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Relations trophiques et diète des juvéniles du Saumon de l'Atlantique dans l'écosystème de la rivière Ste-Marguerite, Québec, Canada.

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Relations trophiques et diète des juvéniles du Saumon de l'Atlantique
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Sommaire

Les écologistes qui ont fertilisé des écosystèmes lotiques et lentiques ont démontré que la production des jeunes salmonidés peut être contrôlée par les nutriments via la voie trophique. Cependant, à ma connaissance, aucune étude n'a été réalisée sur la limitation de la production des juvéniles du Saumon de l'Atlantique par les nutriments, via les interactions trophiques, en milieux naturels. De plus, bien que plusieurs études portent sur la diète des juvéniles de salmonidés sédentaires, très peu ont été réalisées sur la diète des juvéniles de salmonidés anadromes comme le Saumon de l'Atlantique. Le but de cette recherche est d'identifier les patrons des relations trophiques dans un écosystème lotique du Saumon de l'Atlantique et d'examiner quels sont les facteurs déterminant la sélection des proies de ces jeunes saumons dans l'écosystème de la rivière Ste-Marguerite pour l'été 1995.

Pour tester les hypothèses de la première partie de cette recherche, des échantillons de phosphore total, de périphyton, d'invertébrés benthiques ainsi que de juvéniles du Saumon de l'Atlantique ont été récoltés dans cinq ruisseaux et dans quatre sites de la rivière principale. Pour la deuxième partie, des échantillons d'invertébrés de la dérive et de contenus stomacaux de juvéniles du Saumon de l'Atlantique ont été récoltés dans cinq ruisseaux et dans trois sites de la rivière principale. L'échantillonnage s'échelonnait sur une période de deux mois, soit Juillet et Août de l'année 1995.

Le premier chapitre porte sur les interactions entre chaque niveau trophique de l'écosystème de la rivière Ste-Marguerite. Le périphyton semble être le seul niveau trophique à être contrôlé par la voie ascendante (ressources). En effet, aucune dépendance significative à cette voie n'a été trouvée pour les niveaux supérieurs au périphyton. Les différences abiotiques entre les habitats (ruisseaux et rivières) semblent contrôler davantage la communauté des juvéniles du Saumon de l'Atlantique que leurs ressources via les interactions trophiques.

Le second chapitre porte sur les facteurs déterminant le choix des proies par les juvéniles du Saumon de l'Atlantique. Seulement deux types d'invertébrés sur six sont sélectionnés en fonction de leur taille ou de leur abondance. Ces paramètres ne semblent donc pas être des facteurs primordiaux pour contrôler la sélection des proies par les jeunes saumons. L'augmentation de la taille des proies consommées suite à un accroissement de la taille des juvéniles du Saumon de l'Atlantique est probablement mieux expliquée par la limitation morphologique de la gueule des poissons, la bioénergétique et la base saisonnière de l'échantillonnage que par le phénomène de la sélection en taille.

En conclusion, dans un écosystème oligotrophe naturel comme celui de la rivière Ste-Marguerite, il s'avère que la production des juvéniles du Saumon de l'Atlantique n'est pas exclusivement contrôlée par les ressources via la voie trophique. Il semble également que contrairement à la majorité des études publiées, les jeunes saumons ne sélectionnent pas principalement leurs proies en fonction de l'abondance et de la taille de celles-ci.

Mots-clés: *phosphore, périphyton, invertébrés benthiques, brouteurs et de dérive, poissons.*

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Chapitre 2

Liste des sigles et abréviations

ANOVA: Analyse de variance

CF: Facteur de condition

Chl a: Chlorophylle a

E: Indice d'électivité d'Ivlev

MLI: Taille moyenne de tous les invertébrés benthiques

MLG: Taille moyenne de tous les invertébrés brouteurs

n: Effectif de l'échantillon

p: Probabilité

r: Coefficient de corrélation de Pearson

r^2: Variance

SMR: Rivière Ste-Marguerite

TIB: Biomasse totale de tous les invertébrés benthiques

TGB: Biomasse totale de tous les invertébrés brouteurs

TP: Phosphore Total

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Introduction

Le Saumon de l'Atlantique (*Salmo salar*) est une ressource naturelle importante pour le Québec tant pour l'aspect économique que pour l'activité récréative. Au cours de la dernière décennie, une baisse importante de la population de ce poisson est apparue dans la province, à un tel point que la pêche commerciale est désormais interdite (Tremblay et Caron 1998). La pollution, la surpêche, les changements climatiques dans l'océan Atlantique et l'augmentation de la prédation sont quelques causes probables mentionnées pour expliquer ce déclin. L'étape dulcicole (ruisseaux et rivières) dans le cycle de vie du Saumon de l'Atlantique est généralement considérée comme une étape critique pour la limitation de la production de ce salmonidé (DeGraff et Bain 1986). De plus, la productivité des ruisseaux et des rivières ainsi que la disponibilité de la nourriture s'avèrent des facteurs primordiaux pour le contrôle de la production de poissons dans les écosystèmes lotiques (McFadden et Cooper 1962). Cependant, malgré le déclin des populations du Saumon de l'Atlantique, peu d'études ont été réalisées sur les interactions entre les juvéniles et leur environnement ainsi que sur les facteurs influençant la diète de ces jeunes poissons en milieu naturel.

Relations trophiques

Est-ce que les interactions trophiques contrôlent l'abondance et la distribution des organismes biologiques? Depuis plusieurs années, les écologistes se posent la question sans être encore arrivés à un consensus. Pour ceux qui croient à l'importance des interactions trophiques, deux écoles de pensées se sont développées. L'une croit que les organismes vivants sont principalement contrôlés par les ressources (voie ascendante) et l'autre par la prédation (voie descendante) (Power 1992). Conformément à la théorie de la voie ascendante, les organismes de chaque niveau trophique sont limités par la disponibilité de la nourriture (Power 1992). Selon celle de la voie descendante, les organismes situés à la fin de la chaîne alimentaire sont restreint par l'abondance de nourriture et à chaque niveau trophique inférieur, ils sont successivement contrôlés par la prédation et la nourriture (Carpenter et al. 1985). Plusieurs écologistes du milieu aquatique ont tenté de confirmer l'une ou l'autre des théories par des expériences réalisées sur le terrain. Néanmoins, le débat reste ouvert car un nombre considérable d'études appuient les deux théories. Ces résultats contradictoires ont permis à certains écologistes de penser que les organismes vivants peuvent être contrôlés à la fois par les ressources et par la prédation (Fretwell 1977; Oksanen et al. 1981; Power 1992).

Les études réalisées jusqu'à maintenant sur l'écologie des salmonidés mettent l'emphase sur l'importance de la voie ascendante pour contrôler la production de ces poissons. Par exemple, de nombreuses études ont démontré que les nutriments, via la voie trophique, peuvent limiter la production de salmonidés en lacs (LeBrasseur et al. 1978; LeBrasseur et al. 1979; Stockner 1987) et en ruisseaux (Johnston et al. 1990; Deegan et Peterson 1992). Il faut toutefois spécifier que ces études ont été réalisées après un ajout de nutriments à une concentration de beaucoup supérieure à celle retrouvée dans les écosystèmes naturels de salmonidés. L'objectif d'ajouter des nutriments (fertilisation) est d'augmenter la production de poissons en stimulant la production de chaque niveau trophique, soit les algues et les invertébrés brouteurs. Ces invertébrés étant la diète principale des juvéniles du Saumon de l'Atlantique (Maynard et Mazumder *soumis*), leur augmentation en nombre et en taille, stimule par la suite la production de jeunes saumons. Le but ultime de la fertilisation d'un milieu aquatique est donc de déséquilibrer la chaîne alimentaire vers le haut afin d'atténuer les effets descendants de la prédation, et de confirmer que les salmonidés sont principalement contrôlés par les ressources. Cependant, est-il possible de voir ce patron lorsqu'un écosystème est à l'équilibre. Les études qui évaluent les effets de la limitation des nutriments sur les populations de niveaux trophiques supérieurs sont très peu nombreuses sur des écosystèmes complets sans manipulation humaine (Peterson et al. 1983).

Des études révèlent que la biomasse du périphyton est beaucoup plus importante dans des rivières ou ruisseaux riches en nutriments que dans ceux où la concentration en éléments nutritifs est faible (Peterson et al. 1985; Hershey et al. 1988; LaPerriere et al. 1989; Johnston et al. 1990; Mundie et al. 1991). Il a été également observé que dans les ruisseaux et les rivières où la biomasse du périphyton était élevée, la biomasse (Johnston et al. 1990; Winterbourn 1990; Crowl et Schnell 1991;

Suren et Winterbourn 1992; Biggs et Lowe 1994) et la taille (Peterson et al. 1985; Hart et Robinson 1990; Hill 1992; Hill et al. 1992; Suren et Winterbourn 1992) des invertébrés aquatiques étaient plus grandes. De plus, la biomasse, la densité et la croissance des poissons semblent être corrélées positivement à l'abondance de la nourriture (Warren et al. 1964; Masson 1976; Murphy et al. 1981; Wilzbach 1985; Bowlby et Roff 1986). Il semble alors qu'un milieu riche en éléments nutritifs doit avoir une biomasse, une densité et/ou une croissance des poissons plus élevées qu'un milieu pauvre en nutriments. Ceci confirmerait la prédominance de la voie ascendante pour la limitation de la production de poissons. Cependant, selon Hunter et Price (1992), dans une chaîne alimentaire à l'équilibre, plusieurs facteurs biotiques et abiotiques peuvent dissimuler les forces relatives de la voie ascendante ou descendante. Particulièrement, ces facteurs peuvent être la voie hétérotrophe, la lumière, la température, la qualité du substrat, la vitesse du courant, l'azote et les herbivores (Rounick et Grégory 1981; Krewer et Holm 1982; Hyatt et Stockner 1985; Hill et Knight 1988).

Plusieurs études ont révélé que la production hétérotrophe est augmentée suite à un ajout de nutriments (Hyatt et Stockner 1985; Peterson et al. 1985; Hershey et al. 1988; Hullar et Vestal 1989; Mundie et al. 1991; Peterson et al. 1993) et qu'elle est corrélée avec la productivité autotrophe (Peterson et al. 1985; Peterson et al. 1993; Hepinstall et Fuller 1994). Une hausse de la production hétérotrophe aurait donc pour effet de court-circuiter une augmentation de la biomasse algale après un ajout de nutriments. Ceci pourrait contrecarrer un accroissement de l'abondance et/ou de la taille des invertébrés benthiques brouteurs et, par conséquent, la production de poissons.

La vitesse du courant peut également jouer un rôle dans l'impact des nutriments sur la biomasse du périphyton. Selon Horner et Welch (1981), le taux d'absorption des éléments nutritifs par ces algues en dépend. Un courant insuffisant emmène trop peu de nutriments aux algues sessiles pour que leur production augmente de façon significative après une fertilisation (Horner et Welch 1981). Cependant, un courant d'une vélocité trop élevée peut limiter la production de celles-ci par son effet abrasif. Dans mon étude, les différences de vitesse du courant dans chaque site d'échantillonnage peuvent alors masquer une relation entre le phosphore total et la biomasse du périphyton.

Pour plusieurs scientifiques, le périphyton des ruisseaux en régions forestières est principalement limité par la lumière (canopie) et non par la concentration en éléments nutritifs (Minshall 1978; Vannote et al. 1980; Lowe et al. 1986; Hill et Knight 1988). Une relation entre le phosphore total et la biomasse du périphyton peut donc être masquée si la lumière s'avère plus importante que les nutriments.

La production primaire autotrophe peut aussi être régularisée par l'azote (Krewer et Holm 1982). Toutefois, le phosphore total a été préféré lors de la présente étude pour représenter la concentration en nutriments puisque, dans la majorité des études publiées, il s'avère le principal facteur limitatif de la production primaire (Horner et Welch 1981; Peterson et al. 1985; Hart et Robinson 1990; Winterbourn 1990). Une étude a cependant spécifié que l'azote, tout en étant moins limitant que le phosphore, joue sur la régularisation de la production primaire autotrophe (Winterbourn 1990). Par conséquent, ceci peut affaiblir en partie une relation entre la concentration en phosphore total et la biomasse du périphyton.

Des études ont également reconnu que le broutage effectué par les invertébrés aquatiques brouteurs avait une influence prépondérante sur le périphyton soit en diminuant la biomasse, en altérant le taux de productivité primaire, et/ou en changeant la composition et la structure de la communauté (Hill et Knight 1988; Hill et al. 1992; Walton et al. 1995). Ceci implique que ces invertébrés ont la possibilité d'exercer un contrôle descendant sur le périphyton des ruisseaux comme il a été également observé en lacs (Carpenter et al. 1985; McQueen et al. 1986; Mazumder 1994a). Toutefois, les jeunes saumons de l'écosystème de la rivière Ste-Marguerite semblent se nourrir de façon préférentielle d'invertébrés brouteurs comme les chironomides, les Éphéméroptères et les Trichoptères (Maynard et Mazumder *soumis*). Les poissons peuvent donc exercer un contrôle descendant important sur la communauté d'invertébrés brouteurs ce qui empêcherait ceux-ci d'avoir un impact négatif sur le périphyton.

La voie hétérotrophe, la vitesse du courant, la lumière, l'azote ainsi que le contrôle descendant par les invertébrés brouteurs et/ou les poissons peuvent potentiellement affaiblir ou complètement masquer une corrélation entre la biomasse ou la taille des invertébrés versus la biomasse du périphyton, ainsi qu'une corrélation entre la biomasse du périphyton et les nutriments dans l'écosystème de la rivière Ste-Marguerite. Conséquemment, il peut apparaître que la production de poissons n'est pas principalement contrôlée par la voie ascendante comme l'ont prédit la majorité des études réalisées jusqu'à maintenant.

Diète des juvéniles du Saumon de l'Atlantique

La diète des jeunes salmonidés sédentaires comme l'Omble de fontaine (*Salvelinus fontinalis*) (Griffith 1974; Allan 1981), la Truite brune (*Salmo trutta*) (Elliot 1970, 1973; Suarez et al. 1988; Hubert et al. 1993), la Truite rouge (*Salmo clarki*) (Griffith 1974) ainsi que la Truite arc-en-ciel (*Oncorhynchus mykiss*) (Elliot 1970, 1973) a été étudiée de façon intensive. Cependant, très peu d'études similaires ont été réalisées sur les salmonidés anadromes comme le Saumon de l'Atlantique (Allen 1941; Suarez et al. 1988).

Une revue exhaustive de la littérature indique que les jeunes salmonidés choisissent leurs proies en fonction de la taille (Ricker 1932; Allen 1941; Martin 1952; Zorbidi 1970; Moore et Moore 1974; Ringler 1979; Allan 1981; Newman et Waters 1984), ce qui est un mécanisme qui permet d'optimiser l'efficacité de la prédation et donc, la croissance (Paloheimo et Dickie 1965, 1966; Kerr 1971 a, b). Il est alors préférable pour les poissons de choisir les plus grosses proies disponibles pour allouer plus d'énergie à leur croissance. Ce phénomène de sélection en taille a été démontré pour les juvéniles du Saumon de l'Atlantique par les études en laboratoire de Wankowski (1979) et Wankowski et Thorpe (1979).

Pendant que des études suggèrent la prédation selon la taille, d'autres proposent que les proies sont choisies selon leur abondance dans l'environnement du prédateur. Plusieurs écologistes ont observé une corrélation entre la faune disponible et la nourriture consommée par de jeunes saumons dans quelques rivières (Alm 1919 dans Allen 1941; Power 1969; Keeley et Grant 1997). Griffith (1974) et Allan (1981) ont également trouvé une relation similaire en ce qui concerne les juvéniles de Truite rouge et d'Omble de fontaine. Cependant, très peu d'études ont été effectuées sur les facteurs influençant la diète des juvéniles du Saumon de l'Atlantique en ruisseaux naturels. Comme dans le cas des autres jeunes salmonidés, les juvéniles du Saumon de l'Atlantique peuvent sélectionner leurs proies en fonction de l'abondance ou de la taille de celles-ci. Il est aussi possible que d'autres particularités des proies, autres que la taille ou la densité, modifient leur sélection par les prédateurs. Par exemple, il est probable que leur composition biochimique joue un rôle dans cette sélection (Carr et Derby 1986a; Zimmer-Faust et al. 1988; Jones 1992).

Des études sur les jeunes salmonidés ainsi que chez d'autres espèces de poissons ont démontré que la taille des proies consommées augmente avec celle des poissons (Elliot 1970; Suarez et al 1988; Hubert et Rhodes 1992; Hubert et al. 1993; Lavoie et Hubert 1994). Cette augmentation sert à compenser la croissance de la demande métabolique du prédateur avec l'âge. Une telle observation implique que la prédation en fonction de la taille est fonctionnelle chez le poisson. Par contre, cette observation peut dépendre également de la relation morphologique entre la dimension des proies et celle de la gueule des poissons (Moore et Moore 1976; Hart et Ison 1991). Ceci pourrait expliquer pourquoi la taille des proies ingérées s'accroit avec celle des poissons indépendamment du phénomène de la sélection en taille.

Objectifs de l'étude

Les deux principaux objectifs de la présente étude sont d'identifier les patrons des relations trophiques dans un écosystème lotique du Saumon de l'Atlantique et de vérifier quels sont les facteurs qui déterminent la sélection des proies de ces juvéniles dans l'écosystème de la rivière Ste-Marguerite, Québec, Canada. Afin d'accomplir le premier objectif, je vérifie si les niveaux trophiques adjacents sont positivement corrélés. Des corrélations positives entre les nutriments, le périphyton, les invertébrés benthiques et/ou brouteurs, et les poissons suggéreraient une forte dépendance des niveaux trophiques supérieurs aux ressources dans l'écosystème de la rivière Ste-Marguerite. Ceci confirmerait la prédominance de la voie ascendante pour la limitation de la production des poissons. Cependant, il est possible qu'une forte densité d'invertébrés brouteurs soit corrélée avec une faible biomasse du périphyton, et qu'une densité élevée de jeunes saumons soit reliée avec une faible biomasse ou densité d'invertébrés benthiques. Pour le deuxième objectif, je tente de déterminer si les juvéniles du Saumon de l'Atlantique sélectionnent leurs proies en fonction de l'abondance ou de la taille de celles-ci et s'il y a une corrélation positive entre la taille des proies consommées et celle des poissons.

Même si l'écosystème de la rivière Ste-Marguerite est un habitat important pour le Saumon de l'Atlantique au Québec, aucune recherche sur l'écologie des jeunes saumons n'a été réalisée à cet endroit. De plus, les patrons des relations trophiques des écosystèmes lotiques sont très peu connus par rapport à ceux des écosystèmes lentiques (Carpenter et al. 1985; McQueen et al. 1986; Mazumder 1994a; Mazumder et Lean 1994). Selon moi, cette recherche va servir à comprendre les effets limitatifs des nutriments via la voie trophique sur la production du Saumon de l'Atlantique dans un écosystème naturel de rivière. Elle va également contribuer à discerner quels sont les processus écologiques qui régularisent la diète des juvéniles du Saumon de l'Atlantique ainsi qu'à comprendre les écosystèmes lotiques en général.

Méthodes

Phosphore total

Pour analyser la concentration du phosphore total (TP) pour chaque site d'échantillonnage, des échantillons d'eau sont collectés à trois reprises à l'aide d'une bouteille Van Dorn et analysés au laboratoire le même jour selon le protocole proposé par Menzel et Corwin (1965). Plus particulièrement, une solution de persulfate à 5% est ajoutée à chaque échantillon et ceux-ci sont ensuite placés à l'autoclave pendant 30 minutes. Après cette période, un réactif chimique est ajouté à la solution autoclavée et l'absorbance de cette solution est par la suite mesurée avec un spectrophotomètre à une longueur d'onde de 885nm. La formule proposée par ces auteurs est finalement utilisée pour calculer la concentration du TP pour chaque échantillon.

Périphyton

La biomasse du périphyton est quantifiée à partir de la teneur en chlorophylle a (Chl a) de chaque échantillon. Pour chaque site d'échantillonnage, six échantillons (3 en rapides et 3 en fosses) sont collectés à l'aide d'un quadrat de $9 cm^2$ d'aire placé de façon aléatoire sur le fond du ruisseau ou de la rivière. Les roches, à l'intérieur de chaque quadrat, sont lavées dans un litre d'eau provenant du site échantillonné. Cette eau est incorporée dans une bouteille protégée de la lumière et placée ensuite à 4^0C jusqu'aux futures analyses en laboratoire. En laboratoire, 800ml de chaque échantillon d'eau est filtré à travers un filtre de $400 \mu m$ afin d'éliminer les impuretés (particules de substrat, invertébrés, etc...). Ensuite, deux réplicats de 20ml sont filtrés à travers un filtre de fibre de verre de $1.5 \mu m$. Ceux-ci sont protégés de la lumière et congelés à -80^0C. La teneur en chlorophylle a sur chaque filtre est déterminée selon la méthode décrite par Webb et al. (1992). En fait, chaque filtre est bouilli dans une solution d'éthanol à 90% de pureté pour extraire la Chl a du périphyton. Après une journée à 4°C, la solution contenant la Chl a est filtrée à travers un filtre de $0.45 \mu m$. L'absorbance de cette solution filtrée est estimée à l'aide d'un spectrophotomètre à 649, 665 et 750nm de longueur d'onde. La concentration de la Chl a (non-corrigée pour les phéopigments) de chaque échantillon est déterminée selon la formule de Bergman et Peters (1980).

