UNIVERSITÉ DU QUÉBEC

RÔLE DE LA PLAINE D'INONDATION DU LAC SAINT-PIERRE COMME HABITAT DE PRODUCTIVITÉ D'UN SUBSIDE ÉCOLOGIQUE À LA COMMUNAUTÉ ICHTYENNE

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« Nous n'héritons pas de la terre de nos parents,
nous l'empruntons à nos enfants. »

Antoine de Saint-Exupéry

« On ne triomphe de la nature qu'en lui obéissant. »

Francis Bacon

« On dit d'un fleuve emportant tout qu'il est violent
Mais on ne dit jamais rien de la violence
Des rives qui l'enserrent »

Bertolt Brecht

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Les chapitres I, II et III de cette thèse sont présentés sous forme d'articles scientifiques. Ceux-ci sont rédigés en anglais pour convenir au format des journaux scientifiques dans lesquels ils sont publiés ou soumis. Les données analysées dans ces trois chapitres proviennent des travaux de terrain auxquels j'ai activement participé. Les plans d'échantillonnage ont été développés en collaboration avec mes co-directeurs (Gilbert Cabana, Christiane Hudon et Antonia Cattaneo). Je confirme que j'ai travaillé comme premier auteur sur les trois articles.

Le premier chapitre de cette thèse (*Seasonality of a Floodplain Subsidy to the Fish Community of a Large Temperate River*) est publié dans la revue *Ecosystems* (2019). https://doi.org/10.1007/s10021-019-00374-w.

Le second chapitre (*Hydrological control of a floodplain subsidy to littoral riverine fish*) est actuellement en révision dans la revue *Canadian Journal of Fisheries and Aquatic Sciences*.

Le troisième chapitre (*Estimating the duration and contribution of a pulsed subsidy: the benefits of multi-tissues isotopic approach*) sera soumis à la revue *Food webs*.

TABLE DES MATIÈRES

RÉSUMÉ

Les subsides spatiaux sont des ressources (nutriments, détritus ou proies) contrôlées par l'écosystème donneur qui sont mobilisées au-delà des limites d'un écosystème modifiant la dynamique des populations et communautés de l'écosystème receveur. Les effets de ces apports sur l'écosystème receveur varient en fonction de la quantité, la qualité, la durée de disponibilité et du timing des subsides. Les plaines inondables sont des écosystèmes très productifs qui peuvent exporter un subside contribuant à la productivité de la rivière adjacente. Toutefois, les études en milieu tempéré montrent des résultats variables quant à la présence et à l'importance de la contribution d'un subside à la productivité ichtyenne, qui varie en fonction de multiples facteurs tels que le système, le régime hydrologique et l'espèce. Pour ces raisons, il est difficile d'émettre des prédictions sur l'importance du rôle du subside provenant de la plaine inondable à la productivité des poissons.

Par l'entremise de l'analyse du ratio isotopique du carbone ($\delta^{13}C$), cette thèse vise à évaluer la présence et l'importance du subside provenant de la plaine inondable pour la communauté de poisson du lac Saint-Pierre, un grand lac fluvial du fleuve Saint-Laurent. Cette thèse se divise en quatre grands objectifs principaux : (I) identifier la présence du subside et analyser sa dynamique spatio-temporelle; (II) évaluer l'impact du régime hydrologique sur la contribution du subside provenant de la plaine à la productivité et la condition physique de cinq espèces littorales; (III) développer une approche isotopique multi-tissulaire (foie et muscle) afin de mesurer la durée de disponibilité du subside; (IV) évaluer les effets de la sélection du tissu sur les conclusions lors de l'utilisation de l'approche isotopique.

Les résultats révèlent que la plaine inondable contribue à un important subside alimentaire aux poissons littoraux du lac Saint-Pierre, sous forme de biomasse de proies invertébrées. La contribution trophique du subside à la productivité ichtyenne suit un patron saisonnier en accordance avec le cycle hydrologique. La contribution du subside provenant de la plaine est à son maximum à la fin de la crue printanière et décroît au courant de l'été lorsque la production locale du lac Saint-Pierre augmente. Spatialement, la contribution augmente à mesure qu'on s'approche de la plaine inondable, en fonction de l'élévation du site de capture. Les 4 années d'échantillonnage permettent de contraster l'effet du régime hydrologique, indiquant que la taille et la durée de l'inondation dictent le niveau de contribution de la plaine en influençant la productivité et la période de disponibilité du subside. De plus, l'ampleur et la durée de l'inondation sont positivement corrélées avec la condition physique de cinq espèces littorales (perchaude, méné d'herbe, méné jaune, crapet-soleil et fondule barré). La corrélation positive de la condition physique du fondule barré et du méné jaune avec la contribution du subside suggère en outre sa bonne qualité trophique. Finalement, l'approche isotopique multi-tissulaire développée dans le cadre de cette thèse permet de déterminer précisément la durée de disponibilité du subside en relation avec le régime hydrologique. L'utilisation de tissus musculaires, dont le taux de renouvellement isotopique est plus lent que les tissus hépatiques, aura pour effet de sous-estimer la contribution du subside tôt en période de croissance, biaisant ainsi les conclusions.

En conclusion, cette thèse nous a permis d'identifier une source d'énergie importante supportant la productivité ichtyenne du lac Saint-Pierre, incluant la dynamique spatio-temporelle et les facteurs affectant la contribution de la plaine inondable. Les travaux présentés dans cette thèse sont les premiers, à notre connaissance, à avoir mesuré l'importance de la ressource trophique provenant de la plaine inondable du lac St-Pierre pour la communauté ichtyenne de ce système. Le travail réalisé au cours de ce doctorat a permis d'établir des bases solides sur le rôle important, mais très peu étudié, qu'est le subside en provenance de la plaine inondable au lac Saint-Pierre en plus de bonifier les connaissances sur les subsides dans les systèmes rivière/plaine inondable en milieu tempéré et de développer une approche mesurant la durée d'un subside transposable dans système biologique.

Mots-clés : $\delta^{13}C$, communauté ichtyenne, durée de disponibilité, fleuve Saint-Laurent, isotopes stables, lac Saint-Pierre, plaine inondable, perchaude, régime hydrologique, subside spatial.

INTRODUCTION GÉNÉRALE

Subside spatial

Au cours des dernières décennies, un grand nombre de travaux de recherches ont montré que les écosystèmes sont étroitement liés entre eux et que des facteurs externes à un système peuvent influencer, voire même dominer, les patrons et les dynamiques locaux (Polis *et al.* 1997, Nakano *et al.* 1999). Un subside spatial, aussi appelé subside écologique (le terme subside sera utilisé afin d'alléger la lecture de la thèse), est une ressource (nutriments, détritus ou proies) contrôlée par l'écosystème donneur qui est mobilisée au-delà des limites d'un écosystème modifiant la dynamique des populations et communautés de l'écosystème receveur (Polis *et al.* 1997, Subalusky et Post 2019). Un subside peut donc provoquer un changement dans la productivité (Polis *et al.* 1997, Nakano et Murakami 2001, Rooney *et al.* 2006, Anderson *et al.* 2008), la diversité du système receveur (Power 2001, Nakano et Murakami 2001, Wagner et Reynolds 2019) et influencer la stabilité et la structure de son réseau trophique (Huxel et McCann 1998).

Un subside peut être mobilisé entre deux écosystèmes de mêmes types (ex. aquatique vers aquatique ou terrestre vers terrestre) ou de types distincts (ex. aquatique vers terrestre), avec un flux pouvant se produire dans les deux directions. De plus, la distance parcourue par les subsides entre le système donneur et receveur peut couvrir plusieurs échelles spatiales, variant de quelques mètres à des milliers de kilomètres. Des exemples typiques de subsides entre deux écosystèmes de même type et à grande échelle sont : la migration des saumons anadromes (*Oncorhyncus spp.*) transportant des nutriments et du carbone d'origine marine vers les rivières (ex. Kline *et al.* 1998, Mitchell et Lamberti 2005, Scheuerell *et al.* 2007); et la migration massive d'oie des neiges (*Anser caerulescens atlanticus*) vers leur site de reproduction dans l'arctique canadien transférant des nutriments et de l'énergie provenant des terres agricoles en milieu tempéré jusqu'au renard arctique (*Vulpes lagopus*) (Gauthier *et al.* 2005, Giroux *et al.* 2012). À plus petite échelle et entre des écosystèmes de différents types, l'émergence d'insectes aquatiques offre un subside à de nombreux prédateurs terrestres distribués sur de multiples niveaux trophiques (Power et Rainey 2000, Baxter *et al.* 2005, Walters *et al.* 2018 et référence à l'intérieur). Réciproquement, les invertébrés terrestres sont également un subside pour les prédateurs aquatiques (ex. poissons) lorsque ceux-ci tombent dans l'eau (Nakano *et al.* 1999, Nakano et Murakami 2001, Baxter *et al.* 2005).

Les subsides peuvent avoir des répercussions sur la structure, la dynamique ainsi que sur le comportement des organismes du réseau trophique receveur (Murakami et Nakano 2002, Kawaguchi *et al.* 2003). Ces derniers ont le potentiel d'affecter l'écosystème receveur et son réseau trophique de diverses façons en fonction de multiples facteurs. Tout d'abord, le niveau trophique du subside dicte les effets directs et indirects sur les composantes du réseau trophique receveur. Un subside sous forme de nutriments va généralement avoir un effet ascendant (traduction libre de l'anglais « Bottom-up ») et engendrer une augmentation de la production primaire pouvant remonter le long de la chaîne trophique (Polis *et al.* 1997). Par exemple, de multiples expériences ont démontré clairement par l'addition de carbone dans un lac que cette ressource allochtone est utilisée par le phytoplancton et supporte la productivité du zooplancton pélagique ainsi que celle de leurs prédateurs (Pace *et al.* 2004, Carpenter *et al.* 2005, Cole *et al.* 2011). En contraste, une importation de proies (consommateur primaire) peut augmenter la pression de broutage sur les producteurs primaires tout en faisant croître le bassin de ressources disponibles pour les consommateurs secondaires (prédateurs), augmentant donc la productivité des niveaux trophiques supérieurs et exerçant une pression sur le niveau inférieur (effet descendant, traduction libre de l'anglais « Top-down effect »). Toutefois, l'arrivée d'un consommateur primaire peut avoir un effet négatif (compétition apparente) ou positif (mutualisme apparent) indirect sur les consommateurs primaires locaux (Abrams et Matsuda 1996, Polis *et al.* 1997, Baxter *et al.* 2005). De plus, l'apport d'un subside sous forme de proie peut accroître la densité des prédateurs dans un système, engendrant une croissance de la pression des prédateurs sur les proies locales suivant la fin de cet apport (compétition apparente) (ex. Murakami et Nakano 2002). Cependant, si la densité des prédateurs n'est pas affectée par l'apport de nouvelles proies potentielles dans un système, ceci peut impliquer une dilution de la pression des prédateurs sur les proies locales (mutualisme apparent, Nakano *et al.* 1999, Lee *et al.* 2016). Par conséquent, l'impact d'un subside sur la structure et la dynamique d'un réseau trophique variera en fonction de son point d'entrée dans le réseau trophique, du niveau trophique de l'organisme de l'écosystème receveur à l'étude ainsi que de sa relation avec le subside (prédateur, proie ou même niveau trophique).

De plus, l'effet d'un subside sur un écosystème peut différer en fonction de quatre caractéristiques générales définissant le subside soit, sa durée, son timing, sa quantité et sa qualité (Subalusky et Post 2019). Dans ce contexte, je les définirai de la façon suivante : la durée est définie comme la période de temps où le subside est disponible pour les consommateurs de l'écosystème receveur. Le timing est le patron temporel de disponibilité en relation avec d'autres facteurs environnementaux. La quantité est l'importance du flux du subside qui est ajouté à l'écosystème receveur. La qualité du subside est définie par les caractéristiques chimiques de la ressource comme sa labilité et sa stœchiométrie (Marcarelli *et al.* 2011, Sitters *et al.* 2015, Subaluski et Post 2019). Afin de prédire l'effet d'un subside sur un écosystème, les caractéristiques du subside doivent être analysées de la perspective de l'écosystème receveur (Subalusky et Post 2019).

Le taux d'apport d'un subside peut être constant tout au long de l'année (soutenu, traduction libre de l'anglais « pressed ») ou varier temporellement (pulsé, traduction libre de l'anglais « pulsed ») supportant le système receveur à différents degrés au cours de l'année (durée). Par exemple, lors de subsides pulsés, le découplage de la disponibilité du subside (timing) à la productivité locale (*in situ*) stabilise la population des consommateurs du système receveur en leur procurant un niveau de ressources continu pendant leur période de croissance (Nakano et Murakami 2001, Takimoto *et al.* 2002, Marczak *et al.* 2007). À l'opposé, lorsque la disponibilité du subside et celle de la ressource *in situ* sont en synchronie, il se produit un effet déstabilisant sur la dynamique consommateur-ressource (Takimoto *et al.* 2002, Leroux et Loreau 2012).

De multiples études ont montré que la taille de l'impact d'un subside dans un écosystème est directement liée à la quantité de subsides importée dans l'écosystème receveur (Leroux et Loreau 2008, Cottingham et Narayan 2013, Graham *et al.* 2018). Cependant, l'effet du subside peut varier aussi en fonction de la productivité locale au moment de l'apport du subside comme mentionné précédemment (Takimoto *et al.* 2002). La réponse d'un consommateur est directement reliée au ratio entre le subside et la ressource équivalente du système receveur (Marczak *et al.* 2007). Il est donc important de prendre en considération les caractéristiques du système receveur lors d'études sur l'effet d'un subside.

Pour conclure, la qualité du subside peut avoir une grande influence sur la réponse du système receveur et son réseau trophique (Baxter *et al.* 2005, Marcarelli *et al.* 2011, Kelly *et al.* 2014). Par exemple, le carbone terrestre est souvent perçu comme un subside à la production zooplanctonique des lacs (Pace *et al.* 2004, Carpenter *et al.* 2005, Cole *et al.* 2011) puisqu'une importante proportion de la biomasse zooplanctonique en est dérivée, pouvant même atteindre jusqu'à 80 % dans certains systèmes (Solomon *et al.* 2011). Cependant, dans certaines situations, l'apport de carbone d'origine terrestre semble diminuer la productivité zooplanctonique en venant modifier les caractéristiques physiques du lac, limitant ainsi la productivité phytoplanctonique, une ressource de haute qualité (Kelly *et al.* 2014). Conséquemment, il y a un remplacement d'une ressource locale de haute qualité, le phytoplancton, pour un subside de qualité moindre, le carbone organique d'origine terrestre (Brett *et al.* 2009), ayant pour résultat de faire décroître la productivité zooplanctonique. Cet exemple démontre bien un des mécanismes pouvant mener au paradoxe de l'enrichissement (un apport de ressource allochtone réduit la productivité dans le système receveur plutôt que de l'augmenter).

Les subsides n'engendrent pas toujours une réponse numérique directe chez la population consommatrice, mais peuvent toutefois avoir des effets bénéfiques au niveau de l'individu. De nombreuses recherches ont montré que les individus vivant dans un système où il y a l'apport d'un subside ont des taux de croissance ainsi qu'un indice de condition physique (traduction libre de l'anglais « body condition index ») supérieurs aux individus se trouvant dans des systèmes n'étant pas soumis à l'apport d'un subside (Wipfli *et al.* 2003, Hoeinghaus *et al.* 2006, Briggs *et al.* 2012, Sato *et al.* 2016). Par exemple, Briggs *et al.* (2012) ont démontré que certains traits morphologiques (taille du corps et indice de condition physique) de deux espèces de geckos sont positivement liés à la quantité de subsides d'origine marine apportée à leur habitat par le biais d'oiseaux marins. En milieu aquatique, l'indice de condition physique d'une espèce de poisson euryhaline (*Centropomus undecimalis*) est plus élevé chez les individus migrant en eau douce afin d'avoir accès au subside en provenance de la plaine d'inondation sous forme d'invertébrés (écrevisse) et de petits poissons (*Hoplosternum littorale*) que pour les individus résidant dans l'estuaire (Blewet *et al.* 2017). L'indice de condition physique est corrélé positivement avec le taux de survie, la réponse immunitaire, la fécondité à long terme ainsi que la valeur sélective (traduction libre de l'anglais « fitness ») d'un individu (Stevenson *et al.* 2006 et les références à l'intérieur, Briggs *et al.* 2012 et les références à l'intérieur). Puisque l'indice de condition physique est relié avec la valeur sélective d'un individu, la présence d'un subside dans un système peut avoir un impact différé sur la population et possiblement influencer les futures générations des consommateurs.

En somme, les subsides ont des répercussions directes ou indirectes sur la structure et la dynamique du système receveur. La taille et la direction de l'effet du subside sur les organismes locaux (ex. abondance, productivité, croissance, condition physique) sont régies par la quantité et la qualité du subside, sa période de disponibilité (durée et timing), sa relation avec l'organisme (prédateur, proie, compétiteur) ainsi que la structure du réseau trophique receveur complexifiant les prédictions de l'effet global d'un subside dans un système pour lequel les connaissances sur l'ensemble de ces variables sont limitées.

Les plaines inondables comme sources potentielles de subsides

Les plaines inondables sont des zones de basse altitude qui sont périodiquement sujettes aux inondations latérales des rivières ou lacs auxquels elles sont associées (Junk et

Welcomme 1990). Par leur positionnement entre la ligne des basses et hautes eaux, les plaines inondables sont des écotones liant les milieux terrestres et aquatiques (Gregory *et al.* 1991). Ce positionnement fait en sorte qu'elles comprennent des habitats hétérogènes et des écosystèmes fortement productifs, abritant une biodiversité supérieure aux écosystèmes purement aquatiques ou terrestres (Tockner et Stanford 2002).

Les plaines inondables remplissent une multitude de services et de fonctions écosystémiques (Costanza *et al.* 1997). En matière de fonctions écosystémiques, les plaines inondables assument plusieurs rôles importants dans le cycle hydrologique : réduction ou retardement de l'inondation des terres, diminution de l'ampleur de l'inondation et recharge des eaux souterraines (Bullock et Acreman 2003). Elles sont aussi reconnues comme des zones de rétention de carbone et de sédiments (He et Walling 1997), un écosystème propice à de forts taux de dénitrification (Pinay *et al.* 2002), en plus d'avoir un rôle prépondérant dans le maintien de la communauté ichtyenne (Tockner *et al.* 2010). Pour un grand nombre de rivières, un ensemble de preuves s'est accumulé au cours des dernières années supportant que la productivité des plaines inondables agît comme un subside soutenant de façon significative la productivité des rivières (Junk *et al.* 1989, Gutreuter *et al.* 1999, Wantzen *et al.* 2002, Jardine *et al.* 2012).

Le concept des poussées de crue (traduction libre de l'anglais « Flood Pulse Concept ») stipule que la majorité de la productivité d'une rivière est dérivée de sa plaine inondable et que le régime hydrologique joue un rôle crucial en connectant la rivière à sa plaine inondable, favorisant ainsi les échanges de nutriments, de détritus et d'organismes (Junk *et al.* 1989, Junk et Wantzen 2004). Toutefois, puisque le modèle est principalement dérivé à partir d'observations provenant de rivières situées en milieu tropical, Tockner *et al.* (2000) ont ajusté le concept pour tenir compte des différences du climat, de la géomorphologie ainsi que du niveau d'impacts des activités anthropiques existant entre les milieux tropicaux et tempérés. Par exemple, les inondations en milieu tempéré sont majoritairement de plus courte durée, de plus faible prévisibilité et plus variables dans leur synchronicité avec le régime de température comparativement aux inondations en milieu tropical (Tockner *et al.* 2000).

Généralement, lors des inondations, une eau turbide et chargée en nutriments déborde sur la plaine inondable, où la matière en suspension sédimente en raison de la faible vélocité du courant. Ceci résulte en une augmentation de la transparence de l'eau, ce qui favorise le développement du phytoplancton (Tockner *et al.* 1999). La croissance de la production primaire a un effet positif sur la production secondaire. Plusieurs études ont établi un lien entre la productivité zooplanctonique d'une plaine inondable et le régime hydrologique de la rivière, suggérant que l'inondation de la plaine inondable est un processus important pour la productivité zooplanctonique d'un système rivière-plaine inondable (Górski *et al.* 2013). De plus, ces derniers ont aussi observé des relations entre la complexité structurelle de l'habitat inondé et la productivité ainsi que la composition de la communauté zooplanctonique. Complémentairement, Baranyi *et al.* (2002) ont montré que l'abondance du zooplancton dans les plaines inondables augmente avec le temps de résidence de l'eau, suggérant que la dynamique des crues (amplitude et durée) a un effet sur la productivité et donc sur la taille du subside potentiel en provenance de la plaine.

D'ailleurs, une relation positive entre la quantité de poissons capturés et la superficie maximale de la plaine inondable submergée a été observée dans les rivières africaines, soutenant l'importance de ces habitats pour la productivité de la faune ichtyenne d'une rivière (Welcomme 1975, 1979, Bayley 1988). Les poissons migrant latéralement vers la plaine ont accès à cette ressource alimentaire lorsque le niveau d'eau connectant la rivière à la plaine est élevé. Également, une portion de cette ressource alimentaire (p. ex. zooplancton) produite dans la plaine inondable est rejetée dans la rivière lors du retrait de l'eau de la plaine inondable, devenant un subside potentiel pour la faune aquatique (King *et al.* 2003, Jardine *et al.* 2012, Furst *et al.* 2014).

Beaucoup de recherches ont montré l'importance d'un subside en provenance de la plaine d'inondation à la productivité de la rivière et à sa communauté ichtyenne en milieu tropical (ex. Wantzen *et al.* 2002, Jardine *et al.* 2012). Toutefois en milieu tempéré, la contribution de ce subside à la productivité ichtyenne semble varier en fonction de la rivière (Thorp *et al.* 1998, Gutreuter *et al.* 1999, Dettmers *et al.* 2001, Schramm et Eggleton 2006) et de l'espèce à l'étude (Gutreuter *et al.* 1999, Luz-Agostinho *et al.* 2008, 2009). Par exemple, des études faites sur la rivière Ohio et Illinois (États-Unis) n'ont trouvé aucune évidence que les ressources provenant de la plaine supportent la productivité de la communauté de poisson (Thorp *et al.* 1998, Dettmers *et al.* 2001) contrairement aux études menées par Schramm et Eggleton (2006) et Gutreuter *et al.* (1999) sur la rivière Mississippi. En supplément, Gutreuter *et al.* (1999) ont montré que les espèces littorales sont fortement influencées par l'apport de cette ressource, tandis que d'autres espèces exploitant les zones pélagiques de la rivière Mississippi ne semblent pas bénéficier de cette ressource.

De plus, puisque les inondations sont de plus courte durée en milieu tempéré relativement au milieu tropical, il en résulte une plus faible productivité de la plaine inondable, réduisant ainsi la quantité et la durée de disponibilité du subside. Ceci suggère que le rôle du subside comme source d'énergie potentielle à la productivité de la rivière sera restreint à la période de crue et de décrue. En effet, Huryn *et al.* (2001) et Hladyz *et al.* (2012) ont observé une variabilité saisonnière dans la contribution des sources d'énergie supportant la productivité de rivières tempérées. Cette variabilité temporelle de l'importance du subside et des autres sources potentielles d'énergie serait reliée aux différents stades du régime hydrologique de la rivière (crue, plateau, décrue et niveau de base) responsable de la productivité et de l'accessibilité de ces ressources selon le concept proposé par Humphries *et al.* 2014; concept de la vague de rivière (traduction libre de l'anglais : « River Wave Concept »).

D'une part, des effets positifs sur la croissance et l'indice de condition physique ont été rapportés pour certaines espèces de poissons tropicaux et tempérés, pour lesquels le subside provenant de la plaine inondable semble être une source d'énergie majeure. En effet, Glémet et Rodríguez (2007) ont observé une relation positive entre le ratio ARN/ADN, un proxy de la croissance à court terme, et le niveau de l'eau chez les perchaudes (*Perca flavescens*) du lac Saint-Pierre, suggérant une importance de la plaine d'inondation comme d'habitat propice à la croissance et source d'énergie potentielle. Dans la Peace River (FL), Blewet *et al.* (2017) rapportent que l'indice de condition physique chez le *Centropomus undecimalis* (ang. Common snook) est supérieur chez les individus ayant accès au subside provenant de la plaine. D'autre part, les inondations et les subsides venant de la plaine inondable avaient un effet négatif sur la croissance et l'indice de condition physique des détritivores, insectivores, et invertivores de 3 sous-bassins du fleuve Paranà (Abujanra *et al.* 2009). De plus, certains systèmes tels que le Cosumnes River (CA) affichent une variabilité interspécifique dans l'effet du subside sur la condition physique des poissons (Ribeiro *et al.* 2004).

En conclusion, le rôle de la plaine inondable comme système donneur d'un subside de qualité à la productivité ichtyenne de la rivière adjacente diffère selon le système à l'étude. De plus, de nombreuses recherches ont montré une variabilité interspécifique de la contribution du subside venant de la plaine, avec des effets parfois positifs et parfois négatifs sur la croissance et l'indice de condition physique des individus. Puisqu'un ensemble de facteurs influençant l'impact du subside en provenance de la plaine inondable est présent au sein d'une rivière, les aspects spatio-temporels de la contribution trophique du subside de la plaine inondable à la communauté de poissons sont encore mal compris. Il est donc essentiel d'étudier une grande portion de la communauté de poisson d'une rivière, et ce, à différentes périodes de l'année afin de confirmer la présence d'un subside et en mesurer son importance sur la productivité et sur la condition physique des espèces.

Isotopes stables en écologie

Au cours des dernières décennies, l'analyse des isotopes stables s'est avérée un outil de recherche puissant en écologie et particulièrement pour l'étude des subsides (Peterson et Fry 1987, Hobson 1999, McCutchan et Lewis 2002, Layman *et al.* 2012). Les isotopes stables sont souvent utilisés comme marqueurs intrinsèques pour étudier le mouvement et l'assimilation d'un subside (ex. Huryn *et al.* 2001, Doucett *et al.* 2007, Degerman *et al.* 2018). Leur utilisation pour l'analyse des liens trophiques est fondée sur le principe que le ratio isotopique d'un organisme (δX) procure de l'information sur la composition de son régime alimentaire ainsi que sur sa provenance (Hobson, 1999).

Le choix de l'élément utilisé varie en fonction du type de recherche ainsi que des conditions biogéochimiques du système étudié. Les ratios isotopiques du carbone ($\delta^{13}C$) et de l'azote ($\delta^{15}N$) ont été grandement étudiés et utilisés lors d'études sur les liens trophiques. Le $\delta^{13}C$ de la majorité des tissus, tels le muscle et le foie, est entièrement dérivé du régime alimentaire (Fry et Arnold 1982, Tieszen *et al.* 1983, Grey, 2001). De plus, le $\delta^{13}C$ ne subit que peu ou pas de fractionnement trophique, qui est défini par la différence du ratio isotopique entre la ressource alimentaire et le consommateur ($\Delta\delta^{13}C$ organisme aquatique = -0,1 ± 0,96 ‰) (Peterson et Fry 1987, Vander Zanden et Rasmussen 2001, Post 2002), ce qui laisse le ratio isotopique de la source pratiquement inaltéré dans les tissus du consommateur. Pour ces raisons, le $\delta^{13}C$ est un indicateur idéal pour identifier les sources énergétiques composant le régime alimentaire d'un organisme (Harrigan *et al.* 1989).

En contraste, le ratio isotopique de l'azote ($\delta^{15}N$) démontre un grand fractionnement trophique constant ($\Delta\delta^{15}N$ = 3,4 ± 0,99 ‰) le long de la chaîne alimentaire (Vander Zanden et Rasmussen 2001, Post 2002, McCutchan *et al.* 2003). Donc, plus un organisme est haut dans la chaine alimentaire plus son $\delta^{15}N$ sera élevé (ex. : $\delta^{15}N$ producteur primaire = 0 ‰; $\delta^{15}N$ consommateur primaire = 3,4 ‰; $\delta^{15}N$ prédateur = 6,8 ‰). Le $\delta^{15}N$ a donc été fortement utilisé pour déterminer la position trophique d'une espèce ainsi que pour la reconstruction des réseaux trophiques (Vander Zanden *et al.* 1997). En dépit de sa grande utilité pour suivre et mesurer la contribution d'un subside, l'approche isotopique ne peut être utilisée que si les sources alimentaires (subside et autres ressources *in* situ) ont des ratios isotopiques distincts (Rubenstein et Hobson 2004, Durbec *et al.* 2010).

L'approche isotopique permet d'évaluer la contribution trophique relative de chaque source alimentaire potentielle au régime alimentaire d'un individu par l'entremise du modèle de mélange isotopique (Eq. 1.1 et Eq. 1.2) (Philips et Gregg 2001, Layman *et al.* 2012).

$$\delta X_I = f_A \delta X_A + f_B \delta X_B \qquad \text{(Eq. 1.1)}$$

$$f_A + f_B = 1 \qquad \text{(Eq. 1.2)}$$

Où X est l'élément utilisé, δX_I est le ratio isotopique d'un individu pour cet élément, f_A et f_B représentent la contribution relative des sources A et B et δX_A et δX_B sont les ratios isotopiques des sources A et B. Cependant, ce type de modèle de mélange isotopique linéaire est sujet à certaines contraintes. Le nombre de sources potentielles (p) ne peut pas dépasser le nombre d'éléments utilisés (*q*) plus 1 ($p \leq q + 1$). De plus, ce type de modèle de mélange isotopique est généralement trop simple pour étudier les réseaux trophiques en milieu naturel puisque ceux-ci ont un nombre de sources potentielles supérieur au nombre de traceurs isotopiques disponibles (Layman *et al.* 2012). Lorsque ce scénario se produit ($p \geq q + 1$), il est impossible d'obtenir une solution unique pour la contribution relative (*f*) de chacune des sources et nous obtenons plutôt un ensemble de solutions mathématiquement possibles (Phillips et Gregg 2001, Layman *et al.* 2012). Plus récemment, des modèles de mélange isotopique ancrés dans un cadre bayésien ont été développés, se libérant de cette contrainte ($p \leq q + 1$) tout en incorporant l'incertitude et la variabilité dans les paramètres d'entrée représentant ainsi plus adéquatement la réalité des systèmes naturels (Parnell *et al.* 2008, 2010, Layman *et al.* 2012). De plus, l'approche statistique bayésienne permet d'inclure de l'information obtenue a priori (traduction libre de l'anglais : « prior »), offrant donc une représentation plus réaliste de la variabilité des paramètres d'entrée. Les modèles de mélange isotopique du type bayésien donnent également comme résultat final une distribution de probabilité de la contribution pour chacune des sources incluses dans le modèle. Ce faisant, l'approche isotopique, plus particulièrement l'application d'un modèle de mélange isotopique, est une méthode de choix lors d'études visant à identifier et mesurer la contribution relative des subsides au réseau trophique d'un système.

Toutefois, si l'on veut estimer et interpréter la contribution trophique relative d'une source alimentaire potentielle, il faut considérer le renouvellement isotopique de l'organisme et son niveau trophique (Zohary *et al.* 1994, Cabana et Rasmussen 1996, Kidd *et al.* 1999). Le renouvellement isotopique n'est pas immédiat lorsqu'un changement de source nutritionnel survient, ce qui engendre un décalage temporel avant que l'organisme soit à l'équilibre isotopique avec sa nouvelle source d'alimentation (Hesslein *et al.* 1993, MacAvoy *et al.* 2001, Maruyama *et al.* 2001). L'ampleur de ce décalage temporel est directement liée au taux de renouvellement du tissu (λ, Hobson et Clark 1992, Sakano *et al.* 2005). Ce taux de renouvellement est déterminé par la croissance (c) et le remplacement métabolique des tissus (m) ($\lambda = c + m$, Fry et Arnold 1982, Hesslein *et al.* 1993, MacAvoy *et al.* 2001, Maruyama *et al.* 2001). La croissance, et par le fait même le taux de renouvellement des tissus d'un individu, est variable au cours de l'ontogenèse chez de nombreuses espèces de poissons. Notamment, les nouveau-nés ont un taux de croissance très rapide, qui se manifeste par un fort taux de renouvellement des tissus. À l'opposé, les adultes ont une croissance plus lente, ce qui réduit de façon considérable la contribution de la croissance au taux de renouvellement (Gerking 1966, Fry et Arnold 1982).

De plus, les tissus d'un individu ont des taux de renouvellement différents (Tieszen *et al.* 1983). Par exemple, le muscle est considéré comme un tissu lent en comparaison au foie puisque son renouvellement isotopique est plus lent que ce dernier dû à un remplacement métabolique moins élevé (Carleton *et al.* 2008, Wolf *et al.* 2009, Carleton et Martinez del Rio 2010). L'approche isotopique multi-tissulaire tire avantage de la variabilité du taux de renouvellement entre les tissus d'un même organisme. Cette approche utilise la différence des taux de renouvellement entre un tissu à renouvellement rapide (ex. foie, plasma sanguin) (Guelinckx *et al.* 2007) et un tissu relativement lent (ex. muscle) pour déterminer le moment où un organisme a subi un changement de régime alimentaire ou d'habitat (Philips et Eldridge 2006, Guelinckx *et al.* 2008, Carleton *et al.* 2008). Il devient donc théoriquement possible de mesurer la période de disponibilité d'un subside par l'entremise de cette approche.

Des études ont montré que les ratios isotopiques des organismes diffèrent selon qu'ils s'alimentent dans les plaines inondables ou les rivières et que l'utilisation des isotopes stables du carbone permet d'évaluer la contribution trophique relative du subside provenant de la plaine inondable (Thorp *et al.* 1998, Wantzen *et al.* 2002, Jardine *et al.* 2012). La différence isotopique du carbone entre les deux systèmes provient des processus biogéochimiques spécifiques à chaque système. Par exemple, la décomposition de plantes C_3 et C_4, le recyclage du carbone par la réutilisation du dioxyde de carbone (CO_2) lors de la respiration algale ou par l'activité bactérienne méthano oxydante, la production de méthane par des bactéries méthanogènes comme source de carbone ($\delta^{13}C_{CH4}$ = -52 to -80 ‰) sont des processus présents dans la plaine inondable qui appauvrissent la signature isotopique du carbone comparativement à celle observée dans la rivière (Bunn et Boon 1993, Thorp *et al.* 1998, Fry 2002, Wantzen *et al.* 2002, Jardine *et al.* 2012).

Mise en contexte, secteur d'étude et objectifs de la thèse

Les subsides ont la capacité d'influencer de façon significative la productivité ainsi que la structure et la dynamique du réseau trophique du système receveur. Comme mentionné précédemment, les plaines inondables ont le potentiel de soutenir la productivité dans la rivière adjacente, voire même d'en être la principale source énergétique. Toutefois, la contribution des subsides peut varier fortement d'un écosystème à l'autre. Des études menées en milieu tempéré sur le rôle de la plaine d'inondation comme lieu de productivité d'un subside pour les rivières rapportent des résultats contradictoires selon le système et les espèces étudiées. De plus, les plaines inondables font partie des écosystèmes les plus altérés dans le monde entier (Tockner et Stanford 2002). L'empiètement humain (Vitousek *et al.* 1997), la modification des régimes hydrologiques (Ward et Stanford 1995, Merritt et Cooper 2000, Nilsson *et al.* 2005) et les changements climatiques (IPCC 2007, Naiman *et al.* 2008) altèrent les processus responsables de la production et de la distribution du subside de la plaine. Dans un tel contexte, il est important d'approfondir nos connaissances sur les aspects spatiaux temporels de la contribution du subside et d'identifier les variables environnementales qui en régissent la productivité et la distribution.

Le lac Saint-Pierre (LSP) est le plus grand et dernier lac fluvial du fleuve Saint-Laurent (FSL). Celui-ci est situé à 75 km en aval de Montréal, entre les villes de Sorel-Tracy et de Trois-Rivières. Le LSP fait environ 30 km de long par 15 km de large et couvre une superficie fluctuant entre 387 et 501 km^2 en fonction des niveaux d'eau (Hudon 1997). Ce lac fluvial fait en moyenne 3 m de profond à l'exception du chenal de navigation (largeur $\approx$ 250 m) ayant une profondeur d'environ 11 m (Hudon et Carignan 2008). Onze tributaires se déversent directement le long des rives du LSP, créant des masses d'eau distinctes s'écoulant côte à côte sans se mélanger (Frenette *et al.* 2003). On retrouve au LSP une forte diversité faunique et végétale. Soixante-dix-neuf espèces de poissons ont été observées dans le LSP et son archipel, représentant 70 % des espèces de poissons d'eau douce du Québec (La Violette *et al.* 2003). De plus, le LSP abrite plus de 20 % des milieux humides de l'ensemble du fleuve (Langlois *et al.* 1992). En 2000-2002, les milieux humides naturels du LSP s'étendaient sur plus de 197 km^2 (Hudon *et al.* 2018).

