.18	0.21
TOC	-0.45	-0.04
TN	-0.48	0.08
Pheophytin	-0.48	-0.11
TP	-0.38	0.30

(b)

Variable	Axis 1	Axis 2
Ordination statistics for each axis		
Eigenvalue	0.06	0.03
Growth indices score on each axis		
Length	-0.15	0.09
Weight	-0.48	0.28
RNA/DNA ratio	0.41	0.36
Biplot score of constraining variables on each axis		
Temperature	-0.70	0.40
Chlorophyll a	-0.58	-0.26
TOC	-0.19	-0.11
TN	-0.28	-0.68
Pheophytin	-0.49	-0.50

2.10 Figures

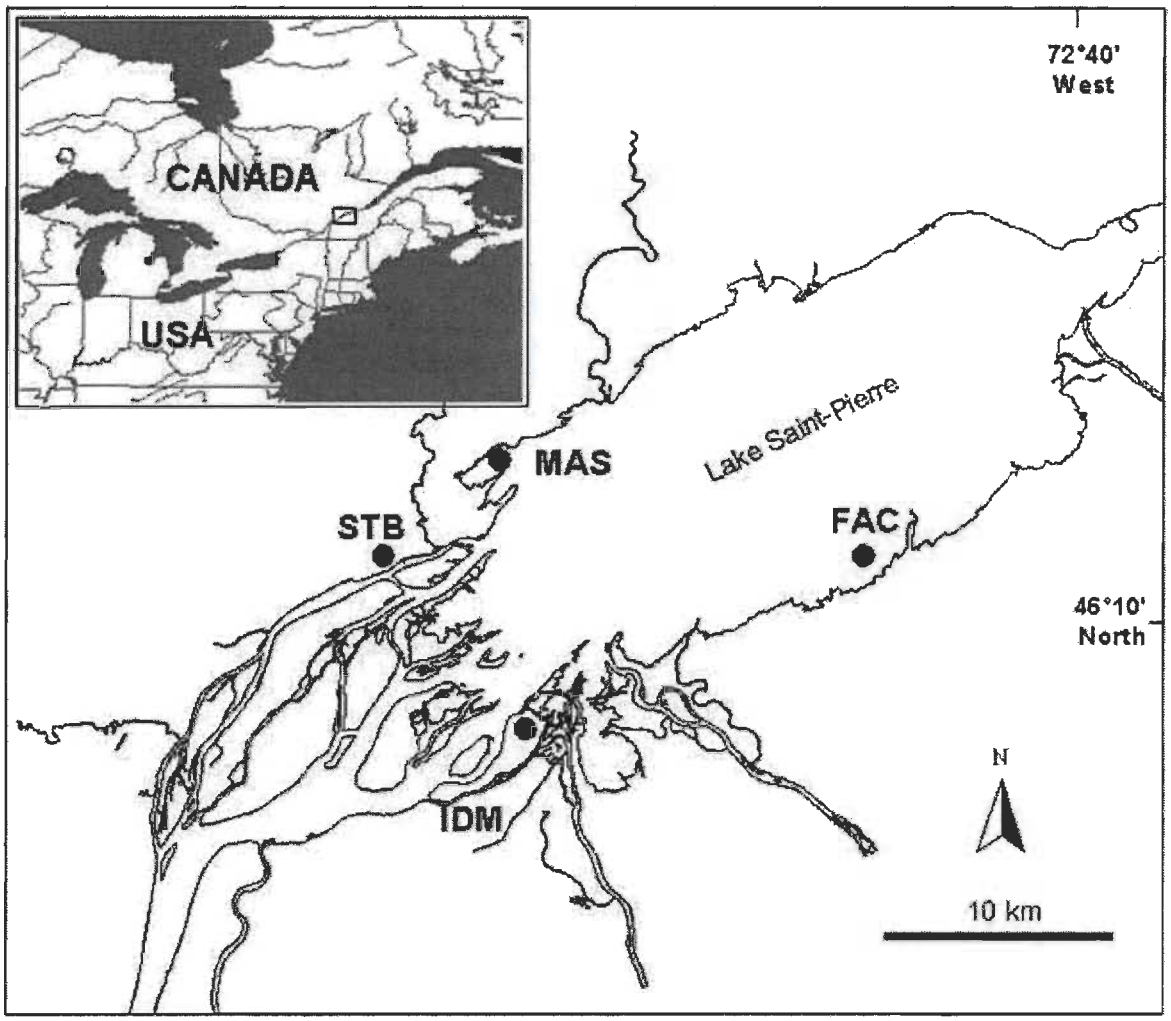

Figure 2.1 Map of the Lake Saint-Pierre highlighting the location of the marshes (Fer-à-Cheval (FAC), Maskinongé (MAS), Ile-du-Moine (IDM), Saint-Barthélemy (STB)) sampled over a 5-week period during May and June 2005.