Invertébrés benthiques

Pour estimer la biomasse totale de tous les invertébrés (TIB), la biomasse totale des invertébrés brouteurs (TGB), la taille moyenne de tous les invertébrés (MLI), et la taille moyenne des invertébrés brouteurs (MLG) pour chaque site d'échantillonnage, les invertébrés benthiques sont échantillonnés à six reprises (3 en rapides et 3 en fosses) à l'aide d'un filet Surber d'ouverture de $9.29 cm^2$ et de $200 \mu m$ de taille de maille. Ce filet est placé aléatoirement sur le fond de chaque site échantillonné. Les roches à l'intérieur du filet Surber sont lavées à la main avec précaution pour que les invertébrés soient ensuite recueillis dans une bouteille fixée à la fin du filet. L'échantillon dans la bouteille est transféré à l'intérieur d'un récipient de plastique et congelé à -20^0C pour de futures analyses. Afin de déterminer l'abondance et la taille des invertébrés, un analyseur d'images lié à un microscope zoom-stéréo est utilisé. Chaque invertébré est identifié jusqu'à l'ordre et dans certains cas jusqu'à la famille selon Merrit et Cummins (1978). La taille des invertébrés est mesurée au 0.5mm près à partir de la tête jusqu'au bout de l'abdomen, en excluant les antennes ou les appendices. Tous les invertébrés de chaque échantillon sont placés dans une bouteille pré-pesée, et ensuite séchés à 60^0C pour un minimum de 48 heures afin d'estimer la biomasse sèche de chaque échantillon.

Invertébrés de la dérive

Je me dois de mentionner que selon une revue exhaustive de la littérature (Elliot 1970; Griffith 1974; Allan 1978; Bachman 1984; Hubert et al. 1993) ainsi que d'après mes observations visuelles des jeunes saumons dans l'écosystème de la rivière Ste-Marguerite, les jeunes salmonidés semblent se nourrir principalement d'invertébrés de la dérive. C'est pourquoi j'ai préféré utiliser ces invertébrés afin d'étudier quels sont les facteurs qui influencent la diète des juvéniles du Saumon de l'Atlantique dans l'écosystème de la rivière Ste-Marguerite.

Pour d'échantillonner les macro-invertébrés de la dérive, deux filets de dérive d'ouverture de $396.5cm^2$ et de $200\mu m$ de taille de maille sont utilisés. Ils sont placés à proximité de l'un de l'autre mais à différentes profondeurs (surface et fond) pour capturer les invertébrés de toute la colonne d'eau. Ces filets sont installés en amont de l'endroit où la pêche est effectuée. Les invertébrés de la dérive sont collectés sur deux périodes de 2 heures précédant la pêche et sur une période de 2 heures pendant la pêche. Des observations préliminaires m'ont permis de constater que sur une période de 2 heures, il n'y a pas d'obstruction des filets par des débris. Après chaque période, les échantillons dans les collecteurs de chaque filet sont recueillis et congelés à -20^0C. Les invertébrés de la dérive sont pour chaque échantillon, identifiés, mesurés et énumérés en laboratoire à l'aide de la même méthode utilisée pour les invertébrés benthiques.

Poissons

Pour calculer le facteur de condition des poissons (CF), à chaque site d'échantillonnage, trois pêches électriques sont effectuées sur une section de 100m afin de capturer au minimum 20 poissons. La masse et la longueur à la fourche de chaque poisson sont mesurées au centigramme et millimètre près. Ces paramètres me permettent de calculer le facteur de condition de Fulton's (Bagenal and Tesch 1978) de chaque poisson selon la formule qui suit:

$$CF = (\text{masse (g)} / \text{longueur à la fourche (cm)}^3) \times 100.$$

Afin d'estimer la biomasse et la densité des juvéniles du Saumon de l'Atlantique pour chaque site d'échantillonnage, une pêche électrique est réalisée sur une section de $300m^2$ pour les ruisseaux et $600m^2$ ($300m^2$ en aval et $300m^2$ en amont de l'embouchure de chaque ruisseau) pour la rivière principale. Cependant, la biomasse et la densité des juvéniles du Saumon de l'Atlantique n'ont pas été échantillonnées pour le ruisseau Xavier.

Dans le but d'étudier la diète des juvéniles du Saumon de l'Atlantique, une pêche électrique est réalisée tôt le matin, sur une section de 100m pour chaque site d'échantillonnage. À chaque site, 9 à 25 poissons sont capturés totalisant 126 individus pour tous les sites d'échantillonnage. Chaque poisson est mesuré et pesé au millimètre et centigramme près. Le contenu stomacal de chacun est retiré en lavant leur estomac à l'aide d'une pompe manuelle qui contient de l'eau du site échantillonné. Les invertébrés trouvés dans chacun des estomacs sont identifiés, mesurés et énumérés en laboratoire à l'aide de la même méthode utilisée pour les invertébrés benthiques et de la dérive. Cependant, les invertébrés brisés retrouvés dans les contenus stomacaux sont seulement énumérés à l'aide de leur tête mais ne sont pas mesurés.

Analyses statistiques

Des tests de t de Students (t-test) sont utilisés pour vérifier s'il y a des différences significatives entre les sites d'échantillonnage en ruisseaux et ceux en rivière principale pour chaque paramètre relié aux niveaux trophiques. Des tests d'analyse de variance (One way Anova) et de comparaison multiple sont utilisés pour comparer chaque paramètre entre les ruisseaux, puis entre les sites d'échantillonnage de la rivière principale. Des régressions linéaires simples sont employées afin de déterminer s'il y a des relations significatives entre chaque niveau trophique pour tous les sites échantillonnés de l'écosystème de la rivière Ste-Marguerite.

L'indice de sélection d'Ivlev (E) (1961) est utilisé afin d'examiner si les poissons sélectionnent préférablement un taxon d'invertébré donné en fonction de son abondance dans l'environnement. Un indice de sélection près de zéro indique qu'un taxon est choisi par les poissons en fonction de son abondance dans la dérive. Un indice au-dessus ou au-dessous de zéro désigne respectivement qu'un taxon est sélectionné ou rejeté en fonction d'un ou des facteurs autres que l'abondance. Le coefficient de corrélation de Pearson (Pearson Product Moment Correlation) est utilisé afin de vérifier s'il y a une relation entre le ratio (% d'un taxon dans la diète / % de ce même taxon dans la dérive) versus la taille des invertébrés de la dérive pour la totalité des invertébrés présents dans l'écosystème de la rivière Ste-Marguerite. Une corrélation positive significative indique que les poissons effectuent la sélection des proies en fonction de la taille. Finalement, une régression polynomiale est employée pour établir s'il y a une relation significative entre la taille moyenne des invertébrés consommés versus la taille des poissons. La signification est déterminée à $P \leq 0.05$

pour tous les tests. Les analyses statistiques sont réalisées à l'aide du logiciel SigmaStat 1.0 (Statistical software, 1992).

Trophic relationships in the Ste-Marguerite river ecosystem, Quebec, Canada.

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Abstract

Trophic relationships were studied in the Ste-Marguerite river ecosystem (SMR), Quebec, in 1995. Five sites in five streams and four sites in the principal river were chosen to collect samples for total phosphorus, Aufwuchs, benthic invertebrates, and juvenile Atlantic salmon (*Salmo salar*). We found that Aufwuchs may be controlled mainly by nutrients but also in part by the grazers. It seems that the benthic invertebrates were neither controlled by Aufwuchs biomass nor by fish biomass or density. It seemed also that the biomass, density and condition factor (CF) of fish may not be controlled by the biomass or the size of the benthic invertebrates. The habitat differences between streams and principal river seemed a more important determinant of the fish community than the trophic pathways. However, a high variability at each trophic level and the physical habitat differences between the streams and the principal river might have interfered in the results of the trophic relationships of the SMR ecosystem.

Introduction

During the last decades, important declines in Atlantic salmon (*Salmo salar*) stocks have been reported in the east coast of Canada (Trembaly and Caron 1998). Over-fishing, pollution, changes in ocean climate, habitat degradation in streams, loss of genetic diversity, increased predation have been proposed to explain this decline. The freshwater (rivers and streams) stage in the life cycle of Atlantic salmon is generally considered to be a critical stage limiting salmonid production (DeGraff and Bain 1986). Food availability and productivity of rivers and streams have been suggested to be major controlling factors in fish production in lotic ecosystems (McFadden and Cooper, 1962).

Many studies have demonstrated that trophic pathways (transfer of nutrients via primary and secondary productivity) can limit salmonid production in streams (Johnston et al. 1990; Deegan and Peterson 1992) and lakes (LeBrasseur et al. 1978; Stockner 1987). All these studies, however, have been based on enriched nutrient concentrations much higher than usually found in natural salmon streams. Whole ecosystem studies to ascertain the extent to which nutrient limitation in natural lotic ecosystems affect populations at higher trophic levels are scanty (Peterson et al. 1983).

Ecologists have long debated the importance of trophic interactions in determining the abundance of living organisms. The ecologists who accept that trophic interactions are important, still debate if primary production is mainly limited by resources (bottom-up) or by predation (top-down). From the bottom-up view, organisms on each trophic level are food limited (Power 1992). From the top-down view, organisms at the top of food chain are food limited, and at successive lower levels, they are alternatively predator, then food limited (Carpenter et al. 1985; Bowlby and Roff 1986; Power 1992). However, some ecologists believe that it is a combination of resource and predation that control the biomass or abundance of each trophic level (Fretwell 1977; Oksanen et al. 1981; Power 1992). Partcularly, those ecologists have mentioned that depending on the ressource range and the number of trophic levels found in the community, the ressource augmentation would increase the algae (bottom-up) or herbivores (top-down). For example, bottom-up control of Aufwuchs would be observed when grazers are reduced by low resources or predation in odd-numbered trophic chain. On the other hand, under intermediate resources in even-numbered trophic chain, the top-down control would prevail.

Previous studies have suggested that streams and rivers with higher concentrations of nutrients have a greater biomass of Aufwuchs (Peterson et al. 1985; Hershey et al. 1988; Johnston et al. 1990). It has been observed that streams and rivers with a high biomass of Aufwuchs have greater biomass (Johnston et al. 1990; Crowl and Schnell 1991; Suren and Winterbourn 1992) or bigger size (Peterson et al. 1985; Hill et al. 1992; Suren and Winterbourn 1992) of aquatic invertebrates. However, several studies have shown that heterotrophic production is enhanced by addition of nutrients (Hyatt and Stockner 1985; Peterson et al. 1985; Hershey et al. 1988; Peterson et al. 1993) and also that heterotrophic productivity is correlated with autotrophic productivity (Peterson et al. 1985; Peterson et al. 1993). The heterotrophic pathway may thus mask some good relationship between Aufwuchs and nutrients.

Grazing by aquatic invertebrates has been shown to have an overriding influence on periphyton in many situations, as evidenced by a decrease in biomass, an altered rate of primary productivity, and/or a change in composition and community structure (Hill and Knight 1988; Hill et al. 1992; Walton et al. 1995). This means that the invertebrate population may exert an important top-down control upon the periphyton as it has been observed in lakes (Carpenter et al. 1985; McQueen et al. 1986; Mazumder 1994a). The young salmon in the Ste-Marguerite river ecosystem in Quebec seemed to feed upon invertebrate grazers like chironomids, Ephemeroptera, and Trichoptera (Maynard and Mazumder, *submitted*). Therefore, it is possible that the fish population can also exert a significant top-down control on the grazer invertebrate populations. Consequently, the heterotrophic pathway and the top-down controls by the invertebrates and/or by the fish communities may potentially weaken the correlation between the biomass or the size of invertebrates and the biomass of Aufwuchs and also, the correlation between the biomass of Aufwuchs and the nutrients in the Ste-Marguerite river ecosystem.

Several studies have demonstrated that fish density and growth are correlated with nutrient status and food supply in streams (Murphy et al. 1981; Bowlby and Roff

1986). Warren et al. (1964) observed that a fourfold increase in the invertebrate production induced by sucrose addition to a hatchery stream resulted in a sevenfold increase in the weight gain of young-of-the-year (YOY) trout. Sucrose enhanced fungal growth which in turn induced an increase in chironomid production. Mason (1976) found an increased growth of YOY salmonids by supplemental feeding in a natural stream. Positive correlations were found between measures of food abundance in streams and the salmonid biomass (Murphy et al. 1981; Bowlby and Roff 1986). Moreover, salmonid biomass in five stream sites in Newfoundland was related to the type of habitat and the level of nutrients (Gibson and Haedrich 1988). Therefore, it may be possible that the biomass, density, growth and the condition of fish are positively related to the abundance of the invertebrates. Thus, in streams and rivers with high invertebrate density, there may be a greater biomass and/or greater density and/or better condition of fish. This expectation is consistent with Huntsman's (1948) suggestion that inorganic fertilization could increase fish production by stimulating the growth of aquatic invertebrates. Thus, we expect that the biomass, density, growth and condition of fish to be positively correlated with the biomass and size of the aquatic invertebrates under natural conditions in our study sites of Atlantic salmon ecosystem.

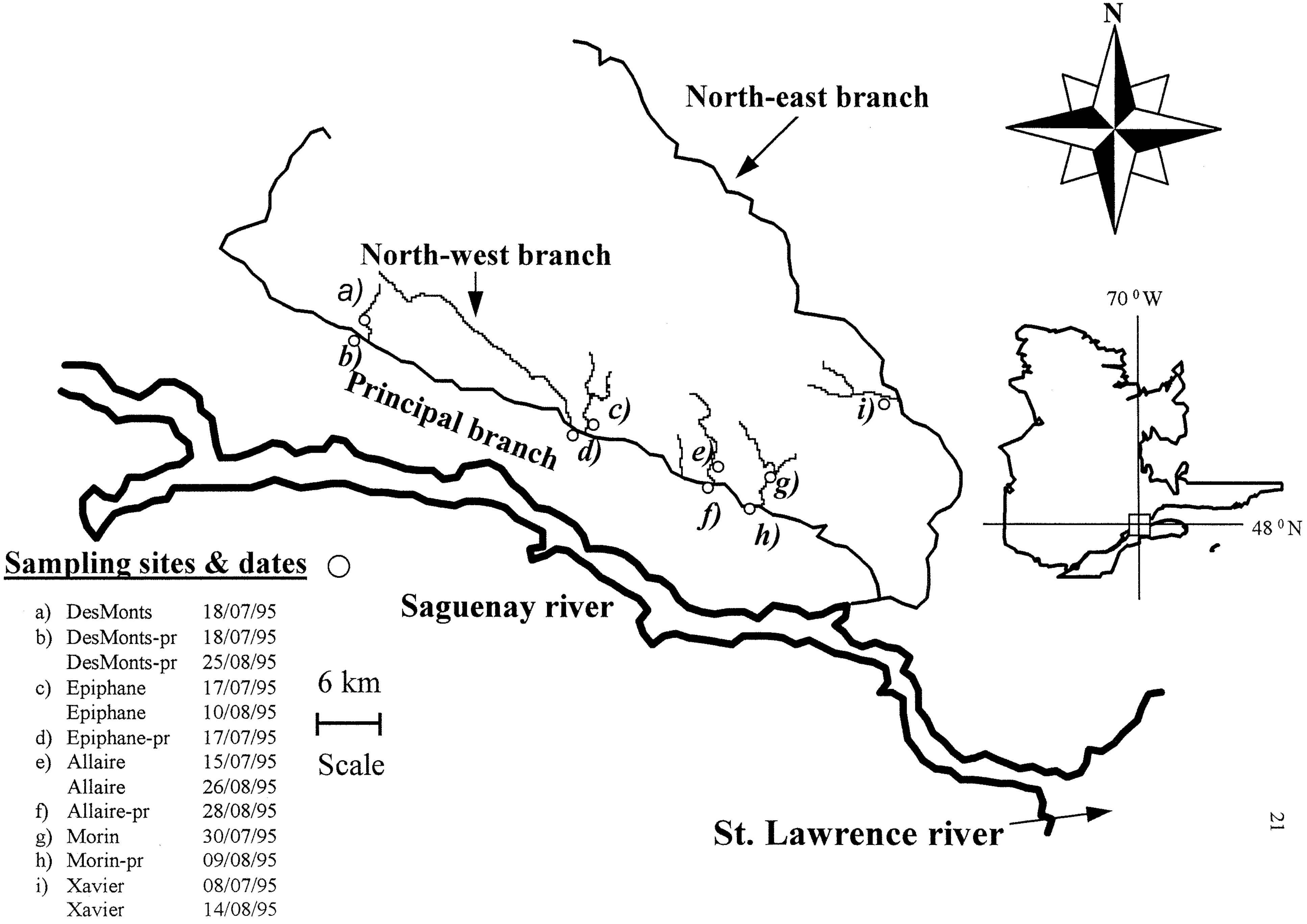
The main objectives of this study is to identify the patterns of trophic relationships in a number of streams and principal river of an Atlantic salmon ecosystem (river and streams), and to test if the resource or predation can explain the variability in each trophic level in this ecosystem. Specifically, we test whether the adjacent trophic levels are positively correlated. Positive correlations among nutrients, Aufwuchs (Chl a), invertebrates and fish would suggest a dominating resource-dependence of higher trophic levels in Ste-Marguerite river ecosystem. However, a high density of grazing invertebrates may be correlated with low biomass of Aufwuchs, and a high density of juvenile fish may be correlated with low invertebrate density or biomass. The patterns of trophic relationships in lotic ecosystems have not been extensively studied, while this area of research is well developed for lentic (lake) ecosystems (Carpenter et al. 1985; McQueen et al. 1986; Mazumder 1994a; Mazumder and Lean 1994). Consequently, this study will not only contribute significantly to the ecology of juvenile Atlantic salmon, but also to the understanding of lotic ecosystems in comparison to trophic patterns in lake ecosystems.

Study site

Our research station (Centre Interuniversitaire de Recherche sur le Saumon de l'Atlantique (CIRSA) is located near the Ste-Marguerite river (SMR) in Sacre-Coeur, 150 Km north of Quebec City. SMR is a tributary of the Saguenay river located in the Saguenay region, Quebec (48°N, 70°W, see map, Fig. 1). It extends 100 km from Monts Valin to Saguenay River near the Sacre-Coeur township. It has a 2130 km^2 of drainage area and is characterized by mountains and dense forests mainly of black spruce (*Picea mariana*). The hydrologic regime is characterized by a spring peak and a low but permanent summer flow with a mean annual discharge of 53 m^3/s (CIRSA *unpublihed data*). Because of particularly low precipitations during the study year (summer 1995), the river had a very low discharge (2.89 m^3/s: CIRSA *unpublished data*). We collected samples from five streams (Allaire, Des Monts, Epiphane, Morin and Xavier) and also from four sites in the main Ste-Marguerite River (Al-pr, DM-pr, Epip-pr and Mor-pr) from 8 July to 25 August of 1995 (Fig. 1). The four sites in the main river corresponded to the upstream section of the mouths of Allaire, Des Monts, Epiphane and Morin creeks. The main substratum was cobbles and boulders in the principal river and in the streams but it was mainly sandy in Morin-pr and Morin. Brook trout (*Salvelinus fontinalis*) and the Atlantic salmon (*Salmo salar*) were the two major fish species in the study sites.

FIG. 1: Sampling sites on the Ste-Marguerite river ecosystem.

Ste-Marguerite river ecosystem



Sampling sites & dates ○

a)	DesMonts	18/07/95
b)	DesMonts-pr	18/07/95
	DesMonts-pr	25/08/95
c)	Epiphane	17/07/95
	Epiphane	10/08/95
d)	Epiphane-pr	17/07/95
e)	Allaire	15/07/95
	Allaire	26/08/95
f)	Allaire-pr	28/08/95
g)	Morin	30/07/95
h)	Morin-pr	09/08/95
i)	Xavier	08/07/95
	Xavier	14/08/95

Methods

Water samples for the analyses of total phosphorus (TP) were collected with a Van Dorn bottle and analysed in triplicate following Menzel and Corwin (1965). In fact, we added 5% persulfate solution in each samples and we autoclaved this solution for 30 minutes. Then, we added a mixed reagent (distilled water, Ammonium paramolybdate, Potassium antimonyl tartrate, Sulfuric acid, Ascorbic acid) to the autoclaved solution and mesured the extinction with a spectrophometer at 885nm. We then used the formula proposed by these authors to calculate the concentration of the TP for each sample.