Le LSP diffère de bien des grandes rivières où le rôle de la plaine d'inondation a été étudié de par sa forte saisonnalité en termes de température et des conditions environnementales. En hiver (décembre à avril), l'ensemble de la surface du LSP est recouvert de glace (à l'exception de son chenal de navigation) et la température de l'eau est légèrement sous le point de congélation (Roca *et al.* 2020). Le couvert de glace limitant la pénétration de la lumière inhibe la productivité primaire. De plus, la basse température de l'eau en cette période de l'année réduit le taux de décomposition de la matière organique diminuant son apport au réseau trophique (Cortez 1998, Petraglia *et al.* 2019). Au printemps, l'augmentation de la température de l'air engendre la fonte du couvert de neige dans l'ensemble du bassin versant. Ceci a pour effet d'augmenter les débits du fleuve Saint-Laurent générant ainsi les inondations printanières. De plus, par son action érosive la débâcle emporte les plantes aquatiques du LSP réduisant la ressource alimentaire tôt en période de crue. Donc, les inondations au LSP suivent un patron saisonnier dont le maximum de l'inondation se produit généralement au début du mois de mai. La plaine inondable du LSP (zone de récurrence 0-2 ans) couvre une superficie d'environ 210 km^2 pour une période de 5 à 9 semaines (Lessard 1991). Toutefois, les inondations démontrent une forte variabilité interannuelle dans leur durée et magnitude (Figure 1).

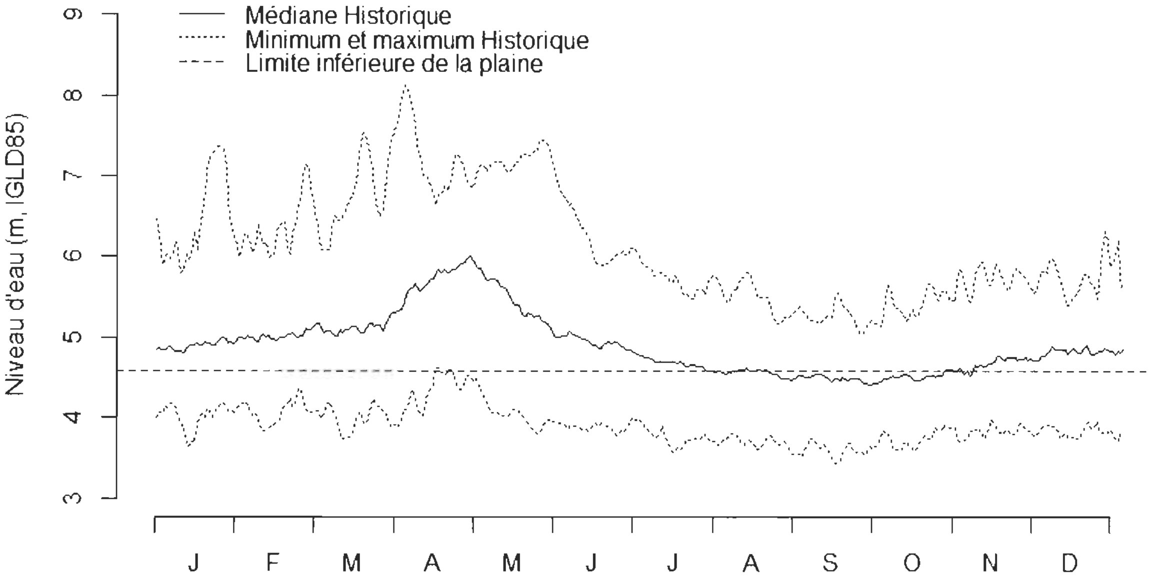

Figure 1. Médiane (ligne pleine), minimum et maximum (lignes pointillées) de la moyenne journalière du niveau d'eau (m, IGLD85) au lac Saint-Pierre observée entre 1966-2017. L'élévation de + 4.57 m IGLD85 (ligne hachurée) coïncidant avec l'élévation à laquelle la rivière déborde dans la plaine d'inondation a été déterminée à partir de la médiane de la valeur minimale des valeurs observées (1966-2017) entre le premier avril (jour de l'année 91) et le premier juillet (jour de l'année 181).

Comme la majorité des plaines inondables en zones tempérées, la plaine est sujette à un ensemble de pressions anthropiques (Tockner et Stanford 2002). Premièrement, le régime hydrologique de la rivière a été modifié par la construction de multiples barrages sur le cours principal du fleuve ainsi que sur un grand nombre de ses tributaires (Morin et Coté 2003, Talbot 2006). Ces constructions altèrent les patrons naturels d'écoulement de l'eau ce qui influence négativement la connectivité entre la rivière et la plaine inondable affectant ainsi les fonctions écosystémiques de la plaine inondable (Bunn et Arthington, 2002). De plus, un chenal de navigation a été creusé le long du fleuve Saint-Laurent afin de permettre la navigation commerciale. Ce chenal concentre une forte portion du volume de l'écoulement au centre du fleuve et diminue le volume d'eau se déversant dans la plaine inondable. Dans l'ensemble, les modifications du régime hydrologique réduisent la magnitude et la durée des inondations et peuvent influencer la période à laquelle la crête de l'inondation se produit (Morin et Bouchard 2000, Nilsson *et al.* 2005, Moyle et Mount 2007). À ceci s'ajoute la dégradation des habitats naturels de la plaine inondable par l'empiètement humain. Au LSP, 14 km^2 de la plaine inondable ont été remblayés et convertis en terres agricoles (Hudon *et al.* 2018). Au cours des décennies précédentes, les pratiques agricoles ont changé, passant des cultures pérennes fourragères à des cultures annuelles à grand interligne, telles que le maïs et le soja. Lors de l'inondation printanière, les champs labourés des cultures annuelles s'avèrent être des habitats de qualité inférieure aux cultures pérennes en ce qui a trait à la productivité d'invertébrés aquatiques (Savignac 1983, 1985, Côté *et al.* 2011).

De plus, les changements climatiques devraient modifier de multiples processus prenant place dans la plaine d'inondation. Les études prédisent que les changements climatiques affecteront le régime hydrologique et par le fait même, les patrons d'inondations des rivières dans le monde entier (Arnell et Gosling 2016, Burn et Whitfield 2016, 2017). Plus spécifiquement pour le nord-est de l'Amérique du Nord, et donc pour le fleuve Saint-Laurent et le LSP, les recherches prévoient une diminution de l'ampleur et de la durée des inondations ainsi qu'une crue printanière plus hâtive (Boyer *et al.* 2010, CEHQ 2015, Burn and Whitfield 2016). Ces pressions anthropiques ont le potentiel d'altérer les processus contrôlant la productivité et la distribution du subside provenant de la plaine inondable soutenant potentiellement la productivité de la rivière.

Plusieurs études antérieures suggèrent que la plaine inondable joue un rôle dans la production globale du LSP, sans toutefois évaluer l'importance des subsides alimentaires qu'elle procure à la communauté piscicole. Au fil des années, le rôle de la plaine inondable comme site de reproduction et d'alevinage pour plusieurs espèces, notamment la perchaude (*Perca flavescens*) et le grand brochet (*Esox lucius*) ont été reconnus

(Mingelbier *et al.* 2008, Magnan *et al.* 2017), supportant la notion que la ressource produite dans la plaine pouvait supporter la productivité de la rivière. De plus, Bertrand *et al.* (2011) ont observé une grande variabilité du $\delta^{13}C$ chez la perchaude, mettant en lumière que différentes sources énergétiques contribuent à la productivité des espèces du LSP. Bertrand *et al.* (2011) ont aussi noté une relation des ratios isotopiques ($\delta^{13}C$) des invertébrés en relation avec la distance de leur lieu de capture à la plaine inondable dans le LSP, suggérant qu'une des sources énergétiques potentielles proviendrait de la plaine d'inondation en plus de soutenir l'applicabilité de l'approche isotopique comme outil.

L'objectif principal de cette thèse est d'étudier la présence d'un subside en provenance de la plaine inondable et faire un portrait des quatre grandes caractéristiques décrivant un subside (durée, timing quantité et qualité) ainsi que de clarifier l'influence du régime hydrologique sur la contribution et les caractéristiques du subside à la communauté ichtyenne du LSP. Premièrement, nous caractériserons les patrons spatio-temporels de la contribution du subside à la communauté de poisson du LSP (timing). Deuxièmement, nous étudierons l'impact du régime hydrologique (ampleur et durée de l'inondation printanière) sur l'importance de la contribution et de la période de disponibilité du subside pour les espèces littorales ainsi que sur leur condition physique (durée, quantité et qualité). Dernièrement, nous examinerons l'importance de la sélection du tissu lors d'études visant à quantifier la contribution d'un subside de durée variable et développerons une approche visant à mesurer la période de disponibilité d'un subside pulsé (durée).

Pour le premier chapitre de cette thèse, l'objectif est de démontrer la présence d'un subside provenant de la plaine et de caractériser ses patrons spatio-temporels de sa contribution à la communauté de poisson du LSP. Nous émettons les hypothèses que la contribution trophique du subside provenant de la plaine inondable aux poissons sera à son maximum tôt en période de croissance suivant l'inondation printanière et diminuera en fonction de la distance de la plaine inondable. Pour tester cette hypothèse, nous avons échantillonné un grand nombre d'espèces de poisson tôt (juin et juillet) et tard (août et septembre) en période de croissance selon un gradient d'élévation et analysé leur ratio isotopique. Nous avons par la suite utilisé un modèle de mélange isotopique afin de quantifier la contribution relative du subside et analyser les effets de l'élévation (spatial), de la date (temporel) et de l'espèce sur la contribution sur la contribution relative du subside.

Pour le second chapitre, l'objectif général est d'étudier l'effet des régimes hydrologiques sur la disponibilité et l'assimilation du subside ainsi que sur la condition physique des individus. Nous avons testé les hypothèses selon lesquelles 1) le régime hydrologique affecte positivement le niveau de contribution trophique du subside ainsi que la durée de disponibilité du subside; 2) que le régime hydrologique et le niveau de contribution affectent positivement la condition physique des individus. Nous avons échantillonné cinq espèces de la zone littorale de la rive sud tôt et tard durant la période de croissance pendant 4 années successives ayant des régimes hydrologiques distincts. Par la suite, nous avons mesuré la contribution du subside provenant de la plaine à l'aide de l'approche isotopique et l'indice de condition physique afin d'étudier l'effet de variables hydrologiques sur ces dernières.

Pour le troisième et dernier chapitre, l'objectif général est de définir les implications de l'utilisation de tissus ayant des taux de renouvellement isotopique distinct lors d'études visant à comprendre l'importance d'un subside pulsé dont la durée varie inter-annuellement. Les hypothèses de base qui sous-tendent ce chapitre de la thèse sont que 1) dans un contexte de subside pulsé l'utilisation de tissu à renouvellement isotopique lent (ex. muscle) engendrera une sous-estimation de la contribution réelle du subside en comparaison aux tissus à renouvellement rapide (ex. foie); 2) que l'utilisation combinée de tissus à renouvellement isotopique lent et rapide permet d'estimer le moment de changement de sources énergétiques. Ce chapitre comporte deux objectifs spécifiques : (1) analyser l'impact du choix du tissu lors d'études sur les subsides spatiaux sur les conclusions générales, et (2) développer une approche isotopique multi-tissus visant à mesurer la période de disponibilité d'un subside montrant une variabilité interannuelle. Pour ce faire nous avons utilisé une étude de cas analysant le flux trophique saisonnier d'invertébrés dérivés de la plaine d'inondation à la perchaude (*Perca flavescens*).

Pour l'étude de cas, nous avons mené annuellement deux campagnes d'échantillonnage (tôt et tard en période de croissance) visant à capturer des perchaudes pendant quatre années successives montrant de fortes divergences dans leur régime d'inondation. Par la suite, nous avons mesuré la contribution du subside dans deux tissus (foie et muscle) ayant des taux de renouvellement isotopiques distincts. Nous avons comparé les résultats obtenus, nous permettant d'émettre des commentaires sur les possibles répercussions de la sélection d'un tissu inapproprié dans le cadre de l'étude de la contribution d'un subside pulsé. Finalement nous avons appliqué notre approche isotopique multi-tissulaire sur le jeu de données afin de mesurer la durée de disponibilité du subside dans le LSP et sa relation avec le régime hydrologique.

CHAPITRE I

SEASONALITY OF A FLOODPLAIN SUBSIDY TO THE FISH COMMUNITY OF A LARGE TEMPERATE RIVER

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Résumé

Cette étude examine la variabilité temporelle et spatiale de la contribution trophique d'un subside provenant de la plaine inondable à la communauté de poisson du lac Saint-Pierre, un grand (≈ 300 km^2) élargissement peu profond (≈ 3 m) du fleuve Saint-Laurent (Québec, Canada). Nous avons émis l'hypothèse que la contribution trophique de la plaine inondable au régime alimentaire des poissons sera maximale tôt en période de croissance suivant l'inondation saisonnière aux sites situés plus près de la plaine d'inondation. Les ratios isotopiques du carbone ($\delta^{13}C$) des invertébrés et de 35 espèces de poissons ont été analysés au commencement et à la fin de la saison de croissance suivant un gradient croissant de distance à la plaine inondable. La contribution trophique de la plaine, sous forme d'invertébrés aquatiques exportés, a été estimée au niveau de la communauté (littoral vs rivière principale), de l'espèce et de l'individu chez les poissons par l'entremise d'un modèle de mélange isotopique (SIAR) et la sélection de modèles mixtes linéaires (AIC). Comme prévu, les poissons capturés tôt en période de croissance près de la plaine d'inondation ont bénéficié du niveau de contribution trophique de la plaine inondable la plus élevée, qui a décru pendant la fin de la saison de la croissance. De plus, la contribution trophique de la plaine inondable diffère entre les espèces de poisson, atteignant les niveaux de contributions les plus élevés chez les petites espèces littorales ou les individus immatures (grand brochet, perchaude, méné à menton noir et méné jaune) comparativement aux taxons de grande taille exploitant le chenal principal de la rivière (barbue de rivière, chevalier rouge, meunier blanc). Notre étude a révélé que la production se produisant dans la plaine inondable lors des inondations printanières représente une ressource trophique d'importance pour une grande proportion du réseau trophique de la rivière, surlignant ainsi le rôle essentiel de la plaine inondable d'une rivière tempérée altéré par les activités anthropiques.

Mots-clés : $\delta^{13}C$, $\delta^{15}N$, Concept des poussées de crue, Hydrologie, Modèle de mélange, Plaine inondable, Productivité ichtyenne, Rivière Saint-Laurent, Rivière tempérée, Subsides spatiaux, Zone littorale.

Abstract

This study examines the temporal and spatial variability of the floodplain trophic contribution to the fish community of Lake Saint-Pierre, a large (≈ 300 km^2), shallow (≈ 3 m) widening of the St. Lawrence River (Québec, Canada). We hypothesized that floodplain contribution to fish diet would be maximal during the early growth period following the seasonal flood and at sites located closest to the floodplain. Carbon stable isotope ratios ($\delta^{13}C$) of invertebrates and 35 fish species were analyzed at the beginning and at the end of two growing seasons, at increasing distances from the floodplain. Floodplain contribution, in the form of exported aquatic invertebrates, was estimated at the fish community (littoral vs main river), species and individual fish level, using a stable isotopic mixing model (SIAR) and a linear mixed model selection (AIC). As hypothesized, fish captured in the early part of the growing season near the floodplain benefitted from the largest floodplain contribution, which decreased during the late growing season. In addition, floodplain contribution differed among fish species, being higher in small or immature littoral species (northern pike, yellow perch, blackchin and golden shiners) than for larger taxa inhabiting the main river channel (shorthead redhorse, white sucker and channel catfish). Our study revealed that floodplain production during the early growth season represents a key food resource to a large portion of the riverine food web, thus highlighting the essential role of the floodplain in human-altered temperate rivers.

Key words: $\delta^{13}C$, $\delta^{15}N$, Fish productivity, Floodplain subsidy, Flood Pulse Concept, Hydrology, Littoral zone, Mixing model, St. Lawrence River, Temperate river.

Introduction

The movement of resources, as nutrients, detritus, and prey, among habitats is widespread in diverse biomes and often plays a key role in population, consumer-resource, food web and community dynamics. Such subsidized systems have been shown to have higher productivity than systems solely supported by autochthonous production (Polis and others 1997). Furthermore, the incorporation of subsidized resources can have cascading effects potentially strengthening or weakening the stability of the recipient system food web (Polis and others 1997; Nakano and Murakami 2001; Rooney and others 2006). However, the temporal availability of a subsidy can be limited to the period of migration or emergence of key organisms (*e.g.*, Nakano and Murakami 2001; Walters and others 2018) or by a temporary increase in the connectivity between donor and recipient habitats (*e.g.*, Hladyz and others 2012).

Large river/floodplain ecosystems have been documented not only as hotspots of biodiversity but also as highly productive areas (Sparks 1995). Floodplain resources can act as a subsidy to the river, enhancing the productivity of fish and other consumers (Welcomme 1975, 1979; Bayley 1995). However, the functional dynamics of complex lowland rivers, particularly regarding energy flow, is still poorly understood (Delong and Thorp 2006). Identifying the sources of energy and their contribution to the river/floodplain ecosystem food web is crucial to understanding the dynamics of populations, communities or ecosystems (Finlay 2001), as well as to applying adequate measures to manage, restore, and rehabilitate these ecosystems (Delong and Thorp 2006). Subsidy from the floodplain may support higher trophic levels by providing dissolved and particulate organic matter, and algal biomass, therefore increasing the productivity at the base of the river food web (Junk and others 1989; Tockner and others 1999). Exportation of secondary productivity (prey) is another potentially important path for this subsidy. Prey subsidy to the river may depend on two mechanisms: active movement by consumers into the floodplain (Junk and others 1989; Waldhoff and others 1996; Fernandes 1997; Gòrski and others 2010) or passive drifting of prey back to the river as the waters recede (Gòrski and others 2016). Furthermore, the density of prey such as zooplankton can often be many orders of magnitude higher in the floodplain than in the river channel, suggesting a subsidy not only of high dietary value but also high quantity to the fish community during the flood season (Savignac 1985; Reckendorfer and others 1999; Casper and Thorp 2007; Gòrski and others 2013).

These observations support the Flood Pulse Concept (FPC) (Junk and others 1989) which stipulates that the main source of energy supporting riverine fish populations is derived from the floodplain. Although the FPC was developed and largely applied to large unaltered tropical rivers (Galat and others 1998; Roach 2013), a modified version was applied to large temperate rivers (Junk and Robertson 1997; Tockner and others 2000) accounting for inherent differences in climate and geomorphology as well as differences in impacts by extensive anthropogenic activities. In comparison with tropical systems, temperate systems exhibit short flood duration, low predictability, and variability in synchronicity between temperature and flood cycles (Tockner and others 2000). Short flood duration results in a limited period of floodplain production, suggesting strong seasonality in the subsidy role of the floodplain in temperate rivers. Huryn and others (2001) showed that the energy source supporting invertebrate productivity of the Taieri River, a New-Zealand grassland river, shifted from terrestrial origin during the high flow season to aquatic origin during the low flow season. A study on the Ovens River (south-eastern Australia) also showed temporal variability in the importance of multiple sources of energy (terrestrial and aquatic) suggesting that in order to understand energy flow in river/floodplain ecosystem, temporal variability must be taken into consideration (Hladyz and others 2012). Temporal variability is a key element of the River Wave Concept (Humphries and others 2014), which hypothesizes that the contribution of floodplain resource would be maximal at the peak of the flood (crest of the wave) before being replaced by downstream transport of upstream productivity and local instream autochthonous productivity when the flood recedes.

Empirical studies examining subsidies from the floodplain to fish in temperate rivers yield rather variable results (Thorp and others 1998; Gutreuter and others 1999; Dettmers and others 2001; Schramm and Eggleton 2006). For example, Schramm and Eggleton (2006) and Gutreuter and others (1999) demonstrated a positive relationship between flood characteristics and fish growth, supporting the applicability of the FPC to the Mississippi River. In contrast, the floodplain was not identified as a major source of energy in two distinct segments of the Ohio River (USA), including a floodplain and a constricted-channel segment (Thorp and others 1998). These contrasting results suggest that the degree of connectivity and the floodplain inundated area are key variables affecting the role of floodplain subsidy.

Moreover, fish species exploiting the littoral zone showed a higher dependence on floodplain trophic resources than species using main channel habitats (Gutreuter and others 1999; Dettmers and others 2001; Luz-Agostinho and others 2008). In the lower Misssissippi River, Schramm and Eggleton (2006) demonstrated that the growth of blue catfish (*Ictalurus furcatus*), a littoral species, was influenced by water temperature as well as by the area and duration of floodplain inundation. In the upper Mississippi River, two littoral species, largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus)* also showed a positive relationship between their growth and the extent of the flood (Gutreuter and others 1999). In both studies, the growth of non-littoral fishes, such as flathead catfish (*Pylodictis olivaris*: Schramm and Eggleton 2006) and white bass (*Morone chrysops*: Gutreuter and others 1999), was unrelated to floodplain characteristics. These results suggest a spatial trend in the trophic contribution of the floodplain as well as variability among fish species characterized by different habitat preferences. These evidences lead us to hypothesize that spatio-temporal patterns as well as interspecific variability must be accounted for in order to quantify subsidies by floodplains to rivers.

Stable isotope analysis (SIA) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) provide information on the dietary origin of these elements once they are incorporated into the aquatic food web (DeNiro and Epstein 1978; Forsberg and others 1993; Hobson 1999). Several biogeochemical processes active in the floodplain may result in very negative consumer $\delta^{13}C$ value typically observed in this habitat. These processes include high rates of decomposition and respiration leading to low $\delta^{13}C$ of dissolved inorganic carbon at the base of the autotrophic food chain (Keough and others 1996, 98; Barth and Veizer

1999) and bacterial consumption of methane (methanotrophy), which generally has very low $\delta^{13}C$ (Bunn and Boon 1993; Jones and Grey 2011). Indeed, Bertrand and others (2011) observed that consumers from different trophic positions (primary consumers, predatory invertebrates, and larval fish) in the floodplain of Lake Saint-Pierre (hereafter abbreviated as LSP; Québec, Canada) showed much more negative $\delta^{13}C$ than consumers in the main river, supporting that floodplain and main river secondary production can be distinguished using SIA.

We hypothesize that if floodplain secondary production constitutes an important trophic subsidy to the main river in a temperate river/floodplain system, (i) then a strong seasonal isotopic signal corresponding to the flooding phenology should be observed in the fish community, that floodplain contribution (ii) will be highest for fish living close to the floodplain in littoral habitats and (iii) will decrease with distance away from the floodplain toward the main channel.

Here we use stable isotope analysis to assess the temporal and spatial patterns of the floodplain trophic contribution to the fish community of LSP, a large fluvial lake of the St. Lawrence River. To this end, we collected fish and invertebrates at the beginning and at the end of the growing period for two years. We used an isotopic mixing model to assess the trophic contribution of the floodplain at the levels of fish community, species, and individuals. A model comparison approach was then used to determine if there is a temporal and spatial pattern to the contribution of the floodplain subsidy at the individual level.

Materials and Methods

Study area

LSP is the largest ($\approx$ 300 km^2) fluvial lake of the St. Lawrence River, situated 75 km downstream of Montreal, Canada (46°12'N, 72°49'O). LSP exhibits a cycle of seasonal inundations (Fig. 1), although their amplitudes have been reduced by the construction of dams and the excavation of a central navigational channel. The non-constricted central channel allows connection between the river and the floodplain when water level rises. The LSP floodplain (0-2 yr flood recurrence zone) expands over ≈ 210 km^2 for 5 to 9 weeks between the months of April and June (Lessard 1991). In 2000-2002, natural wetlands in LSP covered 197 km^2, although agriculture encroached > 14 km^2 of the littoral and floodplain area (Hudon and others 2018). Eleven tributaries flow directly into the LSP with little mixing with the main channel due to a high width to depth ratio creating three distinct water masses running side by side (Frenette and others 2003). Six of those tributaries (Maskinongé, Du Loup, Richelieu, Yamaska, Saint-François, Nicolet sud-ouest and Nicolet) annually bring large loads of dissolved organic carbon (≈ 142 000 t), total nitrogen (≈ 25 400 t) and total phosphorus (≈ 1 500 t) to the LSP (Hudon and others 2017).

Field sampling

We established 13 stations near the navigation channel in 2009 (hereafter designated as channel stations) and four transects of four stations located perpendicularly to the shore along a gradient of elevations towards the floodplain in 2014 (hereafter designated as littoral stations) (Fig. 2). Over both years, stations were sampled twice a year, coinciding with the early (June-early July) and late growing season (end of August-early September) (Fig. 2). In 2014, the seasonal drop in water level prevented the access to the sampling station closest to shore, prompting the designation of an additional station further away offshore to maintain 4 stations per transect. Two additional stations located at the margin of the floodplain forest were also sampled once during early growing season of 2014, bringing the total number of sampled stations/periods to 60. In 2009, fish were captured using a commercial bottom fishing trawl (9.9 m wide × 2.3 m high opening, 1.3 cm mesh), whereas in 2014 two different seines were used for shallow (12.19 m wide x 1.5 m high, 2 mm mesh) and deep (> 1 m) stations (30.48 m wide x 1.75 m high, 10 mm mesh). In 2014, additional collections of invertebrates were made at the same sites using a kick net (500 μm mesh).

At each site, measurements of water depth (nearest cm) were used to calculate site elevation above sea level, referenced to the International Great Lakes Datum of 1985 (m, IGLD85), from the difference between measured depth and the mean daily (in 2009) or hourly (in 2014) water level recorded at the time of sampling. Water level values were obtained from the Fisheries and Ocean Canada website (http://www.meds-sdmm.dfo-mpo.gc.ca, consulted in February 2018) and daily water temperatures were measured at the Sorel-Tracy gauging station and were obtained from the St. Lawrence Global Observatory (https://ogsl.ca, consulted in July 2018).

In 2009, fish were identified to the species and measured (total length, TL; nearest mm), caudal fins were sampled, and fish were returned live to the river. Fin samples were immediately frozen onboard. In 2014, fish were rapidly anesthetized in a clove oil solution (1 ml oil / 25 l river water), euthanized by cervical dislocation, and immediately put on ice. Invertebrates were placed in plastic bag and immediately put on ice. At the end of the day, fish and invertebrates were frozen at -20 °C at the Centre de Recherche sur les Interactions Bassins Versant-Écosystèmes Aquatiques (RIVE), Université du Québec à Trois-Rivières, until further analysis.

Laboratory analyses

Fish collected in 2014 were thawed, then identified to the species level and measured (total length, TL; nearest mm). For large fish (TL > 50 mm), dorsal muscle tissues were sampled between the lateral line and the dorsal fin, cleared of any remaining skin, scales, or bone. For small fish < 50 mm TL, the entire body (except for the head and gut) was used for stable isotope analysis. Some small specimens were damaged during the thawing process preventing the measurement of their total length, resulting in missing information for this variable (Supplementary Material). Since the stable isotopic ratio of muscle and fin tissues is strongly correlated with little bias (Jardine and others 2005, and references therein; Supplementary Material) and exhibit similar turnover rates (Busst and Britton 2018), both tissues were used to track dietary changes on a similar temporal scale. Invertebrates collected in 2014 were identified and sorted to the family, the shell of the gastropods was removed, and soft tissues were cleared of detritus with demineralized water. Invertebrates and fish samples were dried (60 °C for at least 48 h) and ground to a fine powder with a mortar and pestle.

Stable isotope analyses were carried out on muscle/fin tissues for 809 fish from the 35 species divided in 15 families (a complete list of species captured with common and scientific name is included in Supplementary Material) and 105 invertebrates samples representing 41 families. Isotopic analyses were carried out on weighed amounts of powdered samples (0.9 to 1.4 mg) packed into tin capsules (8 x 5 mm; Bn 202723: ISOMASS), analyzed on a continuous-flow isotope ratio mass spectrometer (Delta V Plus; Thermo Scientific) at the RIVE laboratory. Carbon and nitrogen isotope ratios were expressed in delta (δ) notation, defined as the deviation from an international standard material (carbon: Vienna Pee Dee Belemite; nitrogen: air) in parts per thousand (‰). The $\delta^{13}C$ working standard was USGS40 (L-glutamic acid: $\delta^{13}C$ mean ± SD = - 6.389 ± 0.09; $\delta^{15}N$ mean ± SD = -4.21 ± 0.12) from the International Atomic Energy Agency (IAEA). Two internal standards from muscle tissue of two specimens of brook trout (*Salvelinus fontinalis*) were used to correct for instrument drift during analysis. Fish muscle $\delta^{13}C$ values were corrected for their lipid content through mathematical lipid normalization using a combination of the models from Kiljunen and others (2006) and Post and others (2007) as proposed by Skinner and others (2016).

Animal tissues integrate the isotopic composition of ingested food over a period of time, resulting in a temporal lag before they reach isotopic equilibrium with diet (Woodland and others 2012). This rate to equilibrium (the isotopic turnover rate: λ, %·day^{-1}), is dictated primarily by growth and, to a lesser extent, by metabolic rate (Hesslein and others 1993; Xia and others 2013; Latli and others 2017; Bust and Britton 2018). Within species, relative growth rate decreases with rising size (von Bertalanffy 1957; Jobling 1983) and consequently isotopic turnover rate is inversely related to body size (Carleton and Martinez del Rio 2005; Thomas and Crowther 2015; Vander Zanden and others 2015). Therefore, the ratio of the total length of an individual to its common length at sexual maturity (hereafter referred as Relative Size, RS) can be used as a proxy for its isotopic turnover rate. We therefore used RS as a variable to assess the capacity of individuals to track short-term trophic subsidies, such as those provided by the floodplain.

Data analysis

All statistical analyses were performed using R software version 3.4.3 (R Development Core Team 2017). To investigate the temporal change of the trophic resources used by the fish community, the standard ellipse defining the N-C isotopic signature of fish communities sampled in the early and late growth season were identified using the function "*standard. ellipse*" (Jackson and others 2011) from the package SIAR (Stable Isotope Analysis in R; Parnell and others 2008). The relative contribution of the food resources originating from the floodplain (hereafter referred as floodplain contribution) to the fish community (littoral/floodplain vs main river) was assessed using an isotopic mixing model set in a Bayesian framework. We obtained the posterior probability distribution (median and the 95% credibility interval (95% CI)) for the dietary proportion contributed by the floodplain source for each specimen, and for each species and community by sampling season (early and late growing season) using the function "*siarsolomcmcv4*" and "*siarmcmcdirichletv4*" from the package SIAR, respectively. First, invertebrates were divided into two groups based on their site of capture (littoral/floodplain vs river). Invertebrates from the littoral/floodplain zone (defined as the floodplain and marsh/swamp habitat) were used to define the floodplain source and invertebrates captured outside of the littoral/floodplain zone defined the river food source (Fig. 2). Secondly, the statistical significance of $\delta^{13}C$ and $\delta^{15}N$ differences between invertebrates originating from the floodplain and river sources was tested either with a t-test (when the variance was equal among groups) or with Welch's t-test (in case of variance inequality). Equality of variance was tested using a F-test. We ran a two-sources mixed model focussing on $\delta^{13}C$ only, to avoid the issues of $\delta^{15}N$ signature overlap, trophic fractionation (Post 2002) and of variable trophic level of invertebrates' $\delta^{15}N$ signature. Means and SDs of $\delta^{13}C$ of invertebrates originating from the floodplain and river sources, together with $\delta^{13}C$ values for individual fish and carbon trophic fractionation were included as input for SIAR. We used the carbon trophic fractionation ($\Delta\delta^{13}C$ =-0.1±0.96) proposed by Post (2002). A vague Beta (1, 1) prior distribution for the mixing proportion was used to allow the results to be influenced primarily by the data (Parnell *et al.,* 2010).

Spatial and seasonal effects on the floodplain contribution to the isotopic ratio of individual fish (median of the output from the function "*siarsolomcmcv4*") from the entire LSP community were tested with a generalized linear mixed model using a beta distribution (package: glmmTMB). We also conducted the same set of analyses for the channel (2009) and littoral fish communities separately. The performance of each model was assessed using the Akaike information criterion (AIC), calculated for every possible combination of the fixed effect variables while including station as a random effect variable in all models. The fixed-effect variables were: 1) the elevation of the station where the fish was captured (Elevation), 2) the day of fish capture (Day), 3) the species identity (Species) and 4) the ratio of the total length of the individual over that of the common length at maturity (RS). Station elevation was used as a proxy for space (distance from the shoreline) as well as water depth at each station. The common length at maturity and scientific name used were extracted from the Fishbase website (http://www.fishbase.ca, consulted in Febuary 2018) and completed with the Ministère des Forêts de la Faune et des Parcs website (https://mffp.gouv.qc.ca, consulted Febuary 2018). Sampling station was considered as a random effect in the model to avoid pseudo-replication resulting from multiple captures at the same station. Model selection followed the AIC criterion (Burnham and Anderson 1998, 2002). Finally, we tested for residual spatial autocorrelation in the best model using the function "*moran.test*" from the package spdep (Bivand and Wong 2018).

Results

Hydrology

We used four variables describing the phenology of flooding (day of peak flooding, maximum water level, flood duration, and area under the water level vs date relationship). Analysis of these data confirmed the strong similarity in flooding between the years selected for our study (2009 and 2014) (Supplementary Material) compared to historical data. In 2009, the maximum floodplain area covered by water was similar (≈ 201.58 km^2; 33% of the area underwater occupied by the floodplain) to 2014 (≈ 221.62 km^2; 35% of the area underwater occupied by the floodplain). In contrast, between 1966 and 2017 floodplain area ranged between 43.76 km^2 and 336.52 km^2 (between 9.8 and 45% of the area underwater occupied by the floodplain).

Isotopic ratios of invertebrates

The $\delta^{13}C$ values of invertebrates showed equal variance among groups (F test: F = 0.73924, p-value = 0.5406) and were statistically different (*t*-test: t=-17.402, DF = 103, p-value < 0.001). The $\delta^{15}N$ values of invertebrates captured in the littoral/floodplain zone ($\delta^{15}N$ ± SD of all individuals regardless of species = 6.5 ± 1.33, N = 90) and in the river (mean $\delta^{15}N$ ± SD of all individuals regardless of species = 10.3 ± 2.13, N = 15) showed unequal variance among group (F test: F = 2.5581, p-value = 0.008) and were also statistically different (Welch's *t*-test: t =-6.7432, DF= 15.873, p-value < 0.001), but showed substantial overlap between the two habitats (Fig. 3A), thus prompting us to focus solely on $\delta^{13}C$ in the mixing model. The composition of the invertebrate community comprised a larger number of taxa in the littoral/floodplain zone than in the river (Fig. 3B). However, when taxa could be collected in both locations, individuals from the littoral/floodplain zone showed systematically more negative $\delta^{13}C$ values than those from the river (Fig. 3B).

Characteristics of fish communities

In total, 809 (TL measured, N = 752) fish specimens belonging to 35 species were captured and analyzed (as presented in Supplementary Material). The fish assemblage captured in the river channel (2009) differed greatly from the community captured in the littoral (2014) (as described in Supplementary Material). The river channel zone supported primarily species belonging to the Catostomidae, Hiodontidae, Ictaluridae and

Percidae families. In comparison, the littoral community was mostly composed of species from the Cyprinidae, Percidae and Centrarchidae families. In each habitat, the fish community remained similar between sampling seasons, although only five species (smallmouth bass (*Micropterus dolomieu)*, mooneye (*Hiodon tergisus*), brown bullhead (*Ameiurus nebulosus*), yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*)) were caught in both habitats (Supplementary Material). Fish captured in the main river tended to be large individuals of taxa with large (> 200 mm) common size at sexual maturity whereas fish captured in the littoral zone were commonly immature individuals belonging to small taxa (common length at sexual maturity < 150 mm). Accordingly, RS values in the main river community were larger (mean RS± SD = 0.95 ± 0.390, N = 196) than those recorded for the littoral fish community (mean RS ± SD = 0.42 ± 0.234, N = 556) (F test: F = 2.744, p-value < 0.001; Welch's *t*-test: t = 17.576, DF = 246.89, p-value < 0.001). Thus, fish from the channel were very close to their common size at maturity whereas littoral fish averaged only 42% of their usual size at maturity. Relative size did not differ significantly among fish caught in the early and late part of the growing season, neither in the channel (F test: F = 1.123, p-value = 0.5677; *t*-test: t = 0.6061 DF = 194, p-value = 0.5452) nor in the littoral habitat (F test: F = 2.195, p-value < 0.001; Welch's *t*-test: t = 0.840, DF = 531.77, p-value = 0.4015).