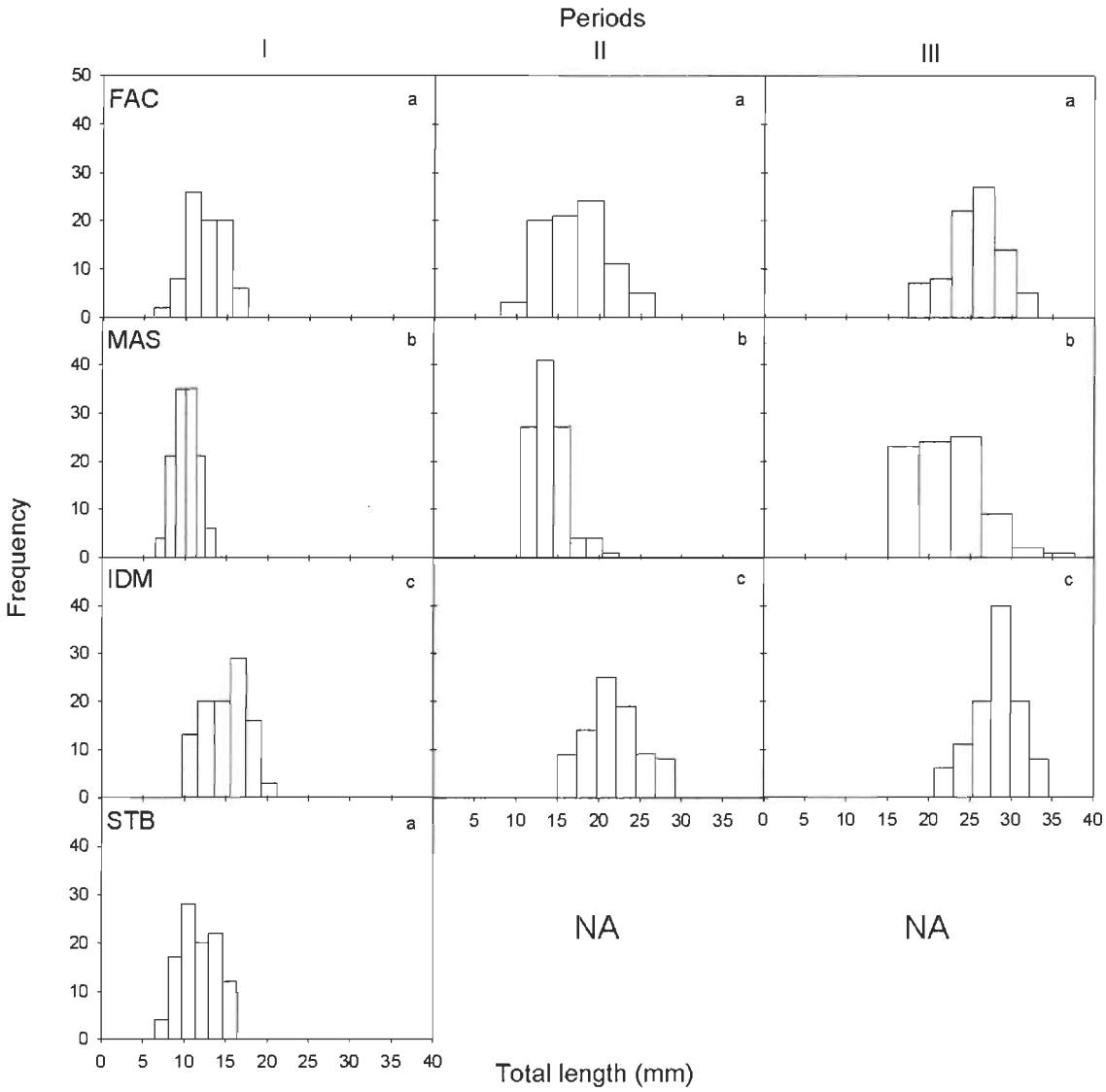

Figure 2.2 Length-frequency distribution of larval yellow perch (*flavescens*) for study sites in Lake Saint-Pierre; Fer-à-Cheval (FAC), Maskinongé (MAS), Ile-du-Moine (IDM), Saint-Barthélemy (STB) over a 5-week growth period. Period I corresponds to DOY 146-157, period II to DOY 159-167 and period III to DOY 171-179. Significant inter-site differences for each period are indicated by different letters ($p < 0.05$).