Aufwuchs biomass was quantified from chlorophyll a (Chl a) estimates. Six samples (3 in riffles and 3 in pools) from each site were collected. At each site, a quadrat (0.09 m^2 area) was placed randomly on the stream bed. The rocks within the quadrat were washed into one liter of stream water. The water was then poured into a dark bottle and kept at 4°C until processed and filtered in the laboratory. We filtered 800 ml of this water through a 400μm filter to eliminate impurities (big particles, insects, etc). We then filtered two replicates of 20ml each through a 1.2μm glass fiber filter. These filters were protected from light and placed in a -80 ^{0}C freezer. Chl a content of Aufwuchs (collected onto the filters) was determined with the method described by Webb et al. (1992). Particularly, we extracted the Chl a of the Aufwuchs by boiling each filter with 90% ethanol solvent. After one day at 4°C, we filtered and collected the solution of Chl a using a 0.45um filter. The absorbance of the solution was estimated using a spectrophotometer at 649, 665 and 750 nm. We then used the formula from Bergman and Peters (1980) to determine the Chl a contents (uncorrected for pheopigments) of each sample.

To estimate the total invertebrate biomass (TIB), total grazer biomass (TGB), mean length of benthic invertebrates (MLI), and the mean length of grazers (MLG), the invertebrates were collected with a Surber net (200μm-mesh) of 0.093 m^2 area, placed randomly on the stream bed. Six replicates were done for each sampling site (3 in riffles and 3 in pools). The rocks enclosed within the mouth of the Surber nets were washed and gently scrubbed. The invertebrates were washed with the flow of water into a bottle attached to the terminal end of the Surber net. The sample in the bottle was transferred into a plastic jar and frozen at -20 ^{0}C. To analyze the abundance and size of benthic invertebrates, we used an image analyzer attached to a zoom-stereo microscope. We identified each invertebrate up to orders or in some cases up to families (Merritt and Cummins 1978). Length of invertebrates were measured from the head to the end of the abdomen, excluding the antennae or tail filaments. All invertebrates were measured to the nearest 0.5mm. All the invertebrates from each sample were placed in a pre-weighted glass bottle and dried at 60 ^{0}C for a minimum of 48 hours to estimate the dry biomass. To estimate the biomass of grazers, we pooled the biomass of chironomids, Trichoptera and the Ephemeroptera together. This combination is based on the functional goup suggested by Merritt and Cummins (1978). According to them, the grazer communities are comprised of several families of Ephemeroptera, Trichoptera and Chironomids. Moreover, Weng (unpublished data) found that in the SMR ecosystem during the summer, these kind of invertebrates feed mainly on Aufwuchs. Therefore, we think that the combination of these insect orders may have some weaknesses but it may reflect adequatly the grazers in SMR ecosystem.

In order to calculate the condition factor of fish (CF), we conducted electrofishing in 100 m sections within each of the sampling sites to capture at least 20 fish. Three fishing trials were carried out for each sampling site. We measured the weight (to the nearest cg) and length (to the nearest mm) of each fish. Fulton's condition factor (Bagenal and Tesch 1978) was calculated as follow:

$$CF = (\text{body weight (g)} / \text{fork length (cm)}^3) \times 100.$$

In order to estimate the biomass and the density of juvenile Atlantic salmon, we did electrofishing in 300m^2 sections in each of the stream sites and 600m^2 (300m^2 below and 300m^2 above the mouth of each stream) at each site of the principal river. Salmon biomass and density were not mesured in Xavier stream. We must mention that the fish biomass and density in our study represent only the salmon. We did not have considered the biomass and the density of Brook trout in our study. Therefore, our estimates do not represent the biomass and the density of total fish community, but of the juvenile Atlantic salmon only.

Statistical analysis

Students t-test was used to determine if there were any significant differences between sampling sites in streams and principal river for each parameter. One way Anova and multiple pairwise comparison analyses were used to compare each parameter related to trophic levels among streams as well as between principal river sampling sites. We used least square linear regressions to asses if there were any significant relationships among trophic levels. Before the analysis, many variables were $\log_{10}$ transformed to stabilize the variance and to linearize the relationships. Significance was determined at $P \leq 0.05$ for all the tests. The statistical analyses were performed using SigmaStat 1.0 (Statistical software, 1992).

Results

Physical and chemical variables

Temperature was always higher in the principal river (approximatly 3°C) than in the streams (Table 1). Dissolved oxygen was also always higher in stream (approximatly 0.6 mg/l) than in the principal river (Table 1). However, for pH, there was no consistent trend during our sampling period (Table 1).

Trophic level patterns

We combined samples in riffles and pools together at each sampling site because there were no significant differences between these two habitats (Students t-test: $p \geq 0.05$). We also combined two different dates (July and August) for Allaire, Xavier and DesMonts-pr because there were no significant differences within site for any of the parameters between July and August (Students t-test: $p \geq 0.05$).

Among the stream sites, Epiphane had significantly higher TP than all other stream sites (One way Anova $p \leq 0.05$; Fig. 2a). Among these stream sites, TP ranged from 3 μg/l to 9 μg/l. Except for Morin, which had only 1.2 mg/m^2, no significant difference in Chl a was observed among the other stream sites sampled (One way Anova $p \geq 0.05$; Fig. 2b). Similarly, no significant difference was observed for the TIB, TGB, MLI and MLG (One way Anova $p \geq 0.05$; Figs. 2c-f) among the stream sites. For the condition factor of fish, however, Epiphane, Morin and Xavier showed significantly higher CF of fish than Allaire and DesMonts streams (One way Anova $p \leq 0.05$; Fig. 3c).

Among the principal river sampling sites, TP was significantly higher in Mor-pr than any other principal river sites with 7.9 μg/l (One way Anova $p \leq 0.05$; Fig. 2a). Among these river sites, TP ranged from 1.8 μg/l to 7.9 μg/l. Although TP was the highest in Mor-pr, Chl a (0.73 mg/m^2) was significantly lower in Mor-pr than all the other principal river sites (One way Anova $p \leq 0.05$; Fig.2b). TIB did not differ significantly among the main river sites (One way Anova $p \geq 0.05$; Fig. 2c). However, Mor-pr and

Table 1: Physico-chemical variables for the SMR ecosystem during summer 1995. Units are: Temperature in °C and oxygen in mg/l. These variables were based upon values for 12 sites sampled during July and August. The sites Epin and Epin-pr were utilised only to obtain these variables.

Sites	T°	O_2	pH
Al-270895	13.8	10.3	6.66
Al-pr-270895	16.2	9.3	6.78
DM-180795	13.9	9.6	7.15
DM-pr-180795	16	9.1	7.6
DM-240895	10.2	10.8	7.82
DM-pr-240895	14.4	10.1	7.23
Epin-010895	13.4	9.6	7.18
Epin-pr-010895	17	8.8	7.85
Epin-190895	15.5	9.2	7.16
Epin-pr-190895	18.8	8.9	7.12
Epip-210795	17.6	9	7.15
Epip-pr-210795	20.6	8.1	6.75
Mor-090895	16.4	9.1	5.5
Mor-pr-090895	19.7	8.6	6.5
Xav-140895	19.7	8.93	6
Xav-pr-140895	19.7	9	7.3
mean stream	15.1	9.6	6.83
mean principal	17.8	8.9	7.14

FIG. 2: Variability in average total phosphorus (a) (n=3 to 6), average chlorophyll a (b) (n=6 to 24), total biomass of benthic invertebrates (c) (n=1 to 11), total biomass of grazer invertebrates (d) (n=1 to 11), mean length of total benthic invertebrates (e) (n=3 to 13), and the mean length of total grazer invertebrates (f) (n=3 to 13), for 9 sites of Ste-Marguerite river ecosystem in summer 1995. The percentage over columns in c) represent the percentage of invertebrate grazers at each site. The bars represent the standard deviation of the parameters at each sites. N represent the repeated estimates at each sites (riffles and pools combined) except the site Allaire, Xavier and DesMonts-pr which we combined these estimates from two differents dates.

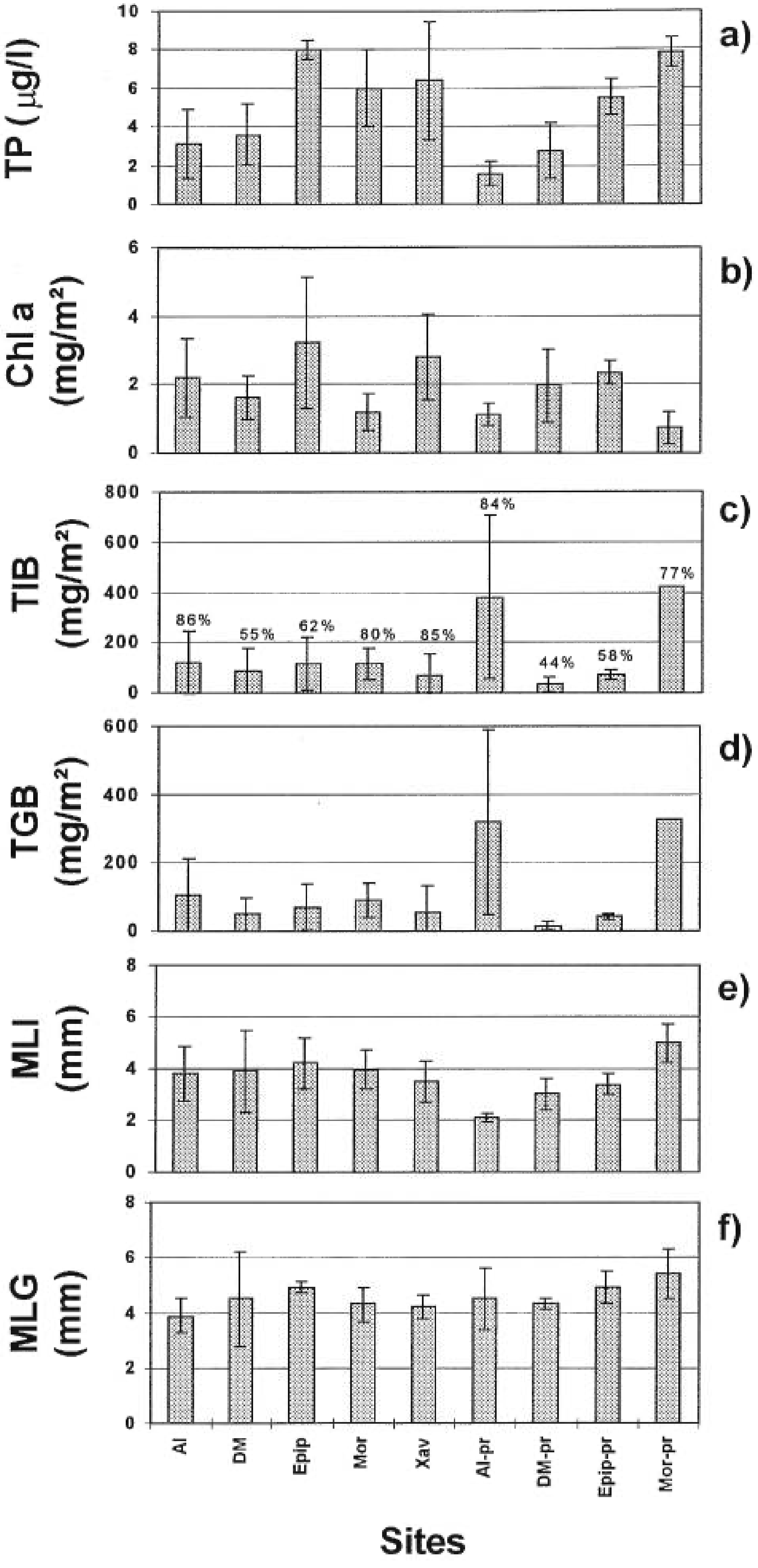
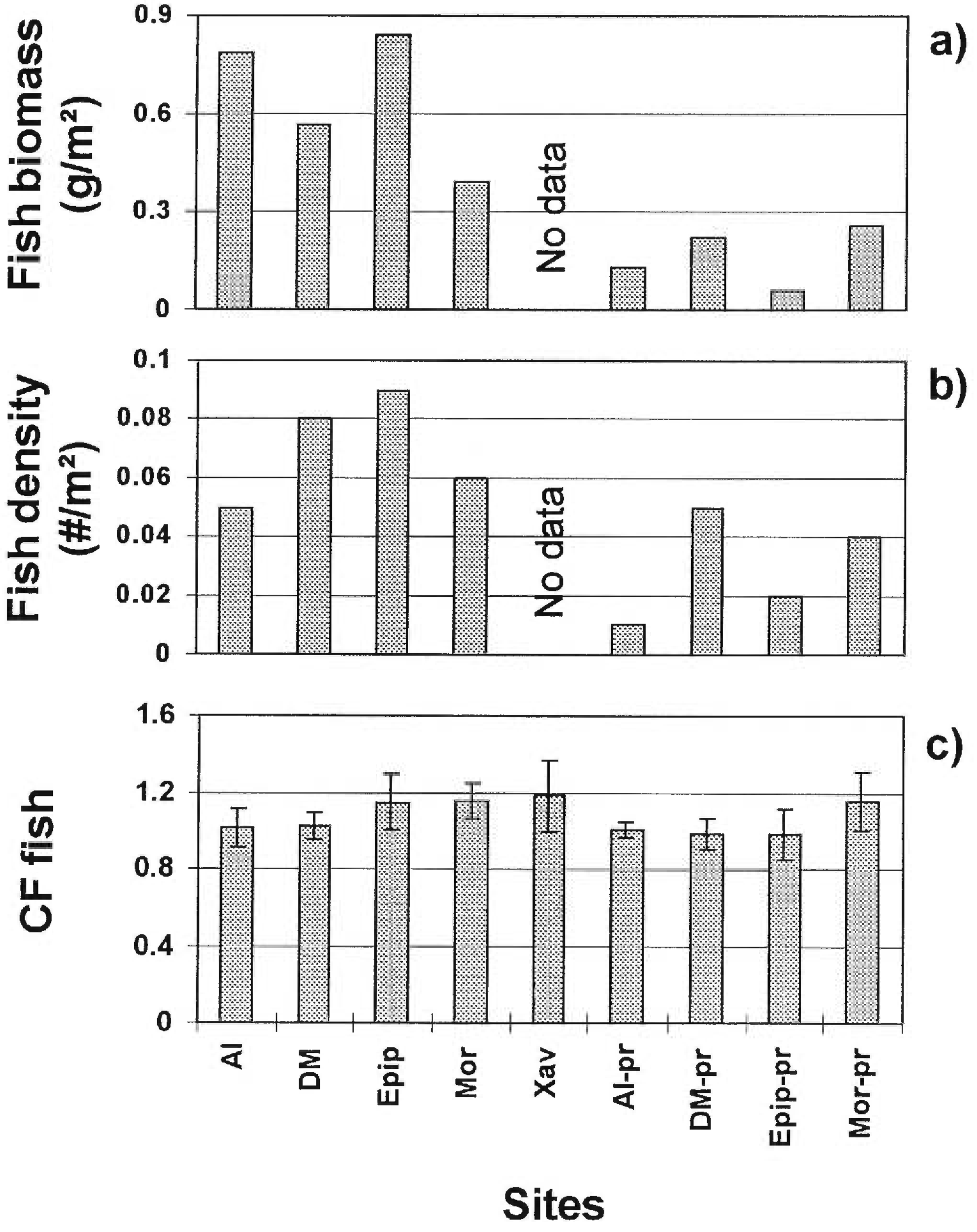

TP (μg/l)
0
2
4
6
8
10
a)
Chl a (mg/m²)
0
2
4
6
b)
TIB (mg/m²)
0
200
400
600
800
86%
55%
62%
80%
85%
84%
44%
58%
77%
c)
TGB (mg/m²)
0
200
400
600
d)
MLI (mm)
0
2
4
6
8
e)
MLG (mm)
0
2
4
6
8
f)
Al
DM
Epip
Mor
Xav
Al-pr
DM-pr
Epip-pr
Mor-pr
Sites

FIG. 3: Variability in average fish biomass (a) (n=1), fish density (b) (n=1), and the condition factor of fish (c) (n=12 to 112), for 8 to 9 sites of Ste-Marguerite river ecosystem in summer 1995. The bars represent the standard deviation of the parameters at each sites. N represent the repeated estimates at each sites.


Fish biomass (g/m²)
0.9
0.6
0.3
0
No data
a)
Fish density (#/m²)
0.1
0.08
0.06
0.04
0.02
0
No data
b)
CF fish
1.6
1.2
0.8
0.4
0
c)
Al
DM
Epip
Mor
Xav
Al-pr
DM-pr
Epip-pr
Mor-pr
Sites

Al-pr sites had significantly higher TGB than Epip-pr and DM-pr sites (One way Anova $p \leq 0.05$; Fig.2d). Epip-pr and Mor-pr had significantly higher MLI than Al-pr and DM-pr (One way Anova $p \leq 0.05$; Fig. 2e). However, there was no difference for the MLG among principal river sites (One way Anova $p \geq 0.05$; Fig.2f). Mor-pr had a significantly higher CF of fish (1.15) than the other sites (One way Anova $p \leq 0.05$; Fig. 3c).

For the overall SMR ecosystem, our results show that streams sustained more biomass and density of fish than the principal river (Student t-test $p \leq 0.05$; Figs. 3a & 3b). The fish biomass ranged between 0.39 to 0.84 g/m^2 in streams and only 0.06 to 0.26 g/m^2 in the principal river (Fig. 3a). The fish density ranged between 0.05 to 0.09 #/m^2 among the six stream sites and 0.01 to 0.05 #/m^2 among the four sites in the main river (Fig 3b). However, other variables like TP, Chl a, TIB, TGB, MLI, MLG and CF of fish were not significantly different between the stream and the river sampling sites (Student t-test $p \geq 0.05$; Figs. 2a-f & 3c).

Nutrients-Aufwuchs relationship

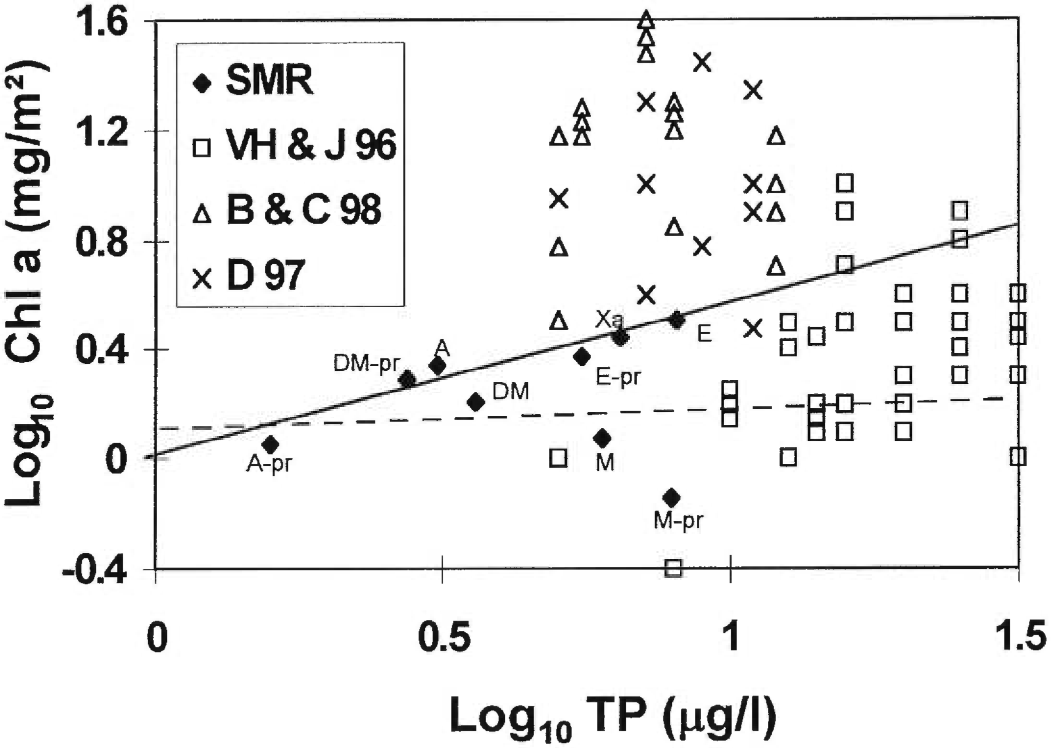
For all the sites sampled in the SMR ecosystem, no significant relationship was found between TP and Chl a ($r^2 = 0.02$; $p=0.7$: Fig. 4). However, by excluding Morin and Mor-pr, there was a significant positive relationship between TP and Chl a with an r^2 of 0.85 (Table 2: eq. 1; Fig. 4) suggesting that phosphorus may control the biomass of the Aufwuchs in the SMR ecosystem. We have excluded the sites Morin and Mor-pr because these sites were characterized by substrate (mainly sandy) different than the other sampling sites.

By plotting similar data of TP-Chl a from Van Nieuwenhuyse and Jones (1996), Dodds et al. (1997) and Bourassa and Cattaneo (1998) with our data points from the SMR ecosystem, we observed extremely variable differences among the three data sets (Fig. 4). We observed that the variability in Chl a for a given TP concentration was too high to see any pattern within such a small range. From the literature data points, for a given TP concentration, Chl a ranged between 0.4 to 39.8 mg/m^2.