Isotopic ratios of fish tissues

All isotopic values ($\delta^{13}C$ and $\delta^{15}N$) of fish tissues were in the range potentially explained by invertebrate food sources originating from the floodplain or the main river (Fig. 4). The standard ellipses of the fish captured in the early and late portion of the growing season showed little overlap, suggesting a major temporal shift in their food resources (Fig. 4). Fish captured early in the growing season exhibited isotopic values similar to those of littoral/floodplain invertebrates whereas fish captured late had isotopic values close to those of main river invertebrates. Fish depended more heavily on food resources produced in the floodplain during the early part of the growing season (floodplain contribution = 54.5%, 95% CI = 51.3:57.7) than fish captured during the late part of the growing season (floodplain contribution = 19.5%, 95% CI = 16.5:22.4). The littoral fish community showed a clear temporal shift in its dependence on the floodplain trophic resource (early growing season floodplain contribution = 67.5%, 95% CI = 65.1:70.1; late growing season floodplain contribution = 26.4%, 95% CI = 23.1:29.7). However, this temporal shift was not found in the main river community (early growing season floodplain contribution = 6.7%, 95% CI = 2.3:11.2; late growing season floodplain contribution = 2.3%, 95% CI = 0.1:6.6).

Modeling the trophic contribution of floodplain secondary production to fish

Of the 16 possible models calculated to predict the trophic contribution from floodplain for all individual fish captured in the littoral and central lake area (N = 752), two models yielded similarly high performance, as shown by their equivalent AIC criterion (ΔAIC = 0.3, Burnham and Anderson 2002). The most efficient models included either all the variables (Elevation, Day of capture, Relative Size, and Species) or all variables excluding the Day of capture (presented in Supplementary Material). The performance of all other models including a reduced subset of variables decreased rapidly, exhibiting ΔAIC greater than 2 (third best model ΔAIC = 7.7). Elevation was positively correlated with floodplain contribution (effect size = 0.082, SE = 0.025), indicating that fish captured at higher elevation in the littoral zone (close to the floodplain) depended more on the floodplain trophic resources than fish captured at lower elevations (closer to the main channel). Day of capture was negatively correlated with floodplain contribution (effect size = -0.002, SE = 0.002), indicating that, as the growing season advanced, fish dependence on floodplain invertebrates declined. Likewise, Relative Size and floodplain contribution were negatively correlated (effect size = -1.464, SE = 0.131) suggesting that, over the whole growing season, individuals with a high Relative Size (a proxy for slow isotopic turnover) depended less on the floodplain subsidy than individuals with a low Relative Size. Species identity was also a significant variable in the most parsimonious model suggesting that floodplain contribution differed among species. Analyses revealed no residual spatial autocorrelation in both best models

(All variables: Moran I = -0.006, p-value = 0.829; Elevation + RS + Species: Moran I = -0.006, p-value = 0.850).

Predictive models derived separately for fish communities sampled in the main channel (in 2009) and the littoral zone (in 2014) yielded similar results, with the same 4 models ranking the best and the same 5 yielding the poorest performance (Supplementary material). Minor differences in the order of the 4 best models were observed between data sets, however, in relation with the variable Day of sampling, which was consistently more important in predicting the contribution of floodplain for littoral fish assemblages. These results showed that the temporal variable (Day of capture) is far more important for the littoral community than for the channel fish community. It is also noteworthy that, for the channel community, the model including only the temporal variable yielded an even lower performance than the null model (Supplementary Material) suggesting that the temporal variable failed to explain any variance on its own for large, mature, channel fish.

Seasonal changes in the floodplain subsidy to different species

In the early growing season, the floodplain contribution differed markedly among fish species, with highest contributions for northern pike and yellow perch (floodplain contribution > 0.75) and lowest values (< 0.1) for other species, such as channel catfish (*Ictalurus punctatus*) and silver redhorse (*Moxostoma anisurum*) (Fig. 5). In contrast, most fish species showed only limited floodplain contribution (< 0.5) during the late growing season with the exception of golden shiner (*Notemigonus crysoleucas*) and largemouth bass (≈ 0.6). For all taxa but two (golden shiner and silver redhorse), a clear temporal shift was observed, from high floodplain contribution during the early growing season to low floodplain contribution during the late growing season (Fig. 5).

Discussion

Our results support our initial hypotheses that the floodplain contribution to the fish community follows clear temporal and spatial patterns. This subsidy decreases as the growing season advances. Spatially, fish captured in the main channel depended less on floodplain subsidy than fish captured in the littoral zone. Furthermore, dependency on floodplain trophic resources differed among fish species, being more important for immature littoral individuals than for mature fish living in the main river channel.

End-members isotopic ratios

The invertebrates $\delta^{13}C$ values in our study covered a wide range from -38.59‰ to -17.60‰, which is similar to that reported in previous studies conducted in Lake Saint-Pierre. Bertrand and others (2011) extensively sampled benthic primary consumers of the LSP and observed $\delta^{13}C$ values ranging from ≈ -37‰ to -14.5‰. Paris and others (2016) also observed a similar wide range of $\delta^{13}C$ values for grazers (-28‰ to -16‰) and filterers (-32‰ to -19‰).

Temporal variability in the floodplain subsidy

Our results showed a clear seasonal shift in the floodplain contribution to the fish community that persisted even when considering the entire lake (littoral zone and main river) (Fig. 4 and Fig. 5). The temporal variable (Day) was indeed included among the two the best models predicting floodplain contribution. However, the separate analyses of the channel and littoral communities showed that the temporal variable was a more efficient predictor of floodplain contribution for littoral fish than for channel fish communities, suggesting that the temporal effect is not homogenous throughout the lake. Therefore, combining both communities together in the same analysis might have weakened the overall seasonality signal. Similarly, temporal variation in the contribution of different carbon sources was found in other studies (Huryn and others 2001; Hladyz and others 2012). Terrestrial organic matter represented more than 50% of the carbon assimilated by the macroinvertebrates community early in the summer but decreased to less than 30% in the autumn in a New Zealand grassland floodplain (Huryn and others 2001). Our study extended these previous findings limited to macroinvertebrates by showing that the floodplain subsidy could also reach numerous fish species including predators (*e.g.*, northern pike (*Esox Lucius*)).

The seasonal switch in resources may result from high productivity of invertebrates (benthos and zooplankton) in the floodplain early in the season, later followed by a post flooding increase in within-river productivity associated with macrophyte and epiphyte growth (Vis and others 2007). Large differences in zooplankton density between the main river and the floodplain have been observed in several temperate rivers (Supplementary Material). In LSP, crude estimates based on average zooplankton densities (Supplementary Material) and river and floodplain morphometry suggest that the total abundance of zooplankton is approximately two times greater in the floodplain (8.11×10^{13} individuals) than in the main channel (3.99×10^{13} individuals) for a 2-year flood recurrence scenario. Thus, even if the LSP floodplain represents only 10% of the total volume of water of the St. Lawrence River in spring, the total biomass of zooplankton generated in the floodplain could greatly exceed that of the main river. This difference in density and abundance between these two zones likely results from differences in abiotic conditions between the two habitats. During the spring flood, high flushing rate (discharge) coupled with elevated turbidity and low water temperature yield low autochthonous productivity in the main river. In contrast, reduced current velocity (high retention), low turbidity, and warm water temperature in the floodplain are conducive to high productivity (Kirk 1985; Tockner and others 2000). As discharge drops and floodwaters recede, primary and secondary production from the floodplain is exported to the littoral zone. However, the stimulation of productivity resulting from floodplain export of primary production (algae) and nutrients might be relatively unimportant in view of the large inputs brought by tributaries to the LSP system. For example, 6 of the main LSP tributaries flowing through the littoral zone carry up 25 400 and 1 500 metric tons of N and P per year, respectively (Hudon and others 2017), most likely resulting in the absence of nutrient limitation for primary production in the littoral zone (Vis and others 2007).

In contrast to our findings, some studies did not find any evidence of floodplain contribution to the fish community in temperate rivers (Thorp and others 1998; Delong and Thorp 2006). The lack of documented floodplain contribution in a highly constricted reach of the Ohio River could result from the sampling period in the late part of the growing season (October 1993 and July 1994) (Thorp and others 1998). In a Mississippi River study, primary and secondary invertebrate consumers were collected only away from the floodplain in the main river channel and long after flood recession (in late July) (Delong and Thorp 2006). The above studies succeeded in tracking the main source of energy on an annual basis but lacked the resolution necessary to document the fine spatial and temporal changes in fish food resource in river/floodplain ecosystems, such as we observed here in the St. Lawrence River.

Spatial patterns in floodplain subsidy

Our data suggest that floodplain contribution followed a spatial gradient, decreasing with distance from the shore and with depth (i.e. decreasing elevation). Similar differences in the importance of floodplain contribution between littoral and pelagic fish species were reported elsewhere (Gutreuter and others 1999). Furthermore, in our study the fish communities in the main river and the littoral zone comprised different taxa (as presented in Supplementary Material). The floodplain subsidy may reach fish inhabiting the littoral zone but may never be assimilated by fish using primarily the central pelagic zone. These results support the findings of Dettmers and others (2001), indicating the presence of a distinct food web in the main channel of large rivers.

Interspecific variation in trophic linkage to the floodplain

To our knowledge, no study has previously investigated the spatial and temporal variability of floodplain subsidy to the productivity of a large number of fish species in a temperate fluvial lake. Trophic linkage with the floodplain was highly variable among 35 fish species early in the growing season, ranging from ≥ 0.70 (northern pike, yellow perch, blackchin shiner (*Notropis heterodon*) and golden shiners) to ≤ 0.25 (shorthead redhorse (*Moxostoma macrolepidotum*), white sucker (*Catostomus commersoni*), channel catfish and silver redhorse). In contrast, all but two fish species (golden shiner, largemouth bass) captured in the late portion of the growing season showed a comparatively low (≤ 0.4) floodplain contribution, indicating that most fish species shifted to within river food sources over the growing season (Fig. 5). Gutreuter and others (1999) found that the growth of largemouth bass and bluegill depended on the inundation pattern but not the growth of white bass, suggesting that the former taxa were more dependent on floodplain food resources than the latter. Herwig and others (2007) also found variability in the dependence on terrestrial C_3 plant among bluegill, freshwater drum (*Aplodinotus grunniens*), and gizzard shad (*Dorosoma cepedianum*) in the Mississippi River.

Relative Size (RS) a proxy for isotopic turnover rate

Relative Size was a significant variable in the most parsimonious model and was negatively correlated with floodplain contribution. As the size of an individual increases and RS approaches 1, tissue turnover rate decreases and tracking the incorporation of the floodplain pulse of secondary production becomes more difficult (Weidel and others 2011). Furthermore, for a given RS, small species (*e.g.*, bridle shiner (*Notropis bifrenatus*)) are expected to have a higher isotopic turnover rate than large species (*e.g.*, silver redhorse), which have slower relative growth rate and metabolism (Vander Zanden and others 2015). To illustrate the effect of RS and the body size of individuals on their capacity to track the trophic contribution of the floodplain, we developed a conceptual model of floodplain contribution through time under different RS and size scenarios (Fig. 6A and B). We estimated the individual floodplain contribution through time from the projected daily isotopic values from the diet switching equation proposed by Hesslein and others (1993). Each scenario was assigned a turnover rate (λ) consistent with their RS or size. We then assumed that the individuals were at equilibrium with the river source (contribution of floodplain = 0) at the start of the year. Also, we assumed that the first diet switch (from river to floodplain source) started at the peak of the flood, when the floodplain resource start to be flushed out of the floodplain with the receding water, and a second diet switch (from floodplain to river source) after the end of the flood when the food resources produced by the floodplain and exported to the river have been exhausted (flushed downstream and/or consumed).

Following the conceptual models described above, the isotopic tracking power of an individual should decrease within a given species as a function of its Relative Size (Fig. 6A) and, for different fish species, its body size at maturity (Fig. 6B). In our study, many littoral individuals showed a high RS. Therefore, floodplain contribution early in the growing season for littoral individuals with high RS was potentially underestimated (Fig. 6A), since tissue turnover rate was too slow to adequately track the pulse of resources exported from the floodplain (Mac Avoy and other 2001). For similar reasons, individuals with a high RS could have carried the signal of floodplain contribution even after water had long receded from the floodplain, leading to an overestimation of the floodplain contribution for the late part of the growing season. Our model suggests that, in general, small fish, both within and among species, tend to track most efficiently the window of opportunity offered by the floodplain subsidy (Fig. 6A and B). The faster isotopic shift in the early season we recorded for small fish also suggested that the floodplain subsidy represented a much more important contribution to their total growth and metabolic requirements than for larger-bodied species. Therefore, years with floods with limited extent and duration should result in low floodplain productivity and reduced growth and survival of small species and early life history stages of larger species (Kirjasniemi and Valtonen 1997).

Conclusion

This paper upholds our hypothesis that the floodplain of LSP is a major source of energy supporting the productivity of many fish species in the early part of the growing season. Fish species associated with the littoral habitats assimilated the subsidy to a larger extent than taxa found in the central river channel, showing a strong spatial variation in floodplain contribution. In conclusion, this study emphasizes the importance of including spatial and temporal patterns to correctly identify the sources of energy supporting ichthyofaunal productivity of temperate river ecosystems. Globally, floods in semi-natural and natural temperate rivers are predicted to be shorter and smaller due to climate change (ACIA 2004) likely resulting in a smaller floodplain subsidy. Therefore, climate change should have a strong negative impact on littoral fish species that are highly dependent on floodplain subsidy early in their development. Human activities such as encroachment of floodplain by agriculture (*e.g.,* Van Dijk and others 2013; Hudon and others 2018), housing, and roads may also lead to reduction of their extent and affect the quality of their water, therefore impacting the ecosystemic function of floodplains.

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Figure legends

Figure 1. Mean daily water level (m, IGLD85) in Lake Saint-Pierre measured in 2009 (grey line) and 2014 (black line) together with the historical median (dotted line, 1966-2017). The elevation of + 4.57 m IGLD85, at which the river enters the floodplain is also shown (dashed line), is the median of the minimal value observed (1966-2017) between April 1st (day of year 91) and July 1st (day of year 181).

Figure 2. Location of sampling sites in Lake Saint-Pierre in 2009 (squares) and 2014 (circles) superimposed on the bathymetry (referenced to chart datum level) and flow direction (arrow). The flood zone (littoral/floodplain zone) lies between the 2-year floodline (fine dashed line) and the limit of dense emergent marsh vegetation (dashed line). Black symbols: sampled only early in the growing season. Grey symbols: sampled both during early and late growing seasons. White symbols: sampled only in the late growing season.

Figure 3. A) Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic ratios of invertebrates in the littoral/floodplain zone (full circles) and in the main river (open squares). B) Distribution of carbon isotopic ratios for each macro-invertebrate taxonomic group caught in the littoral/floodplain zone (grey boxplots and in the main river (white boxplots).

Figure 4. Stable isotopic ratios of muscle and fin tissues for individual fish caught in the early (hairline crosses) and late (open triangles) part of the growing season, superimposed on the standard ellipses for samples taken in the early (full line, crosses) and late (dashed line, open triangles) part of the growing season. Baseline values (mean ± 2 SD) for samples collected in the littoral/floodplain zone (full circle) and the main river (full squares) are corrected for expected trophic fractionations between fish and their prey ($\Delta^{13}C = -0.1 \pm 0.96$; $\Delta^{15}N = 3.4 \pm 0.99$) proposed by Post (2002).

Figure 5. Relative importance of the contribution of floodplain food sources to the diet of different fish species, assessed from the posterior distribution from SIAR. The fish species represented (in decreasing order of floodplain contribution) are only those for which the SIAR model converged. For each species, the median (± 95% credibility interval) contribution assessed for fish captured in the early (full circles), and late (open circles) portion of the growing season are shown. The habitat in which each species was found is identified next to its common name: L (Littoral), C (Channel) and B (both habitats). Sauger (*Sander canadensis*), pumpkinseed (*Lepomis gibbosus*), alewife (*Alosa pseudoharengus*), johnny darter (*Etheostoma nigrum*), trout-perch (*Percopsis omyscomycus*), spottail shiner (*Notropis hudsonius*), round goby (*Neogobius melanostomus*), brook silverside (*Labidesthes sicculus*), largemouth bass (*Micropterus salmoides*), silver redhorse (Moxostoma anisurum), channel catfish (*Ictalurus punctatus*), white sucker (Catostomus commersoni), shorthead redhorse (Moxostoma macrolepidotum), mooneye (*Hiodon tergisus*), eastern silvery minnow (*Hybognathus regius*), walleye (*Sander vitreus*), emerald shiner (*Notropis atherinoides*), banded killifish (*Fundulus diaphanous*), bridle shiner (*Notropis bifrenatus*), golden shiner (*Notemigonus crysoleucas*), blackchin shiner (*Notropis heterodon*), yellow perch (*Perca flavescens*), northern pike (*Esox lucius*).

Figure 6. Conceptual scheme illustrating the relation between the day of the year, water level historical median (dotted line, 1966-2017), and the floodplain contribution for: A) three fish belonging to the same species at three different relative sizes (RS, low/juvenile (λ = 0.84), medium/immature (λ = 0.009), and high/mature (λ = 0.005)) (solid line), B) three fish of the same size, belonging to species characterized by different size at sexual maturity (small (λ = 0.025), medium (λ = 0.01), and large (λ = 0.0015)) for a specific RS (solid line). The flood threshold level of 4.57 m, at which the river enters the floodplain, is also shown (horizontal dashed line).

Figures

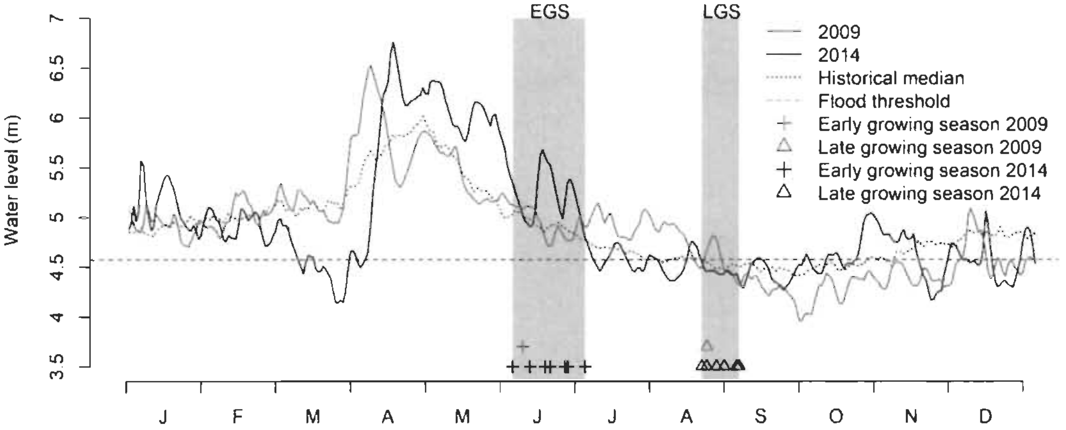


Figure 1.

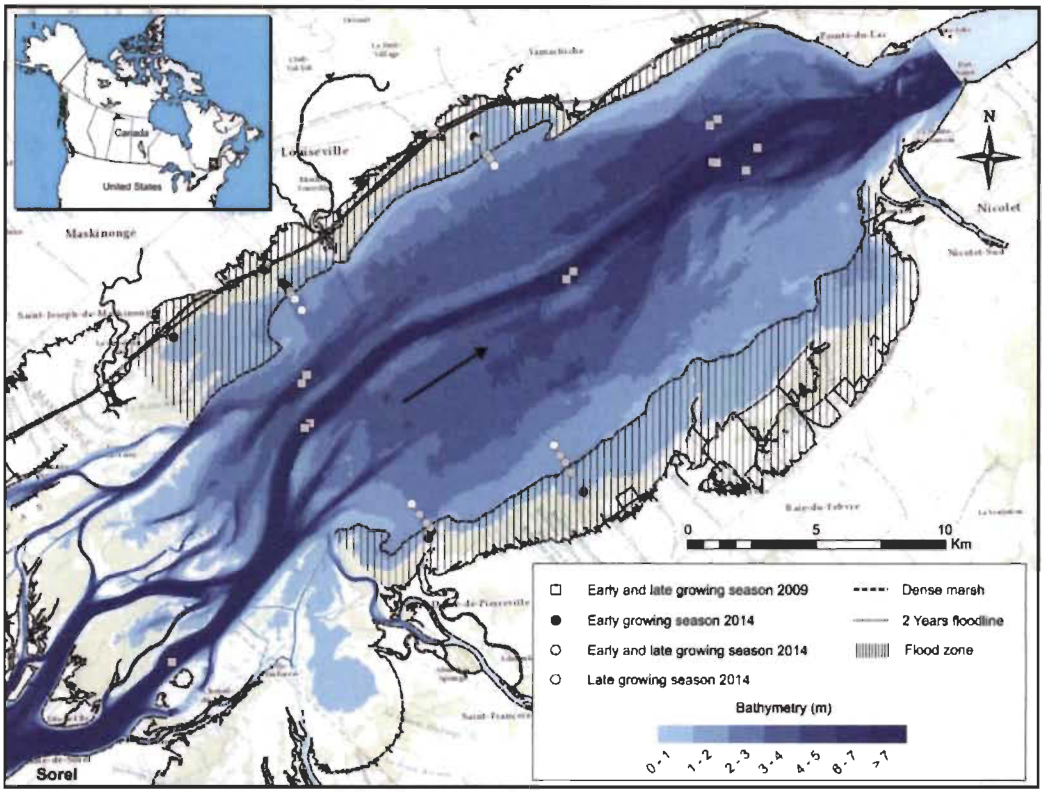

Canada
United States
Louiseville
Maskinonge
Saint-Joseph-de-Maskinongé
Yamachiche
Pointe-du-Lac
Nicolet
Nicolet-Sud
Baie-du-Febvre
Saint-François
Sorel
N
0
5
10
Km
Early and late growing season 2009
Early growing season 2014
Early and late growing season 2014
Late growing season 2014
Dense marsh
2 Years floodline
Flood zone
Bathymetry (m)
0-1
1-2
2-3
3-4
4-5
6-7
>7

Figure 2.

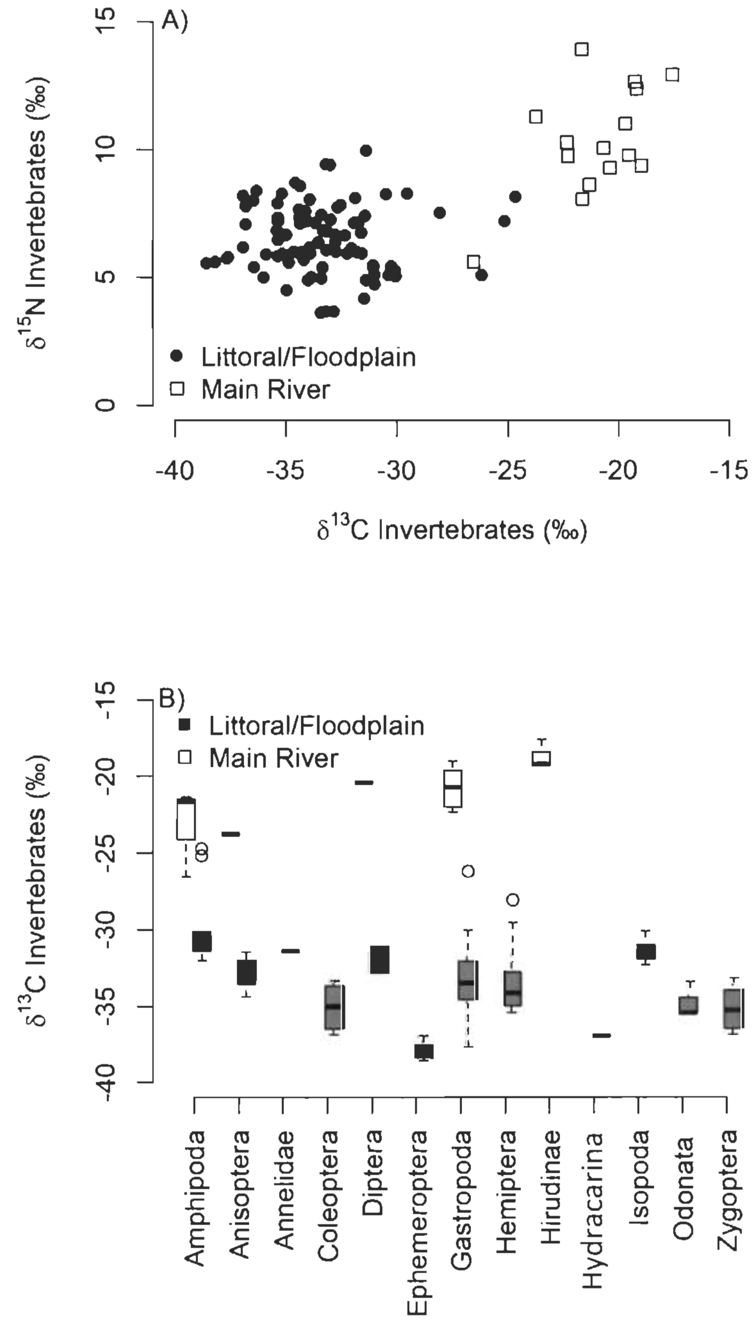

A)
$\delta^{15}N$ Invertebrates (‰)
$\delta^{13}C$ Invertebrates (‰)
0
5
10
15
-40
-35
-30
-25
-20
-15
● Littoral/Floodplain
□ Main River
B)
■ Littoral/Floodplain
□ Main River
$\delta^{13}C$ Invertebrates (‰)
-15
-20
-25
-30
-35
-40
Amphipoda
Anisoptera
Annelidae
Coleoptera
Diptera
Ephemeroptera
Gastropoda
Hemiptera
Hirudinae
Hydracarina
Isopoda
Odonata
Zygoptera

Figure 3.

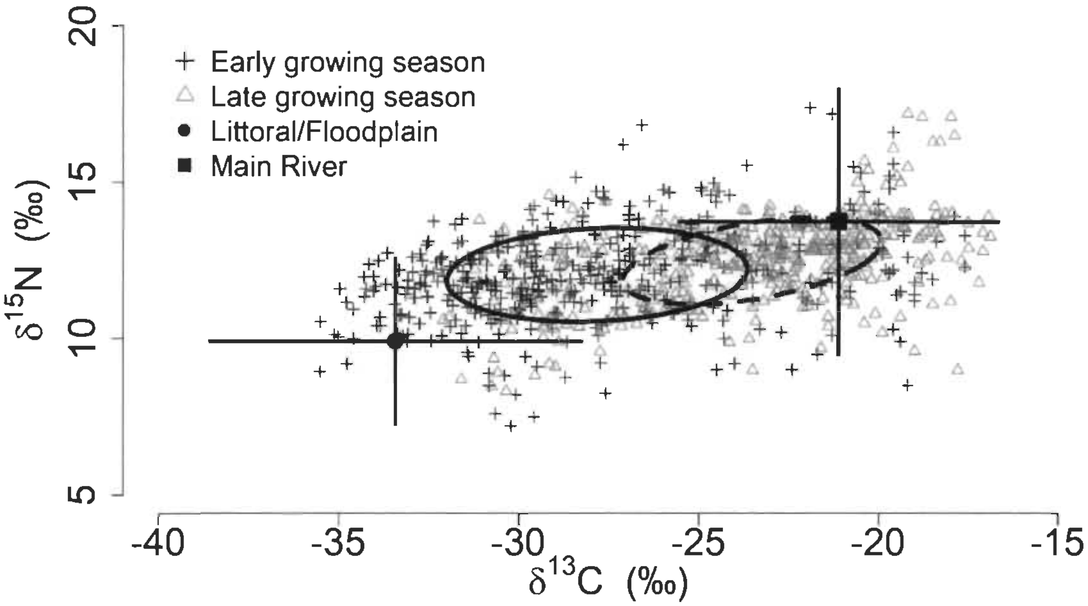

+ Early growing season
△ Late growing season
● Littoral/Floodplain
■ Main River
$\delta^{15}N$ (‰)
$\delta^{13}C$ (‰)
20
15
10
5
-40
-35
-30
-25
-20
-15

Figure 4.

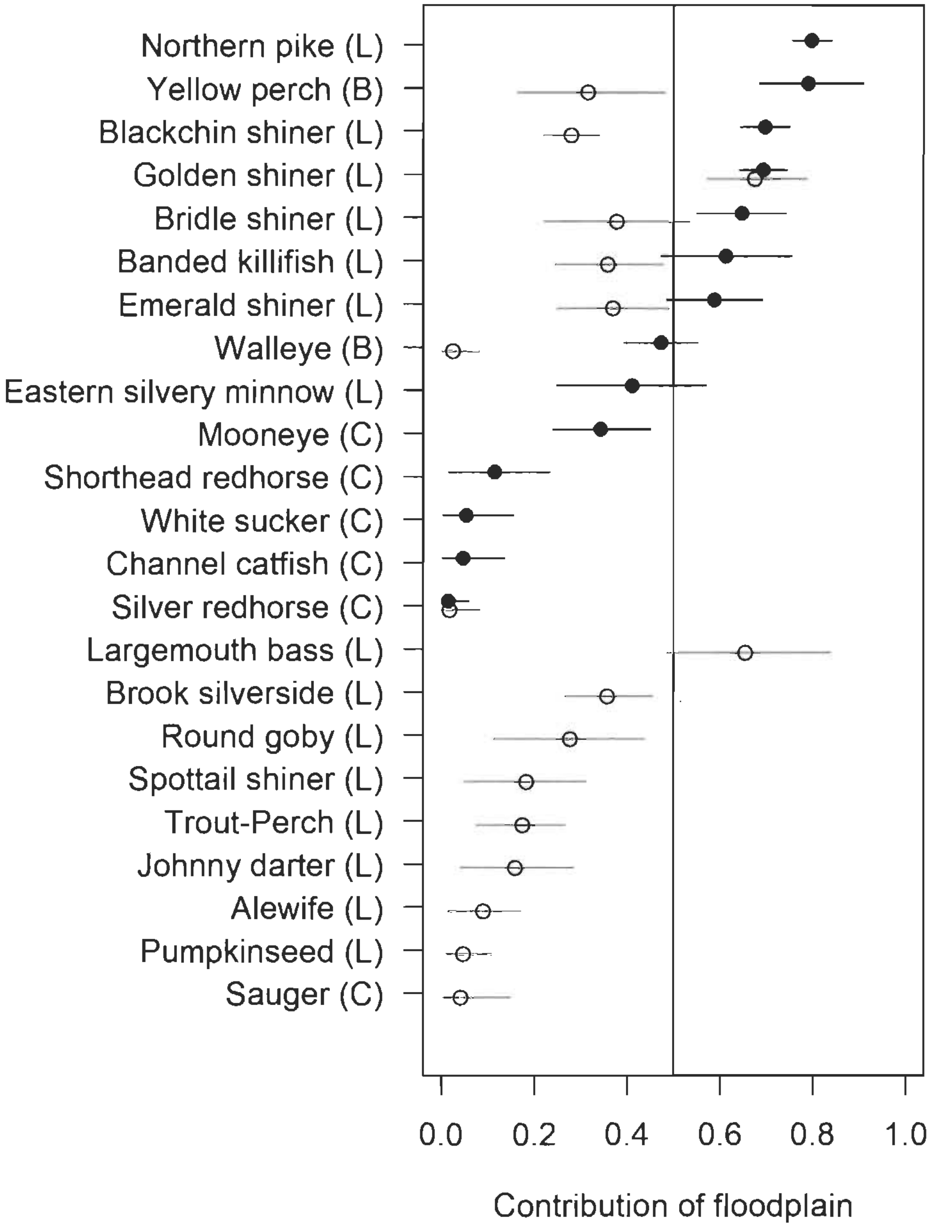

Northern pike (L)
Yellow perch (B)
Blackchin shiner (L)
Golden shiner (L)
Bridle shiner (L)
Banded killifish (L)
Emerald shiner (L)
Walleye (B)
Eastern silvery minnow (L)
Mooneye (C)
Shorthead redhorse (C)
White sucker (C)
Channel catfish (C)
Silver redhorse (C)
Largemouth bass (L)
Brook silverside (L)
Round goby (L)
Spottail shiner (L)
Trout-Perch (L)
Johnny darter (L)
Alewife (L)
Pumpkinseed (L)
Sauger (C)
0.0
0.2
0.4
0.6
0.8
1.0
Contribution of floodplain

Figure 5.

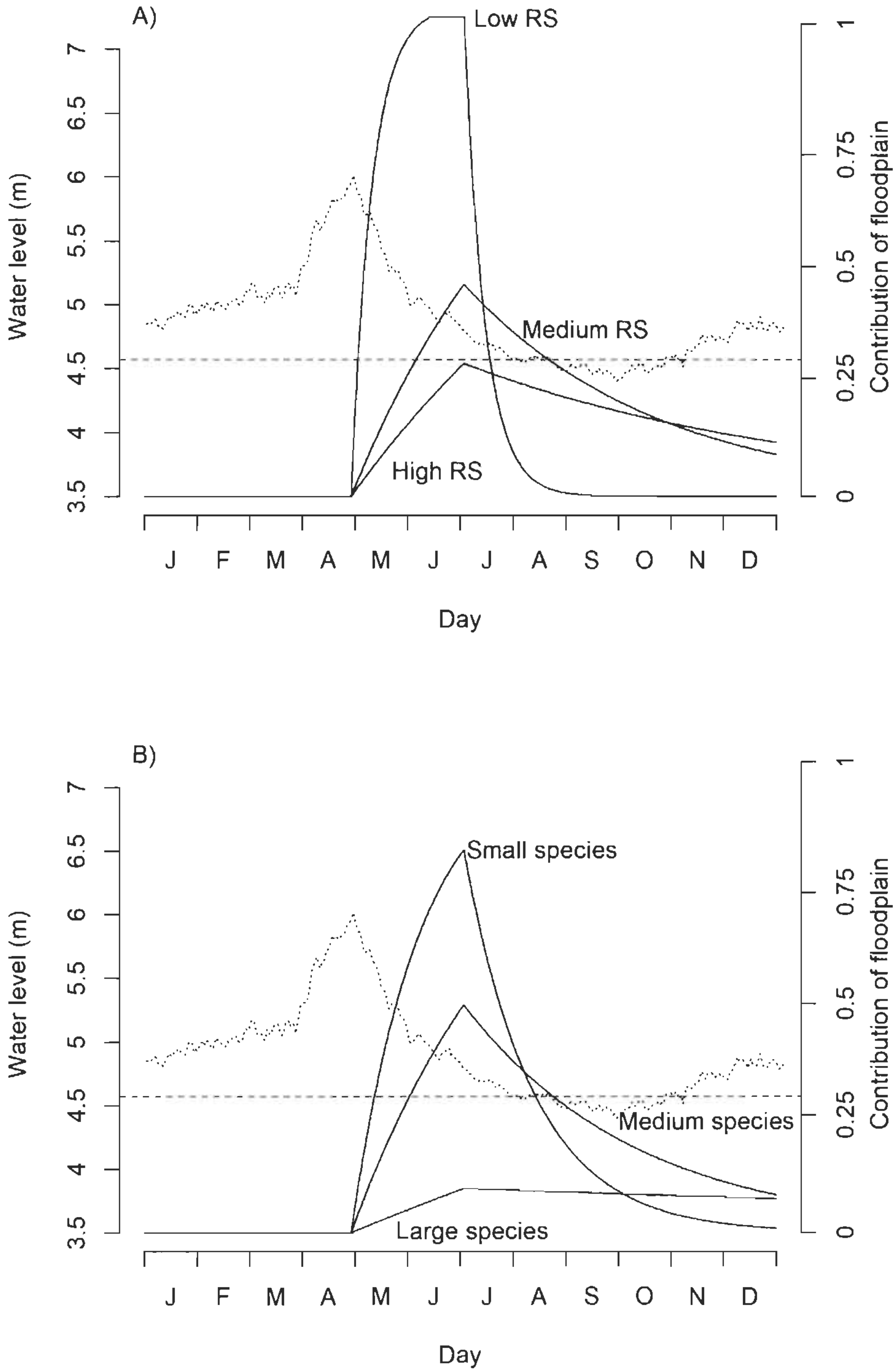

A)
Low RS
Medium RS
High RS
Water level (m)
3.5
4
4.5
5
5.5
6
6.5
7
Contribution of floodplain
0
0.25
0.5
0.75
1
J
F
M
A
M
J
J
A
S
O
N
D
Day
B)
Small species
Medium species
Large species
Water level (m)
3.5
4
4.5
5
5.5
6
6.5
7
Contribution of floodplain
0
0.25
0.5
0.75
1
J
F
M
A
M
J
J
A
S
O
N
D
Day

Figure 6.