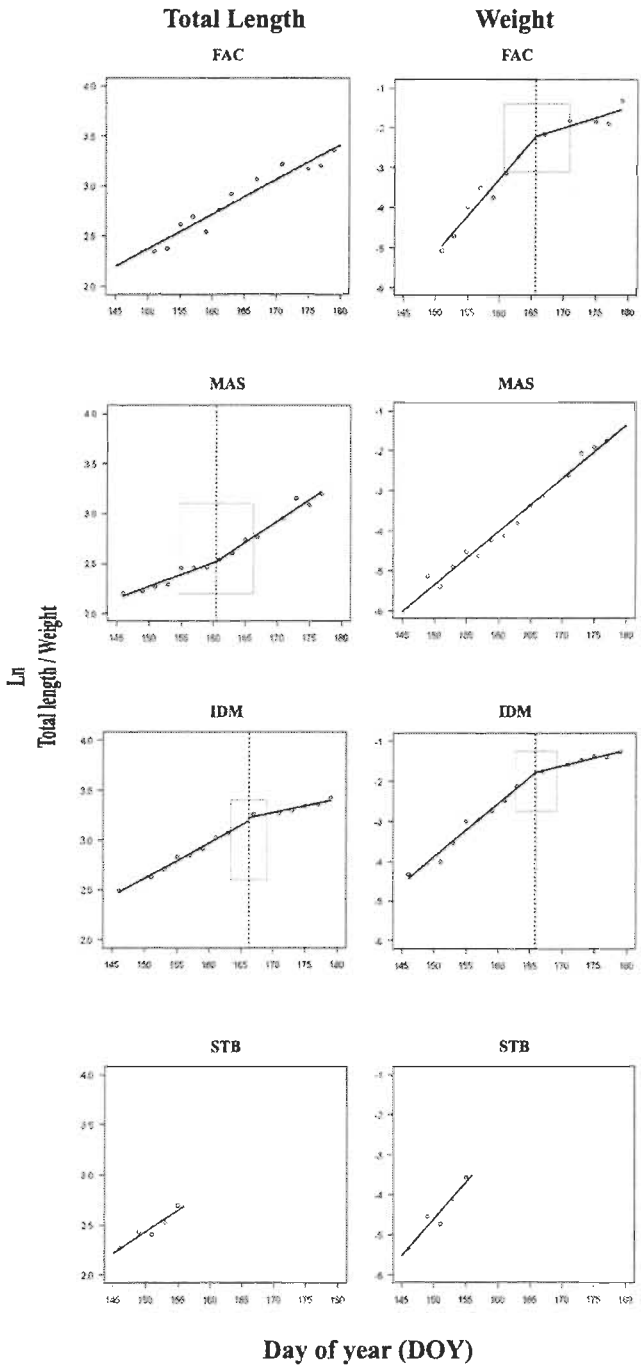

Figure 2.3 Evolution of total length/weight of larval yellow perch (*flavescens*) over a 5-week period for study sites in Lake Saint-Pierre; Fer-à-Cheval (FAC), Maskinongé (MAS), Ile-du-Moine (IDM), Saint-Barthélemy (STB). Values are presented as means with n=21. Solid lines indicate linear regression models. A dotted line indicates the presence of a breakpoint with 95% confidence interval within rectangle.