Table 2: Regressions with chlorophyll a, total invertebrate biomass and grazer biomass as the dependent variables. Units are: TP in µg/l; Chl a in mg/m² ; TIB and TGB in mg/m². The value for the coefficient of regression for each independent variable is given in parentheses. This analysis is based upon values for 8 to 9 sites in the SMR ecosystem during summer 1995. Equations 3 and 5 are calculated after the inclusion of litterature data.

Dependent variable		Independent variables	N	r^2	P
Log_{10} Chl a	intercept	Ist			
1	-0.03	Log_{10} TP (0.579)	7	0.85	0.003
Log_{10} TIB					
2	2.34	Log_{10} Chl a (-1.18)	9	0.5	0.03
3	2.09	Log_{10} Chl a (0.846)	21	0.43	0.001
Log_{10} TGB					
4	2.21	Log_{10} Chl a (-1.31)	9	0.43	0.05
5	2.43	Log_{10} Chl a (-2.38)	43	0.48	0.001

FIG. 4: The linear relationship between Log_{10} total phosphorus and Log_{10} chlorophyll a at 9 sites of Ste-Marguerite river ecosystem in summer 1995. Plain line represent the relationship without Morin and Mor-pr and the dotted line represent the relationship with Morin and Mor-pr. Data were included from Van Nieuwenhuyse and Jones (1996) (□), Dodds et al. (1997)(x) and Bourassa and Cattaneo (1998)(Δ).


SMR
VH & J 96
B & C 98
D 97
Log10 Chl a (mg/m²)
Log10 TP (µg/l)
1.6
1.2
0.8
0.4
0
-0.4
0
0.5
1
1.5
DM-pr
A
DM
Xa
E
E-pr
A-pr
M
M-pr

Aufwuchs-benthic invertebrate relationship

Significant negative relationships were found between the Log_{10} TIB and the Log_{10} Chl a (Table 2: eq. 2; Fig. 5a) and between the Log_{10} TGB and the Log_{10} Chl a (Table 2: eq. 4; Fig. 5b), suggesting that benthic invertebrates had a significant negative impact on the Aufwuchs biomass in the SMR ecosystem.

By plotting data points for Chla-TIB from Reed et al. (1994), Wohl et al. (1995), and Huryn (1998), with our data points, we observed that the relationship was no longer negative but rather significantly positive (Table 2: eq. 3; Fig. 5a). It is interesting to note that the study sites used by these authors had invertebrate communities composed mainly of non-grazer invertebrates while in our sites, the invertebrate community was mainly composed of grazer invertebrates (Fig. 2c).

In our ecosystem, there was a significant negative relationship between TGB and Chl a (Table 2. eq. 4; Fig. 5b). By plotting the data points for Chl a-TGB from Hill and Knight (1987,1988) and Reed et al. (1994) with our data points, the relationship seemed to maintain a significantly negative pattern (Table 2: eq. 5; Fig. 5b). Therefore, our results are consistent with other observations in different lotic ecosystems that the grazer invertebrates may have a significant negative impact on the Aufwuchs biomass.

We plotted biomass of each trophic level related to the ressource (TP). Only the Chl a was related significantly to TP (same equation as above). The other trophic levels were not related significantly to TP ($p \geq 0.05$). These results suggested that the Aufwuchs biomass seem to be mainly controlled by the resources and less by herbivory.

The non-significant positive relationship found between the MLI and Chl a (Fig. 6a) and between the MLG and Chl a (Fig. 6b), suggested that the size of benthic invertebrates were not important determinants of the Aufwuchs biomass in our study sites.

Benthic invertebrate-fish relationship

For the SMR ecosystem, no significant relationship was found between the biomass, density, or CF of fish and the log_{10} TIB (Figs. 7a-c) and Log_{10} TGB (Figs. 8a-c), suggesting that neither the biomass nor the density or the CF of fish seemed to vary

FIG. 5: The linear relationship between Log_{10} chlorophyll a and the Log_{10} of total biomass of benthic invertebrates (a), and the Log_{10} of the total grazer biomass (b) at 9 sites of Ste-Marguerite river ecosystem in summer 1995. Plain line represent the relationship for the SMR ecosystem and the dotted line represent the relationship with the SMR ecosystem and streams elsewhere. Data for total biomass of benthic invertebrate were included from Reed et al. (1994)(□), Wohl et al. (1995)(Δ) and Huryn (1998)(x). Data for grazer biomass were included from Hill and Knight (1987)(x) Hill and Knight (1988)(Δ) and Reed et al. (1994)(□).

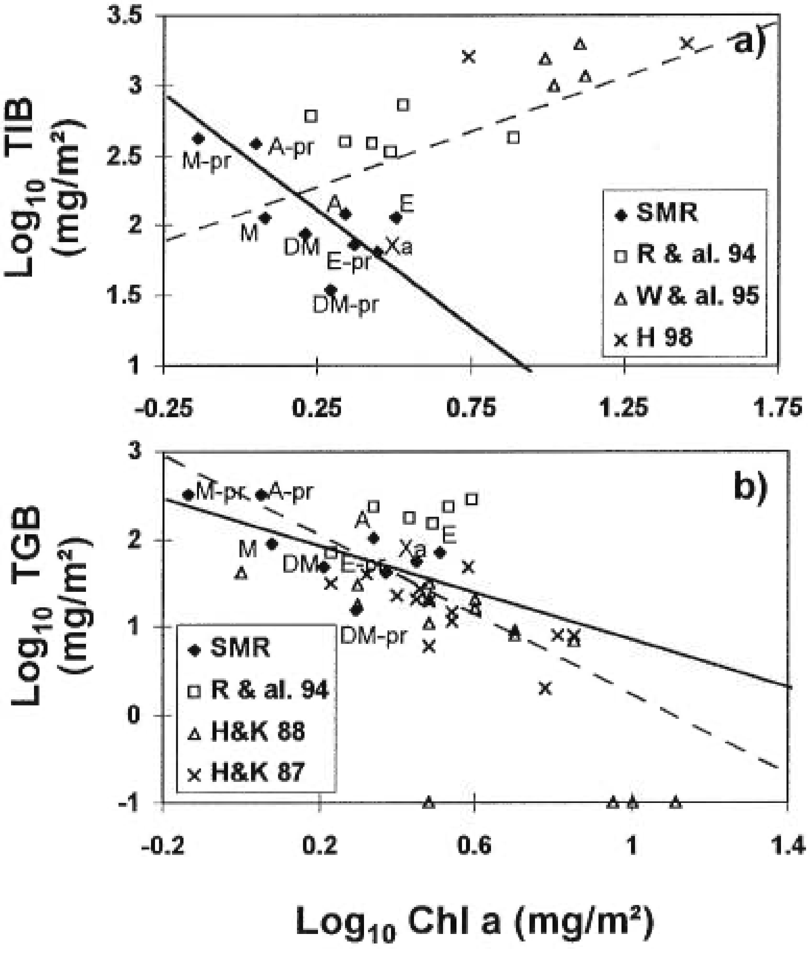

a)
Log10 TIB (mg/m²)
3.5
3
2.5
2
1.5
1
-0.25
0.25
0.75
1.25
1.75
M-pr
A-pr
A
E
M
DM
E-pr
Xa
DM-pr
◆ SMR
□ R & al. 94
△ W & al. 95
× H 98
b)
Log10 TGB (mg/m²)
3
2
1
0
-1
-0.2
0.2
0.6
1
1.4
M-pr
A-pr
A
E
M
DM
E-pr
Xa
DM-pr
◆ SMR
□ R & al. 94
△ H&K 88
× H&K 87
Log10 Chl a (mg/m²)

FIG. 6: The linear relationship between Log_{10} chlorophyll a and the Log_{10} of mean length of total invertebrates (a), and the Log_{10} of the mean length of grazer invertebrates (b) at 9 sites of Ste-Marguerite river ecosystem in summer 1995.

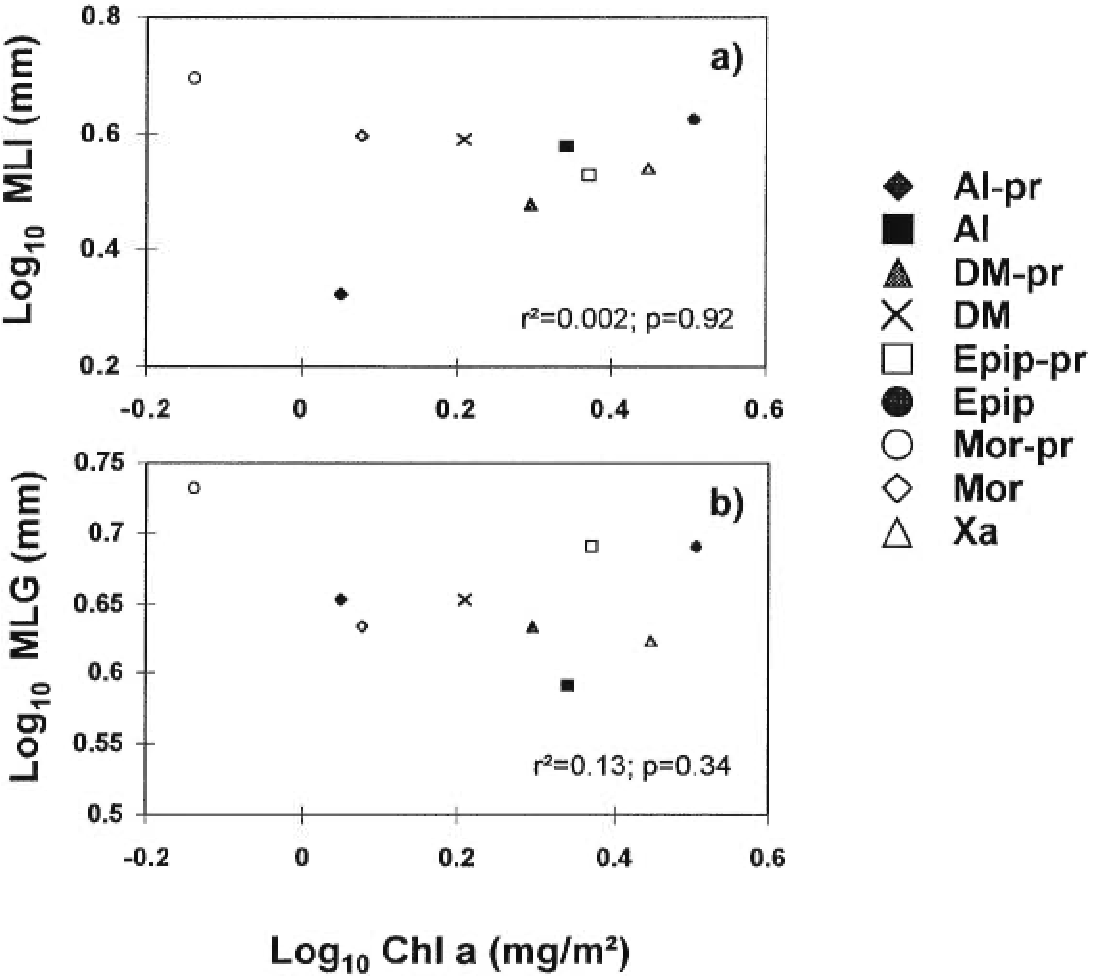
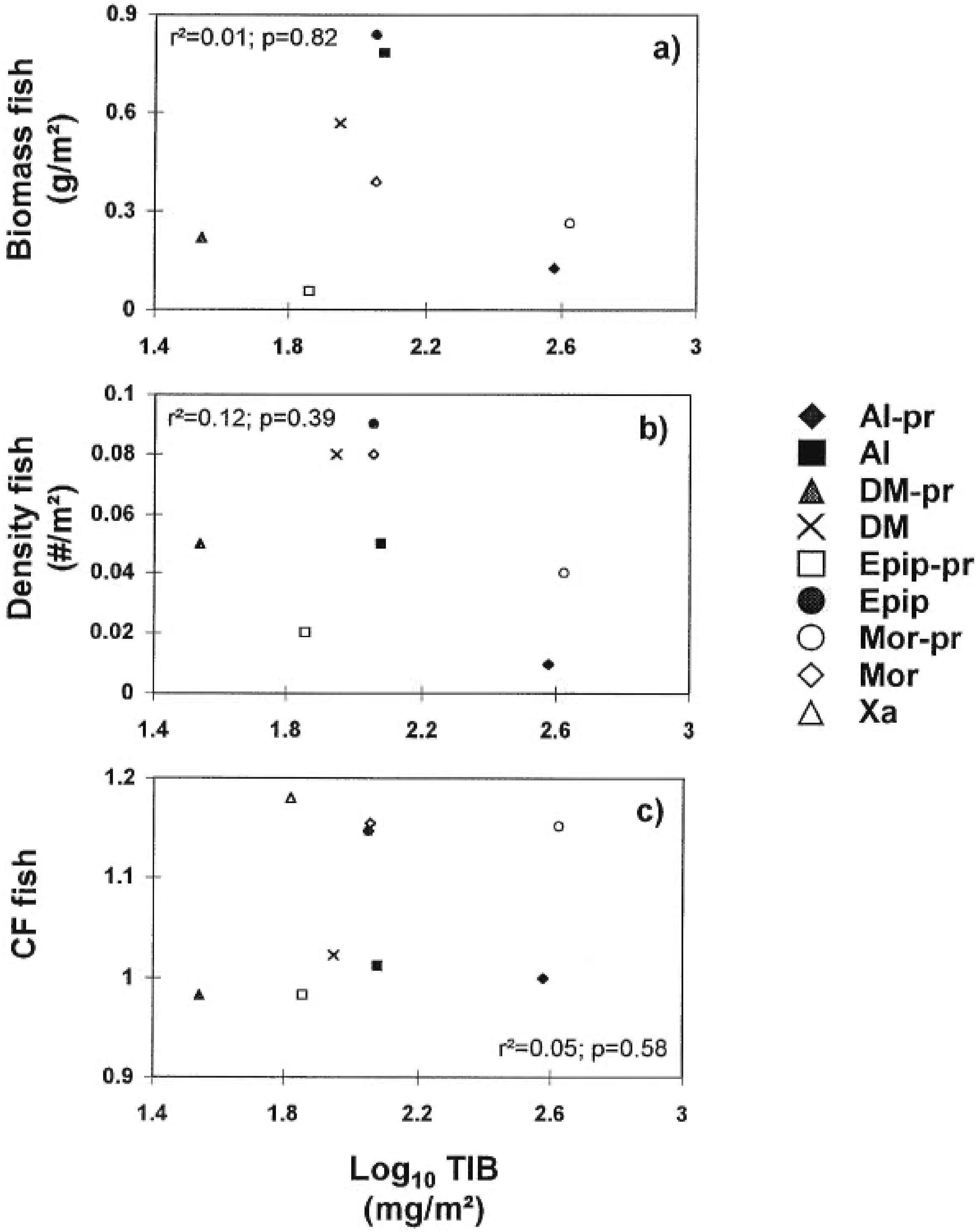
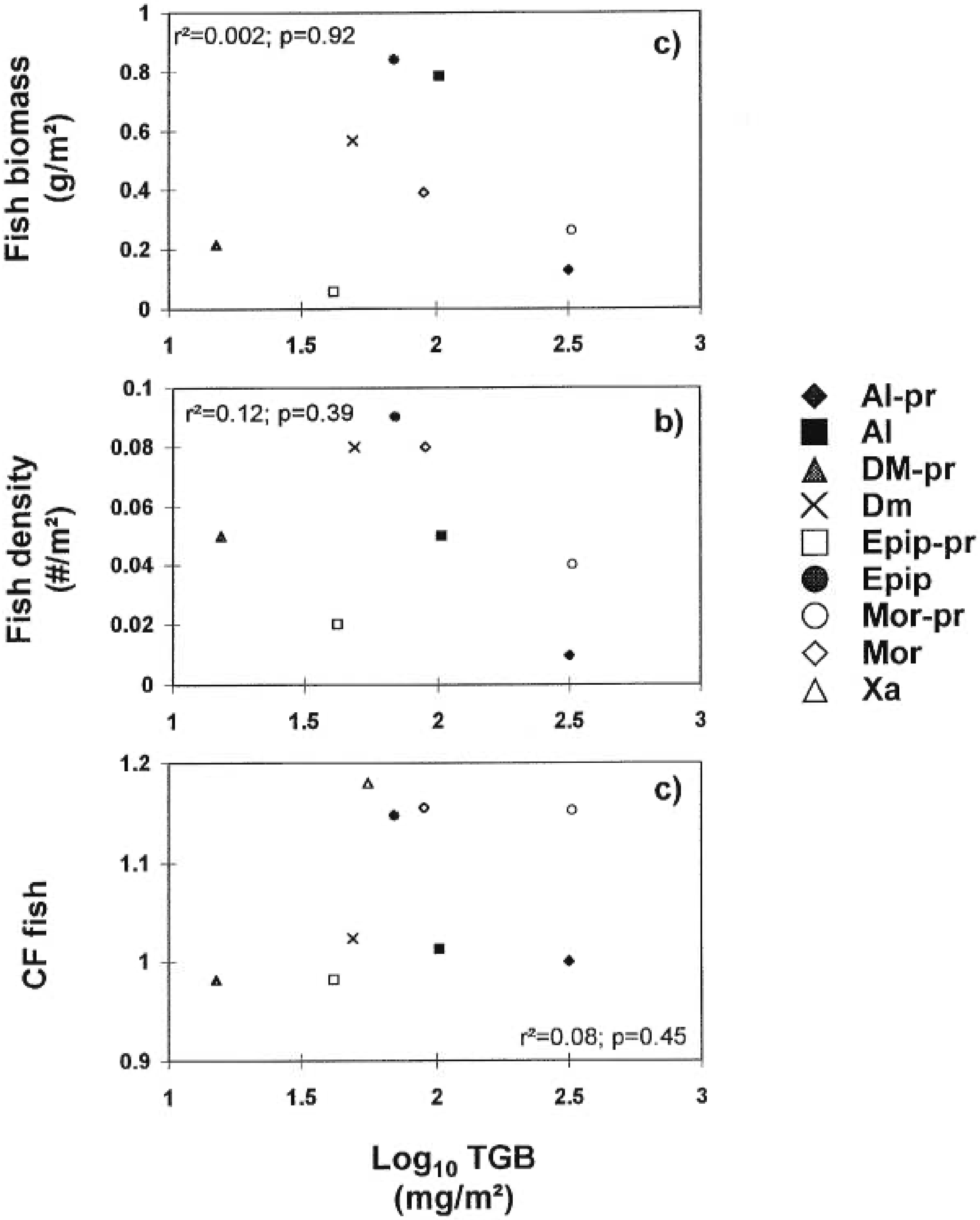

a)
Log10 MLI (mm)
0.8
0.6
0.4
0.2
r²=0.002; p=0.92
-0.2
0
0.2
0.4
0.6
b)
Log10 MLG (mm)
0.75
0.7
0.65
0.6
0.55
0.5
r²=0.13; p=0.34
-0.2
0
0.2
0.4
0.6
Log10 Chl a (mg/m²)
Al-pr
Al
DM-pr
DM
Epip-pr
Epip
Mor-pr
Mor
Xa

FIG. 7: The linear relationship between the $\log_{10}$ of total biomass of benthic invertebrates and the fish biomass (a), the fish density (b) and the condition factor of fish (c) at 8 to 9 sites of Ste-Marguerite river ecosystem in summer 1995.



a)
r²=0.01; p=0.82
Biomass fish (g/m²)
0.9
0.6
0.3
0
1.4
1.8
2.2
2.6
3
b)
r²=0.12; p=0.39
Density fish (#/m²)
0.1
0.08
0.06
0.04
0.02
0
1.4
1.8
2.2
2.6
3
c)
r²=0.05; p=0.58
CF fish
1.2
1.1
1
0.9
1.4
1.8
2.2
2.6
3
Log$_{10}$ TIB (mg/m²)
◆ Al-pr
■ Al
▲ DM-pr
× DM
□ Epip-pr
● Epip
○ Mor-pr
◇ Mor
△ Xa

FIG 8: The linear relationship between the Log_{10} total grazer biomass and the fish biomass (a), the fish density (b), and the condition factor of fish (c) at 8 to 9 sites of the Ste-Marguerite river ecosystem in summer 1995.


Fish biomass (g/m²)
r²=0.002; p=0.92
c)
1
0.8
0.6
0.4
0.2
0
1
1.5
2
2.5
3
Fish density (#/m²)
r²=0.12; p=0.39
b)
0.1
0.08
0.06
0.04
0.02
0
1
1.5
2
2.5
3
CF fish
c)
r²=0.08; p=0.45
1.2
1.1
1
0.9
1
1.5
2
2.5
3
Log₁₀ TGB (mg/m²)
◆ Al-pr
■ Al
▲ DM-pr
× Dm
□ Epip-pr
● Epip
○ Mor-pr
◇ Mor
△ Xa

as a function of the abundance or biomass of total benthic or grazer invertebrates in the SMR ecosystem.

We also explored if the biomass, the density and the CF of fish were related with the MLI or MLG. Again, there was no significant relationship between the biomass, density, CF of fish and the Log_{10} MLI (Figs. 9a-c) and Log_{10} MLG (Figs. 10a-c), suggesting that neither the biomass nor the density or the CF of fish seemed to vary as a function of the size of total benthic or grazer invertebrates in the SMR ecosystem.