Supplementary Material

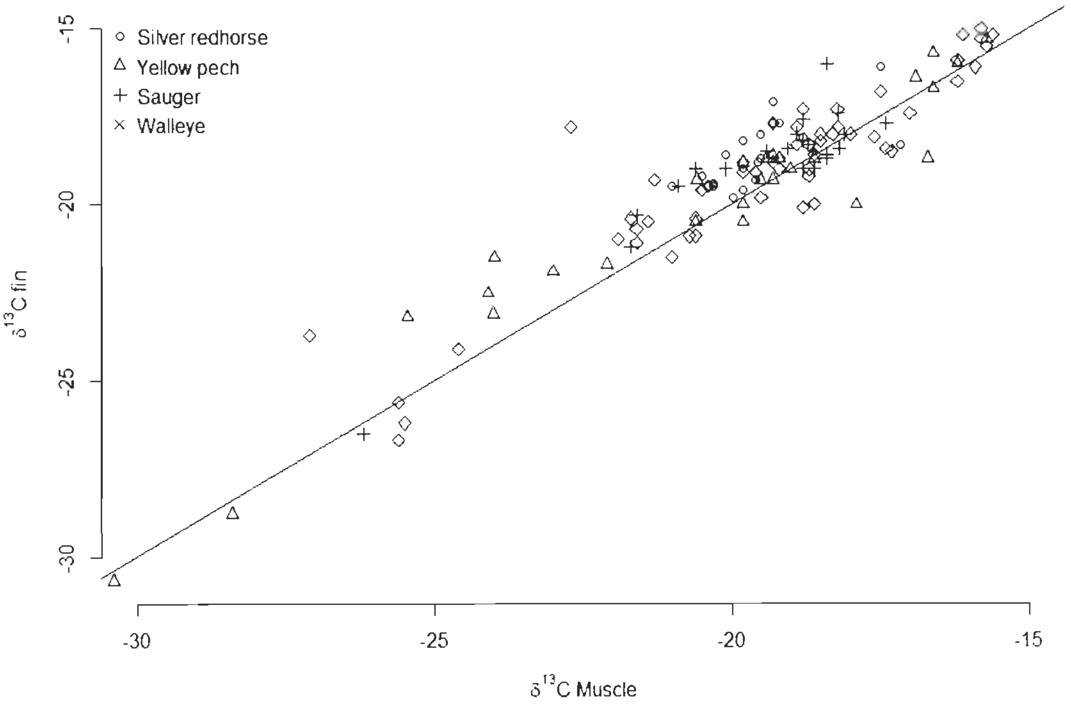
S.M.1. Number of fish captured and measured (measured TL) during the early (Early, June 04 to July 03) and late (Late, August 19 to September 03) portion of the growing seasons in 2009 and 2014 and analyzed in the present study. For each fish taxon, the trophic guild (La Violette and others 2003), main habitats used (littoral, channel), common length at sexual maturity (http://www.fishbase.ca) and Ministère des Forêts de la Faune et des Parcs of Québec website) and median (min-max) length ratio (Total length/common length at maturity) are indicated.

Scientific name **Family** *Species*	Common name	Habitat	Length at maturity (mm)	Relative size Median (Min-Max)	2009 Early (Measured TL)	2009 Late (Measured TL)	2014 Early (Measured TL)	2014 Late (Measured TL)	Total (Measured TL)
Atherinidae									
Labidesthes sicculus	Brook silverside	Littoral	84	0.524 (0.357-0.893)			2 (2)	19 (19)	21 (21)
Catostomidae									
Catostomus catostomus	Longnose sucker	Channel	225	1.823 (1.382-1.862)	3(3)				3 (3)
Catostomus commersoni	White sucker	Channel	407	0.905 (0.455-1.106)	18 (18)	4 (4)			22 (22)
Carpiodes cyprinus	Quillback	Channel	520	0.504 (0.225-1.656)	4 (4)	6 (6)			10 (10)
Moxostoma anisurum	Silver redhorse	Channel	325	1.449 (0.542-1.895)	21 (21)	13 (13)			34 (34)
Moxostoma macrolepidotum	Shorthead redhorse	Channel	408	0.831 (0.363-1.071)	10 (10)	12 (12)			22 (22)
Centrarchidae									
Ambloplites rupestris	Rock bass	Littoral	154	0.377 (0.240-0.383)			2 (2)	2 (1)	4 (3)
Lepomis gibbosus	Pumpkinseed	Littoral	99	0.323 (0.192-1.152)			2 (2)	58 (53)	60 (55)
Micropterus dolomieu	Smallmouth bass	Channel/Littoral	331	0.766 (0.257-1.574)	2 (2)	1 (1)	1 (1)	2 (2)	6 (6)
Micropterus salmoides	Largemouth bass	Littoral	400	0.190 (0.158-0.210)				5 (4)	5 (4)
Pomoxis nigromaculatus	Black crappie	Littoral	275	0.225 (0.204-1.131)			1 (1)	3 (2)	4 (3)
Clupeidae									

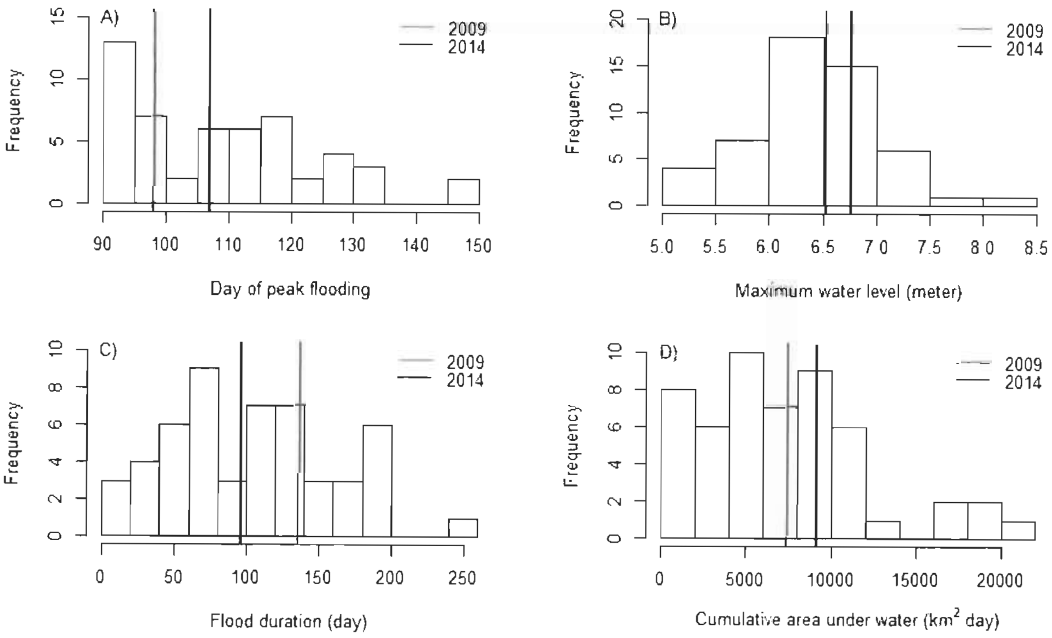
Scientific name **Family** *Species*	Common name	Habitat	Length at maturity (mm)	Relative size Median (Min-Max)	2009 Early (Measured TL)	2009 Late (Measured TL)	2014 Early (Measured TL)	2014 Late (Measured TL)	Total (Measured TL)
Alosa pseudoharengus	Alewife	Littoral	153	0.379 (0.261-0.484)				16 (16)	16 (16)
Cyprinidae									
Cyprinus carpio	Common carp	Channel	310	0.365 (-)	1 (1)				1 (1)
Hybognathus regius	Eastern silvery minnow	Littoral	88	0.648 (0.568-0.886)			8 (8)	5 (5)	13 (13)
Notropis atherinoides	Emerald shiner	Littoral	86	0.529 (0.267-0.814)			26 (23)	17 (17)	43 (40)
Notropis bifrenatus	Bridle shiner	Littoral	50[c]	0.860 (0.520-0.980)			19 (17)	9 (6)	28 (23)
Notemigonus crysoleucas	Golden shiner	Littoral	144	0.441 (0.306-0.6875)			42 (33)	10 (7)	52 (40)
Notropis heterodon	Blackchin shiner	Littoral	56	0.625 (0.393-0.875)			11 (9)	12 (12)	23 (21)
Notropis heterolepis	Blacknose shiner	Littoral	73	0.411 (-)				1 (1)	1 (1)
Notropis hudsonius	Spottail shiner	Littoral	90	0.467 (0.389-0.811)			2 (1)	7 (7)	9 (8)
Cyprinodontidae									
Fundulus diaphanous	Banded killifish	Littoral	63	0.651 (0.460-0.952)			12 (11)	13 (13)	25 (24)
Esocidae									
Esox lucius	Northern pike	Littoral	400	0.183 (0.095-0.912)			72 (65)	1 (1)	73 (66)
Gadidae									
Lota lota	Burbot	Channel	400	0.888 (0.645-1.288)	1 (1)	4 (4)			5 (5)
Gasterosteidae									
Culaea inconstans	Brook stickleback	Littoral	50	0.460 (-)				1 (1)	1 (1)
Gobiidae									
Neogobius melanostomus	Round goby	Littoral	91.5[c]	0.7978 (0.721-0.863)				5 (5)	5 (5)

Scientific name **Family** *Species*	Common name	Habitat	Length at maturity (mm)	Relative size Median (Min-Max)	2009 Early (Measured TL)	2009 Late (Measured TL)	2014 Early (Measured TL)	2014 Late (Measured TL)	Total (Measured TL)
Hiodontidae									
Hiodon tergisus	Mooneye	Channel/Littoral	283	0.714 (0.403-1.809)	17 (17)	1 (1)	3 (3)		21 (21)
Ictaluridae									
Ameiurus nebulosus	Brown bullhead	Channel/Littoral	250	1 (0.236-2.240)	1 (1)	9 (9)	6 (6)		16 (16)
Ictalurus punctatus	Channel catfish	Channel	570	0.535 (0.475-0.846)	11 (11)	1 (1)			12 (12)
Percidae									
Etheostoma nigrum	Johnny darter	Littoral	39	0.910 (0.641-1.179)				10 (10)	10 (10)
Percina caprodes	Logperch	Littoral	125	0.2 (0.192-0.24)			3 (3)		3 (3)
Perca flavescens	Yellow perch	Channel/Littoral	191	0.267 (0.120-1.754)		15 (15)	85 (82)	67 (58)	167 (155)
Sander canadensis	Sauger	Channel	358	0.911 (0.698-1.989)		10 (10)			10 (10)
Sander vitreus	Walleye	Channel/Littoral	422	0.568 (0.081-0.972)	1 (1)	29 (29)	26 (23)	3 (3)	59 (56)
Percopsidae									
Percopsis omyscomycus	Trout-perch	Littoral	88	0.602 (0.466-0.909)			10 (10)	13 (11)	23 (21)
Sciaenidae									
Aplodinotus grunniens	Freshwater drum	Channel	450	0.456 (-)	1 (1)				1 (1)

S.M.2. Relationship between the carbon isotopic ratio of muscle (δ^{13}C Muscle) and fin (δ^{13}C Fin) for 4 species: Silver redhorse (*Moxostoma anisurum*; open circles), Yellow perch (*Perca flavescens*; open triangles), Sauger (*Sander canadensis*; crosses), Walleye (*Sander vitreus*; open diamonds). The line shows the 1:1 relationship between variables.



S.M.3. Hydrological characteristics of floods between 1966 and 2017, recorded at the inlet of Lake Saint-Pierre (Sorel-Tracy gauging station). A) The day of the year when the flood reached maximum water level (Day of peak flooding). B) The highest water level during spring flood (Maximum water level). C) The number of consecutive days in spring when the water level was higher than the inferior limit of the floodplain (Elevation + 4.57 m IGLD85) (Flood duration). D) cumulative area under water during the spring flood using the inferior limit of the floodplain (Elevation + 4.57 m IGLD85) as bench mark (Cumulative area under water). Area under the curve is a combination of flood magnitude and duration. In each panel, the years 2009 (grey) and 2014 (black) for the present study are shown.



S.M.4. **Output of the general linear regression model predicting the floodplain contribution using different combination of explanatory variables: Station elevation (Elevation); Day of fish capture (Day); Ratio of total length to length at maturity (Relative Size); Species (Species).** All models include the station as a random effect. Models are shown in decreasing order of performance, determined from the Akaike Information Criterion (AIC); the difference in performance of each successive model (ΔAIC) with respect to the best one is also shown.

Model	AIC	Δ AIC
Elevation + Relative Size + Species	-1086.1	-
Elevation + Day + Relative Size + Species	-1085.8	0.3
Day + Relative Size + Species	-1078.2	7.9
Relative Size + Species	-1078.0	8.1
Elevation + Species	-964.5	121.6
Elevation + Day + Species	-963.3	122.8
Elevation + Day + Relative Size	-931.9	154.2
Species	-928.6	157.5
Elevation + Relative Size	-928.1	158
Day + Species	-927.2	158.9
Day + Relative Size	-907.6	178.5
Relative_size	-906.6	179.5
Elevation + Day	-853	233.1
Elevation	-848.7	237.4
Day	-813.8	272.3
Null	-813.2	272.9

S.M.5. Comparison of the output of the general linear regression models predicting the floodplain contribution of the littoral (2014, N = 556 fish) and channel (2009, N = 196 fish) fish communities, using different combinations of four explanatory variables: Station elevation (Elevation); Day of fish capture (Day); Ratio of total length to length at maturity (Relative Size); Species (Species). All models include the station as a random effect. For both data subsets, the values of the Akaike Information Criterion (AIC) are shown, indicative of model performance; the difference in model performance (ΔAIC) with respect to the best one is also shown. Models for 2014 are shown in decreasing order of performance and are compared with the ranking of models derived from the 2009 data set, since AIC values cannot be compared among data sets. No residual spatial autocorrelation was observed for the top two ranking models, neither in 2014 (Rank 1 All variables: Moran I = -0.006, p-value = 0.821; Rank 2 Day of capture + RS + Species: Moran I = -0.006, p-value = 0.805) nor in 2009 (Rank 1 All variables: Moran I = -0.003, p-value = 0.377; Rank 2: Elevation + RS + Species: Moran I = -0.002, p-value = 0.301).

	2014 (N = 556) Littoral fish community		Rank 2014	2009 (N = 196) Channel fish community		Rank 2009
Model	AIC	Δ AIC		AIC	Δ AIC	
Elevation + Day + Relative Size + Species	-734.5	-	1	-381.9	0.6	2
Day + Relative Size + Species	-733.6	0.9	2	-372.9	9.6	4
Elevation + Relative Size + Species	-725.1	9.4	3	-382.5	0	1
Relative Size + Species	-712	22.5	4	-373.2	9.3	3
Elevation + Day + Species	-671.6	62.9	5	-333.5	49	5
Day + Species	-670.3	64.2	6	-322.3	60.2	9

	2014 (N = 556) Littoral fish community		Rank 2014	2009 (N = 196) Channel fish community		Rank 2009
Model	AIC	Δ AIC		AIC	Δ AIC	
Elevation + Species	-665.6	68.9	7	-333.4	49.1	6
Species	-653.1	81.4	8	-323	59.5	8
Elevation + Day + Relative Size	-633.5	101	9	-322.2	60.3	10
Day + Relative Size	-627.8	106.7	10	-317.8	64.7	11
Elevation + Relative Size	-624.9	109.6	11	-323.1	59.4	7
Relative Size	-604.5	130	12	319.2	701.7	16
Elevation + Day	-589.7	144.8	13	-299.3	83.2	12
Day	-583	151.5	14	-288.8	93.7	15
Elevation	-580.6	153.9	15	-296.9	85.6	13
Null	-558.6	175.9	16	-289.4	93.1	14

S.M.6. Mean invertebrate density (ind. / l) in the main river and natural floodplain habitats of temperate rivers.

System	Organism	Habitat		References
		Main river (ind. / l)	Floodplain (ind. / l)	
Waikato River	Zooplankton	2.47	19.23	Gòrski and others 2013
Danube River	Zooplankton	161	-	Reckendorfer and others 1999
Danube River	Zooplankton	-	1023	Baranyi and others 2002
St. Lawrence River	Zooplankton	2.18	-	Casper and Thorp 2007
St. Lawrence River	Invertebrates	0.4	-	Cusson 2011
St. Lawrence River (Lake Saint-François and Saint-Pierre)	Zooplankton	11.16	-	Basu and others 2000
St. Lawrence River (Lake Saint-Pierre)	Zooplankton	170.4	1639.2	Savignac 1985
St. Lawrence River (Lake Saint-Pierre)	Invertebrates (zooplankton excluded)	167	1787	Savignac 1985
St. Lawrence River (Lake Saint-Pierre)	Zooplankton	-	831.6	Berger and Cabana Pers. Com.
St. Lawrence River (Lake Saint-Pierre)	Zooplankton	19.4	209.2	This Study (Data not shown)

CHAPITRE II

HYDROLOGICAL CONTROL OF A FLOODPLAIN SUBSIDY TO LITTORAL RIVERINE FISH

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Résumé

Nous avons étudié l'impact des régimes d'inondation sur l'assimilation d'un subside trophique produit dans la plaine inondable et leurs effets sur la condition physique de cinq espèces de poissons littorales du lac Saint-Pierre, un grand ($\approx$ 300 km^2) élargissement peu profond ($\approx$ 3 m) du fleuve Saint-Laurent (Québec, Canada). Examinant quatre années consécutives démontrant des inondations printanières distinctes, nous avons émis l'hypothèse que l'incorporation du carbone dérivé de la plaine inondable dans la biomasse des poissons et leur valeur sélective individuelle (traduction libre de l'anglais « fitness »), mesurée par la condition physique, devrait augmenter les années de fortes inondations.

Nous avons analysé les ratios isotopiques du carbone (δ^{13}C) de cinq espèces invertivores de poissons littorales (la perchaude, le crapet-soleil, le méné d'herbe, le méné jaune et le fondule barré) et des invertébrés capturés au commencement et à la fin de la saison de croissance. La contribution de la plaine a été estimée au niveau de la communauté, de l'espèce et de l'individu, par l'utilisation d'un modèle de mélange isotopique (SIAR). La sélection de modèles linéaires mixtes (AIC) a été utilisée pour l'analyse de l'impact de l'hydrologie sur la contribution de la plaine et la condition physique. Nous avons utilisé les valeurs des résidus générés par la régression spécifique entre le ln de la masse totale et le ln de la longueur totale comme indice de la condition physique.

Les analyses isotopiques ont démontré que les poissons capturés pendant les années de fortes inondations avaient une plus forte dépendance au subside provenant de la plaine inondable, et ce, pour une plus longue période que les poissons capturés les années d'inondation plus modeste. Les cinq espèces ont montré des tendances temporelles similaires de l'assimilation du subside de la plaine inondable. Ceux-ci étaient influencés par le régime d'inondation et la date de capture. De plus, la condition physique chez toutes les espèces était positivement corrélée avec l'intensité et durée de l'inondation. Notre étude mutli-spécifique a quantifié la contribution alimentaire de la plaine inondable à la communauté littorale de poissons et identifié son effet positif sur la valeur sélective des individus. De plus, cette recherche met de l'avant l'importance du régime hydrologique pour déterminer la contribution de la plaine inondable au réseau trophique de la rivière et les conséquences potentielles de futures altérations hydrologiques découlant de la régulation des débits et des changements climatiques.

Mots-clés : Analyse des isotopes stables, Condition physique, Hydrologie, Poissons littoraux, Rivière Saint-Laurent, Subside de la plaine d'inondation.

Abstract

1. We studied the impact of the flood regime on the assimilation of a trophic subsidy produced in the floodplain and its effect on body condition of five littoral fish species of Lake Saint-Pierre, a large ($\approx$ 300 km^2) and shallow ($\approx$ 3 m) widening of the St. Lawrence River (Quebec, Canada). Examining four consecutive years with contrasting spring flood events, we hypothesized that the incorporation of floodplain-derived carbon into fish biomass and individual fitness, measured by body condition, would increase in years with more important floods.

2. We analyzed the carbon stable isotope ratios ($\delta^{13}C$) of 5 invertivore littoral fish species (yellow perch, pumpkinseed, bridle shiner, golden shiner, banded killifish) and invertebrates captured at the beginning and at the end of the growing season. Floodplain contribution was estimated at the community, species, and individual fish levels, using a stable isotopic mixing model (SIAR). A linear mixed model selection (AIC) was used to analyze the impact of hydrology on floodplain contribution and body condition. We used the residual values generated by the specific regressions between ln total weight and ln total length as an index of body condition.

3. Isotopic analysis showed that fish captured during years of important floods had a higher dependency on the floodplain subsidy for a longer period than fish caught during years of modest flooding. The five species showed similar temporal trends in the assimilation of the floodplain subsidy, which was influenced by the flood regime and the date of capture. Furthermore, body condition of all species was positively correlated to flooding intensity and duration.

4. Our multi-species study quantified floodplain contribution to the littoral fish community and identified its positive effect on fish fitness. It highlights the importance of the hydrological regime in determining the contribution of floodplain to riverine trophic network, and the possible consequences of future hydrological alterations resulting from discharge regulation and climate change.

Key words: Body condition, Floodplain subsidy, Hydrology, Littoral fish, St. Lawrence River, Stable isotope analysis.

Introduction

Ecological subsidies, defined as fluxes of donor-controlled resources (*e.g.* nutrients, detritus, and prey) across ecosystem boundaries, are key variables altering the dynamics of the recipient populations (Anderson, Wait & Stapp, 2008; Rooney, McCann & Moore, 2008; Nakano & Murakami, 2001; Polis, Anderson & Holt, 1997). They can be described in terms of five general components from the point of view of the recipient system: their trophic level of entrance (Marczak, Thompson & Richardson, 2007), the quantity and quality of the exported resource, and the timing and duration of the flux (Subalusky & Post, 2019). The interaction of these components will drive the overall response of the recipient consumers. Large fluxes of a high-quality resource (Marcarelli, Baxter, Mineau & Hall, 2011; Sitters, Atkinson, Guelzow, Kelly & Sullivan, 2015; Subalusky & Post, 2019), are expected to increase the productivity and fitness of recipient consumers (Baxter *et al.*, 2005, Marcarelli *et al.*, 2011). However, influx of a poor-quality resource could dilute *in-situ* resources and generate a negative response from the consumer (Brett, Kainz, Taipale & Seshan, 2009; Kelly, Solomon, Weidel & Jones, 2014). The timing of the availability of the subsidy relative to that of *in situ* production may also impact the response of the recipient consumers (Nakano & Murakami, 2001; Takimoto, Iwata & Murakami, 2002). Lastly, the duration of a subsidy can affect the consumer's population structure, food web structure and ecosystem functions in the recipient ecosystems (Holt, 2008; Sato, Ueda & Takimoto, 2019; Yang, Bastow, Spence & Wright, 2008). Therefore, analyzing multiple subsidy components simultaneously should provide a better understanding of the dynamics of the recipient food web and the potential impact of the subsidy.

Floodplains export a wide variety of detritus and living organisms acting as ecological subsidies to the adjacent main river, potentially increasing the growth and productivity of invertebrates and fish consumers (Bayley, 1995; Farly, Hudon, Cattaneo & Cabana, 2019; Furst *et al.*, 2014; Junk, Bayley & Sparks, 1989). However, the importance of this subsidy is highly context dependant (*e.g.* type of floodplain, timing and size of the flood, recipient organism under study) and may also affect only a subset of the recipient food web (Opperman, Moyle, Larsen, Florsheim & Manfree, 2017). Using stable isotope analysis (SIA), Farly *et al.* (2019) showed that in a temperate river-floodplain system, littoral fish species showed a higher dependence to the prey exported from the floodplain than the main channel species. Studies on the Mississippi river showed that interannual variations in flood characteristics (magnitude and duration) exerted stronger effects on the growth of littoral fish than on main channel species (Gutreuter, Bartels, Irons & Sandheinrich, 1999; Schramm & Eggleton, 2006). The trophic connection to the floodplain subsidy makes small littoral fish species key organisms to identify the factors driving the floodplain contribution.

In temperate river-floodplain systems, the timing of floodplain-derived resource availability to the main river follows a pattern associated with the seasonal inundations, being at its highest during and soon after the flood, followed by a replacement by autochthonous productivity in the river itself as the growing season progresses (Farly *et al.*, 2019; Humphries, Keckeis & Finlayson, 2014; Huryn *et al.*, 2001). Flood duration and magnitude are important drivers of the productivity of the floodplain (Baranyi, Hein, Holarek, Keckeis & Schiemer, 2002; Górski, Collier, Duggan, Taylor & Hamilton, 2013; Junk *et al.*, 1989; Lansac-Tôha *et al.*, 2009) that can potentially impact the subsidy quantity and duration. Therefore, further investigation is required to measure the effect of flood intensity on floodplain contribution to littoral fish. To achieve this goal, investigating years with contrasting flood phenologies should provide an invaluable assessment of the role of floodplain in sustaining littoral river productivity.

The introduction of a subsidy may impact the fitness of consumers in the recipient habitat. Body condition, the weight of organisms corrected for length (Blackwell, Brown & Willis, 2000; Bolger & Connolly, 1989) is a simple measure of fitness which has been shown to be strongly positively correlated with survival, immune response, fecundity and fitness (Brosset *et al.*, 2016; Millar & Hickling, 1990; Stevenson & Woods, 2006 and references herein). The response of body condition to a subsidy can be either positive (Briggs *et al.*, 2012; Takimoto, Iwata & Murakami, 2002) or negative (Kelly, Solomon, Weidel & Jones, 2014), depending on the quality of the trophic subsidy from the donor ecosystem. A subsidy of good quality will result in consumers having a better body condition leading to an increase in fitness. The impacts of the flood regime and the floodplain subsidy on fish body condition has been shown to be related to the quality of the subsidy (Abujanra, Agostinho & Hahn, 2009; Luz-Agostinho, Agostinho, Gomes, Júlio & Fugi, 2009; Ribeiro, Crain & Moyle, 2004). Therefore, the response of body condition of littoral fish species to different levels of subsidy can provide information on its quality and impact on fitness.

Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope ratios of consumers are entirely derived from their diet (DeNiro & Epstein, 1978; Forsberg, Araujo-Lima, Martinelli, Victoria & Bonassi, 1993; Hobson, 1999), therefore allowing the identification of the food sources contributing to their growth (DeNiro & Epstein, 1978; Vander Zanden & Rasmussen, 2001). Owing to the often contrasting $\delta^{13}C$ values of prey items such as invertebrates produced in the floodplain vs the main river (*e.g.* Bertrand, Cabana, Marcogliese & Magnan, 2011; Farly *et al.*, 2019; Huryn *et al.*, 2001), stable isotope analysis (SIA) offers a valuable context-specific tool to track and quantified the relative contribution of the floodplain subsidy to the littoral fish productivity.

Our main objectives were 1) to identify the effects of flood magnitude and duration on the assimilation of the floodplain subsidy and 2) to assess its contribution to the fitness of invertivore littoral fish. To do so, we quantified floodplain subsidy assimilation of five littoral fish species of a large fluvial lake and its relation to fish body condition under different flood events. The positive relationship between invertebrate prey production in the floodplain with the duration and magnitude of the flood, described in temperate systems, should result at the littoral community level in: 1) a greater level of assimilation of the subsidy, and 2) an increase of the subsidy's duration represented by a higher level of floodplain contribution late in the growing season. At the individual level, floodplain contribution and fitness as measured by body condition will 1) be positively influenced by flood magnitude and duration, 2) decrease as growing season advance in response to a decrease and post-flood disappearing of the subsidy availability.

Here we used SIA to examine among-year variation in the seasonality of trophic linkage between a large fluvial lake of the St. Lawrence River and its extensive floodplain (Lessard, 1991). To this end, we collected five small invertivorous littoral fish species (yellow perch (*Perca flavescens*), pumpkinseed (*Lepomis gibbosus*), bridle shiner (*Notropis bifrenatus*), golden shiner (*Notemigonus crysoleucas*), and banded killifish (*Fundulus diaphanus*)) and invertebrates at the beginning (spring) and at the end of the growing period (late summer) for four consecutive years exhibiting markedly different hydrological characteristics. We focused on those five ubiquitous littoral invertivorous fish species as they were found in abundance and previous SI studies have found them to be linked trophically to the floodplain of Lake Saint-Pierre (LSP) (Farly *et al.*, 2019; Bertrand *et al.*, 2011). Using isotopic mixing-models, we tested the effects of inter-annual variability in flood characteristics on the use of floodplain-derived prey and examined its impact on fish fitness using the condition index.

Materials and methods

Study area

Lake Saint-Pierre (LSP) is the largest (≈ 300 km^2) fluvial lake of the St. Lawrence River, situated 75 km downstream of Montreal, Canada (46°12'N, 72°49'W). Water level in LSP varies seasonally by ≈ 1.8 m in average, under the combined influences of the St. Lawrence main stem (≈ 70% of total discharge at Québec, regulated), the Ottawa River (≈ 20% of total, partly regulated) and numerous smaller (≈ 10%, unregulated) tributaries (Morin & Bouchard, 2000). The water level of the St. Lawrence River is regulated since the 1960's by multiple dams along its main course (Moses-Saunders power dam at Cornwall and Beauharnois dam at Beauharnois) and among its main tributaries (Morin & Bouchard, 2000). The LSP floodplain (0-2 yr flood recurrence zone) expands over ≈ 210 km^2 for 5 to 9 weeks between the months of April and June (Lessard, 1991) with agriculture encroaching 14 km^2 of the littoral and floodplain area (Hudon, Jean & Létourneau, 2018).

Field sampling

We established multiple stations (2014 n = 7; 2015 n = 10; 2016 n = 10; 2017 n = 5) distributed on a 10-km transect in the littoral zone along the south shore of the LSP (Fig. 1). In 2014, the stations were located along two transects perpendicular to the shore and distanced by 5 km from each other. All stations were sampled twice, early (June-early July) and late in the growing season (end of August-early September) (Fig. 1). In some years, the seasonal drop in water level prevented the access to the sampling station at the same exact location and some stations were located further away offshore to maintain the same number of stations and similar water column depth (mean ± SD cm = 91.9 ± 34.56). Three additional stations located at the margin of the floodplain forest or higher elevation were also sampled once early in the growing season of 2014 (n = 1) and 2016 (n = 2), bringing the total number of sampled stations to 66. At each station, multiple hauls (1 to 4 hauls) were made with a seine (12.19 m wide x 1.5 m high, 2 mm mesh). Invertebrates were collected at the same sites using a kick net (500 μm mesh) and sampling was expanded to multiple other stations in 2014 to cover both floodplain and main river habitats (delimited by the presence dense marsh).

Fish were rapidly anesthetized in a clove oil solution (1 ml oil/25 l river water), euthanized by cervical dislocation, and immediately put on ice. Invertebrates were placed in plastic bags and immediately put on ice. At the end of the day, fish and invertebrates were frozen at -20 °C (2014 and 2015) or -80 °C (2016 and 2017) at the Centre de Recherche sur les Interactions Bassins Versant-Écosystèmes Aquatiques (RIVE), Université du Québec à Trois-Rivières, until further analysis.

Laboratory analyses

Fish muscle tissues and invertebrates were prepared for stable isotope analysis following the protocol presented in Farly *et al.* (2019). Organisms captured in 2016 and 2017 were lyophilized for at least 24 hours instead of being dried (60 °C for at least 48 h). Fish muscle $\delta^{13}C$ values were corrected for their lipid content using a combination of models from Kiljunen *et al.* (2006) and Post *et al.* (2007) as proposed by Skinner, Martin & Moore (2016).

Measurement of flooding intensity

All statistical analyses were performed using R software version 3.4.3 (R Development Core Team 2017). First, we looked at the hydrological differences between the four years sampled during our study. Mean daily water level data at Sorel gauge station (station ID: 02OJ022) between 1966 and 2017 were obtained from the Fisheries and Ocean Canada website (http://www.meds-sdmm.dfo-mpo.gc.ca) consulted in February 2018).

Areal biomass production of aquatic invertebrates in floodplains is strongly related to the duration of the presence of water (Baranyi *et al.*, 2002; Górski *et al.*, 2013; Junk *et al.*, 1989; Lansac-Tôha *et al.*, 2009). We therefore sought to integrate the duration of flooding and its daily areal extent by calculating the annual cumulative flooded area for the entire LSP (hereafter designated as ACFA). This index of flooding intensity was defined as the sum of daily floodplain area under at least 5 cm of water between April 1st and the end of the flood. The 5 cm threshold was determined by field observations of the minimal depth at which fish were observed. The lower limit of the floodplain at which the river enters the floodplain (elevation = 4.57 m IGLD85), is defined as the median of the minimal level values observed (1966-2017) between April 1st (day of year 91) and July 1st (day of year 181). The floodplain was divided in sections of 5 cm elevation obtained from the LIDAR and the area for each section was measured (km^2). Then, the floodplain sections under at least 5 cm were identified by the comparison of the ground elevation of their upper limit of the section + 5 cm to the mean daily water level of the entire LSP. Finally, the areas of those sections were summed to estimate the daily floodplain area under at least 5 cm.

Accounting for isotopic turnover time in consumers to track an ecological subsidy

Following a diet switch, the isotope turnover time of a consumer is strongly related to its body size (Weidel, Carpenter, Kitchell & Vander Zanden, 2011). A small-bodied fish, with higher specific metabolic rate and relative growth rate, will quickly reach a new equilibrium and may retain the new asymptotic signal until the subsidy declines, irrespective of its duration. This contrasts with a larger fish that may reach equilibrium only much later or not at all given the same phenology of the subsidy. Thus, even though a fish may hypothetically consume only prey from the floodplain, a complete reliance on this subsidy would not be apparent if equilibrium has not been reached with this new food source. Isotopic turnover time must therefore be considered to track the assimilation of a seasonal subsidy.

Time to reach equilibrium can be estimated at four times the isotopic half-live (HL) of the tissue analyzed (Hobson & Clark, 1992). The turnover time (TT) of the tissue (muscle or entire fish) can be approximated as:

$$TT = 4 \ln(2)/(\lambda) \qquad (1)$$

where λ is the turnover rate of the tissue. λ can be predicted by the allometric model proposed by Weidel *et al.* (2011):

$$\ln(\lambda) = -3.65 - 0.2 \ln (W_i) \qquad (2)$$

where W_i is the weight of the individual in grams. Combining equations 1 and 2, we can express TT (in days) as a function of body weight:

$$TT = 106.7 * W^{0.2} \qquad (3)$$

For example, fish weighing 1 g and 100 g have turnover times of 107 and 268 days, respectively. The window of assimilation of an individual designates the period equals to the turnover time (TT predicted from equ. 3) prior to its capture (Fig. 2). The variable mean flooded area specific to each individual fish (hereafter designed as MFA_i)

describes its potential exposure, scaled for body size, to the trophic resources originating from the floodplain. MFA_I is defined as the integral of the daily floodplain area under at least 5 cm of water divided by the duration in days of the period of time required following a diet switch for the fish individual to reach isotopic equilibrium (based on TT predicted from equ. 3) (Fig. 2). MFA_I focuses only on the time frame directly affecting the isotopic ratio of the individual and is more representative of the influence of the flood characteristics on the floodplain subsidy assimilation of an individual than their annual counterpart (ACFA).

Trophic contribution of the floodplain

To investigate the temporal change of the trophic resource assimilated by littoral fish, we looked at the difference between the early and late growing season standard ellipses of the N-C isotopic ratios. The standard ellipses were defined using the function "*standard.ellipse*" (Jackson, Inger, Parnell & Bearhop, 2011) from the package SIAR (Stable Isotope Analysis in R; Parnell, Inger, Bearhop & Jackson, 2008). Secondly, we estimated the relative contribution of the food sources originating from the floodplain (hereafter referred as "floodplain contribution") for fish sampled in the early and late growing seasons. The floodplain contribution was assessed using an isotopic mixing model set in a Bayesian framework. We obtained the posterior probability distribution for the dietary proportion contributed by the floodplain source for each specimen, species, and community (five species combined) by sampling season (early and late growing season) using the function "*siarsolomcmcv4*" (individual level) and "*siarmcmcdirichletv4*" (species and community level) from the package SIAR. First, invertebrates were divided into two groups based on their site of capture (littoral/floodplain vs river) to establish the isotopic signatures of both sources. Invertebrates from the littoral/floodplain zone (defined as the portion of the LSP situated at a higher elevation then the beginning of the dense marsh) were used to define the floodplain source end-member and invertebrates captured outside of the littoral/floodplain zone defined the main river food source end-member. Invertebrates of all years were pooled together due to a reduced sampling campaign in 2015, 2016 and

2017. The statistical significance of $\delta^{13}C$ and $\delta^{15}N$ differences between invertebrates originating from the floodplain and river sources was tested with a t-test. Due to an important overlap between food sources in the LSP, the known large trophic fractionation of $\delta^{15}N$ (Post, 2002) and given that prey may belong to different trophic levels, we ran a two-sources mixing model with $\delta^{13}C$ only. Means and SDs of $\delta^{13}C$ of these sources, together with $\delta^{13}C$ values for individual fish and carbon trophic fractionation were included as input for SIAR. We used the carbon trophic fractionation ($\Delta\delta^{13}C = -0.1 \pm 0.96$) proposed by Post (2002). A vague Beta (1, 1) prior distribution for the mixing proportion was used to allow the results to be influenced primarily by the data (Parnell, Inger, Bearhop & Jackson, 2010).