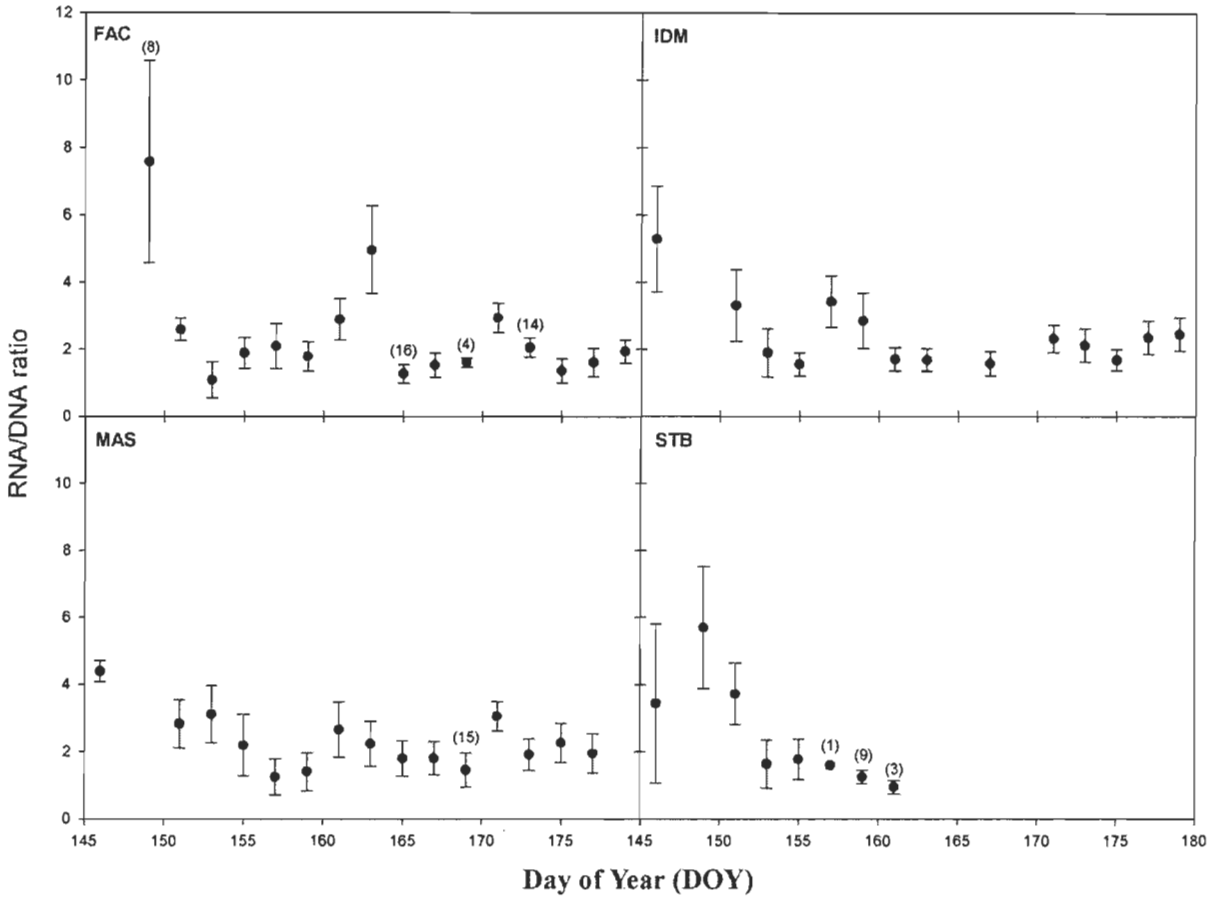

Figure 2.4 Mean larval yellow perch (*flavescens*) RNA/DNA ratio values over a 5-week period in study sites of Lake Saint-Pierre; Fer-à-Cheval (FAC), Maskinongé (MAS), Ile-du-Moine (IDM), Saint-Barthélemy (STB). Values are presented as means ± SD; n=21, unless otherwise indicated in parenthesis.