FIG. 9: The linear relationship between the Log_{10} mean length of benthic invertebrates and the fish biomass (a), the fish density (b), and the condition factor of fish (c) at 8 to 9 sites of Ste-Marguerite river ecosystem in summer 1995.

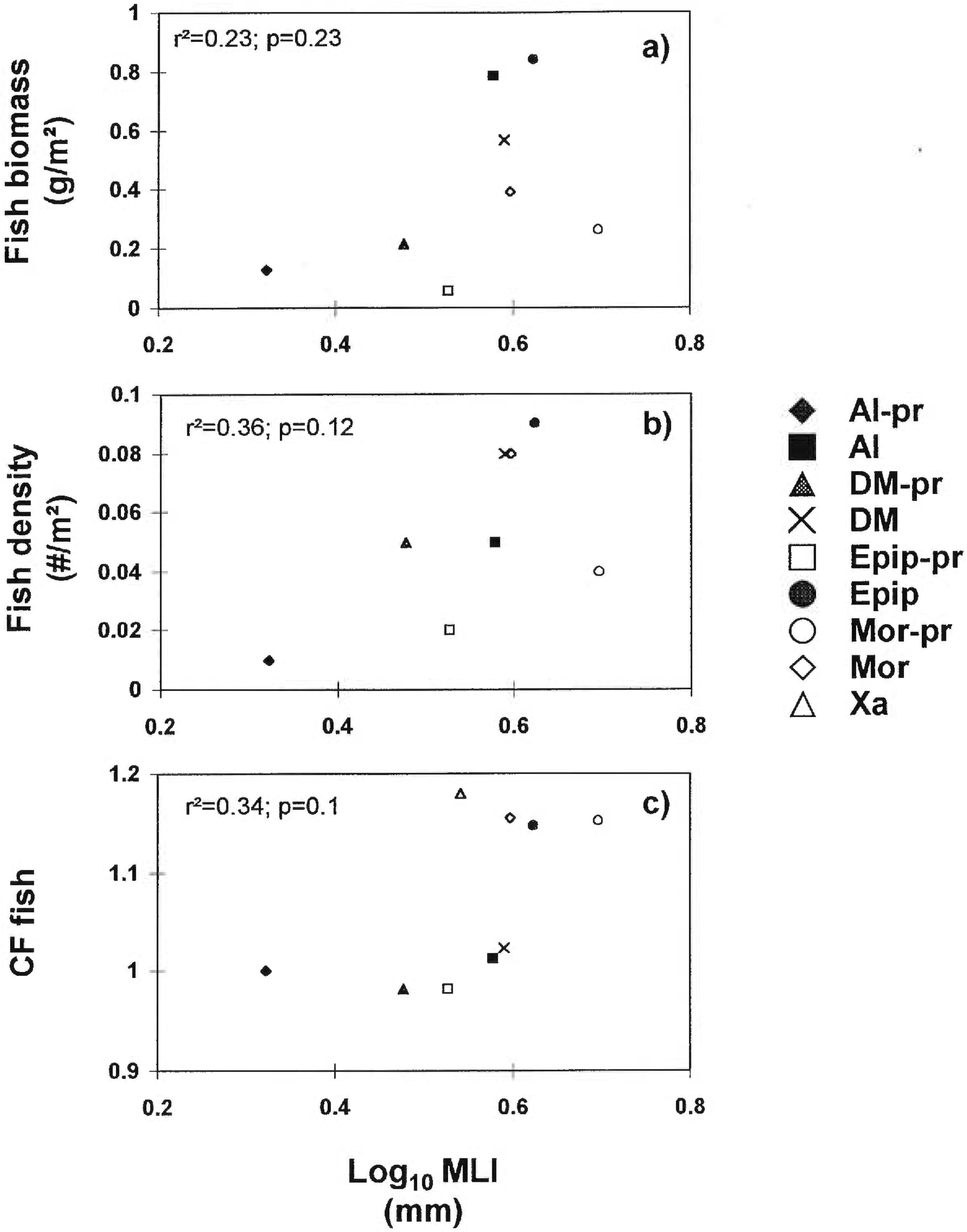
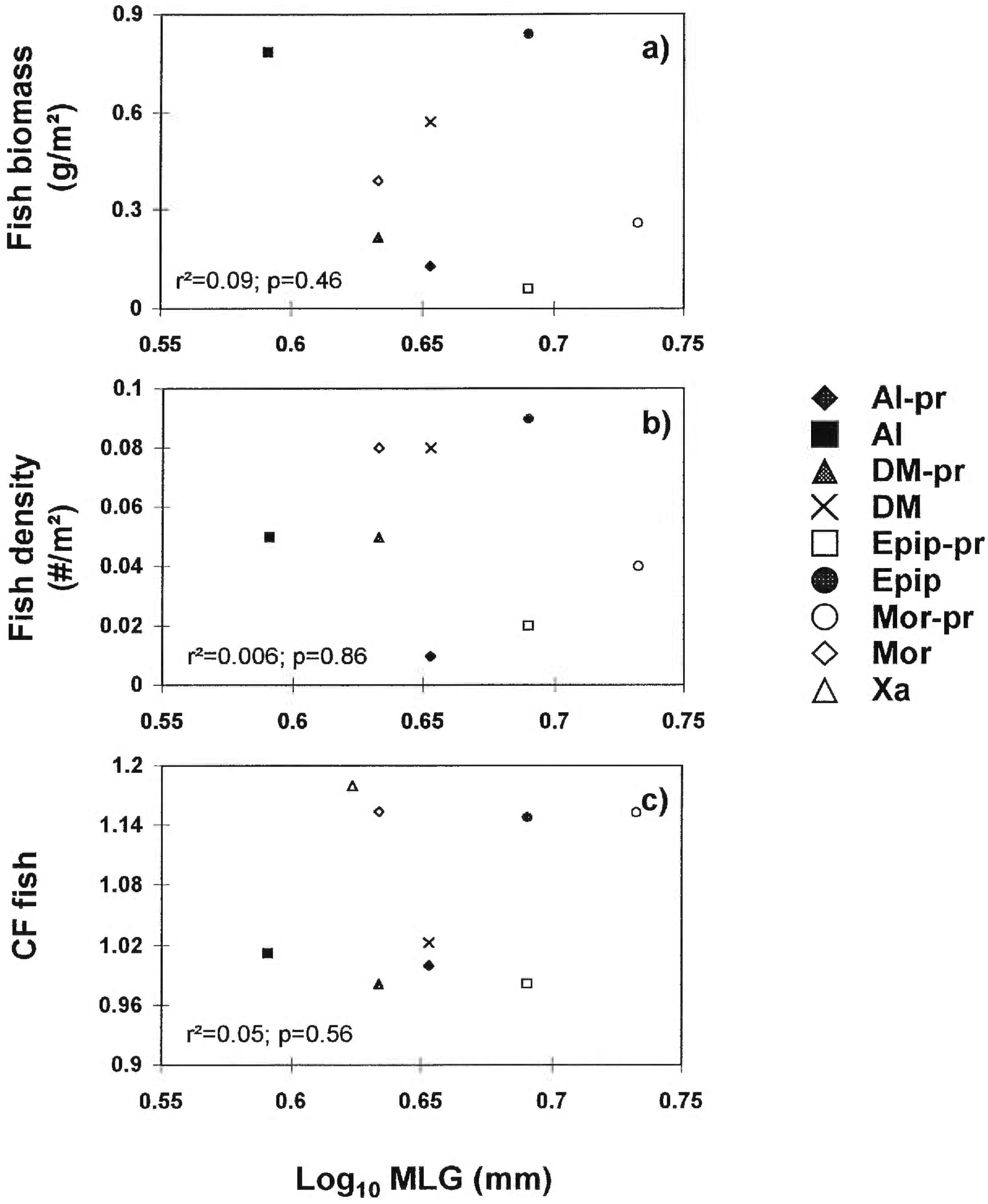

Fish biomass (g/m²)
r²=0.23; p=0.23
a)
1
0.8
0.6
0.4
0.2
0
0.2
0.4
0.6
0.8
Fish density (#/m²)
r²=0.36; p=0.12
b)
0.1
0.08
0.06
0.04
0.02
0
0.2
0.4
0.6
0.8
CF fish
r²=0.34; p=0.1
c)
1.2
1.1
1
0.9
0.2
0.4
0.6
0.8
Log10 MLI (mm)
◆ Al-pr
■ Al
▲ DM-pr
✕ DM
□ Epip-pr
● Epip
○ Mor-pr
◇ Mor
△ Xa

FIG. 10: The linear relationship between the Log_{10} mean length of grazer invertebrates and the fish biomass (a), the fish density (b), and the condition factor of fish (c) at 8 to 9 sites of Ste-Marguerite river ecosystem in summer 1995.


Fish biomass (g/m²)
0.9
0.6
0.3
0
a)
r²=0.09; p=0.46
0.55
0.6
0.65
0.7
0.75
Fish density (#/m²)
0.1
0.08
0.06
0.04
0.02
0
b)
r²=0.006; p=0.86
0.55
0.6
0.65
0.7
0.75
CF fish
1.2
1.14
1.08
1.02
0.96
0.9
c)
r²=0.05; p=0.56
0.55
0.6
0.65
0.7
0.75
Log₁₀ MLG (mm)
◆ Al-pr
■ Al
▲ DM-pr
× DM
□ Epip-pr
● Epip
○ Mor-pr
◇ Mor
△ Xa

Discussion

Periphyton versus Total Phosphorus

It is generally accepted that phosphorus limits the production of phytoplankton in lakes and that there is a positive relationship between phytoplankton biomass and TP (Schindler 1978; Stockner and Shortreed 1985; Prairie et al. 1989; Mazumder 1994a; Mazumder and Havens 1998). However, it is not clear if TP limits the production of Aufwuchs in lotic ecosystems. Significant correlations between stream Aufwuchs and nutrients have been reported in some studies (Biggs and Close 1989; Van Nieuwenhuyse and Jones 1996; Dodds et al. 1997) whereas in others (Jones et al. 1984; Bourassa and Cattaneo 1998) no correlation was found.

For the SMR ecosystem, a significant relationship was found between Log_{10} TP and Log_{10} Chl a only by excluding the sampling sites for Morin and Mor-pr. These two sites were mainly characterized by sandy substrate and because of that, there were few rocks enclosed within our sampling quadrates. It may explain why the high TP concentration in Mor and Mor-pr were not associated with high concentration of Chl a. In addition, grazer invertebrates may have been more segregated and concentrated on these few rocks and thus, had a more negative impact on Aufwuchs than in the the other sampling sites where there are more rocky substrates.

Many studies have shown that invertebrate grazers can limit the growth of pelagic (Mazumder et al. 1988; Hansson 1992; Sarnelle 1992; Mazumder 1994a) and periphytic (Hunter 1980; Hill and Harvey 1990; Rosemond 1993; Rosemond et al. 1993; Bourassa and Cattaneo 1998) algae. Grazers are also known to counterbalance the impact of nutrient addition in natural streams (Stewart 1987; Rosemond et al. 1993). Therefore, a significant grazer impact on Chl a may potentially cancel the positive impact of TP on Chl a such that no relationship would be observed. We have observed that there were significant negative impact of TIB and TGB on Aufwuchs. Therefore, based on the patterns of the relationships observed, we suggest that while the biomass of Aufwuchs seemed to be controlled by the nutrient concentration (TP), the substrate quality and the grazers are also important in determining algal biomass. However, our results seem to suggest that bottom-up forces (TP) were more important in determining the biomass of Aufwuchs than the top-down forces (TIB, TGB). Therefore, our results support hypotheses (Fretwell 1977; Oksanen et al. 1981; Power 1992) that predict that bottom-up control of algal biomass will prevail in low ressource ecosystem. An increase of nutrients would result to an increased algal biomass rather than herbivore in a 3-level trophic chain. In the SMR ecosystem, the range of the ressouce was too narrow to influence significantly the trophic levels above the Aufwuchs.

We wanted to evaluate if the results from a selected site of Atlantic salmon river and streams conform with data from other stream sites. Our comparison show that within a small range of TP, there is more than 2 orders of magnitude variability in Chl a. Because the SMR ecosystem was oligotrophic, we chose a similar range of TP (1 to 32 µg/l) to compare our study sites with other stream ecosystems. It is possible that the differences in hydrology, light, grazing impact, and temperature, in different streams may be more important than the difference of nutrients within such a small range of TP. Because we compared different stream and river sites within a large watershed, these biotic and abiotic parameters were likely less variable among our sampling sites than among different ecosystems.

In stream ecology, the primary factor which limits the Aufwuchs of streams and river is often suggested to be light rather than the phosphorus in forested stream ecosystems (Vannote et al. 1980; Hill and Knight 1988). On the other hand, some studies seem to suggest nutrients as more important determinants of algal biomass than light (Stockner and Shortreed 1978; Peterson et al. 1985). Our results seem to suggest TP as the primary factor limiting the Aufwuchs, perhaps because we had a relatively open canopy among the stream and principal river sites. However, our results suggest that even if the Aufwuchs of our sampling sites was mainly limited by nutrients, the substrate quality and the grazer invertebrates were also the important determinants of Aufwuchs.

Benthic invertebrate biomass versus periphyton biomass

Previous studies have suggested that an increase in periphyton biomass or productivity should increase the abundance of benthic invertebrates (Jonhston et al. 1990; Crowll and Schnell 1991; Suren and Winterbourn, 1992). However, in the SMR ecosystem, instead of finding a positive correlation, we found a significant negative relationship between Log_{10} TIB or Log_{10} TGB and Log_{10} Chl a. Thus, it seems that in the SMR ecosystem, grazers had a negative impact on the biomass of Aufwuchs. It seems also that the biomass of benthic invertebrates was not controlled by the bottom-up pathway (resources).

It is interesting to note that we had a significant negative relationship between Chla-TIB in our ecosystem, but by including data points from literature for Chl a-TIB, the relationship became significantly positive. These studies had invertebrate communities composed mainly of non-grazer invertebrates (Reed et al. 1994; Wohl et al. 1995; Huryn 1998). Perhaps the negative relationship in our ecosystem may be due to the fact that the invertebrate communities were composed mainly of grazer invertebrates and saw a positive relationship with other ecosystems because the invertebrate communities were composed mainly of non-grazer invertebrates in the other ecosystems. We also found a significant negative impact of TGB on the biomass of Aufwuchs. By adding literature data points for Chl a-TGB, the relationship was more significantly negative. Therefore, our results are consistent with others studies that found a significant negative impact of grazers on Aufwuchs biomass in stream. Consequently, it seemed more important to consider the biomass of grazing invertebrates than total invertebrate biomass to discern the real impact of benthic invertebrates on Aufwuchs biomass in lotic ecosystems.

Many studies in lakes have shown that the planktivore fish population exert a top-down control on zooplankton communities and thus mask a correlation between zooplankton biomass and the biomass of pelagic algae (Hrbácek et al. 1961; Brook and Dodson 1965; Galbraith 1967; O'Brien and de Noyelles 1974; Shapiro 1980; Carpenter et al. 1985; Mazumder 1994a). Unlike lentic ecosystems, the studies on the quantitative impact of fish, especially of juvenile salmonids on benthic invertebrates are scarce for lotic ecosystems. However, many studies on the diet of juvenile salmonids have shown that they preferentially select benthic invertebrates for food (Allen 1941; Griffith 1974; Allan 1981; Gibson 1993; Maynard and Mazumder *submitted*). It may thus be suggested that juvenile salmonids should have a significant top-down impact on the benthic invertebrate communities in streams. Among our study sites, the biomass of benthic invertebrates was mainly composed of invertebrate grazers (Chironomids, Trichoptera, Ephemeroptera). Maynard and Mazumder (*submitted*) found that juvenile Atlantic salmon in the SMR ecosystem mainly selected invertebrate grazers for food and that the invertebrate population was numerically dominated (40%) by Chironomid larvae. Also, the juvenile Atlantic salmon seemed to select Chironomid larvae as a function of their abundance in the environment. Therefore, the juvenile Atlantic salmon may be expected to exert an important top-down control on the invertebrate grazer populations and may thus decouple the relationships between Aufwuchs biomass and the TIB or TGB. However, our results show that there were no significant negative impact of the biomass or density of fish on the TIB or TGB. It can be suggested that although the young Atlantic salmon prey on grazers, their density was too low in our study sites to exert a significant top-down control on the invertebrate communities. However, this assumption can be biased by the fact that we considered only the density of the juvenile Atlantic salmon to represent the total fish density. Therefore, it may underestimate the total fish density in our sampling sites. By including the trout density to the density of the salmon, it may show a different pattern.

It seems that the biomass of benthic invertebrates and grazing invertebrates were not regulated by the biomass of Aufwuchs and/or the fish community. Instead, the abundance of grazing invertebrates seemed to have a negative impact on Aufwuchs. However, we would like to point out that our conclusions are based on a small number of sampling sites.

Length of benthic invertebrates versus periphyton biomass

An increase in the biomass or productivity of periphyton seems to be associated with greater mean lengths of benthic invertebrates under enriched conditions (Peterson et al. 1985; Hill et al. 1992; Suren and Winterbourn 1992). However, in the SMR ecosystem, no significant positive relationship between Log_{10} MLI or MLG and Log_{10} Chl a were observed. Thus, it seems that the average size of the benthic or grazer invertebrates is not a function of the Aufwuchs biomass in these nutrient poor streams.

As juvenile salmonids preferentially select their prey as a function of prey size (Moore and Moore 1974; Ringler 1979; Allan 1981; Newman and Waters 1984), they can be expected to exert an important top-down impact on the size of the invertebrates. However, Maynard and Mazumder (*submitted*) found that the juvenile Atlantic salmon did not select their prey as a function of prey size in the SMR ecosystem. Our results showed that there were no significant negative impact of the biomass or density of fish on the MLI or MLG. Similar to the biomass of benthic invertebrates, it can be suggested that although the young Atlantic salmon prey on grazers, their density was too low in our study sites to exert a significant top-down control on the invertebrate communities. However, as discussed above, this asumption may also be biased by the trout density.

Biomass and density of fish versus benthic invertebrates

Earlier studies have shown that fish density and biomass are dependent on nutrient status and food abundance in lotic ecosystems (Murphy et al. 1981; Bowlby and Roff 1986; Gibson and Haedrich 1988). However, for the SMR ecosystem, no significant relationships were found between Log_{10} TIB, Log_{10} TGB, Log_{10} MLI and Log_{10} MLG versus the biomass or the density of fish. Therefore, it seems that the biomass and the size of benthic invertebrates did not control the biomass or the density of juvenile Atlantic salmon. Our observations also suggest that the biomass and density of juvenile Atlantic salmon may not control the abundance or the size of benthic invertebrates in the SMR ecosystem. Nevertheless, in our study, all the streams had a significantly higher biomass and density of fish than the principal river. Thus, the juvenile Atlantic salmon seemed more controlled by other environmental factors than by trophic pathways in the SMR ecosystem. However, the lack of a significant relationship between the biomass and/or the size of the invertebrates versus the biomass and/or the density of fish may be due to the small range of these variables.

Gibson and Haedrich (1988) have mentioned that the salmonid biomass in the streams of Newfoundland was dependent on the type of available habitats. In our study, streams support a higher biomass and density than the sites in the principal river. Thus, it is possible that the stream habitats are better suited for the juvenile Atlantic salmon than the principal river. Abundant accumulation of organic debris in natural stream channels are essential components of salmonid rearing habitat (Swanson and Lienkaemper 1978; Bryant 1983). The stream habitat may be better because it has more obstacles (logs, bigger rocks, etc) which provide more shelter to the fish from predation than the principal river. In the SMR ecosystem, we observed a greater abundance of logs and bigger rocks in streams than in the principal river. Thus, the stream sites in our study may have provided more shelter to the juvenile salmon than the sites in the principal river. The stream habitats may also be better because of their faster current. DeGraaf and Bain (1986) have demonstrated that water velocity is the principal factor determining summer habitat used by juvenile Atlantic salmon. Moreover, parr survival was found to be positively related to the summer discharge in some rivers (Huntsman 1973). With higher current velocity, stream water is more oxygenated. A reduced flow, and therefore low oxygen supply in the gravel, has been shown to have a negative effect on alevins (Wickett 1958). Thus, streams with higher current provide more suitable habitat for the juvenile Atlantic salmon than the principal river. In our study, the level of oxygen was always higher in streams than in the principal river. Temperature can also play an important role in the choice of habitat by the juvenile Atlantic salmon in North America (Power 1990). The juvenile Atlantic salmon prefer cooler water (Elliott 1991). Our study streams had more canopy cover than the principal river, and thus, the temperature in the stream was cooler than in the principal river. In the SMR ecosystem, streams had on an average 3°C lower temperature than the principal river. Current, temperature and debris are probably the three main reasons why we found higher biomass and density of fish in streams than in the principal river and that we did not see a dependence of fish on the trophic pathways in the SMR ecosystem.