Inter-annual, seasonal and species effect on the floodplain contribution

First, we analysed the effect of ACFA on the level of floodplain contribution estimated for the early and late growing season for our five species pooled together to detect the influence of the flood regime on the contribution of the floodplain subsidy to littoral species and the duration of the subsidy availability. Secondly, we looked at the specific pattern of assimilation of the subsidy in each season to test for the presence of a general pattern of floodplain contribution common for each species independently.

Impact of MFA_I on floodplain contribution and body condition

Lastly, we looked at the impact of flood regime on the floodplain contribution and body condition at the individual level since each individual has a distinct turnover time and date of capture leading to unique potential levels of exposure to the annual flood regime. The impact of flood regime on floodplain contribution for individual fish (median of the output from the function *"siarsolomcmcv4")* was tested with a generalized linear mixed model using a beta distribution (package: glmmTMB) for both early and late growth seasons combined. The best models were identified using the Akaike information criterion (AIC, Burnham & Anderson, 1998, 2002) calculated for every possible combination of the fixed effect variables while including station as a random effect variable in all models. The fixed-effect variables were: 1) mean flooded area for each individual fish (MFA_I), 2) the day of fish capture (Day), 3) year of capture (Year), 4) the interaction between Day and Year (Day * Year), and 5) the species identity (species). The temporal and species variables were included in the analysis because prior analysis and results presented in Farly *et al.* (2019) suggest a negative effect of the day of capture and the presence of potential inter-specific differences in the pattern of assimilation of the subsidy. Therefore, to isolate the impact of the hydrology on the floodplain contribution at the individual level those variables must be taken into consideration. We include year of capture and its interaction with the variable day of capture due to different effect size of day of capture on the floodplain contribution when looking at each year separately. Furthermore, to avoid pseudo-replication resulting from multiple captures at the same station, sampling station was considered as a random effect in every model.

We repeated the analysis using the same independent variables but with body condition as the dependent variable to assess the impact of hydrology on the fish body condition. In this case, we used the function "lmer" (package: lme4) to fit the generalized linear mixed model using a normal distribution and then we used the function "dredge" (package: MuMin) to identify the best model based on their AIC score. The body condition for each individual fish was calculated from the residual values centered on the mean generated by the specific regressions between ln total weight and ln total length (Blackwell *et al.*, 2000). Lastly, we used the function "lm" to fit linear regressions using a normal distribution between floodplain contribution (independent variable) and body condition (dependent variable) for each species separately.

Results

Inter-annual patterns in floods

The four years (2014 to 2017) investigated exhibited sharp differences in flood phenology (Fig. 3) covering most of the historical hydrological variability observed throughout 1966-2017 (see Supplementary Material S.M.1. and S.M.2.). Floods observed in 2014 and 2016 had magnitudes (highest water level recorded during the flood) and durations close to the historical median (Fig. 3 and S.M.1.). The flood recorded in 2015 showed one of the lowest magnitudes (47th) and shortest durations (46th) (Fig. 3 and S.M.1.). Conversely, the year of 2017 had a flood of extreme magnitude (5th) and duration (8th). Thus, the serendipitous comparison of those four consecutive years allowed us to investigate the impact of different flood regimes on the temporal pattern of assimilation of the floodplain subsidy by the littoral fish community and its potential effect on fish condition.

Isotopic ratios of invertebrate prey

The $\delta^{13}C$ values of invertebrates from the littoral/floodplain zone (mean $\delta^{13}C \pm SD$ = -33.2‰ ± 2.82, N = 125) were significantly more negative than the isotopic values of invertebrates collected in the main river (mean $\delta^{13}C \pm SD$ =-21.7‰ ± 3.21, N = 47) (*t*-test: t = -22.841, DF = 170, p-value < 0.001, all years combined) (Fig. 4). The $\delta^{15}N$ values of invertebrates from the littoral/floodplain zone ($\delta^{15}N \pm SD$ =7.1 ± 1.81, N = 125) and the main river (mean $\delta^{15}N \pm SD$ = 10.0 ± 1.71, N = 47) also differed statistically (*t*-test: t =-9.5883, DF = 179, p-value < 0.001), but showed a substantial overlap between floodplain and main river habitats (Fig. 4). Inter-annual comparison of the $\delta^{13}C$ of invertebrates did not show difference amongst year in each zone (Fig. 4) allowing us to pool all invertebrates together regardless of the years of capture for further analysis.

Fish isotopic ratios

In total, we captured 810 individuals belonging to five species (yellow perch, bridle shiner, golden shiner, pumpkinseed, banded killifish). All species were captured in the early and late growing seasons of each year with very few exceptions (see Supplementary Material S.M.3.). Isotopic ratios of all fish fell within the isotopic range covered by the invertebrates from the floodplain and the main river (Fig. 5). No overlap between the early and late growing season ellipses were found in 2014 and 2016 (seasonal overlap = 0%) suggesting a seasonal switch in the food sources exploited. In contrast, the seasonal ellipses in 2015 and 2017 overlapped, indicating that fish exploited similar trophic resources during both the early and late growth season.

Floodplain contribution to the littoral fish community

For fish captured in the early part of the growth season, floodplain contribution was always high (> 0.60), except for 2015 (0.52), which coincided with the smallest floodplain extent (ACFA = 1 287 km^2 Day) (Table1). In contrast, fish captured late in the season exhibited a substantial drop (2-4-fold) in floodplain contribution for all years, except for fish caught in 2017, which were influenced by the floodplain much later in the season (0.60) owing to the extended flooding period (ACFA = 18 217 km^2 Day) (Table 1).

All five species followed a similar general trend of decreasing floodplain contribution from the early to late growing season. Furthermore, for a specific season (early and late growing seasons) inter-annual comparisons showed that as ACFA increases the trophic contribution of the floodplain to higher level for all species (Fig. 6).

From all possible models explaining the floodplain contribution at the individual level for the entire growing season, the model including all variables and the interaction had statistically better performance than the others (second best model Δ AIC =11.6) (see Supplementary Material S.M.4.). The MFA_I had a positive effect size (effect size = 0.008, SE = 0.001), supporting our initial hypothesis that high water level during the temporal window of assimilation of the individual should result in a high floodplain contribution (see Supplementary Materials S.M.5.). Conversely, the variable day of capture had a negative effect (effect size = -0.011, SE = 0.002) suggesting that floodplain contribution decreased as the growing season progressed. However, the significant interaction between day of capture and year of capture suggested that the annual flood regime impacted the effect size of day of capture. Species identity was also a significant variable in the best model suggesting that floodplain contribution differed among species. The regression coefficients specific to each species were, in growing order of magnitude, banded killifish < pumpkinseed ($B = 0.178$) < yellow perch ($B = 0.194$) < golden shiner ($B = 0.259$) < bridle shiner ($B = 0.333$). However, only banded killifish was significantly different to all other species (see Supplementary Material S.M.6.). Other species were statistically similar to at least one other specie (S.M.6.).

Body condition and integrated flooded area (MFA_I)

From all possible models explaining body condition for the entire growing season, the model including only the variable MFA_I had a statistically better performance than the others (second best model Δ AIC = 6.65) (see Supplementary Material S.M.7.). MFA_I had a positive effect size (effect size = 0.001, SE = 0.0002), supporting our hypothesis that larger and longer flood results in littoral fish with higher body condition (Fig. 7). Models including species identity had the lowest AIC values meaning that it had a low predicting power and there is no inter-specific difference in the body condition response among the five littoral species.

The linear relationship between body condition and MFA_I showed a significant positive relationship for all species when combined ($p < 0.001$) (Fig. 7). This result supports our initial hypothesis that an increase in flood duration and magnitude (leading to an increase in MFA_I) increases body condition. The analysis performed on each of those five species separately revealed a statistically significant positive relationship between body condition and MFA_I for all 5 species ($p < 0.05$) (Fig. 7). However, the explained variance by the linear relationship was low (r^2: 0,025 to 0.146); all relationships were positive.

Only body condition of golden shiner (effect size = 0.344; $p < 0.001$) and banded killifish (effect size = 0.28; $p = 0.038$) showed a significantly positive relationship to floodplain contribution (see Supplementary Material S.M.8.) suggesting inter-specific variability in the response of body condition to the level of floodplain contribution.

Discussion

Results from our four-year study supported our initial hypothesis that flood regime plays an important role determining the temporal aspect of the source of energy sustaining the littoral food web by affecting three of the four main characteristics of the floodplain subsidy (timing, duration and quantity). As flood increases in magnitude and duration, the littoral fish community relies more heavily and for a longer period on floodplain subsidies (Fig. 6). Furthermore, fish body condition of all species responded positively to longer and higher floods and the body condition of two species showed a positive relationship with floodplain contribution indicating a subsidy of good quality exported from the floodplain.

Inter-annual floodplain subsidy assimilation

The results obtained during the four years of our study support a strong seasonal pattern in the source of energy sustaining the littoral food web. These results were also found in other temperate river/floodplain systems (Hladyz, Nielsen, Suter & Krull, 2012; Huryn *et al.*, 2001; Humphries *et al.*, 2014). The level of floodplain contribution and its rate of decrease through the growing season showed variability among years driven by the flood regime (Table 1 and 2; Fig. 6). As expected, years of extreme hydrological regimes (2015 and 2017) showed distinct patterns of temporal floodplain contribution compared to average flood years (2014, 2016). The lowest flood year (2015) yielded lower and shorter-term floodplain contributions than the highest flood year (2017), which brought high and prolonged contributions. Nevertheless, even in the low-flood year (2015), floodplain subsidies still accounted for half of the energy of fish captured early in the growing season (52.1%, Table 1, Fig. 6). In contrast, the large and long flood of 2017 sustained littoral species throughout the growing season, with no apparent shifting to resources from the main river during the growing season (Table 1, Fig. 6).

As we hypothesized, lower MFA_I resulted in a decrease in the relative contribution of the subsidy provided by the floodplain. This should be the result of the lower secondary productivity associated with short and small flood (Baranyi *et al.*, 2002; Górski *et al.*, 2013; Lansac-Tôha *et al.*, 2009). Consequently, this limits the amount of subsidy available to be ingested during the window of assimilation of the individual, diminishing its contribution. Although, the size of the window of assimilation of an individual, the annual hydrological regime and the moment of capture determine the MFA_I values of an individual. Low MFA_I values are generally observed at the end of the growing season for small individuals (small temporal window of assimilation) in an average flood year (Table 1). However, low values can also be observed early in the growing season during years with small floods. Conversely, large floods such as recorded in 2017, can produce high MFA_I during the entire growing season leading to high level of floodplain contribution over the entire growing season (Table 1).

Species patterns and Lake Saint-Pierre fish community

Species identity was a variable found in the best model suggesting interspecific variability in the assimilation of the floodplain subsidy. The studied species were mostly small littoral invertivorous species with similar high turnover rates (S.M.3.). Therefore, the interspecific differences observed were most likely due to a disparity in the level of dependency to the floodplain subsidy emerging from factors other than different turnover rates or trophic level among species. Even tough interspecific variation was found, all five species level of floodplain contribution exhibited a similar negative response to the reduction of flood magnitude and duration (ACFA; Fig. 6 A and B) supporting the idea that the overall annual pattern of resources sustaining the littoral fish species is mainly driven by the hydrological regime.

Although, our sampling did not cover the entire LSP fish community, earlier studies concluded that species mostly associated with the main channel do not display a strong dependency to the floodplain subsidy (Dettmers, Wahl, Soluk & Gutreuter, 2001; Gutreuter *et al.*, 1999). Furthermore, a previous study in the LSP also showed that the main river fish community, mostly composed of large individuals and large catostomids, did not strongly rely on floodplain subsidies and did not respond to temporal variability in the main source of energy sustaining their productivity during a typical year of flooding (Farly *et al.*, 2019). This suggests that a portion of the LSP food web (the main river) is not or at least only minimally influenced by the effect of the inter-annual variability in the flood regime. Therefore, the main river community should exhibit less variability in their productivity among years compared to the littoral fish community.

Body condition

Our study is one of the few that directly measured the impact of a subsidy on the fitness of the recipient consumer. Our results clearly support that the conditions induced by larger and longer flood have a positive impact on the body condition of five abundant invertivore littoral species in our system (Fig. 7, S.M.7.). Positive responses to an increase in flood magnitude and duration have been also observed among fish species in other systems. Gutreuter *et al.* (1999) showed that largemouth bass (*Micropterus salmoides*) growth is higher during years of large floods than years of smaller floods. In the LSP system, yellow perch growth has shown to be positively impacted by high water level through the growing season (Glémet & Rodríguez, 2007). Therefore, years exhibiting floods of large magnitude and long duration should result in higher growth and productivity of littoral fish species.

Our results showed inter-specific variation in the response of body condition to floodplain contribution (S.M.8.), as observed in other systems (Ribeiro *et al.*, 2004; Luz-Agosthino *et al.,* 2009). Only two species (golden shiner and banded killifish) displayed statistically significant evidence of a positive impact of the assimilation of the subsidy on their body condition. Golden shiner and banded killifish have high tolerance to low dissolved oxygen compared to the other species (Tang *et al.*, 2020), allowing them to exploit the subsidy directly in the floodplain during period of low dissolved oxygen concentration (Górski *et al.*, 2013; Hennings, Gresswell & Fleming, 2007). By accessing the floodplain, those species would be exposed in the cold spring to higher water temperature than fish in the main river and potentially to lower predation pressure due to high habitat complexity (Schneider & Winemiller, 2008), all factors favorizing higher growth and body condition.

Human impacts on flow regime

A meta-analysis by Gounand, Little, Harvey & Altermatt (2018) concluded that the low primary production of streams and lakes ($\approx$ 55 g C m^{-2} yr^{-1}) in comparison to the important fluxes of allochthonous carbon that they receive, might render them especially vulnerable to alteration of subsidy flow. The annual primary production of LSP (105 g C m^{-2} yr^{-1}, Vis *et al.*, 2007) is slightly above the mean reported by Gounand *et al.* (2018) for freshwater systems. However, Vis *et al.* (2007) showed that the annual primary production is not evenly distributed through the year and that epiphyton and phytoplankton productivity exhibited low level in May and early June before reaching their highest value in July and August. Zooplankton biomass also follows a similar temporal pattern in in the LSP (Savignac, 1985). However, zooplankton biomass in the floodplain was 3 to 60 times higher in April and May compared to the river during the same period. Therefore, the peak of subsidy availability coincides with the period of low *in situ* production (spring and early summer) in the main river. This strongly suggests that the main river should be highly sensitive to changes in the subsidy.

Most of temperate floodplains are subject to anthropogenic pressures, such as flow regulation (e.g., dams), human encroachment and climate change (Tockner & Stanford, 2002). Flow regulation and human encroachment alter the floodplain-river connectivity (Bunn & Arthington, 2002) and negatively affect two main flood characteristics (magnitude and duration) driving the subsidy production and its delivery to the river (Moyle & Mount, 2007; Nilsson, Reidy, Dynesius & Revenga, 2005; Whipple, Viers & Dahlke, 2017). The impacts of climate change on the flood regime of rivers are expected to vary worldwide based on their region and their flood generating mechanism, such as intense rainfall on saturated soil or snow melt (Arnell & Gosling, 2016; Burn & Whitfield, 2016, 2017). Consequently, by altering the flood regime, anthropogenic pressures affect the resources sustaining the littoral food web by lowering the quantity of subsidy produced and exported as well as modifying its temporal pattern of availability to the littoral fish community. Thus, their impacts on floodplain subsidy and potentially on fish fitness will be negative in systems with flood regime response similar to the LSP.

Furthermore, those same anthropogenic pressures can potentially affect other sources of subsidies (Giling, Mac Nally & Thompson, 2015) and also negatively impact the availability of spawning and nursery habitat of littoral fish species such as the northern pike (*Esox lucius*) (Foubert, Lecomte, Brodeur, Le Pichot & Mingelbier, 2020; Mingelbier, Brodeur & Morin, 2005). By altering multiple essential aspects (food resource, spawning and early development), those cumulative negative impacts combined to other human induced pressures affect profoundly littoral fish species as already observed in the LSP (reduction of their abundance; Magnan *et al.,* 2017) leading to a fish community mainly composed of main river fish and alien species (Galat & Lipkin, 2000; Moyle, Crain & Whitener, 2007; Moyle & Mount, 2007).

Conclusion

In conclusion, by measuring the floodplain contribution during four distinct hydrological years with SIA, this study shows that flood regime drives the contribution and the period of availability (duration) of the subsidy to the productivity of the littoral fish community and demonstrates a clear positive relationship between the flood magnitude and duration and body condition of five littoral fish species. Furthermore, the positive response of body condition for two of the five species we investigated indicated that the floodplain exported good quality subsidies for some littoral fish species. Therefore, anthropic pressures altering the hydrological regime of a river have a negative effect on the capacity of a floodplain to sustain the littoral fish community and producing individuals with high fitness. Our study enriches the understanding of the influence of the hydrological regime on the structure and dynamics of the food web of a temperate river/floodplain system.

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Tables

Table 1 Annual Cumulative flooded area (ACFA, km2 day) for years 2014-2017, number of individuals, individual mean flooded area (MFAI) (mean ± 95% confidence interval) and proportion of floodplain contribution to fish muscle tissue (median ± 95% credibility interval) for the early (EGS) and late (LGS) portion of the growing season of each year.

		Number of individuals		Mean MFA_I (km^2 day) (95% CI)		Floodplain contribution to fish muscle tissue Median proportion (95% CI)	
Year	ACFA (km^2 day)	EGS	LGS	EGS	LGS	EGS	LGS
2014	9 148	72	61	91.5 (87.1-95.9)	44.9 (39.7-50.1)	0.62 (0.57-0.67)	0.15 (0.09-0.20)
2015	1 287	80	121	18.2 (17.7-18.6)	8.2 (7.7-8.6)	0.52 (0.48-0.56)	0.34 (0.30-0.38)
2016	6 448	211	165	92.4 (91.1-93.8)	19.4 (16.7-22.1)	0.65 (0.63-0.68)	0.28 (0.24-0.32)
2017	18 217	54	46	138.2 (132.8-143.6)	77.8 (72.5-83.2)	0.65 (0.60-0.71)	0.60 (0.54-0.66)

Figure legends

Figure 1. Location of sampling sites in Lake Saint-Pierre in 2014 (circle), 2015 (squares), 2016 (triangles) and 2017 (crosses). Flow direction is indicated by the arrow. The annual floodplain (littoral/floodplain zone) lies between the annual maximum level and the limit of dense emergent marsh vegetation represented by the northern limit of the red area (2014: green area; 2015: red area; 2016: yellow area; 2017: purple). White symbols: sampled only early in the growing season. Grey symbols: sampled both during early and late growing seasons. Black symbols: sampled only in the late growing season.

Figure 2. Conceptual models showing the window of assimilation and its impact on MFA$_I$ for two hypothetical fish of different size: A) a larger fish with an isotopic half-life = 25 days, duration of the window of assimilation = 100 days; B) a smaller fish with an isotopic half-life = 12.5 days, duration of the window of assimilation = 50 days. The historical median flooded area under at least 5 cm of water is plotted against the day of the year. Annual cumulative flooded area (ACFA) is represented by the area under the curve between April 1st and the end of the flood.

Figure 3. Hydrographs of the four sampled years and the historical median of the last 51 years. Mean daily water level (m, IGLD85) in Lake Saint-Pierre measured in 2014 (black line), 2015 (red line), 2016 (green line) and 2017 (blue line) together with the historical median (dotted grey line, 1966-2017). Elevation of the lower limit of the floodplain (4.57 m IGLD85) (dashed black line). Colored dots indicate the sampled date. Mean daily water level data at Sorel gauge station (station ID: 02OJ022) were obtained from the Fisheries and Ocean Canada website (http://www.meds-sdmm.dfo-mpo.gc.ca, consulted in February 2018).

Figure 4. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic ratios of invertebrates in the littoral/floodplain zone (black symbols) and in the main river (red symbols) for 2014 (open circles), 2015 (open triangle), 2016 (hairline crosses) and 2017 (hairline x).

Figure 5. Isotopic ratios of individual fish from five species pooled (yellow perch, bridle shiner, golden shiner, pumpkinseed, banded killifish) captured during the early (EGS, open circles) and late (LGS, crosses) growth season, with their standard ellipses (EGS, full black line; LGS, full grey line). For each year, the intensity of the flood, measured as the annual cumulative floodplain area (ACFA, km^2) is indicated. Baseline values (mean ± 2 SD) for invertebrates (four years combined) collected in the littoral/floodplain zone (full circle) and the main river (full squares) are corrected for the expected trophic fractionation between fish and their potential prey ($\Delta\ \delta\ ^{13}C$ = -0.1 ± 0.96; $\Delta\ \delta\ ^{15}N$ =3.4 ± 0.99; Post, 2002).

Figure 6. Floodplain contribution (Median proportion ± 95% credible interval) to muscle tissue of five fish species in relation to the annual cumulative flooded area (ACFA) during A) the early growing season and B) the late growing season. For clarity, the points were spread horizontally and the species positions along the x-axis were adjusted to eliminate overlap between species from the same years. For each year the actual ACFA value is represented by the banded killifish.

Figure 7. Relation between body condition (residuals generated from the species-specific relationship between the ln-transformed mass and ln-transformed total length of fish individuals) and the individual mean flooded area (MFAI) for both seasons combined (early and late growing season).

Figures

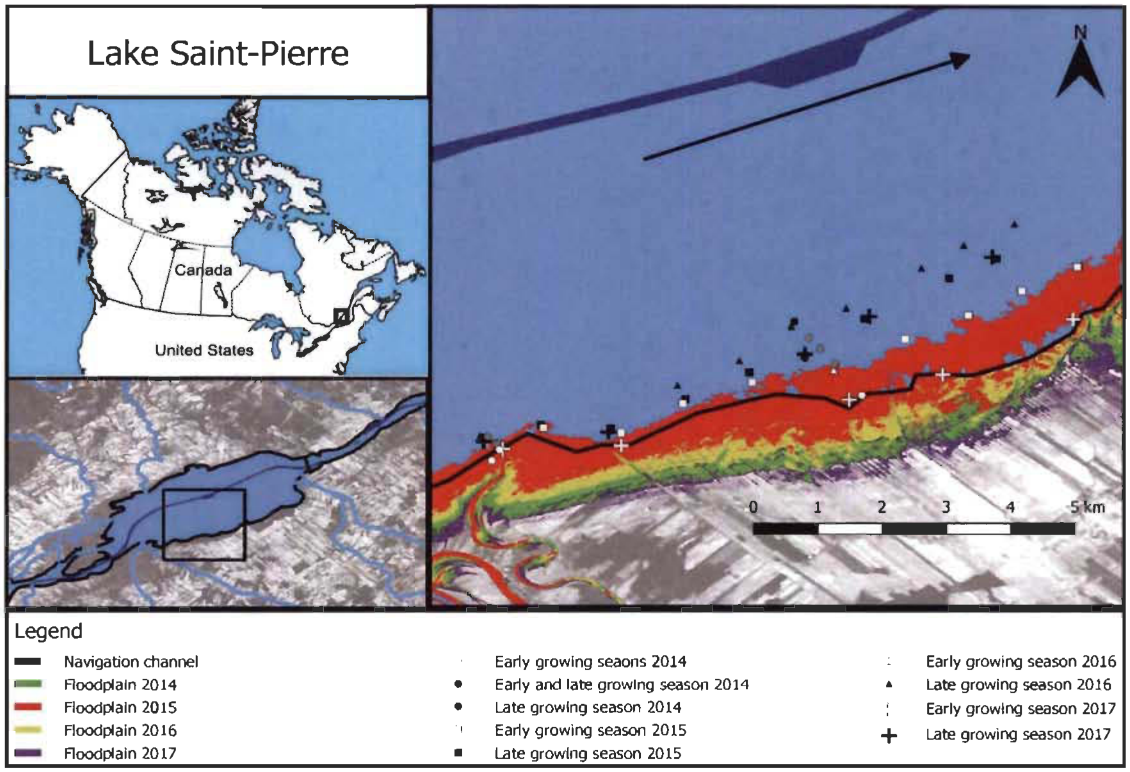


Figure 1.

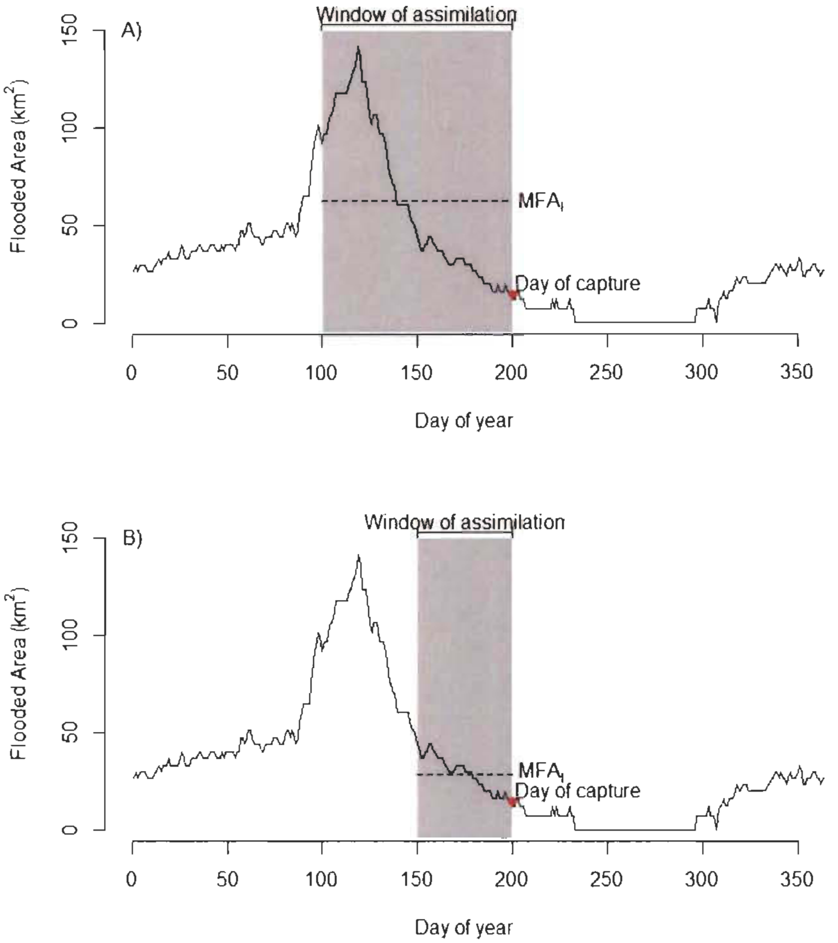

A)
Window of assimilation
MFA$_i$
Day of capture
Flooded Area (km^2)
0
50
100
150
0
50
100
150
200
250
300
350
Day of year
B)
Window of assimilation
MFA$_i$
Day of capture
Flooded Area (km^2)
0
50
100
150
0
50
100
150
200
250
300
350
Day of year

Figure 2.

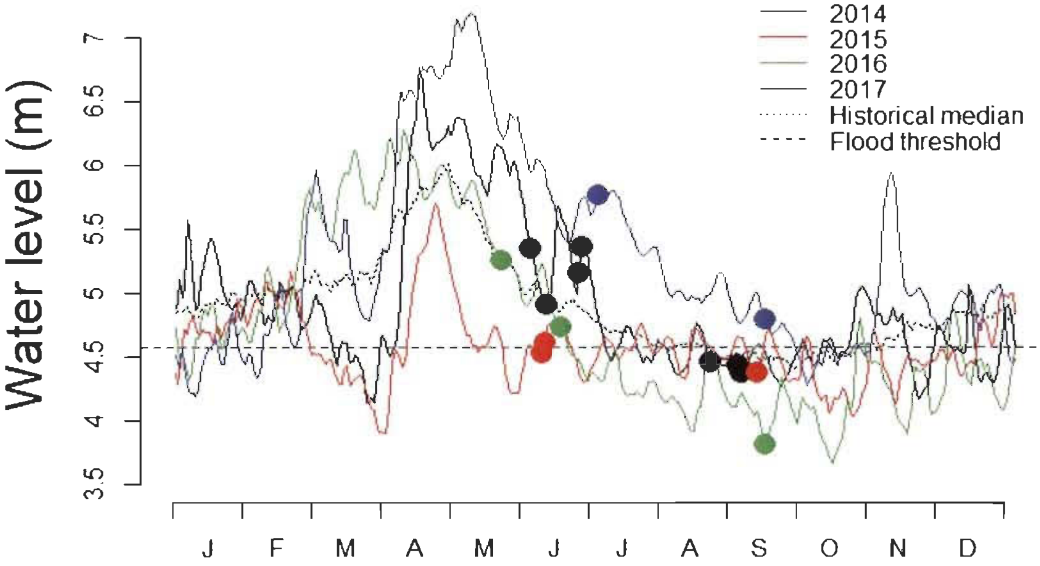

Water level (m)
3.5
4
4.5
5
5.5
6
6.5
7
J
F
M
A
M
J
J
A
S
O
N
D
2014
2015
2016
2017
Historical median
Flood threshold

Figure 3.

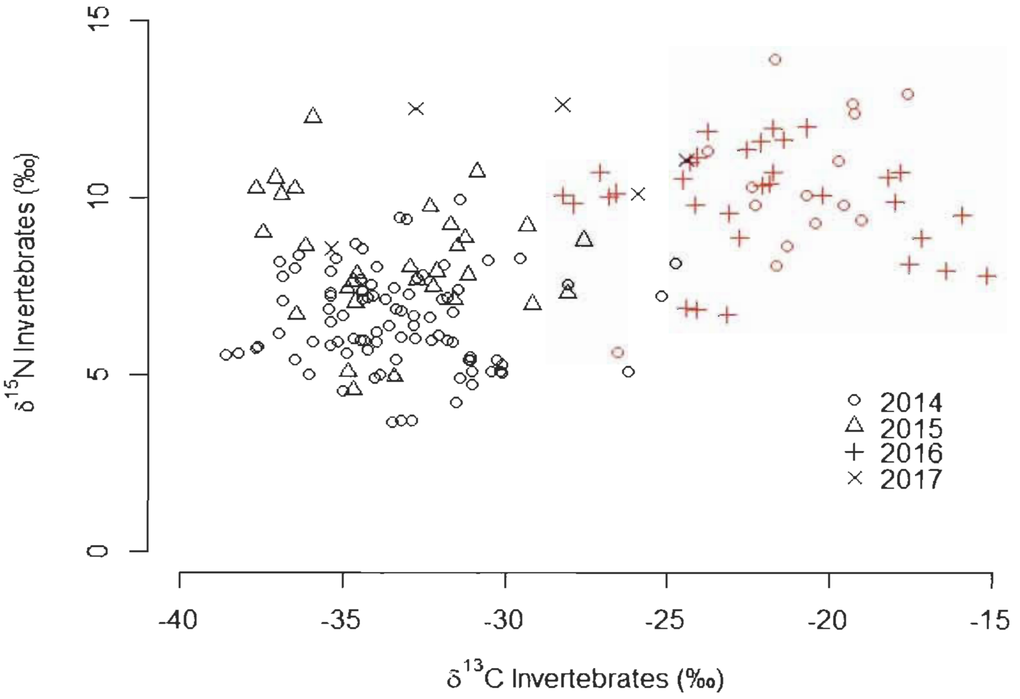

0
5
10
15
δ^{15}N Invertebrates (‰)
-40
-35
-30
-25
-20
-15
δ^{13}C Invertebrates (‰)
○ 2014
△ 2015
+ 2016
× 2017

Figure 4.

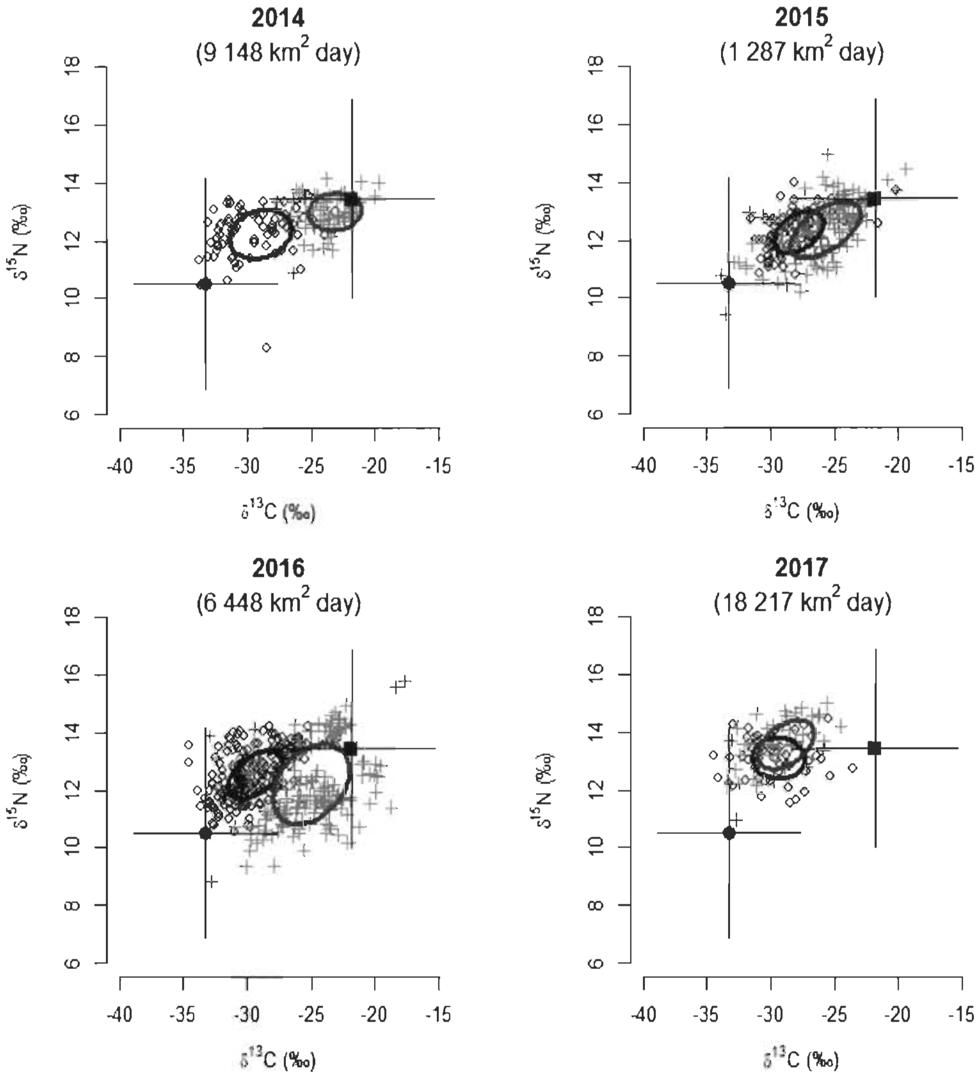

2014
(9 148 km^2 day)
2015
(1 287 km^2 day)
2016
(6 448 km^2 day)
2017
(18 217 km^2 day)
δ^{15}N (‰)
δ^{13}C (‰)
6
8
10
12
14
16
18
-40
-35
-30
-25
-20
-15

Figure 5.

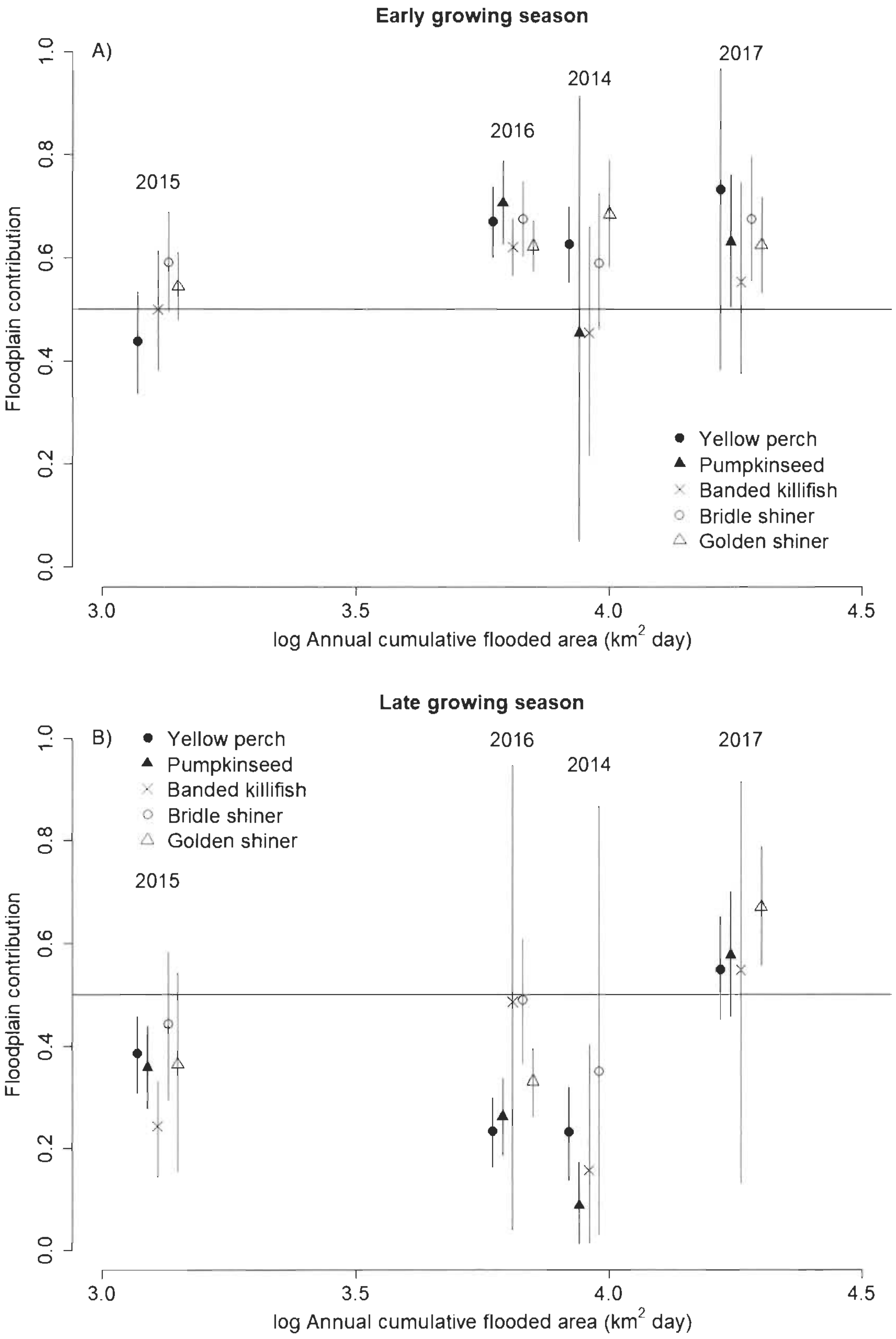

Early growing season
A)
Floodplain contribution
0.0
0.2
0.4
0.6
0.8
1.0
2015
2016
2014
2017
● Yellow perch
▲ Pumpkinseed
× Banded killifish
○ Bridle shiner
△ Golden shiner
3.0
3.5
4.0
4.5
log Annual cumulative flooded area (km^2 day)
Late growing season
B)
● Yellow perch
▲ Pumpkinseed
× Banded killifish
○ Bridle shiner
△ Golden shiner
Floodplain contribution
0.0
0.2
0.4
0.6
0.8
1.0
2015
2016
2014
2017
3.0
3.5
4.0
4.5
log Annual cumulative flooded area (km^2 day)

Figure 6.

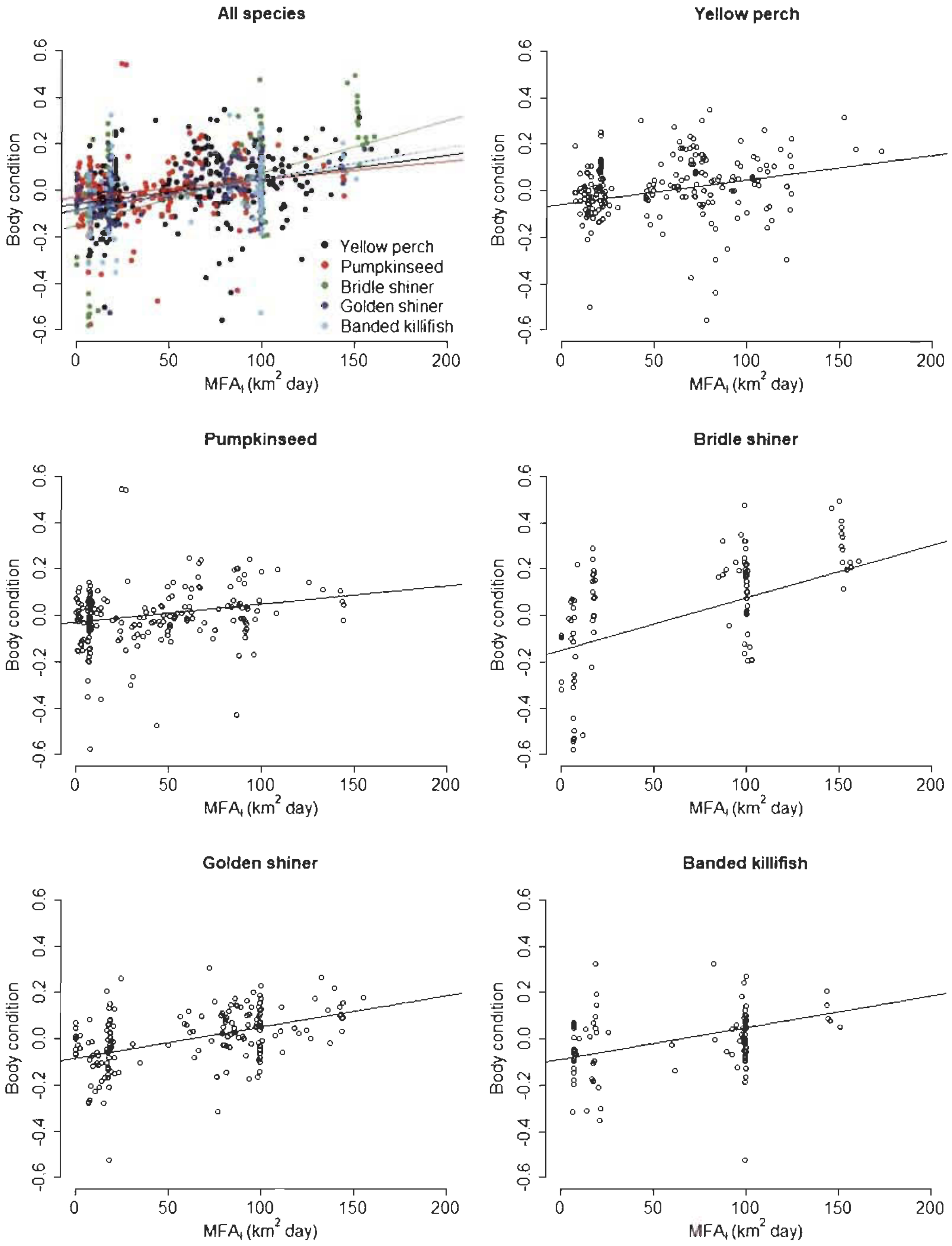
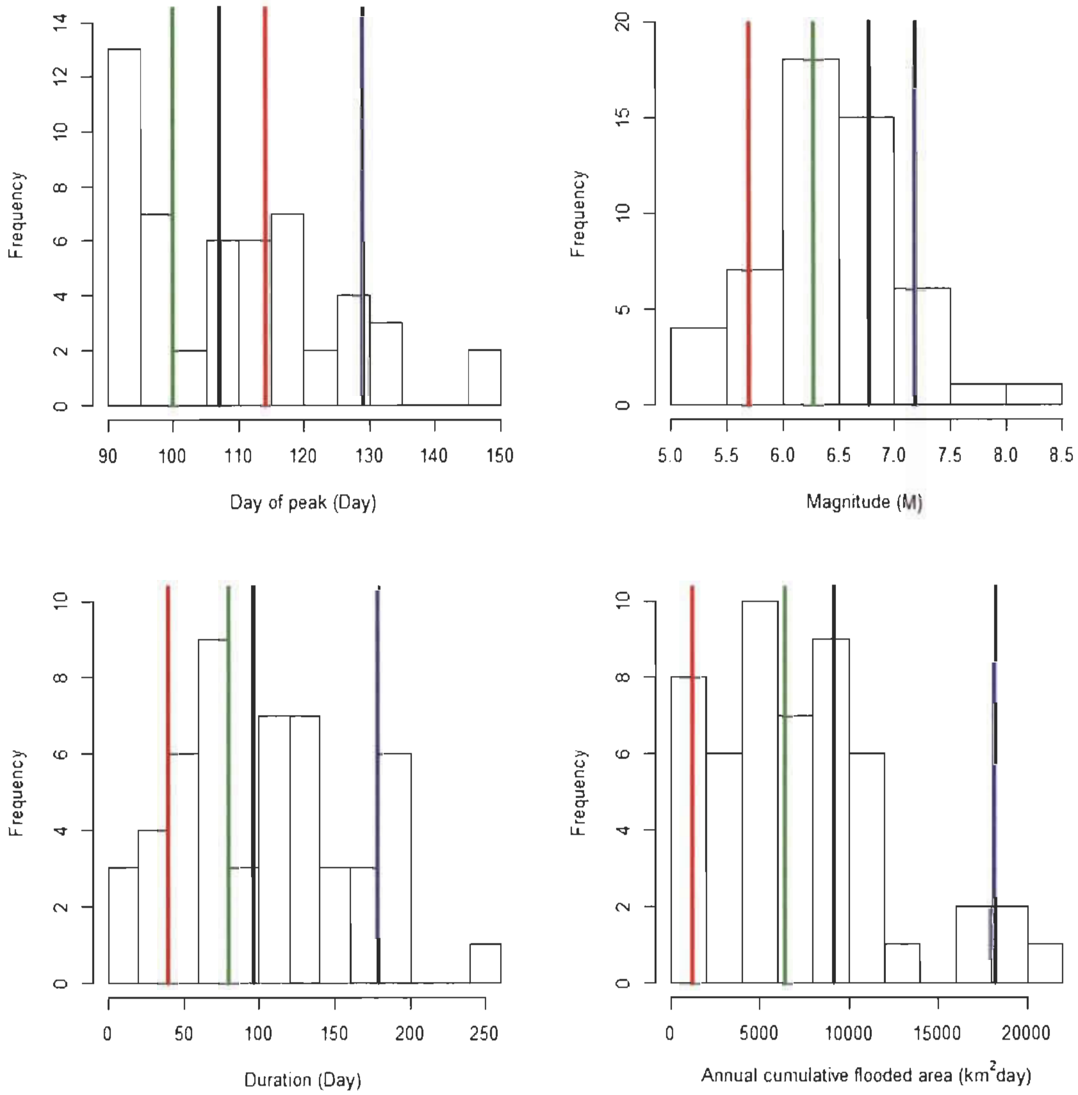

All species
Yellow perch
Pumpkinseed
Bridle shiner
Golden shiner
Banded killifish
Yellow perch
Pumpkinseed
Bridle shiner
Golden shiner
Banded killifish
Body condition
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
0
50
100
150
200
MFA$_i$ (km^2 day)

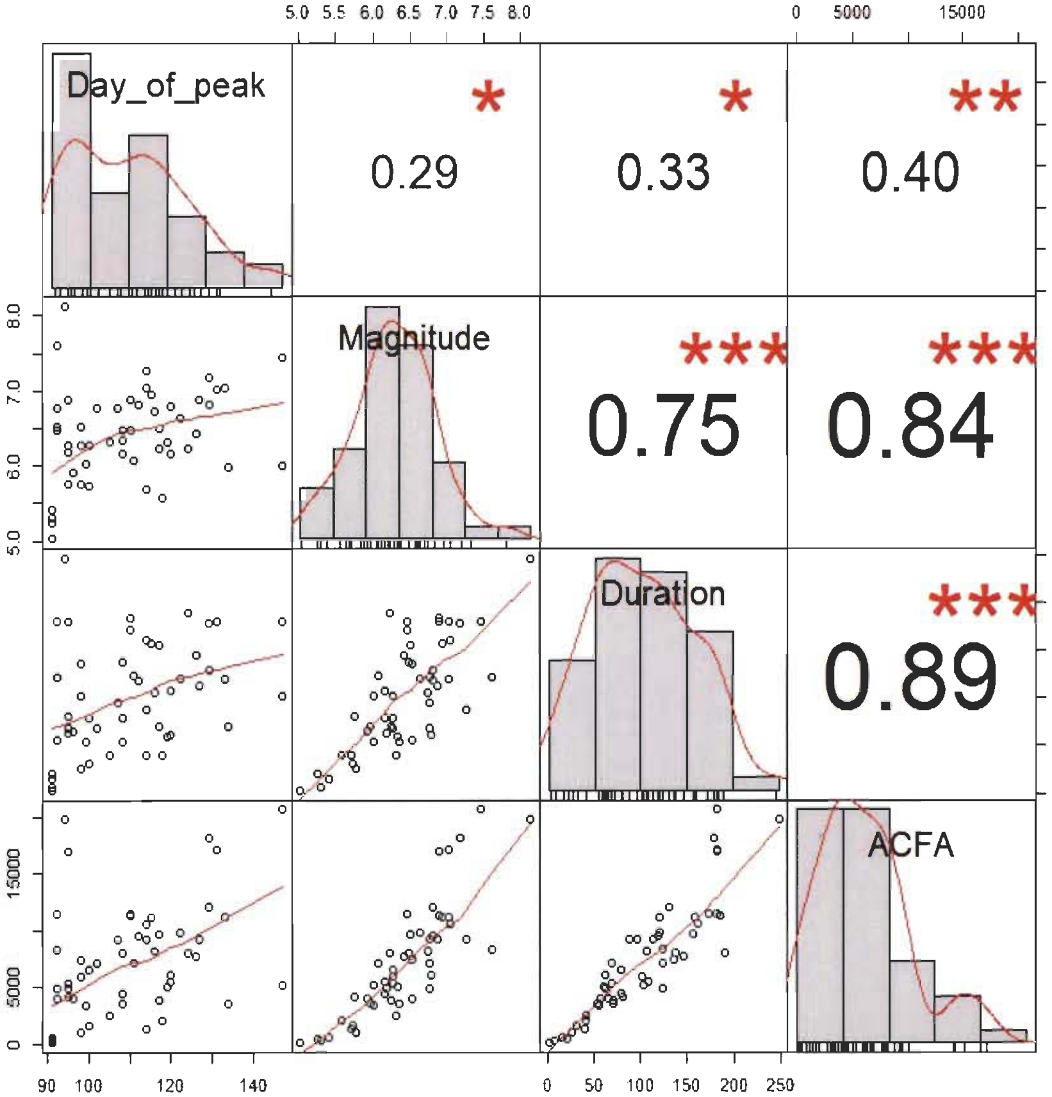
Figure 7.

Supplementary material

S.M.1. Histogram of the distribution of four flood characteristics between 1966 and 2017. The four years of the present study are shown by vertical coloured bars: 2014 (black), 2015 (red), 2016 (green), 2017 (blue).



S.M.2. Distribution of individual variables (histograms) and correlation plots between the flood characteristics: day of flood peak (Day_of_peak), magnitude, duration and annual cumulative flooded area (ACFA) (1966-2017). Values of the correlation (Pearson correlation) and level of significance of the associated probability (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) are indicated above the diagonal.



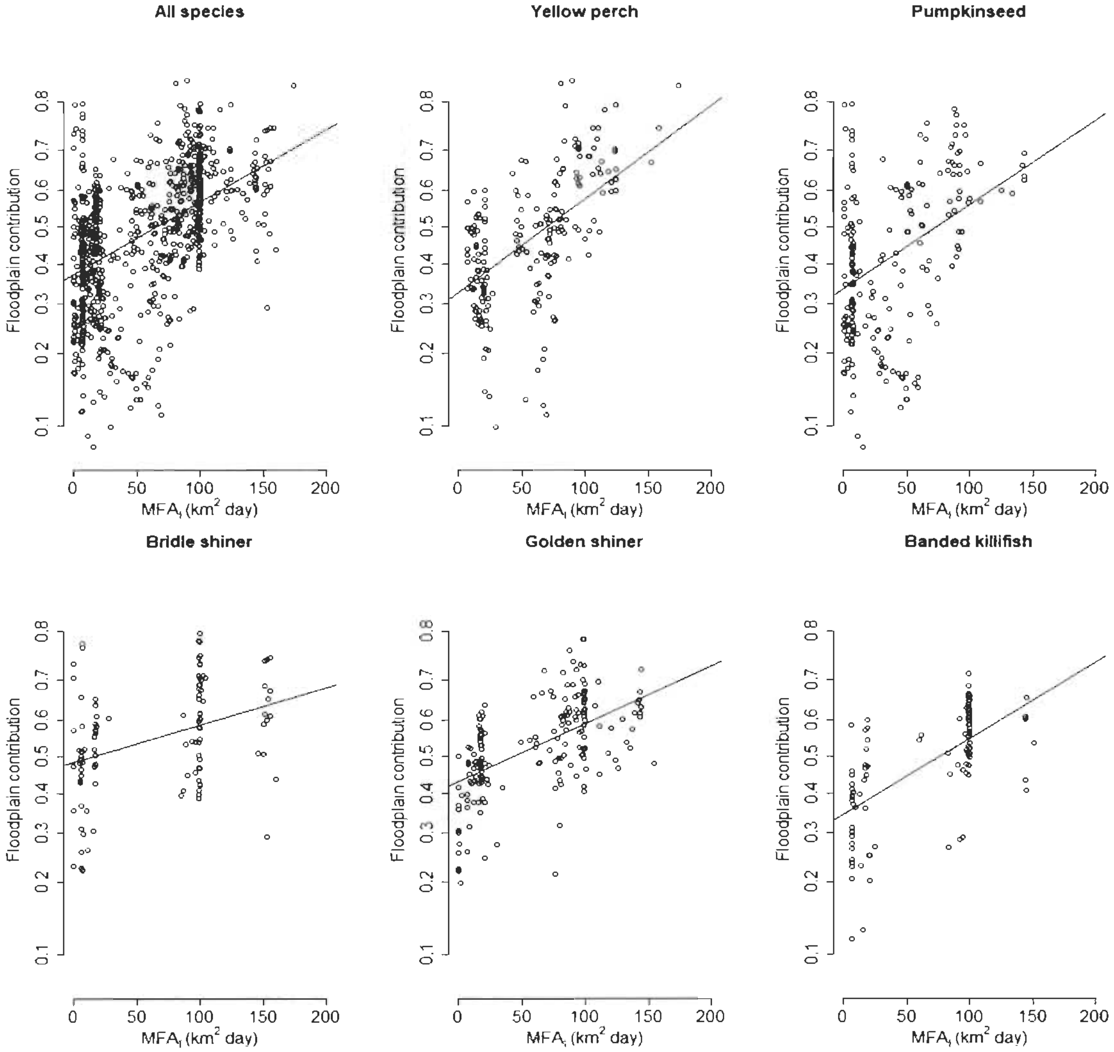
S.M.3. Table of the spawning season, diet, average isotopic half-live (HL) and number of captures for each fish taxa during the early (EGS, dates) and late (LGS, dates) growing seasons for the four sampling years.

Scientific name	Common name	Average HL (SD)	2014 EGS	2014 LGS	2015 EGS	2015 LGS	2016 EGS	2016 LGS	2017 EGS	2017 LGS	Total
Fundulus diaphanous	Banded killifish	27 (2.5)	5	5	11	23	50	1	6	2	103
Lepomis gibbosus	Pumpkinseed	30 (9.3)	2	27	0	49	28	67	11	16	200
Notropis bifrenatus	Bridle shiner	24 (3.0)	11	3	16	16	36	13	15	0	110
Notemigonus crysoleucas	Golden shiner	30 (5.5)	17	0	32	6	61	38	18	13	185
Perca flavescens	Yellow perch	34 (10.7)	37	26	21	27	36	46	4	15	212
Total			72	61	80	121	211	165	54	46	810

S.M.4. Output of the general linear regression model predicting the floodplain contribution to individual fish during the entire growing season (early and late growing season combined) using different combinations of explanatory variables: Species (Species); Day of fish capture (Day); Year of capture (Year); Individual average flooded area prior to fish capture (MFA_I). All models included the station as a random effect. Models are shown in decreasing order of performance, determined from the Akaike Information Criterion (AIC); the difference in performance of each successive model (ΔAIC) with respect to the best one is also shown.

Model	AIC	Δ AIC
Species + MFA_I + Day + Year + Day * Year	-1218.6	0
Species + MFA_I + Day + Year	-1207.0	11.6
Species + MFA_I + Day	-1202.1	16.5
Species + MFA_I + Year	-1200.8	17.8
MFA_I + Day + Year + Day * Year	-1197.8	20.8
Species + MFA_I	-1193.9	24.7
MFA_I + Day + Year	-1186.4	32.2
Species + Day + Year + Day * Year	-1183.6	35
MFA_I + Day	-1182.3	36.3
MFA_I + Year	-1178.7	39.9
MFA_I	-1173.0	45.6
Species + Day + Year	-1170.0	48.6
Day + Year + Day * Year	-1164	54.6
Species +Day	-1161.9	56.7
Day + Year	-1151.5	67.1
Day	-1142.7	75.9
Species	-1137.6	81
Species +Year	-1136.6	82
Null	-1117.0	101.6
Year	-1116.1	102.5

S.M.5. Relationship between individual mean flooded area (MFAI) and floodplain contribution for selected species together and individually. The linear regression was calculated with the package "betareg" using the function betareg with a link logit.



S.M.6. Regression coefficients of the variable species identity with different reference species as baseline for the best model predicting the floodplain contribution to individuals captured over the entire growing season.

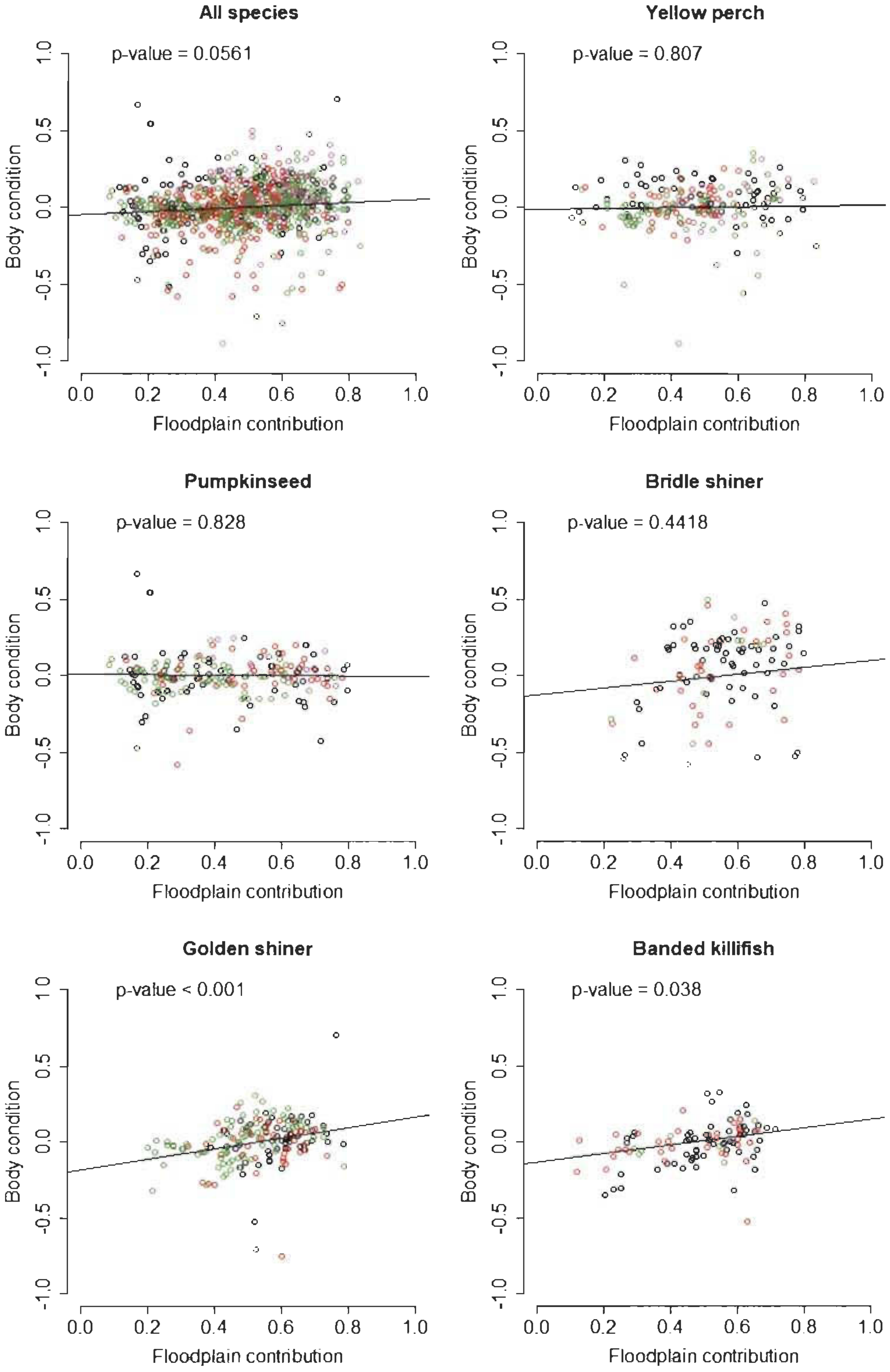
Reference species	Banded killifish	Pumpkinseed	Bridle shiner	Golden shiner	Yellow perch
Banded killifish		0.1785*	0.3327*	0.2591*	0.1937*
Pumpkinseed	-0. 1785*		0.1542*	0.0806	0.0152
Bridle shiner	-0. 3327*	-0. 1542*		-0.0736	-0.1390*
Golden shiner	-0.2591*	-0. 0806	0.0736		-0.0654
Yellow perch	-0. 1937*	-0.0152	0.1390*	-0.0654	

*Statistically different to the reference baseline species $P < 0.05$

S.M.7. Output of the general linear regression model predicting fish body condition during the entire growing season (early and late growing season combined) using different combinations of explanatory variables: Species (Species); Day of fish capture (Day); Year of capture (Year); Individual average flooded area prior to fish capture ($\mathrm{MFA}_{\mathrm{I}}$). All models included station as a random effect. Models are shown in decreasing order of performance, determined from the Akaike Information Criterion (AIC); the difference in performance of each successive model (ΔAIC) with respect to the best one is also shown.

Model	AIC	Δ AIC
$\mathrm{MFA}_{\mathrm{I}}$	-134.8	0
Null	-128.2	6.65
Day	-128.1	6.75
Day + Year	-125.1	9.71
$\mathrm{MFA}_{\mathrm{I}}$ + Day	-123.2	11.65
Year	-121	13.80
$\mathrm{MFA}_{\mathrm{I}}$ + Year	-115.3	19.51
$\mathrm{MFA}_{\mathrm{I}}$ + Day + Year	-109.5	25.34
Species + $\mathrm{MFA}_{\mathrm{I}}$	-107.7	27.07
Species + Day	-103.3	31.55
Species + Day + Year	-100.0	34.83
Species	-99.4	35.42
Species + $\mathrm{MFA}_{\mathrm{I}}$ + Day	-99.0	35.79
Species + Year	-91.7	43.15
Species + $\mathrm{MFA}_{\mathrm{I}}$ + Year	-88.0	46.85
Species + $\mathrm{MFA}_{\mathrm{I}}$ + Day + Year	-84.5	50.36
Day + Year + Day * Year	-83.2	51.66
$\mathrm{MFA}_{\mathrm{I}}$ + Day + Year + Day * Year	-68.2	66.61
Species + Day + Year + Day * Year	-58.1	76.71
Species + $\mathrm{MFA}_{\mathrm{I}}$ + Day + Year + Day * Year	-43.6	91.23

S.M.8. Relationship between floodplain contribution and body condition for selected species together and individually. Year of capture is represented by the colour of the symbol (2014 = black, 2015 = red, 2016 = green, 2017 = purple).



CHAPITRE III

ESTIMATING THE DURATION AND CONTRIBUTION OF A PULSED SUBSIDY: A MULTI-TISSUE ISOTOPIC APPROACH

This article will be submitted to the journal *Food webs*.

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Résumé

Les subsides écologiques peuvent altérer la stabilité, la structure, et la productivité de l'écosystème receveur. La durée du subside devrait moduler ces effets. Les objectifs principaux de cette étude sont : 1) examiner les potentiels problèmes d'utiliser un modèle uni-tissulaire afin d'estimer l'assimilation d'un subside comparer à un modèle multi-tissulaire, et 2) developper une approche isotopique multi-tissulaire permettant d'estimer la durée d'un subside pulsé. L'approche estime la durée du subside pulsé en se basant sur la différence des ratios isotopiques entre deux tissus ayant des taux de renouvellement isotopique distincts. Pour ce faire, nous avons utilisé une étude de cas examinant la contribution trophique d'un subside provenant de la plaine inondable à la productivité de la perchaude (*Perca flavescens*) pendant quatre années consécutives démontrant des régimes d'inondation contrastant dans le lac Saint-Pierre (Québec, Canada). Nos résultats montrent qu'un modèle uni-tissulaire utilisant un tissu à renouvellement lent produit une sous-estimation de la contribution du subside provenant de la plaine tôt en saison de croissance et en une sur-estimation tard en saison de croissance. De plus, nous avons démontré que l'approche développée peut estimer la durée du subside provenant de la plaine et identifier le régime d'inondation comme une des forces principales agissant sur la durée du subside dans ce système. L'utilisation de plusieurs tissus préviendrai les conclusions biaisées à propos de l'importance du support des subsides pulsés au réseau trophique récepteur.

Mots-clés : Approche isotopique multi-tissulaire, Hydrologie, Modèle de mélange isotopique, Pechaude, Rivière Saint-Laurent, Rivière tempérée, Subside pulsé.

Abstract

Ecological subsidies have the capacity to alter the stability, structure, and productivity of the recipient ecosystems. The duration of a subsidy should modulate these effects. The main objectives of this study are 1) to examine the potential shortcomings of single-tissue models to estimate the assimilation of a subsidy compared to two-tissue models and 2) to develop a multi-tissue isotopic approach allowing the estimation of the duration of a subsidy. The approach estimates the duration of a pulsed subsidy based on the stable isotope ratio dissimilarities between two tissues with different stable isotope turnover rates. We looked at the trophic contribution of a subsidy from the floodplain to the productivity of yellow perch (*Perca flavescens*) over four consecutive years exhibiting contrasting flood regimes in Lake Saint-Pierre (Québec, Canada). Our results show that relying solely on a slow tissue, the floodplain contribution is underestimated early in the growing season and overestimated in the late growing season. Furthermore, we show that the approach developed can be used to estimate the duration of the floodplain's subsidy and its environmental drivers. We identified the flood regime as the main driver in our system. Using multiple tissues prevents biased conclusions about the importance of a pulsed subsidy to the recipient food web.

Key words: Hydrology, Isotopic mixing model, Multi-tissue isotopic approach, Pulsed subsidy, St. Lawrence River, Temperate river, Yellow perch.

Introduction

Identifying sources and fluxes of energy supporting ecosystems is a central goal of ecology. The occurrence of spatial subsidies, defined as donor-controlled resources (e.g. nutrients, detritus, and prey) mobilized across ecosystem boundaries, is a key feature altering the stability, structure and productivity of the recipient system (Polis *et al.* 1997, Nakano and Murakami 2001, Anderson *et al.* 2008, Rooney *et al.* 2008). The effect of a subsidy on a recipient food web is mainly shaped by the trophic level, quantity, quality, timing and duration of the subsidy (Marczak *et al.* 2007, Subalusky and Post 2019). The duration of a subsidy can be a critical component altering the consumer's population structure, food web structure and ecosystem functions (Holt 2008, Yang *et al.* 2008, Sato *et al.* 2019). The availability of a subsidy can be sustained (pressed subsidy), or ephemeral (pulsed subsidy) (McInturf *et al.* 2019). Variability in the subsidy duration generates distinct levels of subsidy assimilation by recipient organisms among pulsed episodes. In turn, different levels of assimilation induce variability in the direction and magnitude of the response produced in the recipient system (Yang *et al.* 2010, Uno 2016, Sato *et al.* 2019). Organisms living in an ecosystem subjected to a pulsed subsidy are facing multiple modifications of their diet's origin over a relatively short period of time (switches from *in situ* resources to subsidy and back to *in situ* resources). Therefore, an approach aiming to estimate the duration of a pulsed subsidy must be able to track multiple diet switches. Such an approach would provide a valuable tool to assess the subsidy dynamics and its impact on the recipient's food web.

Stable isotope analysis (SIA) have been shown to be a useful tool to track the assimilation of a subsidy by recipient organisms (e.g. Huryn *et al.* 2001, Farly *et al.* 2019, submitted). Different tissues integrate the isotopic composition of the subsidy at different speed based on their isotopic turnover rates (λ) (Tieszen *et al.* 1983, Perga and Gerdeaux 2005, Yohannes *et al.* 2017). By assimilating the subsidy at different rates, two tissues from the same consumer could exhibit contrasting level of dependency to a pulsed subsidy, potentially generating distinct conclusions about the importance of the subsidy. The dynamic pattern of the subsidy availability and its assimilation by organisms can be unveiled by looking at the isotopic difference between tissues with distinct turnover rates in the consumer, allowing an estimation of the timing of the diet switch and consequently the duration of a pulsed subsidy. Most proposed multi-tissue stable isotope models estimate the timing of a single diet switch rendering difficult to measure the duration of a pulsed subsidy producing two diet switches (Philips and Eldridge 2006, Boecklner *et al.* 2011).

In this study, we aim to 1) examine the potential shortcomings of single-tissue models to estimate the assimilation of a subsidy compared to two-tissue models, and 2) develop an approach based on the model of Philips and Eldridge (2006) to estimate the duration of a pulsed subsidy based on multi-tissue SIA. To do so, we used the case study of the seasonal trophic flux of floodplain-derived invertebrates to yellow perch (*Perca flavescens*). We investigated the duration of this trophic linkage over four years exhibiting contrasting flood regimes (Farly *et al.* 2019, submitted) using stable carbon isotopic ratios ($\delta^{13}C$) of two tissues (muscle and liver) with different isotopic turnover rates.

Materials and Methods

Study area and model species

Lake Saint-Pierre (LSP) is situated 75 km downstream of Montreal, Canada (46°12'N, 72°49'O) and is the largest (≈ 300 km^2) and last fluvial lake of the St. Lawrence River. LSP exhibits a cycle of seasonal inundations, in part influenced by dams controlling the flow (Morin and Bouchard 2000). The LSP floodplain (0-2 years flood recurrence zone) expands over ≈ 210 km^2 for 5 to 9 weeks between the months of April and June (Lessard 1991). Previous studies in the LSP showed that invertebrates captured in the floodplain are isotopically distinct from the ones captured in the main river, rendering SIA usable in our system. (Farly *et al.* 2019, submitted). Moreover, they identified only two potential sources, main river vs floodplain, of production in the system (Farly *et al.* 2019, submitted). The subsidy originating from the floodplain of LSP contributes to the largest extent to the productivity of the littoral fish community during the early growing season (Farly *et al.* 2019, submitted) when the *in situ* river production is low (Savignac 1985, see Supplementary Materials S.M.1). The contribution level and period of availability of the subsidy are dictated by the highly variable magnitude and duration of the floods across years (Farly *et al.* submitted). This high variability in the flood's magnitude and duration observed during our sampling years (2014-2017, Table 1) will most likely result in variable duration in the availability of the flood plain subsidy. For these reasons, the LSP is a suitable system to test if the period of subsidy's availability can be estimated by a multi-tissue SIA approach.

In LSP, the yellow perch is a ubiquitous species strongly trophically linked to the floodplain (Farly *et al.* 2019, *submitted*). Therefore, using the yellow perch as a model organism to test our multi-tissue SIA approach allows us to highlight the ecological importance of the floodplain while testing the applicability of the model with real data.