Condition Factor (CF) of fish versus benthic invertebrates

We did not observe positive relationships between the CF of fish and Log_{10} TIB, Log_{10} TGB, Log_{10} MLI and Log_{10} MLG. Our results also showed that the combination of the biomass to the size of invertebrates did not improve the variability of the CF of fish. Therefore, it seems that the CF of fish may not be controlled by trophic pathways in the SMR ecosystem.

Several studies have demonstrated that the growth (Hyatt and Stockner 1985; Johnston et al. 1990; Peterson et al. 1993) and condition (Deegan and Peterson 1992) of young salmonids increases after stream fertilization. This result is explained by the fact that nutrient enrichment increases the abundance of food (invertebrates) for the juveniles. Other studies also mentioned that the growth rate of juvenile Atlantic salmon is correlated to the size of their prey (Wankowski and Thorpe 1979) and that the fertilization of a tundra stream with phosphorus increased the size of larval blackflies (Peterson et al. 1985) and *Orthocladius* larvae (Hershey et al. 1988). Therefore, we expected to have a significant relationship between the TIB, TGB, MLI, MLG and the CF of fish for the SMR ecosystem. However, no relationships were found between these trophic parameters in our study.

Two reasons can probably explain why we did not observe a significant relationship between the Log_{10} MLI, Log_{10} MLG and the CF of fish. The ranges for MLI and MLG were too small to have any impact on the CF of fish. Also, juvenile Atlantic salmon of the SMR ecosystem do not select their food by prey size (Maynard and Mazumder, *submitted*).

Unlike the studies mentioned above, there was no significant response of the CF of fish as a function of TIB or TGB. This may be because the ranges of TIB and TGB in our study were not large enough to exhibit a significant pattern in the CF of fish. The other studies found an increase of CF of fish because they had a greater range of biomass of invertebrates due to stream enrichment. In natural oligotrophic lotic ecosystems like our study sites, it is likely that the differences in resources (TP or Chl a) were too small to induce a large range in benthic invertebrate biomass, and thus, induce no significant response in the fish community.

Conclusion

In the SMR ecosystem, Aufwuchs biomass seemed to be significantly correlated with nutrients (TP) and grazer invertebrates. However, TP seemed to be more important in determining the biomass of Aufwuchs than the grazing impact of the benthic invertebrates. It seemed that the benthic invertebrates were not controlled exclusively by either Aufwuchs biomass or fish biomass or density. It seemed also that the biomass, density and CF of fish may not be controlled by the biomass or the size of the benthic invertebrates. The habitat differences between streams and principal river seemed more important determinants of the fish community than trophic pathways. Therefore, unlike studies in enriched streams, the fish community in natural streams with low gradients of nutrients may not be controlled by trophic pathways, but rather by physical characteristics of streams. However, a high variability at each trophic level and physical habitat differences among the streams and the principal river might have decoupled the relationships amongst trophic levels in the SMR ecosystem.

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Prey selection patterns of juvenile Atlantic salmon (*Salmo salar*) in the Ste-Marguerite river ecosystem, Quebec, Canada.

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Abstract

Prey choice of juvenile Atlantic salmon (*Salmo salar*) was studied in the Ste-Marguerite river ecosystem, Quebec, in 1995. Five sites in five streams and three sites in the main river were chosen to collect fish and drifting invertebrates. Only the chironomid larvae were selected according to their abundance in the drift and only the water mites were rejected because of their size. The increase in the length of the prey consumed with the length of the fish was explained more by the morphological limitation of the fish than by the positive size selection by the fish. Our observations tend to show that in the Ste-Marguerite river ecosystem, the juvenile Atlantic salmon select their prey neither according to prey abundance nor according to prey size.

Introduction

Diet of juvenile landlocked salmonids such as brook trout (*Salvelinus fontinalis*) (Griffith 1974; Allan 1981), brown trout (*Salmo trutta*) (Elliot 1970, 1973; Suarez et al. 1988; Hubert et al. 1993), cutthroat trout (*Salmo clarki*) (Griffith 1974) and rainbow trout (*Oncorhynchus mykiss*) (Elliot 1970, 1973) have been extensively studied. In contrast, similar studies on anadromous salmonids, such as the Atlantic salmon (*Salmo salar*) are very few (Allen 1941; Suarez et al. 1988). Despite the fact that Canadian East Coast has been facing alarming declines in wild population of Atlantic salmon (Tremblay and Caron 1998), very few studies have considered the diet of their juveniles under natural conditions.

An extensive review of literature indicates that young salmonids choose their prey according to the size of the prey (Ricker 1932; Allen 1941; Martin 1952; Zorbidi 1970; Moore and Moore 1974; Ringler 1979; Allan 1981; Newman and Waters 1984). Prey selectivity is a mechanism to optimize foraging efficiency and hence, growth. The relationship between prey body size and predator (fish) body size, in terms of energy gathering and utilization efficiency, has been established using mathematical models (Paloheimo and Dickie 1965, 1966; Kerr 1971a, 1971b). These studies have suggested that fish tend to select their prey according to the size of the prey to channel more energy into growth. Wankowski (1979), and Wankowski and Thorpe (1979) have demonstrated that the juvenile Atlantic salmon show size-selective predation under laboratory conditions.

While some studies have suggested size-selective predation, others have suggested that prey are chosen according to their abundance in the predator's environment. Alm (1919), as reported in Allen (1941), observed a positive correlation between the fauna available and the food eaten by the young salmon in some Swedish rivers. Griffith (1974) found that cutthroat trout select Ephemeroptera, Plecoptera and Trichoptera larvae as a function of their abundance in the drift. Allan (1981) also found a similar relationship for juvenile brook trout. However, for Atlantic salmon, not much is known about how the juveniles choose their prey in natural habitats. Like other juvenile salmonids, juvenile Atlantic salmon may select prey by abundance and/or size. It is also possible that some attributes other than size or density may modify prey selection. For example, the biochemical composition of the food items may have a role in diet selection (Carr and Derby 1986a; Zimmer-Faust et al. 1988; Jones 1992).

Many studies of juvenile salmonids as well as other fish have demonstrated that the length of prey consumed increases with the length of the fish (Allen 1941; Elliot 1970; Suarez et al. 1988; Hubert and Rhodes 1992; Hubert et al. 1993; Lavoie and Hubert 1994). This increase would be to meet the growing metabolic demands of the predator with age. Such an observation implies that size-selective predation by fish is effective. If size-selective predation is occurring for juvenile Atlantic salmon in our study, then increases in the size of prey would be expected with increasing size of fish. However, such observations may also be dependent on the morphological relationship between the dimensions of the prey and the mouth gape of the fish (Moore and Moore 1976; Hart and Ison 1991).

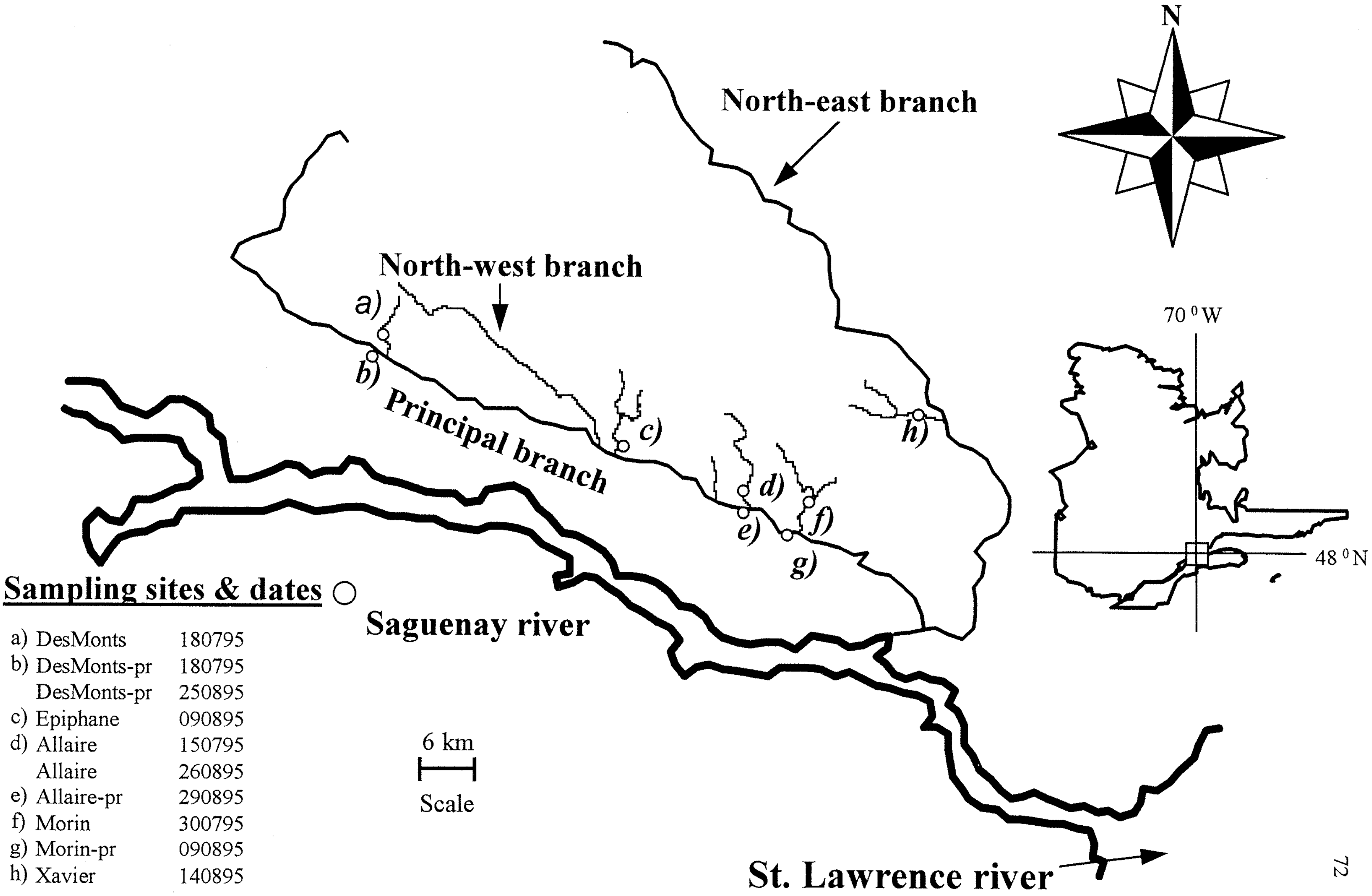
The objective of our study was to investigate which factors determine the selection of prey by juvenile Atlantic salmon along the Ste-Marguerite river (SMR) system in the East coast of Quebec, Canada. Specifically, we tested if juvenile Atlantic salmon select their prey according to the prey size as well as to the relative density of prey groups. We used relationship between fish size versus consumed prey size to test prey selection by size, and we used electivity indices to test prey selection by the abundance of prey groups. Although SMR is an important Atlantic salmon habitat in Quebec, not much is known about the feeding ecology of juvenile salmon in this area. Because juvenile production has significant consequences for adult production, we feel that our results will contribute significantly to our understanding of the ecological processes regulating Atlantic salmon fisheries.

Study site

Ste-Marguerite river is a tributary of the Saguenay river located in the Saguenay region, Quebec (48°N, 70°W, see map, Fig. 11). It extends 100 km from the Monts Valin to the Saguenay river near Sacre-Coeur township. It has a 2130 km² of drainage area and is characterized by mountains and dense forests mainly of black spruce (*Picea mariana*). The hydrologic regime is characterized by a spring peak and low but permanent summer flow with a mean annual discharge of 53 $m^3 \cdot s^{-1}$ (CIRSA *unpublihed data*). Because of particularly low precipitation during the study year (summer 1995), the river had a very low discharge (2.89 m^3/s: CIRSA *unpublished data*). We collected samples from five streams (Allaire, Des Monts, Epiphane, Morin and Xavier) and also from three sites in the principal river (Al-pr, DM-pr and Mor-pr) from 15 July to 29 August of 1995 (see map, Fig. 11). The three sites on the main river corresponded to the mouth of the streams Allaire, Des Monts and Morin. Only two sites were sampled twice in our sampling period. DM-pr and Allaire was sampled on 15,18 of July and 25,26 of August respectively (see map, Fig.11). The main substratum was cobbles and boulders in the principal river and in the streams but it was mainly sandy in Morin-pr and Morin. Brook trout (*Salvelinus fontinalis*) and the Atlantic salmon (*Salmo salar*) were the major fish species in the SMR ecosystem.

FIG. 11: Sampling sites on the Ste-Marguerite river ecosystem.

Ste-Marguerite river ecosystem



Sampling sites & dates ○

a)	DesMonts	180795
b)	DesMonts-pr	180795
	DesMonts-pr	250895
c)	Epiphane	090895
d)	Allaire	150795
	Allaire	260895
e)	Allaire-pr	290895
f)	Morin	300795
g)	Morin-pr	090895
h)	Xavier	140895

Materials and Methods

Literature survey (Elliot 1970; Griffith 1974; Allan 1978; Bachman 1984; Hubert et al. 1993) and our personal video observations in the SMR ecosystem suggest that juvenile Atlantic salmonids are predominantly feeding on drifting invertebrates. To collect drifting macro-invertebrates, we used two drift nets of 200 µm mesh size with an opening of 396.5 cm². They were placed near each other but at different depths to capture drifting invertebrates from the entire water column. Drift nets were installed upstream of the selected fishing sites. Drifting invertebrates were collected for 2 hours before fishing and 2 hours during fishing. After every two hours, (our preliminary observations suggested no net clogging within 2 hours), we took the collector of each drift net and the samples were placed in a -20 ^{0}C freezer. We collected the drifting invertebrates during the early morning (approximately at 5h00) because the major peak of drifting invertebrates is generally during the early morning or during the dusk (Elliot 1970; Merrit and Cummins 1978; Allan 1996) and because the fish eats mainly during the periods of low light intensity (Jorgensen and Jobling 1989; Jorgensen and Jobling 1992; Amundsen et al. 1999). We also choose a period of 2h before the fishing period because the stomach contents of fish collected during a any period reflect what the fish had eaten before and during the fishing time. To analyze the abundance and size of drifting invertebrates, we used an image analyzer attached to a zoom-stereo microscope and identified invertebrates to order or family (Merritt and Cummins 1978). All invertebrates were measured to nearest 0.5mm. Lengths of invertebrates were measured from the head to the end of the abdomen excluding the antennae or tail filaments.

To capture the fish, we did electrofishing on a 100 m section in each sampling site. The number of fish captured for gut analyses ranged from 9 to 25 fish, totalizing 126 fish guts for all the sampling sites. Fish were collected early in the morning. We measured the weight and length of each fish and collected the stomach contents of each by flushing the stomach with stream water using a manual pump. Each fish was measured to nearest millimeter and weighed to the nearest centigram. The invertebrates in each stomach were identified, measured and enumerated in the laboratory in the same manner as for the organisms in the drifting invertebrate samples. We must mention that when we flushed the stomach of the salmons, we collected only the anterior part of the gut content. Because of this, and because we fish soon after the major drifting period, we had mainly complete invertebrates and very few broken invertebrates in our stomach samples. The broken specimens, however, were enumerated using the head capsule but were not used for length estimates.

Statistical analysis

We used the electivity index (E) of Ivlev (1961) to determine if the fish selected for a given invertebrate taxon according to their abundance. An Ivlev electivity index near zero indicates that a given taxon is chosen by the fish according to its abundance in the drift. An index above or below zero, indicates that a given taxon is selected preferentially or rejected, respectively. We used the Pearson Product Moment Correlation to asses the relationship between the ratio (% of a taxon in diet / % of the same taxon in drift) versus the mean length of total drifting invertebrates to determine if the fish followed size-selective predation. Non-linear regression (polynomial) was used to determine if there was a significant relationship between the mean length of invertebrates consumed versus the length of fish. Significance was determined at $P \leq 0.05$ for all tests. The statistical analyses were performed using SigmaStat 1.0 (Statistical software, 1992).

Results

Prey selection

For all the 10 sites studied in the SMR ecosystem, the water mites and the chironomid larvae were the predominant drifting invertebrates during summer of 1995 (Figure 12a). They account for up to 25.1% and 25.3% respectively, of the total invertebrate density found in the drift. Combined together, all the other groups account for 49.6%.

The stomach content of 126 juvenile Atlantic salmon for all the sampling sites in the SMR ecosystem show strong contrast to the composition of drifting communities. The Trichoptera, the chironomids and the Ephemeroptera larvae were the predominant invertebrates found in the stomach of the juvenile salmon (Fig. 12b). They comprised up to 25.2%, 21.1% and 18.3%, respectively, of the total stomach content. These observations suggested that the juvenile Atlantic salmon select mainly the Trichoptera, chironomids and Ephemeroptera larvae as food. Altough water mites were one of the most abundant invertebrates in the drift, the juvenile salmon did not choose water mites. It was interesting to note that the relative abundance of the chironomid larvae in the stomach of the young salmons was approximately the same as the relative abundance of the chironomid larvae in the drift (Fig 12b).

Selection by abundance

To determine if young salmon were feeding on particular invertebrates as a function of their relative abundance, we plotted the $\log_{10}$ percent representation of each invertebrate taxon in the diet against the $\log_{10}$ percent representation of the same taxon in the drift (Fig. 13 a-f). If the drift is a good indicator of prey abundance and if fish take prey in proportion to their relative abundance, the electivity indices should be equal to zero. The electivity index for chironomid larvae was not significantly different from zero (E=-0.07) (Fig. 13a), suggesting that chironomid larvae were selected by the juvenile Atlantic salmon in the Ste-Marguerite river according to their abundance. On the other hand, the water mites (E=-0.81) (Fig. 13b), Simuliidae larvae (E=-0.56) (Fig. 13c), and other Diptera as a group (E=-0.48) (Fig. 13d) were always under represented in the

FIG. 12: Relative abundance of drifting invertebrates and preys in juvenile Atlantic salmon in the SMR ecosystem during summer 1995.

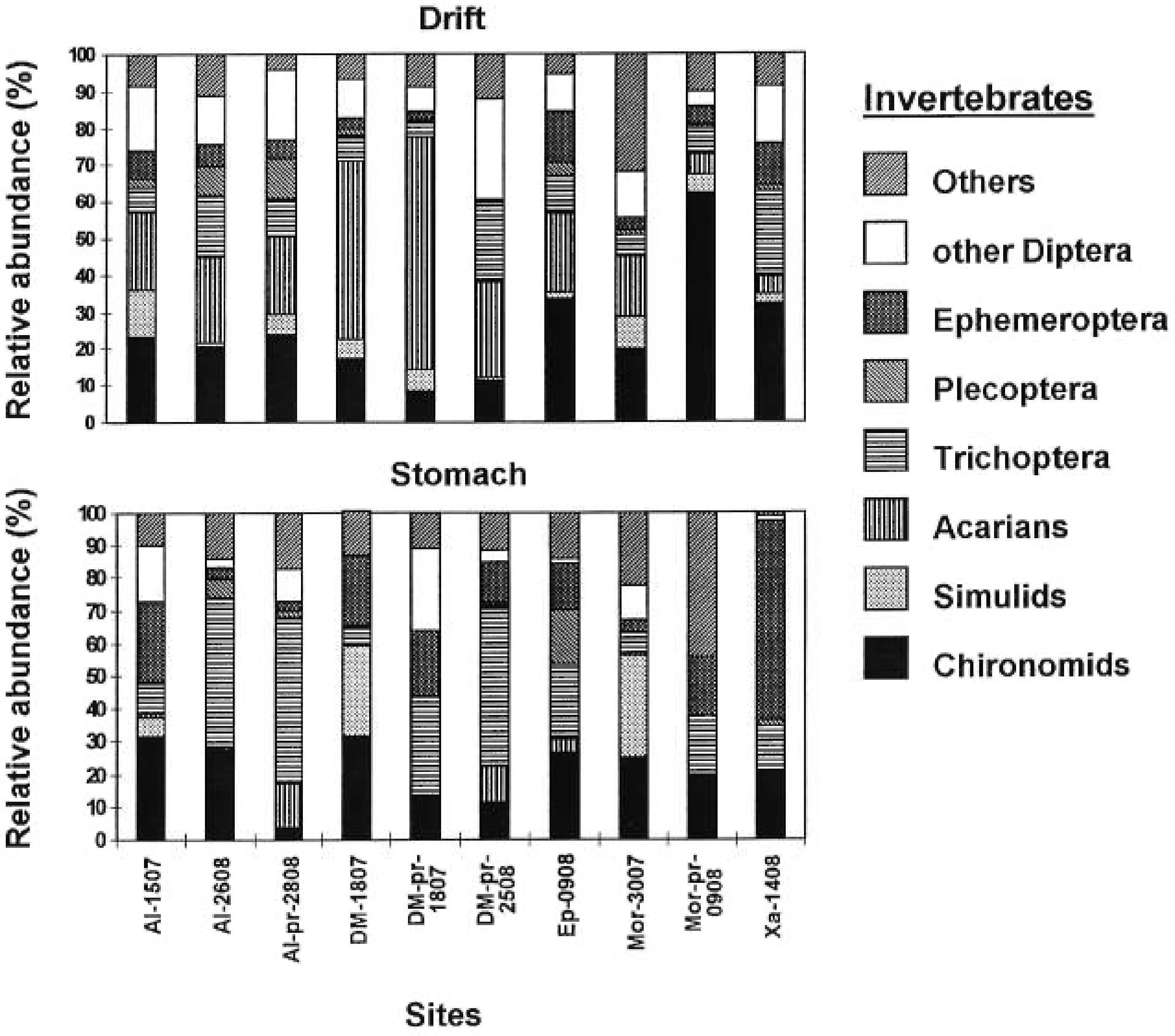
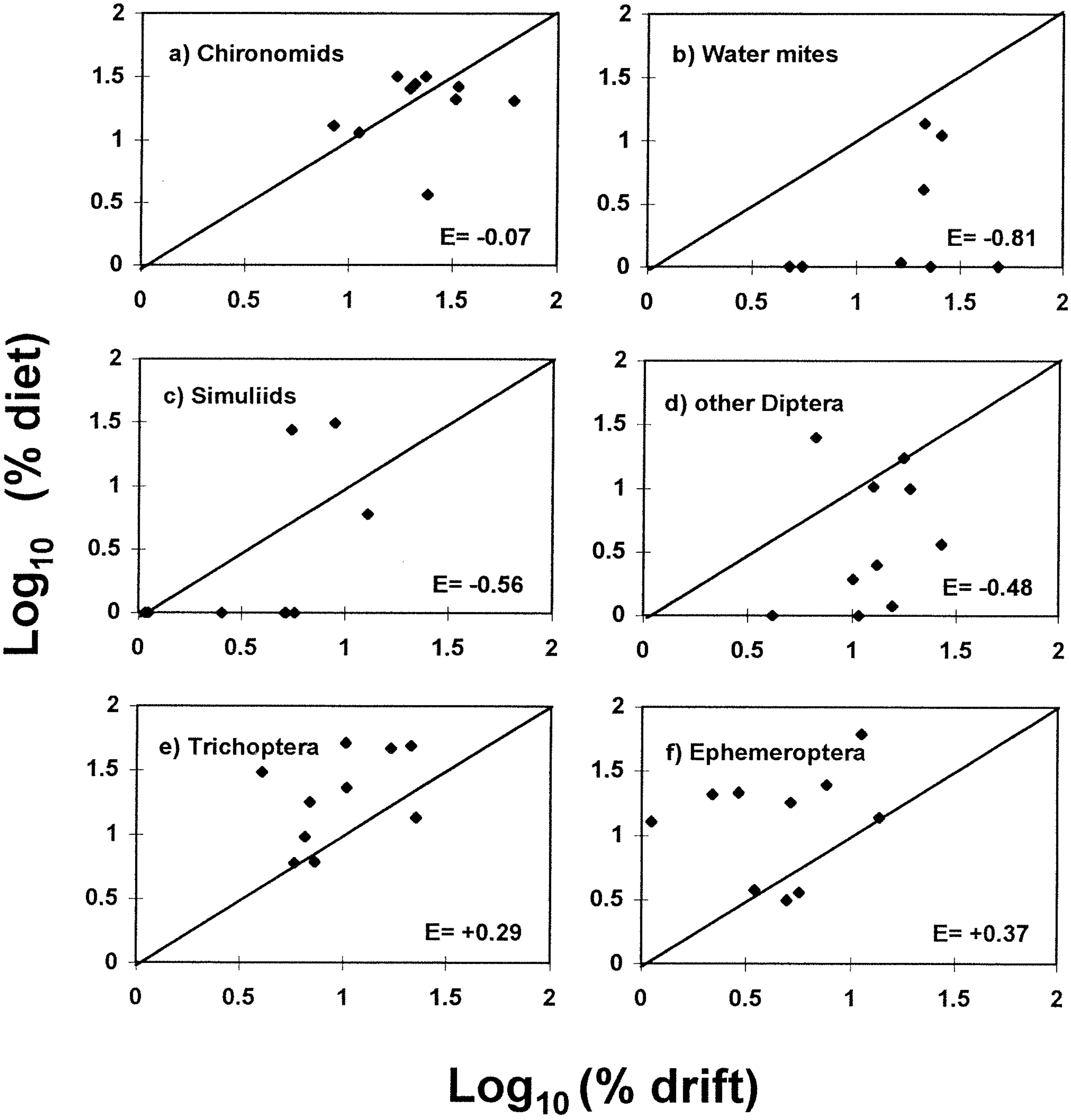

Drift
Relative abundance (%)
0
10
20
30
40
50
60
70
80
90
100
Stomach
Relative abundance (%)
Al-1507
Al-2608
Al-pr-2808
DM-1807
DM-pr-1807
DM-pr-2508
Ep-0908
Mor-3007
Mor-pr-0908
Xa-1408
Sites
Invertebrates
Others
other Diptera
Ephemeroptera
Plecoptera
Trichoptera
Acarians
Simulids
Chironomids

FIG. 13: The relationship between the percentage of a taxon in the diet and the percentage of the same taxon in the drift for 8 to 10 sites of Ste-Marguerite ecosystem during summer 1995. The diagonal lines represent 1:1 relationship or E=0.


a) Chironomids
E= -0.07
b) Water mites
E= -0.81
c) Simuliids
E= -0.56
d) other Diptera
E= -0.48
e) Trichoptera
E= +0.29
f) Ephemeroptera
E= +0.37
0
0.5
1
1.5
2
Log_{10} (% diet)
Log_{10} (% drift)

diet, suggesting that these invertebrates were not preferred by the juvenile Atlantic salmon. The Trichoptera larvae (E=+0.29) (Fig. 13e) and Ephemeroptera larvae (E=+0.37) (Fig. 13f) showed positive electivity indices, suggesting that these invertebrates were fed upon selectively by the juvenile Atlantic salmon.

Selection by size

In the SMR ecosystem, the ratio of invertebrates in diet to drift is positively correlated with the size of the invertebrates only if we included the points which described the water mites in the correlation (Pearson's $n=63$; $r^2=0.43$: $p \leq 0.05$) (Fig. 14). If we excluded the water mites, the correlation is not significant (Pearson's $n=57$; $r^2=0.14$: $p>0.05$) (Fig. 14). Thus, the juvenile salmon rejected only the water mites according to their size and the other groups of invertebrates were neither selected nor rejected for their size.

Relationship between prey size and fish size

A positive significant relationship was observed between the size of invertebrates consumed and the length of fish ($n=95$; $r^2=0.12$; $p \leq 0.05$) (Fig. 15a), but only 12% of the prey size selection was explained by the size of juvenile fish. Our results showed also, that the fish bigger than 8cm had a wider diet (Fig. 15a). Therefore, it seems that the length of the prey increased significantly with the length of the young salmon. However, the relationship is not strong ($r^2=0.12$) probably because the variability in size selection is greater for larger fish than smaller fish. This result show that the small fish eat only small prey but as the fish become bigger, the fish consumed bigger prey while they continue to consume small prey items.

FIG. 14: Size selection index for drifting invertebrates by 126 juvenile Atlantic salmon for 10 sites of Ste-Marguerite river ecosystem during summer 1995 with water mites (Pearson's n=63; $r^2=0.43$: $p \leq 0.05$) and without water mites (Pearson's n=57; $r^2=0.14$: $p > 0.05$). Each data point represent the mean length of each invertebrates group in the drift.

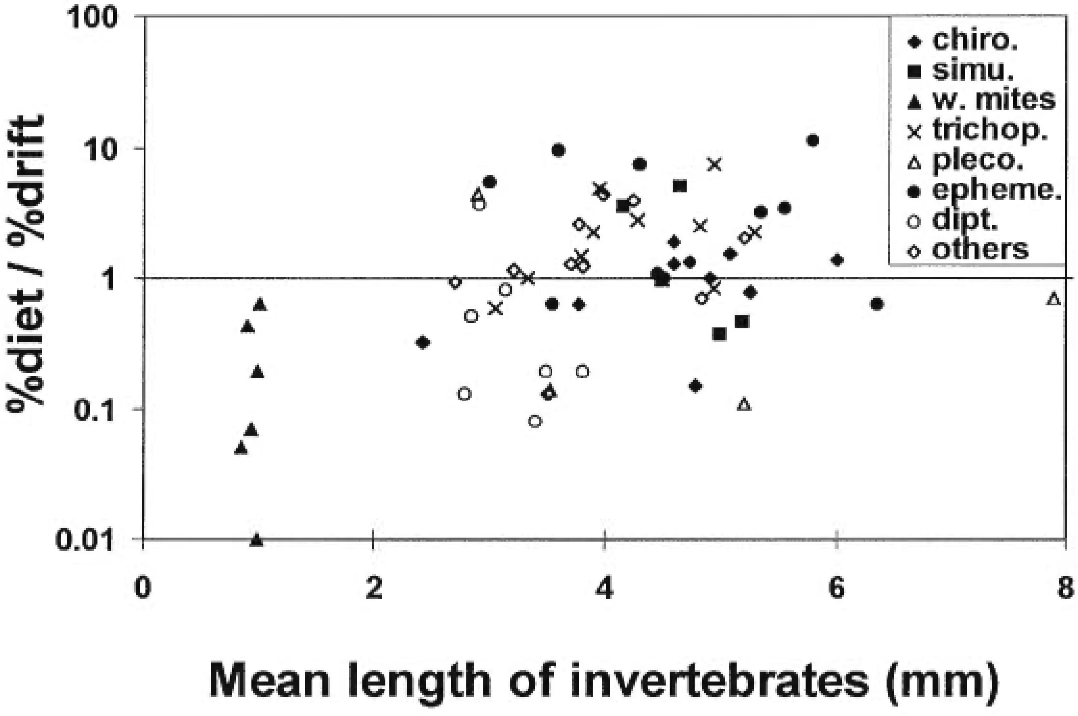
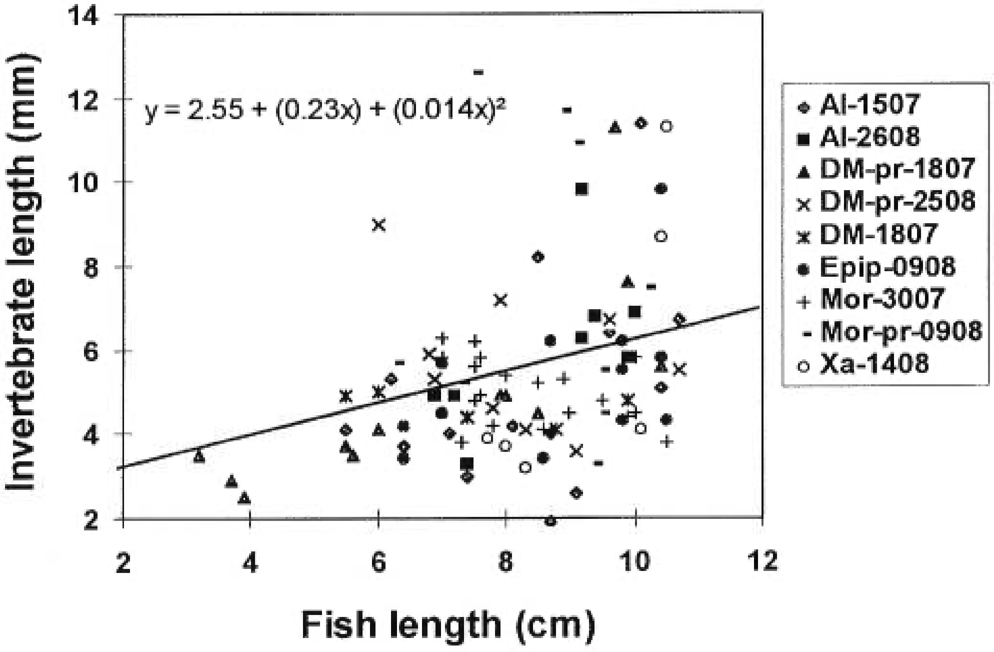

100
10
1
0.1
0.01
0
2
4
6
8
%diet / %drift
Mean length of invertebrates (mm)
◆ chiro.
■ simu.
▲ w. mites
× trichop.
△ pleco.
● epheme.
○ dipt.
◇ others

FIG. 15: Relationship between the length of fish and the mean length of invertebrates consumed for 9 sites of Ste-Marguerite river ecosystem during summer 1995 ($n=95$; $r^2=0.12$: $p \leq 0.05$). Each data point represent an individual fish.


y = 2.55 + (0.23x) + (0.014x)²
Invertebrate length (mm)
Fish length (cm)
14
12
10
8
6
4
2
2
4
6
8
10
12
◇ Al-1507
■ Al-2608
▲ DM-pr-1807
× DM-pr-2508
✱ DM-1807
● Epip-0908
+ Mor-3007
- Mor-pr-0908
○ Xa-1408

Discussion

Our results on prey selection by juvenile Atlantic salmon from the SMR ecosystem indicates a different pattern of prey selection than suggested by others. Studies on the land-locked juvenile salmonids, brook charr (Griffith 1974; Allan 1981) and cutthroat trout (Griffith 1974) suggest that these fishes select their prey according to their abundance in the environment. Moreover, Alm (1919) as reported in Allen (1941) compared the food of juvenile salmonids in some Swedish rivers and found that there was a clear relationship between the diet of fish and the abundance of Chironomidae, Trichoptera and Ephemeroptera larvae in the environment. Power (1969) was the only paper in the litterature which mentioned that the major constituant of the diet of the juvenile Atlantic salmon was Simulidae larvae. He explained his results by the fact that the juvenile Atlantic salmon were opportunists and fed upon Simulidae larvae because it was the most abundant invertebrate in his study sites. Unlike Power (1969), Keeley and Grant 1997 found that the juvenile Atlantic salmon in the Catamaran brook (New Brunswick) select mainly Chironomidae larvae, Diptera pupae and adults, Ephemeroptera and Trichoptera larvae for food. They also mentioned that the young salmons were opportunistic feeders because the stomach contents of the juvenile Atlantic salmon had revealed that the preys were consumed in the same proportion than in the drift. Unlike the study of Power (1969) and Keeley and Grant (1997), only the Chironomidae larvae were selected as a function of their abundance in the SMR ecosystem.

Chironomidae are one of the most abundant insect groups in many streams and most of them live on the upper surfaces of stones (Allen 1941). Moreover, because the life cycles of aquatic invertebrates change during the season, the chironomids may be more abundant probably because the other predominant invertebrates like Ephemeroptera and Trichoptera were already emerged from water when we sampled at the end of the summer (Merrit and Cummins 1978; Allan 1996). Because the feeding of the juvenile Atlantic salmon is opportunistic, they are able to switch prey according to prey relative abundance and profitability (Thonney and Gibson 1989). Because the chironomid larvae were so abundant in the SMR ecosystem during our sampling period, the juvenile Atlantic salmon capture these kind of prey with low cost of energy expenditures. Therefore, the chironomid larvae were highly profitable for the juvenile Atlantic salmon in the SMR ecosystem. This is probably the reason why the fish selected chironomids according to their abundance in the environment. However, this trend can probably change depending on when the sampling is done during the season. However, based on the Ivlev electivity index values for other invertebrates, prey abundance does not seem to be an important determinant of prey selection by the fish at the end of the summer in the SMR ecosystem.

It was also interesting to note that juvenile Atlantic salmon preferred to eat invertebrates which were mainly grazers (Chironomidae, Trichoptera and Ephemeroptera larvae) rather than other invertebrate functional groups as also demonstrated in several other studies (Alm 1919 as reported in Allen 1941; Allen 1941; McCormac 1962; Griffith 1974; Wankowski and Thorpe 1979; Allan 1981; Suarez et al. 1988; Lavoie and Hubert 1994). It is possible that these grazers, because of their greater nutritional value, were preferred as prey items. It is important to note that salmon enhancement methods such as fertilization of streams (Johnston et al. 1990; Deegan and Peterson 1992) succeed in most cases due to an increased density of grazers. However, we must mention that our taxonomic identification of the invertebrates may have some weaknesses because it was difficult to identify the species of the invertebrates found in the stomach content of the fish. Nonetheless, based on the functional goup of Merritt and Cummins (1978), the grazer comprised several families of Ephemeroptera, Trichoptera and Chironomids. Moreover, Weng (unpublished data) found that in the SMR ecosystem during the summer 1996, these kind of invertebrates fed mainly on Aufwuchs. Therefore, we think that the invertebrates found in the stomach of the fish in 1995 were mainly grazer.

Many studies have shown that the juvenile salmonids are size-selective predators (Ricker 1932; Allen 1941; Martin 1952; Zorbidi 1970; Moore and Moore 1974; Ringler 1979; Wankowski and Torpe 1979; Newman and Waters 1984). Allan (1981) mentioned that bigger invertebrates are over-reprensented in the diet and that the smaller invertebrate are under-represented in the diet of fish. The Trichoptera and the Ephemeroptera larvae were the bigger invertebrates found in the SMR ecosystem, so it may be suggested that these invertebrates may be selected by young salmons by size-selection because of their greater size. Water mites were the smaller invertebrates found in the SMR ecosystem. The rejection of this invertebrate may also be explained by their smaller size. Keeley and Grant (1997) have found that the juvenile Atlantic salmon in Catamaran brook select their preys in function of the size of the prey. However, only the rejection of the water mites by the juvenile salmons in the SMR ecosystem can be explained by their smallest size amongst all other invertebrates in the drift. The study by Allan (1978) on the diet of juvenile brook trout have shown that only the invertebrates with a head length below 0.7mm were rejected by the fish. The water mites have a total mean length of 1mm, consequently, they are too small to be eaten by the young salmon. Minimum prey length is thought to be limited by gill raker spacing (Wankowski 1979; Dunbrack and Dill 1983; Lazzaro 1987). Therefore, in our study, the size rejection of the water mites may be explained by the fact that they are too small and thus, can escape from the young salmon through the gill rakers.

In our study however, we have considered only the total length of the invertebrates. Lazzaro (1987) mentioned that the shape of the preys can influence the choice of certain kind of prey by the fish. As demonstrated in Keeley and Grant (1997), the width of the invertebrates can also play a role in the selection of the prey by juvenile Atlantic salmon. Thus, it may explain why the Ephemeroptera larvae were selected preferentially in our study. The surface/volume ratio of this group is greater than other groups of invertebrates. Juveniles Atlantic salmon are visual predators (Wankowski and Thorpe 1979) and if the Ephemeroptera larvae are larger than the other group of invertebrates, they are more visible to the fish. Probably this is why the juvenile salmon selected Ephemeroptera larvae more than other invertebrate groups. However, the surface/volume ratio of the other invertebrates does not explain their rejection or selection by the fish because they have approximately similar surface / volume ratio. It seems that the abundance and the size of prey alone can not determine the selection of the Ephemeroptera and Trichoptera larvae, and the rejection of the other Dipterans and Simuliidae larvae by the juvenile Atlantic salmon in SMR ecosystem.

Allen (1941) mentioned that it is not only the abundance and the size of the prey that are important for the selection of prey but also the smell and/or taste of each kind of invertebrates. Some studies mentioned that four types of common, low-molecular-weight metabolites, acting alone or together, serve as potent attractants or stimulants of feeding behavior. These substances are free amino acids, quaternary ammonium compounds, nucleotides and organic acids (Carr and Derby 1986a; Zimmer-Faust et al. 1988; Jones 1992). Carr et al. (1996) found that four combined biochemical substances (glycine, alanine, proline, and arginine) attract or stimulate the feeding behavior of the smolts of Atlantic salmon in marine ecosystem. However, it seems that no extensive study has been conducted on the biochemical substances of stream invertebrates in relation to their stimulating effects on the feeding behavior of young salmonid. Therefore, we do not know if the invertebrates that were rejected (Simuliidae larvae and other Diptera) or selected (Ephemeroptera and Trichoptera larvae) have a pleasant or unpleasant smell and/or taste. Further studies on biochemical quality of each group of invertebrates in lotic ecosystems are needed to answer this question.

Some studies have found that the length of the invertebrates consumed increases with the length of the fish (Elliot 1970; Pearre 1986; Suarez et al 1988; Hubert and Rhodes 1992; Hubert et al. 1993; Lavoie and Hubert 1994). Burns (1968) found the same trends for zooplankton. She found a strong positive relationship between the diameter of platic bead ingested and the increasing body size of zooplankton (*Bosmina longirostris* and six species of *Daphnia*). Keeley and Grant (1997) have also demonstrated that the length of preys increased with the fork length of the juvenile Atlantic salmon. For them, it implies that the fish select the bigger prey by size selection when the fish grow. Our results seems to be inconsistent with the studies mentioned above. Our results demonstrated that there was an increase in the length of prey with an increase in the length of the fish. However, our observation of a greater variation in prey selection by bigger fish seem to be inconsistent with other studies (ref. cited above). Some authors mentioned that the juvenile Atlantic salmon ingest whole prey items which makes the dependence of fish on the morphological relationship between the dimensions of the prey and the mouth of the fish as an important criterion in prey selection (Moore and Moore 1976; Wankowski 1979; Lazzaro 1987; Hart and Ison 1991; Hart and Gill 1992a). Because of the small size of their mouths, the reduced volume of its buccal cavity, and the resulting weak suction strength and poor aiming, the juveniles fish initially select small preys (Lazzaro 1987). During growth, they feed progressively upon larger prey. This maximum size selection imposed by the fish gape is well documented for juvenile chum salmon (*Oncorhynchus* keta) by Feller and Kaczynski (1975). This may explain why the variation in the length of the prey consumed increases with an increase in the length of juvenile Atlantic salmon. The bigger fish can handle and ingest bigger preys than the smaller fish, but the great variation in the length of the prey consumed by the bigger fish showed that the bigger fish continue to eat mainly on small invertebrates.