Field sampling

Over a four-year period, we sampled yellow perch across multiple stations (Total = 58; 2014 = 21; 2015 = 18; 2016 = 15; 2017 = 4) distributed around LSP. Each year, two sampling campaigns were conducted coinciding with the early (EGS, June to early July, N = 22) and late growing season (LGS, end of August to early September N = 36). For stations located (N = 53) in the littoral zone, multiple hauls (1 to 4 hauls) were made using a seine (12.19 m wide X 1.5 m high, 2 mm mesh). However, in 2014 a larger seine was used in deep (> 1 m) stations (30.48 m wide X 1.75 m high, 10 mm mesh). For stations situated closer to the navigation channel (N = 5), fish were captured using a commercial bottom fishing trawl (9.9 m wide × 2.3 m high opening, 1.3 cm mesh). Additional collections of invertebrates were made at the same sites using a kick net (500 μm mesh) and sampling was expanded to multiple other stations in 2014 to cover both main river and floodplain habitats (further information in Farly *et al.* 2019).

Captured fish were rapidly anesthetized in a clove oil solution (1 ml oil / 25 l river water), euthanized by cervical dislocation, and immediately put on ice. Captured invertebrates were placed in plastic bags and immediately put on ice. At the end of the day, fish and invertebrates were frozen at -20 °C at the Centre de Recherche sur les Interactions Bassins Versant-Écosystèmes Aquatiques (RIVE), Université du Québec à Trois-Rivières, until further analysis.

Laboratory analysis and data analysis

Fish muscle and liver tissues and invertebrates were prepared for stable isotope analysis following the protocol presented in Farly *et al.* (2019, submitted). A combination of models from Kiljunen *et al.* (2006) and Post *et al.* (2007) as proposed by Skinner, Martin & Moore (2016) was used to correct yellow perch muscle and liver $\delta^{13}C$ values for their lipid content.

All statistical analyses were performed using R software version 3.4.3 (R Development Core Team 2017). First, invertebrates were divided into two groups based on their site of capture (littoral/floodplain vs main river) to establish the isotopic signatures of both sources. Invertebrates from the littoral/floodplain zone (defined as the portion of the LSP situated at a higher elevation than the beginning of the dense marsh) were used to define the floodplain source end-member and invertebrates captured outside of the littoral/floodplain zone defined the main river food source end-member. Invertebrates of all years were pooled together due to a reduced invertebrate sampling in 2015-2017. Secondly, the statistical significance of $\delta^{13}C$ differences between the floodplain and main river sources was tested (*t*-test).

Means and SDs of $\delta^{13}C$ of these sources, together with $\delta^{13}C$ values for individual fish and carbon trophic fractionation were included as input for SIAR. We used the carbon trophic fractionation ($\Delta\delta^{13}C \pm SD = -0.1 \pm 0.98$) proposed by Post (2002). A vague Beta (1, 1) prior distribution for the mixing proportion was used to allow the results to be influenced primarily by the data (Parnell *et al.* 2010). Furthermore, we used the function "*siarmcmcdirichletv4*" from the package SIAR (Parnell *et al.* 2008) to assess the floodplain contribution for the liver and muscle isotopic ratios and compared the estimated contribution to observe for discrepancies. When an organism is exposed to a change in its diet, its tissues will assimilate the signal of the new source over a time period related to their turnover rate. In turn, different tissues with distinct turnover rates will generate different estimates of the resource contribution until the tissues reach equilibrium. We used the term "apparent" floodplain contribution to reflect the discrepancies between the results of the mixing models using muscle vs liver data.

A multi-tissue SI approach to estimate the duration of an ecological subsidy

The approach estimates the duration of a pulsed subsidy in a recipient ecosystem by identifying the moment of the diet switch (hereafter designated as DS) from the subsidy to the *in situ* resource. It predicts the isotopic differences between the fast and slow tissue over a determined period for all possible DS and examines which DS value generates the lowest standard error (best model) when comparing the predicted values to an observed dataset. The approach makes three assumptions: 1) individuals are at isotopic equilibrium with the recipient *in situ* resource (recipient end-members) at the beginning of the season (prior to the availability of the subsidy); 2) the moment of the first diet switch is known or can be estimated; 3) there is a complete switch in the resource exploited by the individuals at a specific date.

The isotopic value of a tissue at any time following a diet switch can be estimated as (Hesslein *et al.* 1993):

$$\delta X_{It} = \delta X_S + (\delta X_R - \delta X_S) * e^{-\lambda t} \qquad \text{Eq. 1}$$

where δX_{It} is the isotopic value at time t. δX_S and δX_R are the isotopic values of the subsidy and recipient end-members, respectively, corrected for the trophic discrimination factor specific to each tissue. λ is the turnover rate of the specific tissue under study and t is the number of days since the availability of the subsidy (first diet switch).

In a system receiving a pulsed subsidy there are two diet switches, therefore Eq. 1 is used to predict the isotopic values following the first diet switch (from *in situ* to subsidy resources). To predict the isotopic values after the second diet switch (from subsidy to *in situ* resources), we modified Eq. 1 (Eq. 2).

$$\delta X_{It} = \delta X_R + (\delta X_{ID} - \delta X_R) * e^{-\lambda P} \qquad \text{Eq. 2}$$

where δX_{ID} is the predicted isotopic value of an individual on the potential day of the second diet switch (DS). δX_{ID} is derived from Eq. 1 where t = DS. In Eq. 2, P is the number of days since the second diet switch (DS). Combining both equations, the isotopic value of an individual over two diet switches can be estimated (Fig. 1).

The differences in isotopic values between the fast and slow tissues are then calculated over a period of time ($t = 0$ to t_{max}) for every possible DS by combining Eq.1 and Eq. 2 (DS = 0 to t_{max}) (Fig. 2). t_{max} should exceed the expected duration to extend beyond the second diet switch. Next, for each model (N = t_{max}), the standard errors are calculated by comparing the observed isotopic differences and the predicted values emerging from the models. Finally, the model with the lowest standard error is identified as the best model. The DS value from the best model is identified as the best estimate for the moment of the second diet switch. To account for the variance of the parameters ($\delta^{13}C$ of the end-members, trophic discrimination factors, turnover rate of each tissue), the process is repeated a 1000 times with a combination of new values for each parameter drawn from their normal distribution (mean ± SD estimated for the system under study). Then, the DS distribution obtained provides a plausible time frame for the moment when the recipient consumer changes from the subsidy to the *in situ* resources.

Multi-tissue SIA application to yellow perch

The isotopic turnover rates (λ) used were 0.06 ± 0.02 ($\lambda \pm$ SD) for the liver and 0.012 ± 0.0014 ($\lambda \pm$ SD) for the muscle, resulting in distinct isotopic values following a diet switch (Weidel *et al.* 2011, Yohannes *et al.* 2017). We used the liver turnover rate from the European perch (*Perca fluviatilis*), a closed related species, because no value for the yellow perch was available to our knowledge. We assumed that the first diet switch (main river resource to subsidy) occurs when the water level begins to decrease (Day since peak = 0), exporting the resource produced in the floodplain to the main river and rendering it available to the littoral fish community. Lastly, we set the range of the variable DS between 1 and 200 days. Based on the flood duration and magnitude observed during the four years of this study (Table 1), the duration of the subsidy should not extend over 200 days. All parameters values and their standard deviations are found in Supplementary Materials (S.M.2.).

Results

Invertebrates, muscle and liver $\delta^{13}C$ isotopic ratios

Invertebrates δ^{13}C values caught in the littoral/floodplain zone (mean δ^{13}C ± SD = -33.2‰ ± 2.82, N = 125) were significantly more negative (t-test: t = -22.841, DF = 170, p-value < 0.001, all years combined) than those observed in the main river (mean δ^{13}C ± SD =-21.7‰ ± 3.21, N = 47; see Supplementary Materials S.M.3.). No evidence of inter-annual variability was observed within habitat type, allowing us to pool invertebrates from multiple years together (S.M.3).

We measured the δ^{13}C and δ^{15}N of both muscle and liver from 230 yellow perch (Table 2 and see Supplementary Materials S.M.4.). We observed that the δ^{13}C from individuals captured during the early growing season tended to be more negative than the values observed from the individuals captured later in the growing season (Table 2 and S.M.4.). Furthermore, the comparison between the δ^{13}C values of the liver and muscle followed a trend as predicted from their turnover rates and is coherent with a spring pulse of a resource with a more negative δ^{13}C signature. Individuals captured during the early growing season tended to have more negative δ^{13}C values for their liver (closer to the floodplain end-member signature) than for their muscle (Table 2 and Fig. 3). On the other hand, individuals captured late in the growing season exhibited liver $\delta^{13}C$ values more positive compared to their muscle $\delta^{13}C$ values, indicating a return to less negative $\delta^{13}C$ values and more similar to the main river end-member signature.

Floodplain contribution to liver and muscle of yellow perch

At the population level, apparent floodplain contribution to the liver was always more important than for muscle during the early growing season (floodplain contribution difference: 2014 = 22.4%; 2015 = 9.3%; 2016 = 15.9%) (Fig. 4A). Contrastingly, during the late growing season the apparent floodplain contribution was always smaller in the liver compared to the muscle (floodplain contribution difference: 2014 = 15.6%; 2015 = 6.7%; 2016 = 6.3%; 2017 = 5.5%) (Fig. 4B). At the individual level, apparent floodplain contribution measured from the muscle tissue was underestimated by 10.8 ± 9.7% (mean ± sd) during the early growing season and overestimated by 5.2 ± 6.7 (mean ± sd) during the late growing season compared to that estimated from liver values (see Supplementary Materials S.M.5.).

Estimation of the moment of diet switch

Our approach to estimate the moment of the diet switch from floodplain to river resources (DS) provided reasonable time frames for each year (2014-2017) predicting the duration of the subsidy availability (Fig. 5 and see Supplementary Materials S.M.6.). In relation to the day since the peak, the estimated moment of diet switch increased with the duration of the flood varying from 34 days after the peak of the flood during a small flood year (2015) to 126 days since the peak in a large flood year (2017). The positive linear relation between flood and subsidy duration estimated from isotopic data suggests that subsidy duration and assimilation are directly linked to the magnitude and duration of the flood as expected (Fig. 6).

Discussion

This study provides strong evidence that a multi-tissue SIA approach allows the tracking of the assimilation of the subsidy over multiple diet switches and produces a realistic estimate of the subsidy duration. Our results showed that an isotopic mixing model based on a tissue with slow turnover can underestimate the assimilation of a pulsed subsidized resource.

Estimation of subsidy contribution: two vs one tissue approach

Comparison between liver and muscle $\delta^{13}C$ values showed that both tissues were rarely at equilibrium with each other (Fig. 3). This indicates that resources availability and assimilation supporting yellow perch productivity followed a dynamic pattern through the growing season. More precisely, our results showed a shift in the resources assimilated by yellow perch from floodplain resources in the early growing season to main river resources in the late growing season regardless of the tissue analyzed (Fig. 4). However, the apparent floodplain contribution varied in function of the tissues due to their different turnover rates (Fig. 4). At the population level, the apparent floodplain contribution to the muscle was always underestimated early in growing season (by up to 22.4% in 2014) and overestimated in late growing season (by up to 15.6% in 2014) when compared to the liver. Relying solely on the apparent floodplain contribution of the muscle can result in a miss-identification of the main source of energy supporting the species such as observed in the early growing season of 2014 and 2015 (Fig. 4).

Furthermore, at the individual level, the difference between the floodplain contribution measured with the liver and muscle isotopic values showed high variability among individuals and can differ drastically from the mean of the population (S.M.5.). This high intra-population variability suggests a strong discrepancy in the reliance on the floodplain subsidy among individuals that would be missed by only analyzing the mean of a population (Vander Zanden *et al.* 2010). Tissue selection could potentially have high impact on the results and their interpretation when investigating the relation of stable isotope ratios of individuals against other variables such as contaminant level

(Pinzone *et al.* 2019; Le Croizier *et al.* 2019) and trophic level (Vander Zanden and Rasmussen 1999). Our study provides clear evidence that the tissue analyzed for SIA should be selected according to the ecological questions, their turnover rate and temporal availability of the resources (Thomas and Crowther 2015; Shipley and Matich 2020).

Assumptions of the approach and case study

Our approach makes three assumptions: 1) the individuals are at isotopic equilibrium with the recipient *in situ* resource at the beginning of the growing season; 2) the moment of the first diet switch is known or can be estimated; 3) there is a complete switch in the resource exploited by the individuals at a specific date. Results from the case study showed that individuals reach equilibrium with the main river source by the end of the growing season (Fig. 6), suggesting that they are at equilibrium the following growing season and thus supporting the first assumption. In our case study, most of the specimens analyzed were not sexually mature based on their size and therefore, they were unlikely to migrate into the floodplain for reproductive purposes. Hence, the floodplain subsidy became available at the peak of flood, when the water level starts dropping and exporting the subsidy to the river, thus, supporting the second assumption. Lastly, after the first diet switch, the floodplain productivity is the most abundant food resource by several orders of magnitude since the main river productivity is low due to limiting factors such as low water temperature, high water flow and low water transparency (Savignac 1985, Hamilton and Lewis 1987). This suggests a drastic switch in the resource exploited, as assumed. However, this assumption might not hold for the second diet switch in our system. In the LSP, main river productivity increases progressively during summer (Vis *et al.* 2007; S.M.1.). Conversely, floodplain subsidy exportation decreases toward the end of the flood potentially producing a gradual diet switch rather than an abrupt one.

Tailoring the approach to specific systems

The approach developed in this study was conceived to be simple and general to allow its application to diverse systems and organisms. Although, it would be possible to increase the predictive power of the approach by including specific information of the system. Two general improvements are possible and could be applicable to most systems. First, the isotopic turnover rate of an organism is influenced by the temperature (Thomas and Crowther 2015). Therefore, implementing a function to modulate λ in relation of the temperature should produce a better estimation of the duration of the subsidy. Second, as mentioned above, the assumption of a sudden change in the resource exploited might not be applicable to most systems. This assumption could be omitted by including a density dependent function combined to an isotopic mixing model to determine the isotopic value of the recipient end-member. However, the effect of temperature on the specific λ and the relative density of the trophic resources are lacking in the literature. Therefore, the implementation of these improvements will require an immense amount of work specific to each system and organism under study and will systematically complexify the model.

Applications of the approach and multi-tissue SIA

Our approach provides an interesting tool to researchers that allows a better understanding of the temporality of the subsidy. This may result in a more accurate representation of the food web structure and dynamics in diverse systems. Specific subsidy's duration can be easily measured by monitoring the presence of the subsidy's vector in the recipient ecosystem such as migrating bird as prey (Giroux *et al.* 2012) and emergence of aquatic insects (Nakano and Murakami 2001). On the other hand, when investigating subsidies that are difficult to track or quantify, such as carcasses and feces of migrant animal (Subalusky *et al.* 2014, Pringle 2017), estimating their period of availability in the recipient ecosystem is challenging, rendering our approach highly valuable.

Our study suggests that high temporal variance between tissues with different turnover rates across seasons could be a simple index of the importance of seasonal subsidies. Furthermore, multi-tissue SIA can also identify disparities in the migration pattern among individuals (Davis *et al.* 2015), disentangle temporally and spatially complex diet (Mac Avoy *et al.* 2001, Perga and Gerdeaux 2005, Buchheister and Latour 2010), and identify dietary specialization (Bond, Jardine and Hobson 2016). With such significant benefits and the decreasing monetary cost associated with SIA, we strongly recommend the combination of multiple tissues exhibiting distinct turnover rates in future research using SIA to investigate trophic relationships.

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Tables

Table 1. Annual characteristics of the flood regime of Lake Saint-Pierre. Historical median (1966-2017), Day of year (DOY). Day of peak is defined as the day of the year when the water level reached the highest level. Magnitude is defined as the highest water level reached (m, IGLD85). End of the flood is defined as the day of the year when the water level is for the first time under the floodplain limit (IGLD85 › 4.57 m). Duration is defined as the number of consecutive days that the floodplain is under water (water level IGLD85 › 4.57 m) since April 1st (Julian day = 91). Mean daily water level values at Sorel (station ID: 02OJ022) were obtained from the Fisheries and Ocean Canada website (http://www.meds-sdmm.dfo-mpo.gc.ca, consulted in February 2018).

Year	Day of peak (DOY)	Magnitude (m)	Duration (days)
2014	107	6.77	96
2015	114	5.70	40
2016	100	6.27	80
2017	129	7.19	179
Historical median	109	6.45	102.5

Table 2. Muscle and liver $\delta^{13}C$ and standard deviation (SD) in different years and seasons.

Year	**Early growing season**			**Late growing season**		
	# Specimen	$\delta^{13}C_{muscle}$ (SD)	$\delta^{13}C_{liver}$ (SD)	# Specimen	$\delta^{13}C_{muscle}$ (SD)	$\delta^{13}C_{liver}$ (SD)
2014	37	-27.10 (2.08)	-29.80 (2.03)	44	-24.76 (3.19)	-22.97 (3.76)
2015	19	-26.72 (2.73)	-27.83 (1.29)	50	-25.10 (2.40)	-24.32 (2.56)
2016	19	-28.31 (2.09)	-30.25 (1.67)	47	-24.29(2.65)	-23.44 (2.45)
2017	1	-27.31 (-)	-30.08 (-)	13	-28.20 (1.80)	-27.51 (2.51)

Figure legends

Figure 1. Predicted isotopic values (δX) for a fast (black line) and a slow tissue (grey line) in a system under the influence of two diet switches. The timing of the second diet switch (DS = 100), isotopic signatures of the recipient (δX_R = 10 ‰) and subsidy (δX_S = 0 ‰) end-members are arbitrarily chosen.

Figure 2. Predicted isotopic difference between the fast and the slow tissues following a diet switch from subsidy to *in situ* resources at three different moments (DS = 25 (light gray line), 100 (dark gray line) and 175 (black line)) over a period of time of 200 days following the beginning of the subsidy availability (t_{max} = 200). DS is the variable for the timing (Day since subsidy availability) of the second diet switch from subsidy to *in situ* resources (vertical dashed line).

Figure 3. Difference in the isotopic ratio between the liver and the muscle. Fish captured in the early growing season (black circle). Fish captured late in growing season (grey circle). The 1:1 relationship between isotopic ratios of muscle and liver is shown as the solid line.

Figure 4. Floodplain contribution (median and 95% credible intervals) to the liver (empty circles) and muscle (filled circled) of yellow perch during the A) early growing season, and B) late growing season of four distinct hydrological years.

Figure 5. Observed $\delta^{13}C$ difference between a fast (liver) and a slow (muscle) tissue (empty red circle) and the expected values (solid black line) from the best model estimating the moment of the diet switch (from floodplain to river resources) for four hydrological distinct years superimposed to histograms of the estimated timing of diet switch (DS) from 1000 iterations.

Figure 6. Relation between flood duration and subsidy duration estimated from isotopic data.

Figures

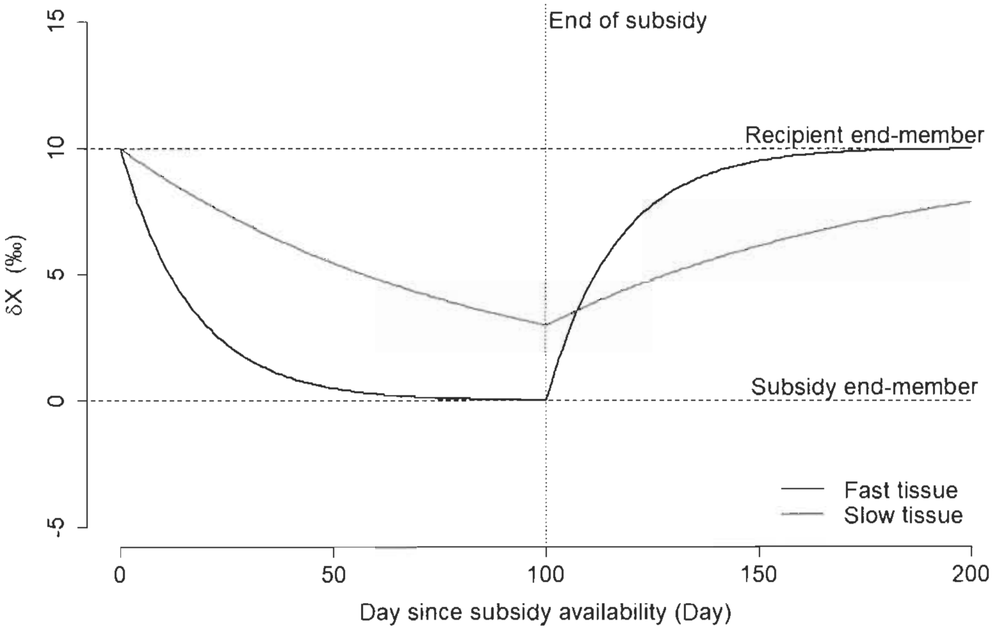


Figure 1.

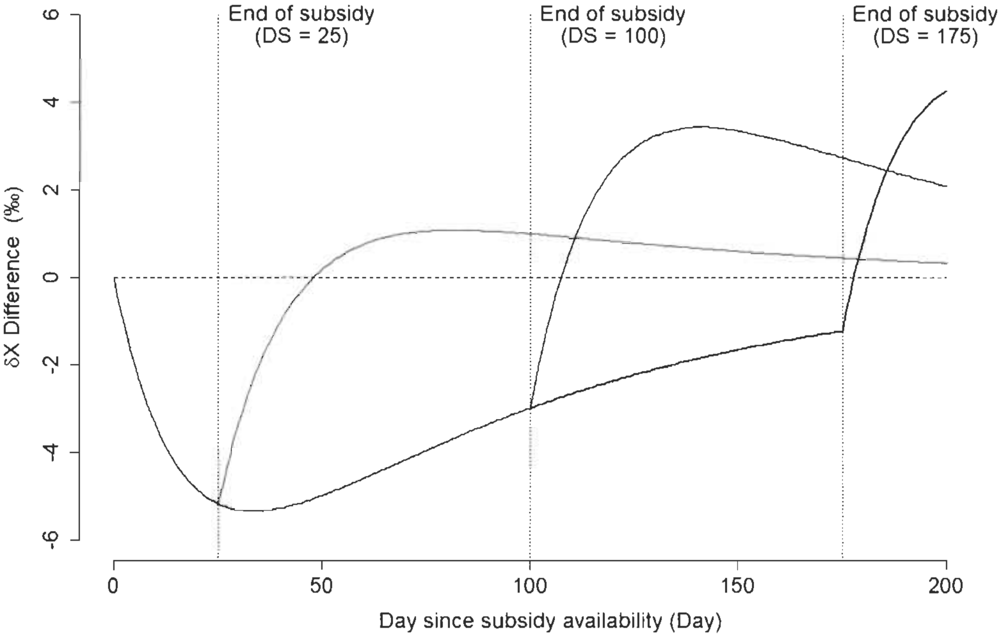

End of subsidy
(DS = 25)
End of subsidy
(DS = 100)
End of subsidy
(DS = 175)
δX Difference (‰)
6
4
2
0
-2
-4
-6
0
50
100
150
200
Day since subsidy availability (Day)

Figure 2.

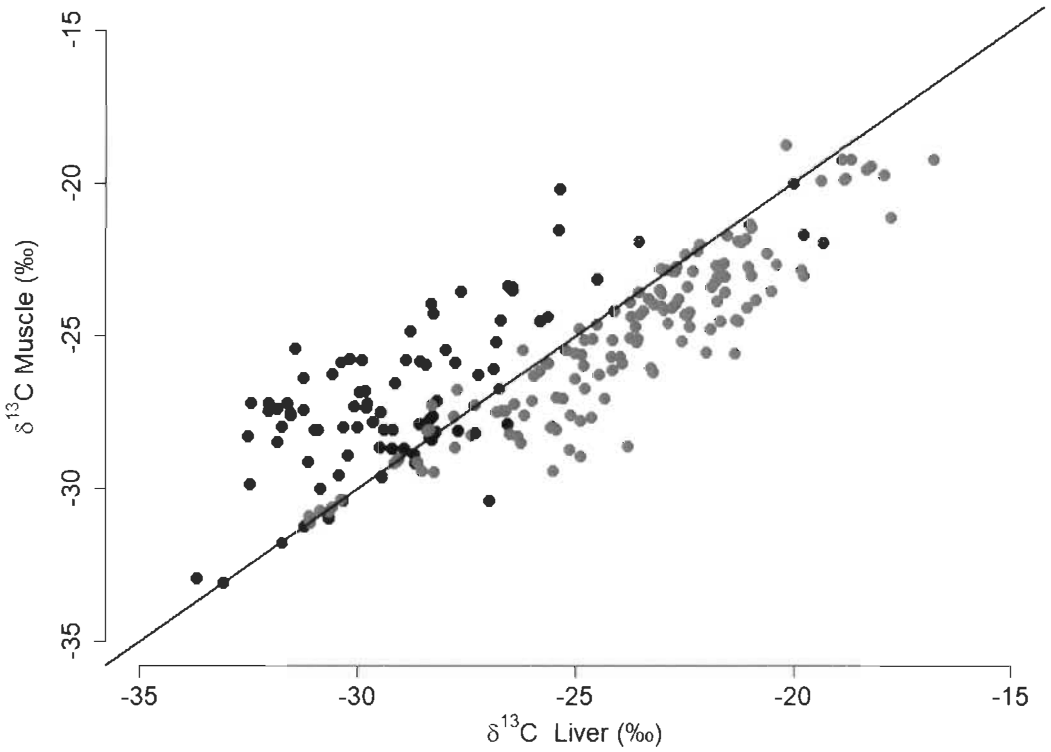


Figure 3.

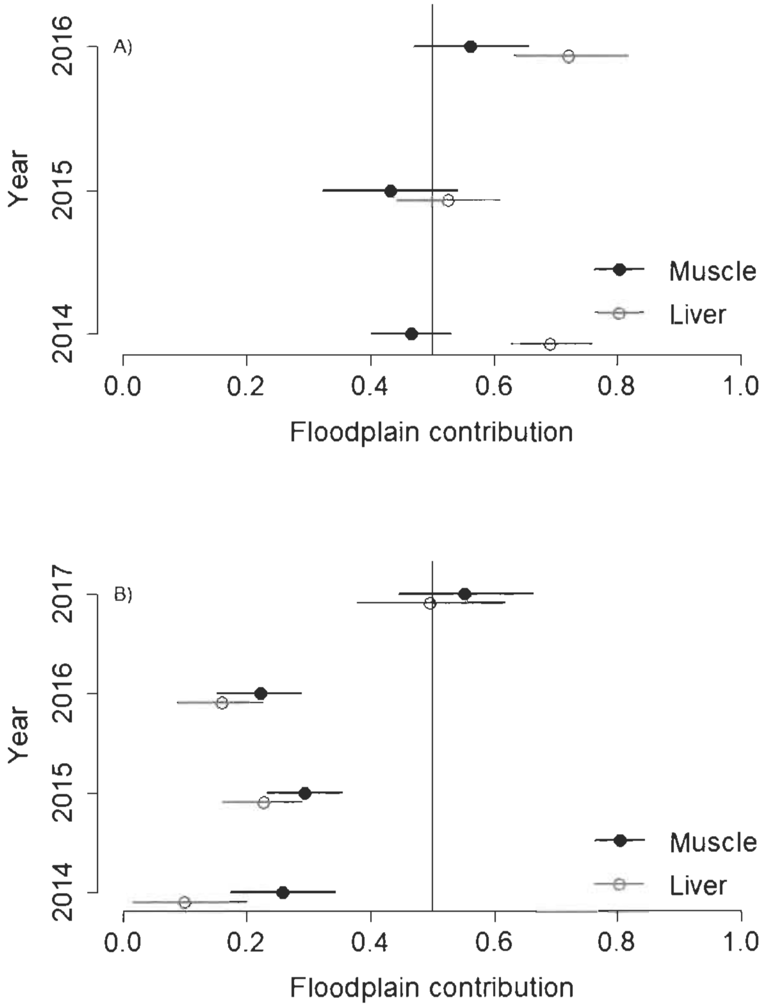

A)
Year
2016
2015
2014
Muscle
Liver
0.0
0.2
0.4
0.6
0.8
1.0
Floodplain contribution
B)
Year
2017
2016
2015
2014
Muscle
Liver
0.0
0.2
0.4
0.6
0.8
1.0
Floodplain contribution

Figure 4.

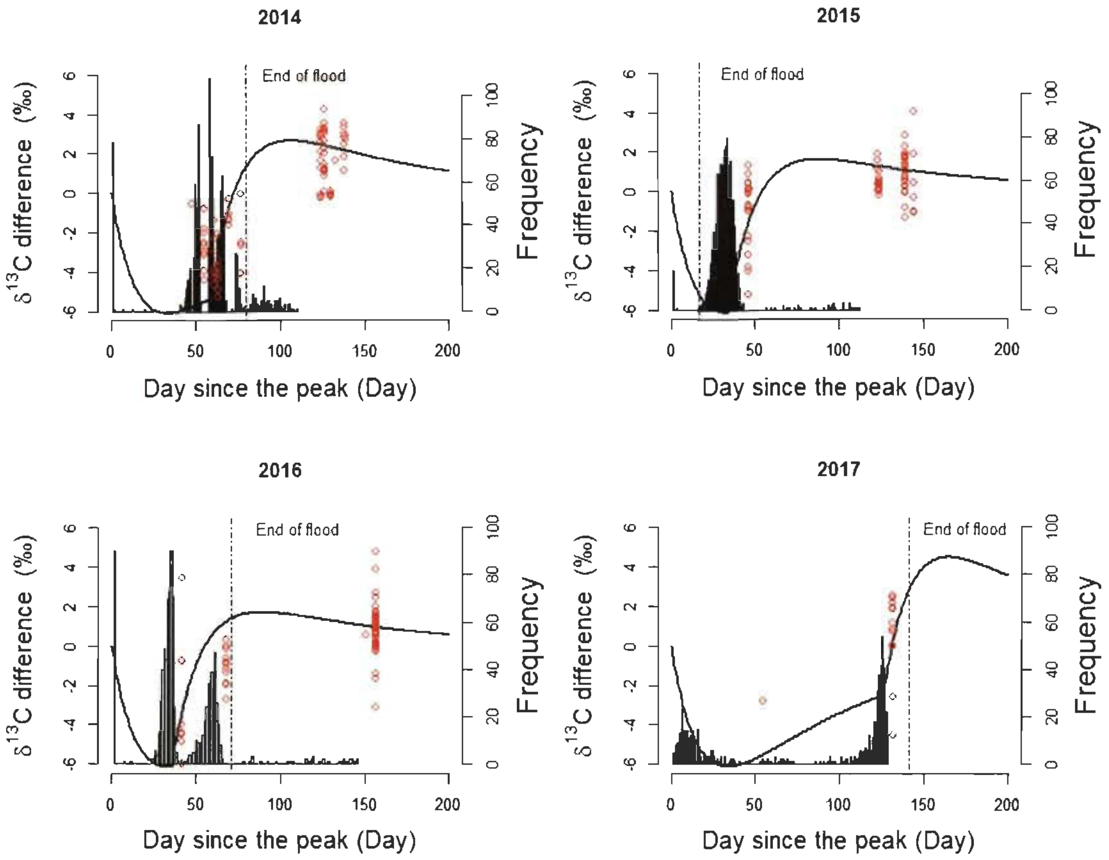
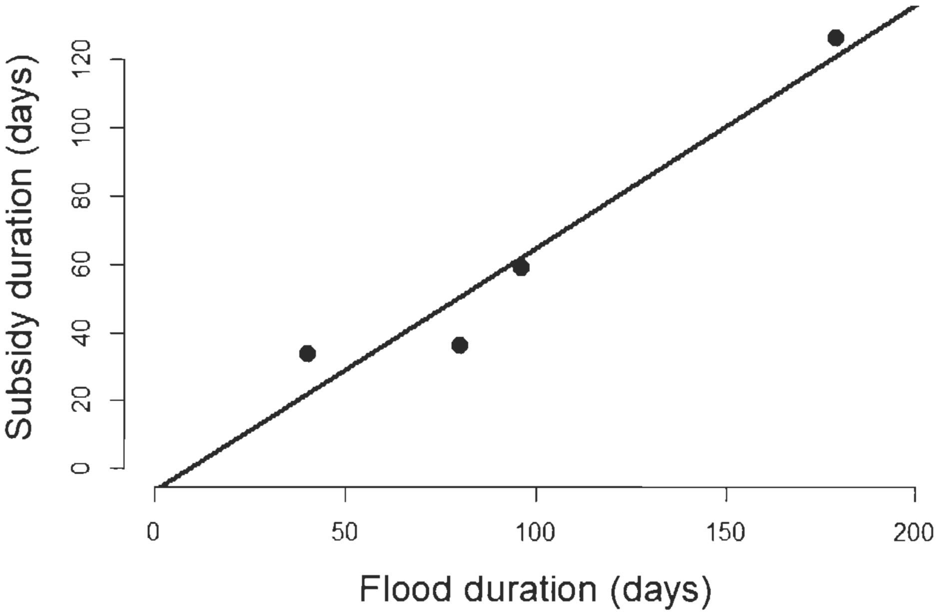

2014
2015
2016
2017
End of flood
δ^{13}C difference (‰)
Frequency
Day since the peak (Day)
6
4
2
0
-2
-4
-6
0
20
40
60
80
100
0
50
100
150
200

Figure 5.

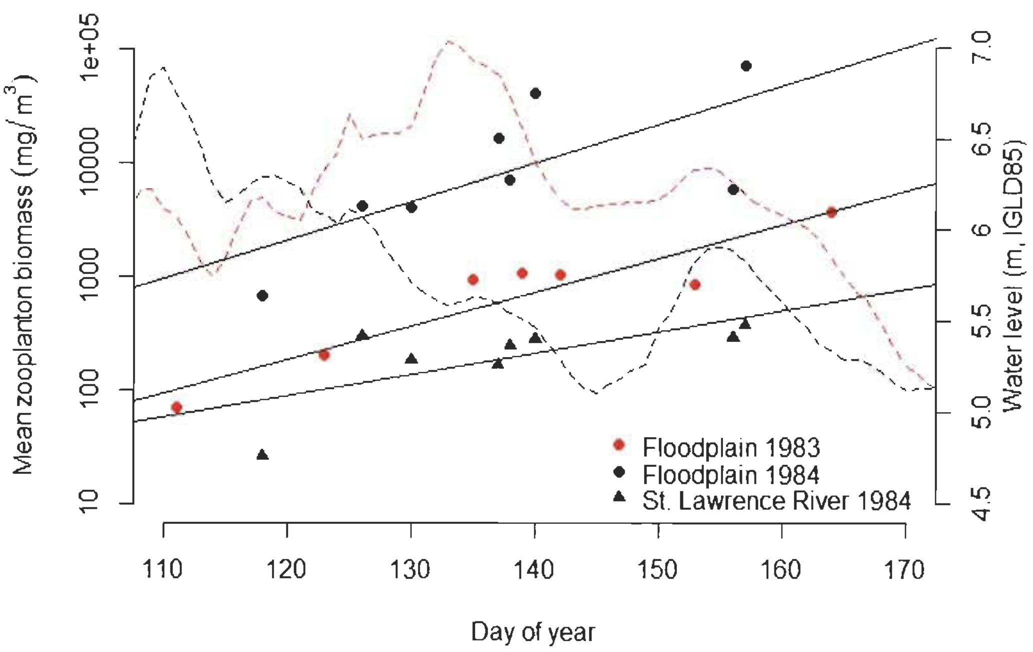


Subsidy duration (days)
0
20
40
60
80
100
120
0
50
100
150
200
Flood duration (days)

Figure 6.

Supplementary materials

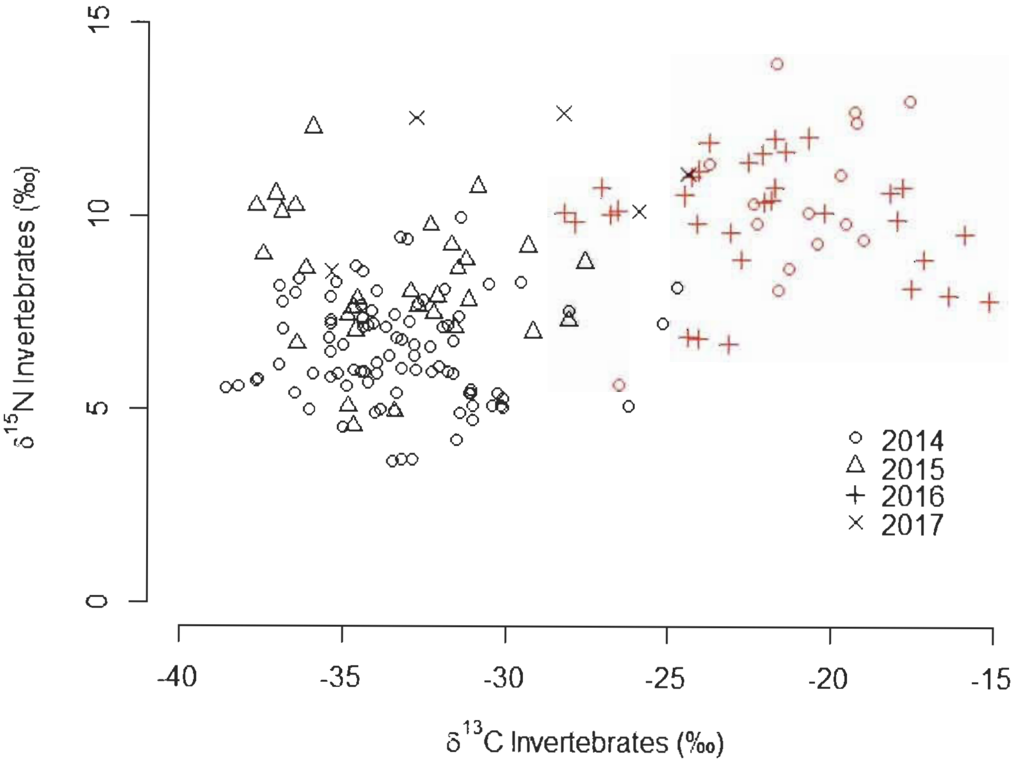
S.M.1. Mean zooplankton biomass (mg/m^3) in the floodplain (dots) and the St. Lawrence River (triangle) during spring floods of 1983 (red dots) and 1984 (black dots and triangles) superimposed to mean daily water level (m, IGLD85) (1983: dashed red line; 1984: dashed black line). Linear regression of the log of the mean zooplankton biomass in function of the day of the year (solid black line). Data come from Savignac 1985.



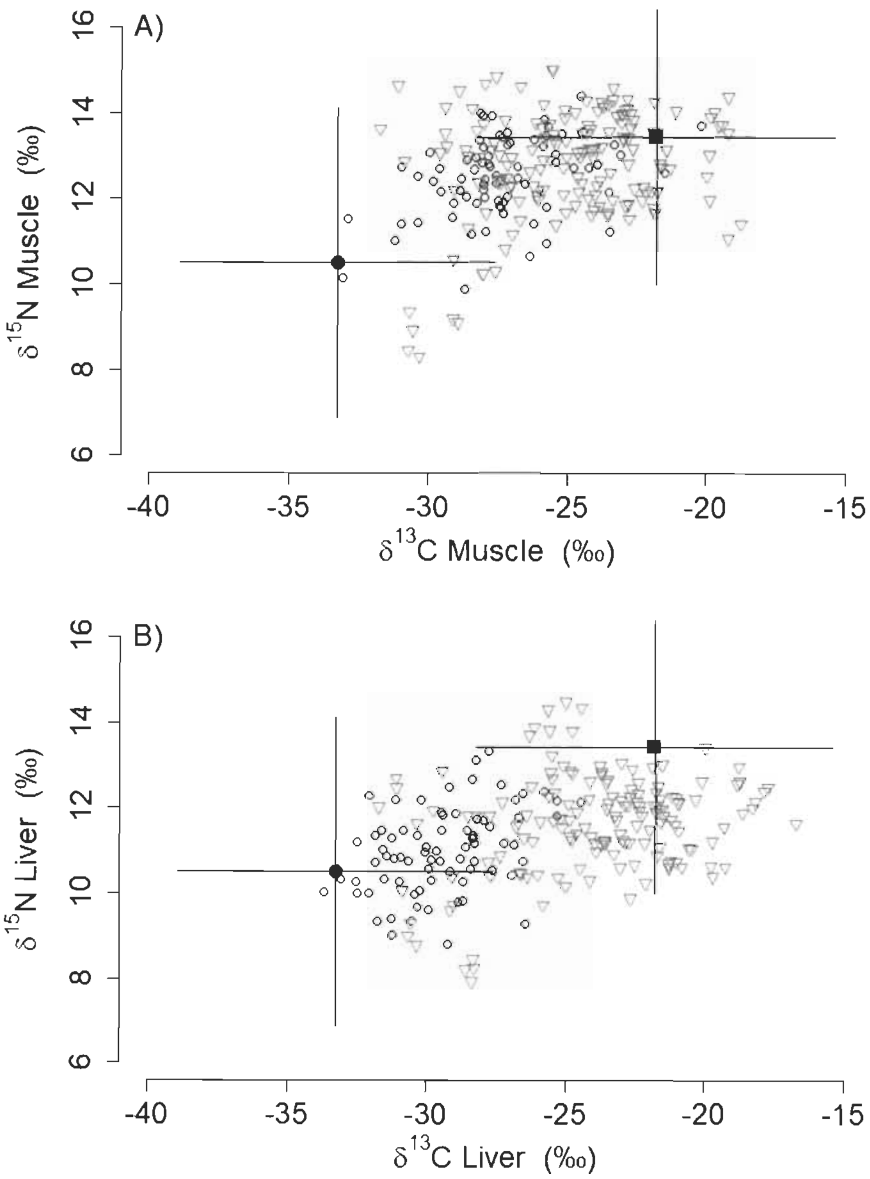
S.M.2. Mean and standard deviation of the parameters used in equation 1 and 2.

Parameter	Mean	Standard Deviation	References
Floodplain end-member ($\delta^{13}C$)	-33.16	2.82	This study
River end-member ($\delta^{13}C$)	-21.72	3.21	This study
Trophic fractionation ($\Delta^{13}C$)	-0.1	0.96	Post 2002
Liver turnover rate (λ_{Liver})	0.06	0.02	Yohannes *et al*. 2017
Muscle turnover rate (λ_{Muscle})	0.012	0.0014	Weidel *et al*. 2011

S.M.3. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopic ratios of invertebrates in the littoral/floodplain zone (black symbols) and in the main river (red symbols) for 2014 (open circles), 2015 (open triangle), 2016 (hairline crosses) and 2017 (hairline x).



S.M.4. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) A) muscle B) liver isotopic ratios for individual yellow perch caught early (circles) and late (inverted triangle) growing period. Baseline values (mean ± 2 SD) for samples collected in the littoral/floodplain zone (full circle) and the main river (full squares) are corrected for the expected trophic fractionation between fish and their prey ($\Delta 13C = -0.1 \pm 0.96$; $\Delta 15N = 3.4 \pm 0.99$; Post 2002).



S.M.5. Differences between floodplain contribution estimated from liver vs muscle isotopic values and their standard deviation (SD) at the individual level per year per season.

Year	Early growing season Mean (SD)	Late growing season Mean (sd)
2014	0.139 (0.075)	-0.082 (0.069)
2015	0.057 (0.094)	-0.040 (0.053)
2016	0.098 (0.119)	-0.043 (0.062)
2017	-	-0.032 (0.100)
Average	0.108 (0.097)	-0.052 (0.067)

S.M.6. Number of specimens, end of flood (day of the year), estimated moment of the diet switch (day of the year), mean values of the DS frequency distribution ± standard deviation (SD) for the 1000 iterations for the diet switch moment estimated and estimation of the duration of the subsidy. End of the flood is defined as the day of the year when the water level is for the first time under the floodplain limit (IGLD85 › 4.57 m. Duration is defined as the difference between the diet switch moment and the peak of the flood.

Year	# specimens	End of flood (DOY)	Diet switch (DOY)	Mean (± SD)	Duration (days)
2014	81	188	166	169.5 (13.63)	59
2015	69	132	148	147.9 (12.38)	34
2016	66	172	136**	146.9 (20.02)	36
2017	14	271	255	210.2 (51.86)	126

* Another possible date for the diet switch were observed for 2016, day of year 161 resulting in a duration of the subsidy of 61 days. Only the date with the highest frequency was included in the table.

DISCUSSION GÉNÉRALE

Synthèse et contributions scientifiques de la thèse

Cette thèse examine l'importance et les caractéristiques (durée, timing quantité et qualité) du subside provenant de la plaine inondable à la communauté ichtyenne d'un lac fluvial situé en milieu tempéré : le lac Saint-Pierre. Le Chapitre I détermine les variations temporelles (timing saisonnier) et spatiales (distance à l'extérieur de la plaine inondable) du subside au régime alimentaire pour la communauté piscicole. Le Chapitre II évalue le rôle des variations hydrologiques dans la régulation de la quantité (durée d'inondation) et de la période de disponibilité (timing de l'inondation) des subsides alimentaires et l'effet potentiel de ces facteurs sur la condition physique de 5 espèces de poissons. Le Chapitre III détermine l'impact du choix du tissu utilisé pour les analyses isotopiques sur l'évaluation de la contribution du subside. Compte tenu des variations saisonnières des apports provenant de la plaine inondable au LSP, le choix du tissu analysé revêt une grande importance lors de l'emploi de l'approche isotopique pour évaluer sa contribution.

Dans le chapitre I, nous avons évalué la présence ainsi que décrit les patrons spatio-temporels de la contribution du subside provenant de la plaine à l'ensemble de la communauté ichtyenne du lac Saint-Pierre. Nous avons testé les hypothèses que 1) le subside provenant de la plaine inondable est assimilé par la communauté ichtyenne du LSP et que 2) sa contribution trophique aux poissons diminuera en fonction de la distance de la plaine inondable et 3) sera à son maximum tôt en période de croissance suivant l'inondation printanière. Pour ce faire, nous avons échantillonné une grande proportion de la communauté de poisson (35 espèces) du LSP tôt et tard en période de croissance et nous avons mesuré le niveau de contribution trophique à l'aide de l'approche isotopique.

L'approche isotopique nous a donné l'occasion de confirmer que la productivité prenant place dans la plaine inondable était assimilée par une grande portion des poissons du LSP supportant notre première hypothèse. De plus, la contribution du subside au régime alimentaire des poissons a montré une variabilité spatiale et temporelle. Tout d'abord, la contribution de cette ressource s'est avérée plus élevée chez les individus capturés dans le littoral comparativement à ceux capturés dans le chenal principal ou à proximité appuyant notre seconde hypothèse. Dernièrement, les individus du littoral ont démontré une variabilité saisonnière dans le niveau de contribution abondant dans le sens de notre troisième hypothèse. Le subside de la plaine inondable constituait la ressource alimentaire principale (> 50 %) assimilée par les espèces littorales (ex. perchaude, grand brochet, méné jaune) tôt en période de croissance (mai et juin), mais son importance s'estompait (< 50 %) tard en période de croissance (août et septembre).

Les résultats de ce chapitre supportent fortement l'hypothèse que le subside en provenance de la plaine inondable contribue au régime alimentaire des espèces littorales d'un grand fleuve en milieu tempéré. Toutefois, puisque la contribution du subside est restreinte aux espèces littorales pour une brève période (tôt en période de croissance lorsque la production *in situ* du fleuve est toujours à un faible niveau) une application directe du concept des poussées de crue (traduction libre de *Flood Pulse Concept,* Junk *et al.* 1989) n'est pas adéquate. Le concept de vague de rivière (traduction libre de *River Wave Concept*) semble décrire plus justement notre système, soit une variabilité temporelle de l'importance des ressources supportant la productivité d'une rivière (Humphries *et al.* 2014). Cependant, les résultats obtenus lors de ce chapitre, soit la diminution de la contribution du subside en fonction de l'élévation, nous permettent de bonifier ce cadre conceptuel en lui ajoutant une dimension spatiale latérale.

Dans le chapitre II, notre objectif était de déterminer le rôle du régime hydrologique sur la disponibilité et la contribution du subside provenant de la plaine inondable au régime alimentaire des espèces de poissons littoraux du LSP ainsi que son impact sur la condition physique des individus. Nous avons testé les hypothèses selon lesquelles 1) les régimes hydrologiques affectent positivement le niveau de contribution trophique du subside ainsi que la durée de disponibilité du subside, 2) que les régimes hydrologiques et 3) le niveau de contribution affectent positivement la condition physique des individus. Pour ce faire, nous avons échantillonné 5 espèces littorales, soit la perchaude (*Perca flavescens)*, le crapet-soleil (*Lepomis gibbosus*), le méné d'herbe (*Notropis bifrenatus*), le méné jaune (*Notomigonus crysoleucas*) et le fondule barré (*Fundulus diaphanus*), au cours de 4 années hydrologiquement distinctes.

Nos résultats montrent que la contribution du subside sur l'ensemble de la période de croissance est influencée par les régimes hydrologiques extrêmes supportant notre première hypothèse. Les années de faible inondation ont démontré une contribution faible du subside à la communauté littorale tôt en période de croissance en comparaison aux années ayant un régime d'inondation normal ou très fort. De plus, lors d'années de forte inondation, le subside provenant de la plaine a été identifié comme source d'énergie principale (> 50 %) pour les espèces littorales tout au long de la période de croissance, ne présentant donc aucune variabilité temporelle. Ce patron n'a pas été observé lors des années de faible ou de moyenne inondation. Au niveau de l'individu, la variable hydrologique (« Individual Mean Flooded Area », MFA_I, Chapitre II) a été reconnue comme étant une variable importante pour expliquer la contribution du subside de la plaine au régime alimentaire de l'individu conjointement avec la date de capture et l'espèce étudiées. De plus, la variable MFA_I était positivement corrélée avec l'indice de condition physique des 5 espèces à l'étude, suggérant qu'une forte inondation exerce un effet positif sur les espèces littorales appuyant notre seconde hypothèse. Une corrélation positive entre la contribution du subside de la plaine et l'indice de condition physique a été observée chez le méné jaune et le fondule barré, supportant que le subside soit de bonne qualité pour ces espèces. Toutefois, notre troisième hypothèse n'est que partiellement validée puisque la condition physique de seulement deux espèces sur cinq répond positivement au niveau de contribution du subside.

Les résultats du chapitre II démontrent l'importance du régime hydrologique comme facteur contrôlant la dynamique du subside provenant de la plaine inondable d'une rivière tempérée. Ces résultats suggèrent que les pressions anthropiques sur le régime hydrologique (diminution de l'ampleur et de la durée des crues) et la plaine inondable (empiètement) réduiront la contribution du subside au régime alimentaire des espèces littorales du LSP. En retour, la réduction de la quantité et de la période de disponibilité du subside provenant de la plaine devrait diminuer la condition physique des poissons.

Dans le chapitre III, nous avons développé une approche isotopique multi-tissulaire nous permettant d'estimer la période de disponibilité d'un subside pulsé. Par la suite, nous avons exploré les possibles répercussions de la sélection de différents tissus ayant des taux de renouvellement isotopique distincts lors de l'utilisation de l'approche des isotopes stables pour mesurer l'importance d'un subside pulsé au régime alimentaire d'une espèce dépendante. Finalement, nous avons appliqué l'approche isotopique multi-tissulaire afin d'estimer la durée du subside provenant de la plaine d'inondation pour quatre années ayant des régimes hydrologiques contrastants. Nous avons testé les hyphothèses que 1) dans un contexte de subside pulsé l'utilisation de tissu à renouvellement isotopique lent (ex. muscle) engendrera une sous-estimation de la contribution réelle du subside en comparaison aux tissus à renouvellement rapide (ex. foie); 2) que l'utilisation combinée de tissus à renouvellement isotopique lent et rapide permet d'estimer le moment de changement de sources énergétiques. À ces fins, nous avons échantillonné des perchaudes tôt et tard en période de croissance au cours de 4 années hydrologiquement distinctes. Par la suite, nous avons mesuré la contribution trophique du subside provenant de la plaine à l'aide de l'approche isotopique pour le foie (tissu à renouvellement isotopique rapide) et le muscle (tissu à renouvellement isotopique lent).

Nos résultats démontrent que le choix du tissu pour l'approche des isotopes stables peut avoir des répercussions majeures sur l'évaluation de la contribution relative des subsides pulsés au régime alimentaire des consommateurs supportant notre première hypothèse. En moyenne, la contribution apparente du subside au muscle (tissu lent) est sous-estimée de 8,8 % tôt en période de croissance et sur-estimée par 5,8 % en comparaison à celle du foie (tissu rapide). Ceci montre que l'utilisation de multiples tissus ayant des taux de renouvellement isotopique distincts permet d'éviter les conclusions erronées et de mieux cerner les patrons temporels de l'utilisation d'un subside pulsé par les consommateurs.

L'approche multi-tissulaire développée dans notre étude permet de modéliser le moment de la transition de régime alimentaire entre le subside et la production fluviale *in situ,* en relation au patron d'inondation pour nos 4 années à l'étude. La capacité de l'approche à définir ce moment de transition soutient notre seconde hypothèse. Les résultats du modèle indiquent que le changement de ressources alimentaires, du subside pour la ressource *in situ*, se produit quelques jours avant la fin de la crue à l'exception de l'année de très faible inondation, où le changement semble se produire après la fin de la crue. Ces résultats suggèrent que les individus changent leur alimentation pour la ressource produite dans la rivière lorsque cette dernière devient plus abondante que le subside de la plaine inondable.

Dans le contexte du LSP, ce chapitre met en relation la durée du subside provenant de la plaine avec les régimes hydrologiques et la productivité primaire. Dans un cadre plus général, le chapitre III propose une approche adaptable permettant d'identifier les variables environnementales influençant la période de disponibilité d'un subside pulsé dans différents contextes environnementaux. De plus, ce chapitre met de l'avant avec un exemple concret, l'importance de la sélection du tissu lors de l'utilisation de l'approche isotopique pour l'étude des subsides pulsés.

Perspectives de recherche

L'étude des subsides dans le contexte des changements climatiques

Les subsides sont un sujet d'actualité en écologie en raison de leur grande importance pour le fonctionnement des systèmes receveurs ainsi que la complexité des mécanismes responsables de la réponse du système receveur (Bampoh *et al.* 2019, Subalusky et Post 2019, Urban *et al.* 2019, Zuercher *et al.* 2019). Dans un contexte de changements climatiques, les impacts vont perturber les facteurs qui régissent la quantité, la qualité, la durée et le timing des subsides modifiant ainsi la réponse des organismes et écosystèmes receveurs (Mcmullin *et al.* 2017, Brett *et al.* 2017, Arimitsu *et al.* 2018, Degerman *et al.* 2018, Pessarrodona *et al.* 2018). Une compréhension profonde de l'impact des subsides sur le système receveur, et plus particulièrement des mécanismes et processus responsables de la réponse, est indispensable pour prédire la trajectoire des écosystèmes dans le futur.

Au LSP, les recherches prévoient que les changements climatiques vont influencer la phénologie du régime d'inondation. Ceux-ci engendreraient une diminution de l'ampleur et de la durée des inondations ainsi qu'une crue printanière plus hâtive (Boyer *et al.* 2010, CEHQ 2015). Ces modifications de la phénologie de la crue printanière provoqueraient une diminution de la production du subside provenant de la plaine engendrant une réduction de sa contribution aux espèces littorales. De plus, un devancement de la crue printanière pourrait découler en un découplage entre le régime d'inondation et les régimes thermiques et d'ensoleillement. Ces régimes fournissent les conditions écologiques favorisant la diversité et la productivité (Tockner *et al.* 2000). Donc, un découplage entre ceux-ci provoquerait un effet négatif majeur sur le réseau trophique littoral du LSP en diminuant la quantité de subside produite et en dissociant la période de disponibilité du subside de la période de forte demande.

Nouvelles approches pour l'étude des subsides spatiaux

Au cours de cette thèse, nous avons démontré que l'utilisation des ratios isotopiques du carbone ($\delta^{13}C$) permet de mesurer adéquatement la contribution du subside provenant de la plaine inondable au régime alimentaire des consommateurs de la rivière adjacente. Toutefois, l'utilisation d'éléments autres que le carbone a aussi une forte pertinence pour l'étude des subsides. Par exemple, l'utilisation des isotopes stables du soufre ($\delta^{34}S$) et de l'hydrogène ($\delta^{2}H$) peut nous informer sur les subsides spatiaux entre les systèmes terrestres et aquatiques (Doucett *et al.* 2007, Cole *et al.* 2011, Nehlich *et al.* 2011, Solomon *et al.* 2011), ainsi qu'entre les systèmes marins et d'eau douce (Porter *et al.* 2014, Novak *et al.* 2017). L'utilisation de plusieurs éléments conjointement permet de discerner la contribution de plusieurs sources potentielles d'énergie à un réseau trophique (Hamilton *et al.* 1992, Finlay 2001). L'approche multi-isotopique offre aux chercheurs la capacité de suivre simultanément plusieurs sources autochtones et allochtones, permettant ainsi d'étudier des réseaux trophiques complexes (Porter *et al.* 2014, Weber *et al.* 2017).

Au cours des dernières années, l'abondance naturelle de l'isotope radioactif du carbone ($\Delta^{14}C$) a émergé comme un traceur naturel des sources de carbone (autochtone et allochtone) dans les écosystèmes, plus particulièrement chez les systèmes aquatiques (Bellamy *et al.* 2017). L'utilisation du $\Delta^{14}C$ permet de distinguer les sources de carbone terrestre des sources aquatiques, parfois impossibles avec le $\delta^{13}C$ en raison du chevauchement de leur signature, ainsi que de nous informer sur l'âge du carbone et de la matière organique consommés par les organismes (Caraco *et al.* 2010, Bellamy *et al.* 2017, Guillemette *et al.* 2017). De multiples études ont démontré que le carbone terrestre ancien (ex. décongélation du permafrost, suintements d'hydrocarbures, fonte des glaciers) est un subside potentiel d'importance pour les écosystèmes aquatiques malgré le paradigme prônant sa faible qualité comparativement au carbone plus moderne (Zigah *et al.* 2012, Guillemette *et al.* 2017 et référence à l'intérieur, Evans *et al.* 2018). De plus, la quantité de carbone terrestre ancien exportée vers les systèmes aquatiques ainsi que son assimilation dans le réseau trophique est positivement corrélée avec l'ampleur des pressions anthropiques (agriculture, urbanisation, déforestation, changements climatiques) présente dans le bassin versant (Wang *et al.* 2014, Butman *et al.* 2015, Bellamy *et al.* 2017, Guillemette *et al.* 2017). Dans un contexte de pressions anthropiques croissantes, l'utilisation $\Delta^{14}C$ peut nous informer sur l'importance du subside terrestre (moderne et ancien) à la productivité des systèmes aquatiques ainsi que sur l'effet des perturbations anthropiques sur celui-ci (Caraco *et al.* 2010, Weber *et al.* 2017). Ces informations seront d'une importance primordiale dans la gestion des systèmes aquatiques d'eau douce dans un futur rapproché (Keaveney *et al.* 2015).

Complémentairement aux approches isotopiques discutées précédemment, l'analyse du profil des acides gras offre une avenue forte intéressante lors d'études sur les relations trophiques. La composition en acide gras varie en fonction du type de producteur primaire (ex. terrestre vs aquatique) offrant un traceur naturel pour suivre les subsides le long du réseau trophique (Thurber *et al.* 2013, Hixson *et al.* 2015, Twining *et al.* 2016). Par exemple, le ratio d'acide gras omega-3 : omega-6 peut être utilisé comme traceur d'un subside d'origine marin vers les milieux d'eau douce puisqu'il est plus élevé chez les organismes marins que d'eau douce (Heintz *et al.* 2004). Puisque les acides gras essentiels (i.e. ne pouvant pas être synthétisés par les organismes consommateurs) sont produits à la base de la chaîne alimentaire par les plantes et bactéries, l'analyse de leur composition chez les organismes consommateurs offre de l'information générale sur les sources d'énergie basales supportant un écosystème (Olsen 1999, Heintz *et al.* 2004). De surcroît, la ressource contenant une forte concentration d'acides gras essentiels est souvent perçue comme une ressource de haute qualité (Hixson *et al.* 2015, Twining *et al.* 2019) et peut même agir comme un composé limitant la croissance dans certaines situations (Gladyshev *et al.* 2013). Par exemple, les acides gras poly-insaturés (PUFA) jouent des rôles physiologiques importants chez un grand nombre d'organismes, en faisant une ressource de qualité et potentiellement limitante pour le consommateur (Fritz *et al.* 2019). Donc l'analyse du profil des acides gras peut nous informer sur la provenance d'un subside, son étendue spatiale dans le système receveur ainsi que sur sa qualité (Twining *et al.* 2016, Fritz *et al.* 2017, 2019).

Une nouvelle approche prometteuse pour l'étude des liens trophiques est l'analyse isotopique des composés spécifiques tels que les acides aminés ou les acides gras. L'analyse isotopique des composés spécifiques de biomarqueurs caractéristiques à certains groupes d'organismes permet de distinguer la composition isotopique des différentes sources parfois impossibles à dissocier en raison de la difficulté de séparer ces sources physiquement (Van den Meersche *et al.* 2009, Bec *et al.* 2011). Par exemple, obtenir la signature isotopique pure du phytoplancton est très difficile en raison des autres composantes du seston (bactéries, détritus et protozoaires) et de notre incapacité de les séparer physiquement. L'analyse isotopique des acides gras spécifiques au phytoplancton offre une signature isotopique purement phytoplanctonique impossible à obtenir par l'approche isotopique traditionnelle (Pace *et al.* 2007). Certaines études ont d'ailleurs démontré des liens trophiques importants par l'analyse isotopique des composés spécifiques, alors qu'ils avaient été jugés inexistants par les approches isotopiques conventionnelles (ex. $\delta^{13}C$, $\delta^{15}N$ et $\delta^{34}S$ du muscle) (Seabrook *et al.* 2019). Donc, l'analyse des ratios isotopiques des composés spécifiques permet d'identifier et mesurer la contribution de certaines sources préalablement impossibles à dissocier ainsi que de déceler des relations trophiques qui étaient négligées par les approches isotopiques dites traditionnelles (Van den Meersche *et al.* 2009, Ishikawa *et al.* 2014, Brett *et al.* 2017, Seabrook *et al.* 2019, Twining *et al.* 2019).

Une avenue forte intéressante dans l'étude des subsides est l'utilisation simultanée des différentes approches soit l'analyse isotopique de multiples éléments (stable et radioactif), l'étude des profils des acides gras ainsi que l'analyse isotopique de composés spécifiques. Ceci permettrait de répondre à de multiples questions qui ne pourraient être résolues par l'usage d'une seule de ces approches (Weber *et al.* 2017, Bellamy *et al.* 2017, Johnson *et al.* 2018). L'approche multiple permettrait aussi de démêler des signaux mixtes résultants de facteurs temporels et spatiaux (Seabrook *et al.* 2019), d'inclure la qualité de la ressource dans les analyses et ainsi de brosser un portrait plus complet de l'utilisation des subsides par les consommateurs pour déterminer le réel impact des subsides sur le système receveur (Van den Meersche *et al.* 2009, Seabrook *et al.* 2019, Twining *et al.* 2019).

Le fleuve Saint-Laurent, un système à explorer

L'introduction de cette thèse signalait la grande variabilité de l'importance des subsides provenant de la plaine inondable entre les différents systèmes de rivière/plaine inondable en milieu tempéré. Cette variabilité résulte en partie du grand nombre de variables environnementales qui entrent en jeu (climatiques, hydrologiques, morphologiques, anthropiques) et des interactions complexes entre ces variables, ce qui réduit notre potentiel de généralisation (Thorp *et al.* 1998, Gutreuter *et al.* 1999, Dettmers *et al.*

2001, Schramm et Eggleton 2006). De plus, le LSP est un écosystème qui diffère grandement, de par la présence d'un couvert de glace pendant près de quatre mois et une forte saisonnalité des températures définissant clairement la saison de croissance, des autres systèmes tempérés où des études sur le rôle de la plaine inondable ont été menées. Bien que cette thèse ait clarifié le rôle de la plaine inondable comme lieu d'origine d'une ressource alimentaire importante pour la communauté de poisson du LSP et ait proposé des concepts plus généraux pouvant s'appliquer à d'autres systèmes tempérés comme la saisonnalité de la contribution, l'ajout d'une dimension spatiale au concept de vague de rivière (traduction libre de River Wave Concept, Humphries *et al.* 2014), et l'impact positif du subside sur les poissons littoraux, il demeure important de détailler les facteurs environnementaux supportant leur applicabilité.

Le fleuve Saint-Laurent (FSL) est un laboratoire à aire ouverte nous permettant d'étudier les subsides provenant de la plaine inondable. Celui-ci abrite une grande diversité et une forte variabilité spatiale dans ses habitats, sa faune ichtyenne et le niveau de pressions anthropiques retrouvées le long de son parcours. Nous pouvons donc, en étudiant le fleuve à différente échelle, répondre à plusieurs questions écologiques sur les subsides spatiaux. Tout d'abord, la section située en amont du lac Saint-Pierre et de son archipel abrite une richesse en milieux humides très faible qui est de plus fortement fragmentée (Talbot, 2006). Complémentairement, la composition et la richesse de la communauté ichtyenne sont changeantes en fonction du tronçon du fleuve à l'étude. Ceci nous permet d'observer de nouvelles espèces qui n'ont pas été capturées dans le LSP au cours de cette thèse (La Violette *et al.* 2003, Foubert *et al.* 2018), ainsi que d'observer la même espèce dans différents habitats. Ceci nous permettrait de tester l'importance du subside provenant de la plaine inondable sous différentes conditions chez la même espèce simultanément. De plus, les pressions anthropiques agissant directement sur le littoral sont très fortes en amont du LSP, avec pratiquement l'entièreté des berges ayant été modifiée pour limiter l'effet des inondations (Talbot, 2006). Par cette configuration spatiale des pressions anthropiques le long du FSL, il est possible d'observer une variabilité saisonnière dans les débits tout le long du FSL, à l'exception du lac Saint-François, mais seulement une forte augmentation des aires inondées au LSP et son archipel. Ceci nous offre l'opportunité d'isoler l'effet de l'ampleur de la plaine inondable sur la contribution des sources alimentaires potentielles, la croissance ainsi que sur la condition physique des poissons.

Au lac Saint-François, un autre lac fluvial du FSL, les niveaux d'eau montrent qu'une très faible variabilité annuelle (‹15 cm) en raison d'un fort contrôle des débits par deux complexes hydroélectriques (Moses-Saunders et Beauharnois-les Cèdres). En comparant ce tronçon avec le reste du FSL nous pouvons isoler l'effet du régime hydrologique des autres variables lors d'étude visant à comprendre l'effet de la variabilité des niveaux d'eau sur les organismes. Puisque les niveaux ne varient pratiquement pas, la contribution de la plaine inondable comme ressource alimentaire est fortement limitée, pour ne pas dire inexistante, rendant possible de comparer les effets d'un subside sur la communauté de poisson et d'étudier des théories écologiques plus larges. Par exemple, nous pourrions vérifier si l'apport d'un subside augmente réellement la longueur réseau trophique (Briggs *et al.* 2012).

À plus petite échelle, le LSP et son archipel abritent une plaine inondable à fort caractère naturel, offrant une forte diversité dans les habitats inondés ainsi qu'une faune et une flore luxuriante. Cette thèse a mesuré et décrit les patrons spatio-temporels de la contribution de ce subside à la communauté ichtyenne, mais n'a pas analysé son importance pour l'ensemble de la communauté faunique démontrant une dépendance à la plaine inondable. Par exemple, un grand nombre d'espèces d'oiseaux utilise la plaine inondable du LSP comme halte migratoire ou utilise directement la plaine inondable comme aire de nidification. L'étude de l'utilisation des ressources alimentaires de la plaine inondable par les espèces migratrices pourrait nous informer sur son importance comme source d'un subside transporté sur de grandes distances et de son possible impact sur les habitats receveurs (voir introduction). Complémentairement, les études se concentrant sur les espèces nicheuses pourraient mettre en relation l'influence de la plaine inondable et du régime hydrologique sur la croissance et le taux de survie des oisillons. Dans l'ensemble, nos connaissances liées au rôle des plaines inondables naturelles sur la communauté sont rudimentaires au LSP et dans les rivières tempérées en général. L'étude de l'ensemble de la communauté faunique offrirait une compréhension holistique et permettrait une gestion plus adéquate de ces écosystèmes.

De plus, au cours de cette thèse, nous nous sommes principalement intéressés au rôle de la plaine inondable en général sans nous attarder à la variabilité pouvant émaner entre les différents habitats inondés. L'archipel du LSP composé de 103 îles offre une grande variabilité d'habitats naturels inondés qui ne sont pas présents dans le reste du Saint-Laurent. Par exemple, on retrouve dans l'archipel des cours d'eau intermittents et des baies de taille variable le tout dans différentes masses d'eau provenant d'effluents différents. De plus, comparativement au LSP, le chenal principal de la rivière se trouve plus près des zones inondées nous offrant la chance de tester si c'est la distance séparant la plaine au chenal principal ou bien les patrons de déplacements des poissons qui agissent comme facteur limitant la distribution du subside dans le système receveur.

À plus petite échelle, il serait intéressant d'identifier les sources d'énergie basales (algale, détritique ou méthanotrophe) supportant la productivité dans les plaines d'inondation et d'observer si la contribution de chaque source varie en fonction du type d'habitat inondé et de son positionnement dans l'axe latéral de l'écoulement de la rivière. Ceci pourrait être accompli en utilisant les différentes approches proposées dans la section précédente.

Amélioration de l'approche isotopique multi-tissulaire

L'approche isotopique multi-tissulaire développée au chapitre III se voulait très générale afin d'élargir son utilisation à une vaste gamme de système. Certaines études pourraient l'optimiser pour leur système tout en répondant à des questions écologiques distinctes. Par exemple, répéter l'étude du chapitre II et III, mais avec un suivi s'étendant tout le long de l'année et un échantillonnage temporel plus serré permettrait de tester l'approche isotopique multi-tissulaire tout au long de la période de croissance afin d'identifier les valeurs des ratios isotopiques de départ et le moment initial de l'utilisation du subside. De plus, les résultats recueillis au cours de cette étude permettraient d'approfondir nos connaissances sur l'écologie hivernale de beaucoup d'espèces ainsi que sur la variation isotopique en période de limitation nutritionnelle et de croissance restreintes. Il a été suggéré à maintes reprises que l'expérimentation en laboratoire devrait être utilisée afin de combler nos connaissances sur les facteurs et processus influençant les ratios isotopiques (Gannes *et al.* 1997, Martínez del Rio *et al.* 2009). Il serait donc avantageux de mener des expériences en laboratoire visant à obtenir des taux de renouvellement précis spécifiques aux espèces étudiées en nature. Par exemple, pour la perchaude (*Perca flavescens*) aucune donnée sur le taux de renouvellement du foie n'était disponible et nous avons dû prendre le taux d'une espèce similaire (*Perca fluviatilis*). Bien que ceci soit acceptable, cette solution n'est pas optimale. De plus, des recherches sur l'influence de la température sur la croissance et le taux de renouvellement isotopique seraient nécessaires puisque la disponibilité du subside se produit dans une période de l'année où la température est fortement variable. L'incorporation de taux de renouvellement spécifique à la population à l'étude ainsi que l'effet de la température journalière augmenteraient significativement la précision du modèle et accroîtraient nos connaissances sur le métabolisme des organismes à l'étude.

Conclusion

Cette thèse s'est intéressée à un champ de recherche d'actualité en écologie, soit les subsides spatiaux. Plus particulièrement, nous nous sommes penchés sur l'importance de la productivité de la plaine inondable comme source d'énergie soutenant le réseau trophique du lac Saint-Pierre, qui jusqu'à ce moment était plutôt anecdotique et méconnue. Par l'utilisation de l'approche des isotopes stables, nous avons clarifié les patrons spatio-temporels de la contribution du subside provenant de la plaine inondable au régime alimentaire de la communauté de poissons et évalué les effets du régime hydrologique sur cette contribution. Les principales contributions de cette thèse sont 1) la démonstration de la présence et de l'assimilation d'un subside pulsé en provenance de la plaine inondable soutenant la productivité des poissons du LSP; 2) La clarification des patrons spatio-temporels de la contribution du subside au régime alimentaire d'une grande proportion de la communauté ichtyenne; 3) La description de l'influence du régime hydrologique sur la disponibilité et l'assimilation du subside provenant de la plaine ainsi que sur la condition physique de cinq espèces littorales. Cette thèse a donc permis d'établir des fondations solides pour de futures études sur les subsides en provenance de la plaine d'inondation dans le LSP. De plus, les connaissances acquises au cours des trois chapitres de cette thèse offrent une nouvelle vision de l'importance des plaines d'inondation comme un habitat de productivité de la principale ressource supportant les poissons (parfois exploités pour la pêche récréative et commerciale) dans un grand fleuve. Dans un contexte plus général, cette thèse a fait avancer les connaissances sur le rôle des plaines inondables en milieu tempéré comme source d'un subside pour supportant la productivité de la rivière. En plus, nous avons mis en évidence certaines faiblesses de l'approche isotopique lorsque celle-ci n'utilise qu'un seul tissu et avons développé une approche isotopique multi-tissulaire permettant d'estimer la durée des subsides pulsés dans de multiples écosystèmes.

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