Feeding energetics may explain the increase in mean prey length with body size. Large prey contain more energy (Smock 1980) but take longer to handle (Bannon and Ringler 1986) than small prey. It may explain why the bigger juvenile Atlantic salmon in the SMR ecosystem select bigger preys than smaller fish but because of the handling time, they continue to eat mainly small invertebrates.

It is mentionned that fish are size-selective but depending of the season, the fish may have some problems to find big prey to feed upon, and subsequently they may fed upon small preys because they dont have the choice (Pearre 1986; Lazzaro 1987). Similar patterns seem to exist for zooplankton grazing on planktonic particules in lakes. McCauley and Downing (1985) found that zooplankton (cladocerans) were size-selective but the very small or very big particules were not preferentially selected because these particules were not enough available to predation. Therefore, the seasonality of the sampling may also explain why the juvenile Atlantic salmon in the SMR ecosystem eat mainly small preys items. As we discussed above, during our sampling period, the chironomid larvae were the most abundant invertebrate in our ecosystem. Because the Atlantic salmon are opportunists, they eat chironomids as a function of their abundance during mid and late summer and then, the small size of the chironomids eaten may be reflected in the Figure 15. Nonetheless, this trend may surely change during the season depending on the availability of other prefered preys like Ephemeroptera and Trichoptera. It would be very interesting to study the seasonnal patterns of this trend but because of the bad weather conditions at the beginning of the summer, we had no choice but to do the sampling only during a narrow period of time. However, we think that the pattern we found in the late summer in the

SMR ecosystem is representative of what really happens in streams at this particular time of the year.

Conclusions

In our study, the juvenile Atlantic salmon select only the chironomid larvae as a function of their relative abundance in the drift. Only the water mites were rejected by the young salmon because of their smaller size. The selection of Trichoptera and Ephemeroptera larvae and the rejection of the Simuliidae larvae and other Diptera was not explained by either their abundance or their size. Therefore, the factors which determine the selection of prey by the juvenile Atlantic salmon in the SMR ecosystem seem to be different from the majority of the other studies done on juvenile salmonids. It would be desirable to conduct further studies on the diet of juvenile Atlantic salmon in several lotic ecosystems to understand more accurately why the young Atlantic salmon select some prey types while rejecting others of similar size and density in freshwater ecosystems.

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Discussion générale

Chapitre 1

Les résultats obtenus concordent avec ceux d'autres études quant à la prédominance de la voie ascendante pour le contrôle de la biomasse du périphyton (Biggs et Close 1989; Van Nieuwenhuyse et Jones 1996; Dodds et al. 1997). Cette biomasse semble en effet contrôlée principalement par les ressources (nutriments) mais seulement en excluant les sites Mor et Mor-pr de la relation. Ces sites sont caractérisés par un substrat composé principalement de sable, ce qui entraîne une faible densité de roches dans les quadrats d'échantillonnage. Ceci peut expliquer pourquoi la forte concentration en phosphore total pour Morin et Mor-pr n'est pas associée à une concentration élevée de Chl a. Il est donc justifié de mentionner que la qualité du substrat est un facteur qui peut masquer une corrélation positive entre les nutriments et le périphyton (Rounick et Grégory 1981). Il y a néanmoins d'autres facteurs qui peuvent dissimuler une telle corrélation comme le contrôle descendant des invertébrés brouteurs et l'intensité de la lumière ambiante.

Selon plusieurs écologistes, les invertébrés brouteurs peuvent limiter la croissance des algues pélagiques (Mazumder et al. 1988; Hansson 1992; Sarnelle 1992; Mazumder 1994a) et du périphyton (Hunter 1980; Hill et Harvey 1990; Rosemond et al. 1993; Bourassa et Cattaneo 1998). Le phénomène du broutage peut même masquer une relation entre les éléments nutritifs et le périphyton (Stewart 1987; Rosemond et al. 1993). Mes résultats confirment partiellement ce phénomène. Pour l'écosystème de la rivière Ste-Marguerite, les invertébrés brouteurs ont un impact négatif significatif sur la biomasse du périphyton. Cependant, il faut indiquer que cet impact reste moins important pour limiter cette biomasse que l'impact positif des nutriments. Ce résultat confirme les hypothèses qui prédisent que la biomasse des algues est principalement contrôlée par la voie ascendante dans un écosystème oligotrophe (Fretwell 1977; Oksanen et al. 1981; Power 1992). En fait, il semble que l'écosystème de la rivière Ste-Marguerite est trop pauvre en éléments nutritifs pour influencer significativement les niveaux trophiques supérieurs au périphyton. Ceci peut probablement expliquer pourquoi la biomasse du périphyton est principalement contrôlée par la voie ascendante et d'un moindre degré par la voie descendante.

Selon la théorie du "River Continuum Concept", la lumière s'avère le plus important facteur pour limiter la croissance du périphyton dans les ruisseaux situés dans une région forestière (Vannote et al. 1980). Dû au fait que la rivière Ste-Marguerite et ses tributaires sont situés dans un milieu forestier, la croissance du périphyton de cet écosystème doit être principalement contrôlé par la lumière et non par les nutriments. Cependant, tel n'est pas le cas. D'après certains, quand la lumière n'est pas limitante, ce sont les nutriments qui contrôlent le périphyton des ruisseaux (Stockner and Shortreed 1978; Peterson et al. 1983). En effet, lors de l'été 1995, la canopie forestière était relativement ouverte pour les ruisseaux et inexistante pour la rivière principale. Par conséquent, la lumière semble suffisamment abondante pour ne pas limiter la croissance du périphyton. Ceci permet probablement à cette biomasse algale d'être principalement contrôlée par les nutriments dans l'écosystème de la rivière Ste-Marguerite.

Certaines études ont suggéré qu'une augmentation de la biomasse ou de la productivité du périphyton entraîne un accroissement de l'abondance (Hart et Robinson 1990; Jonhston et al. 1990; Crowll et Schnell, 1991; Suren et Winterbourn, 1992) et de la taille (Peterson et al. 1985; Hart et Robinson, 1990; Hill, 1992; Hill et al. 1992) des invertébrés benthiques. Cependant, cela ne semble pas s'appliquer pour l'écosystème oligotrophe de la rivière Ste-Marguerite. Un faible gradient en éléments nutritifs fait en sorte que celui du périphyton est sans doute insuffisant pour induire une réponse significative aux invertébrés benthiques.

Un nombre considérable d'études réalisées en lacs ont démontré que les poissons planctonivores peuvent exercer un contrôle descendant sur la communauté zooplanctonique et donc masquer une corrélation entre la biomasse du zooplancton et la biomasse d'algues pélagiques (Hrbácek et al. 1961; Brook et Dodson 1965; Galbraith 1967; O'Brien et de Noyelles 1974; Shapiro 1980; Carpenter et al. 1985; Mazumder 1994a). Cependant, les juvéniles du Saumon de l'Atlantique de l'écosystème de la rivière Ste-Marguerite ne semblent pas avoir d'impact négatif significatif sur l'abondance et la taille des invertébrés benthiques. La densité de ces poissons est sans doute trop faible pour induire un tel impact sur ces invertébrés. De plus, ces juvéniles ne sélectionnent pas leurs proies en fonction de la taille (Maynard et Mazumder *soumis*). Ils ne peuvent donc pas avoir un impact sur l'abondance et/ou la taille des invertébrés benthiques. Il faut toutefois indiquer que seulement les saumons ont été utilisés pour représenter la densité totale des poissons. En ne tenant pas compte des truites, cela sous-estime cette densité totale. Les résultats peuvent alors être biaisés car il peut s'avérer que les truites ont un impact sur les invertébrés benthiques.

Plusieurs écologistes ont remarqué que la biomasse et la densité des poissons sont dépendantes du statut en nutriments et de l'abondance de nourriture en écosystèmes lotiques (Murphy et al. 1981; Bowlby et Roff 1986; Gibson et Haedrich 1988). Par contre, pour l'écosystème de la rivière Ste-Marguerite, la biomasse et la densité des juvéniles du Saumon de l'Atlantique ne s'avèrent pas contrôlées par les ressources (invertébrés). Comme je l'ai déjà mentionné, si le gradient des nutriments est trop faible pour induire une réponse significative aux invertébrés, il est peu probable d'observer une dépendance des poissons aux ressources. Il est intéressant de remarquer que selon les résultats obtenus, la biomasse et la densité des poissons semblent plus contrôlées par les différences abiotiques des milieux que par les interactions trophiques, lorsqu'un écosystème est oligotrophe. Le Saumon de l'Atlantique préfère évoluer en eaux froides et bien oxygénées (Elliot 1991; Gibson 1993). Les ruisseaux de l'écosystème de la rivière Ste-Marguerite démontrent toujours une température et un taux d'oxygène supérieurs à la rivière principale. D'autre part, il y a plus d'abris disponibles pour les jeunes saumons dans les ruisseaux. Bryant (1983) mentionne en effet que l'abondance d'abris à la prédation est une composante essentielle d'un bon habitat d'élevage de saumons. Ces raisons expliquent probablement pourquoi la biomasse et la densité des juvéniles du Saumon de l'Atlantique sont supérieures dans les ruisseaux. Par conséquent, dans un écosystème oligotrophe comme celui de la rivière Ste-Marguerite, les différences abiotiques entre les milieux peuvent surclasser les interactions trophiques en ce qui a trait à la limitation de la production des poissons.

Un bon nombre d'études ont démontré que la croissance (Hyatt et Stockner 1985; Johnston et al. 1990; Peterson et al. 1993) et la condition (Deegan et Peterson 1992) des jeunes salmonidés augmentent après une fertilisation en éléments nutritifs dans les écosystèmes lotiques. Ces résultats s'expliquent par le fait que l'ajout des nutriments stimule la voie ascendante vers les niveaux trophiques supérieurs et que cela accroît l'abondance et/ou la taille des invertébrés qui sont la nourriture des jeunes salmonidés. Cependant, dans un écosystème naturel comme celui de la rivière Ste-Marguerite, la croissance ou la condition des poissons ne s'avère pas dépendante de cette voie ascendante. Cette observation peut être due au fait que les gradients de l'abondance et de la taille des invertébrés benthiques sont possiblement trop faibles dans un écosystème oligotrophe pour induire une réponse significative à la condition des poissons.

Chapitre 2

Certaines études réalisées sur les jeunes salmonidés sédentaires comme l'Omble de fontaine (Griffith 1974; Allan 1981) et la Truite rouge (Griffith 1974) proposent que ces poissons sélectionnent leurs proies en fonction de l'abondance de celles-ci dans l'environnement. Ce phénomène de sélection des proies est aussi observé chez les juvéniles du Saumon de l'Atlantique (Keeley et Grant 1997). Néanmoins, d'autres études suggèrent que les jeunes salmonidés sont des prédateurs choisissant leurs proies principalement en fonction de leur taille (Ricker 1932; Allen 1941; Martin 1952; Zorbidi 1970; Moore et Moore 1974; Ringler 1979; Wankowski et Thorpe 1979; Newman et Waters 1984). Par conséquent, les juvéniles du Saumon de l'Atlantique sélectionnent vraisemblablement leurs proies par l'un ou l'autre de ces phénomènes.

Pour l'écosystème de la rivière Ste-Marguerite, les juvéniles du Saumon de l'Atlantique sélectionnent seulement les chironomides en fonction de leur abondance. Puisque les larves de chironomides sont les invertébrés les plus abondants dans l'écosystème de la rivière Ste-Marguerite, les juvéniles du Saumon de l'Atlantique étant opportunistes (Thonney et Gibson 1989; Keeley et Grant 1997) peuvent capturer ce type de proies sans dépenser beaucoup d'énergie. Par conséquent, ces larves sont probablement des proies très profitables aux jeunes saumons de cet écosystème. Ceci peut certainement expliquer pourquoi les poissons sélectionnent les chironomides en fonction de leur abondance dans la dérive. Toutefois, selon mes résultats, l'abondance des autres invertébrés ne semble pas un facteur important pour influencer le choix de ces invertébrés par les jeunes saumons de l'écosystème de la rivière Ste-Marguerite. Cependant, il est important de mentionner que, sans être sélectionné en fonction de leurs abondances, les larves d'Éphéméroptères et de Trichoptères sont choisies préférentiellement par les jeunes saumons.

Selon les études mentionnées ci-haut, la sélection en taille peut vraisemblablement expliquer pourquoi les larves de Trichoptères et d'Éphéméroptères sont préférées. Pourtant, selon mes résultats, seulement les acariens sont rejetés en fonction de leur dimension. Ceux-ci sont d'ailleurs les plus petits invertébrés retrouvés dans la dérive de l'écosystème de la rivière Ste-Marguerite. L'étude d'Allan (1978) sur la diète des jeunes Ombles de fontaine révèle que seulement les invertébrés ayant une tête de moins de 0.7mm sont rejetés. Les acariens possèdent une dimension moyenne de 1mm, ils sont donc trop petits pour être mangés par les jeunes saumons. Quelques écologistes pensent que la taille minimum des proies ingérées est limitée par l'espace des branchies des poissons (Wankowski 1979; Dunbrack et Dill 1983). Les acariens peuvent ainsi échapper aux jeunes saumons par l'espace des branchies, ce qui peut expliquer pourquoi ces invertébrés sont rejetés en fonction de leur taille.

Lors de mon étude, je n'ai toutefois considéré que la longueur totale des invertébrés pour représenter la taille des proies. Comme Keeley et Grant (1997) l'ont constaté, la largeur des invertébrés peut jouer un rôle dans la sélection des proies par les juvéniles du Saumon de l'Atlantique. Le ratio surface/volume des larves d'Éphéméroptères est plus grand que celui des autres groupes d'invertébrés. Puisque les juvéniles du Saumon de l'Atlantique sont des prédateurs visuels (Wankowski et Thorpe 1979), les larves d'Éphéméroptères étant plus larges que celles des autres groupes d'invertébrés, elles sont plus visibles aux poissons. Ceci peut justifier pourquoi elles sont sélectionnées préférentiellement par les jeunes saumons de mon étude. Par contre, le ratio surface/volume des autres invertébrés ne justifie pas leur rejet ou leur sélection parce qu'ils possèdent approximativement le même ratio.

Suite aux résultats de la présente étude, il semble que l'abondance et la taille ne sont pas des facteurs primordiaux pour influencer la sélection des proies par les juvéniles du Saumon de l'Atlantique de l'écosystème de la rivière Ste-Marguerite. Allen (1941) propose que la sélection des proies par les jeunes saumons n'est pas seulement déterminée en fonction de l'abondance et de la taille mais aussi par l'odeur et/ou le goût de chaque type d'invertébrés. Certaines études indiquent que des substances biochimiques stimulent le comportement de prédation des saumoneaux du Saumon de l'Atlantique dans l'écosystème marin (Carr and Derby 1986a; Zimmer-Faust et al. 1988; Jones 1992; Carr et al. 1996). Étant donné que les juvéniles du Saumon de L'Atlantique sélectionnent préférentiellement les invertébrés brouteurs (chironomides, Trichoptères, Éphéméroptères), ceux-ci peuvent alors posséder ces substances biochimiques. Néanmoins, aucune étude exhaustive n'a été réalisée sur les substances biochimiques des invertébrés de ruisseaux en relation avec leurs effets stimulants sur les jeunes salmonidés. Conséquemment, il est primordial de faire des études en milieux lotiques pour tester si certains invertébrés benthiques possèdent ces substances.

Plusieurs études ont démontré que la taille des invertébrés consommés augmente avec la taille des poissons (Elliot 1970; Suarez et al. 1988; Hubert et Rhodes 1992; Hubert et al. 1993; Lavoie et Hubert 1994; Keeley et Grant 1997). Mes résultats révèlent que ce phénomène existe chez les juvéniles du Saumon de l'Atlantique. Néanmoins, mes observations d'une grande variabilité de la sélection en taille des proies chez les plus gros poissons sont inconsistantes avec les autres études. Cette variation confirme qu'une forte sélection en taille des proies n'existe pas pour les jeunes saumons de l'écosystème de la rivière Ste-Marguerite. Quelques auteurs ont découvert que les juvéniles du Saumon de l'Atlantique consomment leurs proies en entier et que ceci crée une dépendance morphologique entre la dimension des proies et la gueule des poissons (Moore et Moore 1976; Wankowski 1979; Hart et Ison 1991; Hart et Gill 1992). Les poissons de plus grande dimension peuvent donc manipuler et ingérer de plus grosses proies, ce qui peut expliquer pourquoi la variation de la taille des proies consommées augmente avec la taille des poissons. Cependant, il est intéressant de remarquer que malgré ce phénomène, les jeunes saumons continuent de se nourrir principalement de petits invertébrés.

Le principe de la bioénergétique peut également expliquer un accroissement de la taille moyenne des proies ingérées avec l'augmentation de la taille des poissons. Les proies de plus grande dimension contiennent plus d'énergie (Smock 1980) mais prennent plus de temps à être manipulées par les poissons (Bannon et Ringler 1986). Ceci peut expliquer pourquoi dans l'écosystème de la rivière Ste-Marguerite, les juvéniles du Saumon de l'Atlantique choisissent des proies d'une taille moyenne plus grande lors de leur croissance. Cependant, dû au temps de manipulation, ils continuent de se nourrir principalement de petites proies.

La base saisonnière de l'échantillonnage peut aussi expliquer pourquoi les jeunes saumons de l'écosystème de la rivière Ste-Marguerite continuent de se nourrir principalement de petits invertébrés lors de leur croissance. Selon les saisons, les poissons peuvent avoir de la difficulté à trouver des grosses proies en abondance, ils sont alors obligés de se nourrir principalement de petites proies (Pearre 1986; Lazzaro 1987). Mon échantillonnage se passait à la fin de l'été 1995. L'abondance de grosses proies comme les larves d'Éphéméroptères et de Trichoptères est généralement très faible durant cette période de l'année, car ces invertébrés ont déjà émergé (Merritt et Cummins 1978; Allan 1996). En effet, les larves de chironomides étaient les invertébrés les plus abondants pendant mon étude. Par conséquent, les jeunes saumons n'ont probablement pas le choix de se nourrir principalement de petits invertébrés. Il serait intéressant de faire d'autres études pour tester si ce phénomène est observé au début de l'été, lorsque les larves d'Éphéméroptères et de Trichoptères sont en grande abondance.

Conclusion générale

Dans un écosystème de rivière oligotrophe comme celui de la Ste-Marguerite, les nutriments semblent jouer un rôle prépondérant dans la détermination de la biomasse du périphyton. Cependant, cette biomasse peut également être contrôlée à un certain point par l'effet descendant des invertébrés brouteurs. L'abondance et la taille des invertébrés benthiques ainsi que la biomasse, la densité et la condition des juvéniles du Saumon de l'Atlantique ne semblent pas être en fonction des ressources. Alors, dans un écosystème oligotrophe, un faible gradient de phosphore peut induire une réponse significative à la biomasse algale, mais le gradient de cette dernière semble insuffisant pour observer une forte dépendance des niveaux trophiques supérieurs aux ressources. Ceci pourrait expliquer pourquoi les juvéniles du Saumon de l'Atlantique, qui se situent au dernier niveau trophique, s'avèrent davantage contrôlés en fonction des différences abiotiques des habitats de ruisseaux et de rivières que par la voie trophique.

Au moment de mon étude, seulement deux types d'invertébrés sur six ont été sélectionnés en fonction de leur abondance ou de leur taille par les juvéniles du Saumon de l'Atlantique de l'écosystème de la rivière Ste-Marguerite. Il semble alors que les facteurs qui déterminent la sélection des proies par ces juvéniles diffèrent de la majorité des autres études réalisées sur de jeunes salmonidés.

À ma connaissance, cette recherche à été la première à étudier les facteurs influençant le choix de la diète et les relations trophiques dans un écosystème complet de juvéniles du Saumon de l'Atlantique. Il faut toutefois mentionner que mes résultats peuvent être biaisés par plusieurs facteurs comme un nombre insuffisant de sites échantillonnés, la vitesse du courant, l'azote, la voie hétérotrophe, et la base saisonnière de l'échantillonnage. Il serait donc important de réaliser des recherches ultérieures, dans plusieurs écosystèmes lotiques différents, pour savoir si d'autres études corroboreraient mes résultats. Cela servirait également à vérifier si les facteurs mentionnés ci-haut peuvent modifier les patrons des relations trophiques ainsi que le choix de la diète des juvéniles du Saumon de l'Atlantique.

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