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COUPLAGE ENTRE MACRO-HABITATS ET CONTRIBUTION D'UNE PLAINE D'INONDATION À LA PRODUCTIVITÉ D'UN GRAND LAC FLUVIAL

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« Les mots que nous proférons déterminent notre perception du monde.
Il ne tient qu'à nous de les réenchanter. »

Clément Viktorovitch, *Le pouvoir rhétorique*

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Introduction générale

Introduction

Contexte général

Les écosystèmes aquatiques sont parmi les plus productifs et dynamiques de la biosphère (Häder & Gao, 2023). Leur fonctionnement repose en grande partie sur la circulation de matière et d'énergie entre compartiments interconnectés, qu'il s'agisse des liens entre zones pélagiques et benthiques (Stasko et al., 2016), entre amont et aval (Vannote et al., 1980), ou entre chenal principal et habitats latéraux (Jardine et al., 2012). Dans les grands systèmes fluviaux, cette connectivité est particulièrement marquée par l'existence de plaines inondables saisonnières, qui figurent parmi les milieux les plus riches et diversifiés de la planète (Ndehedehe et al., 2021).

La plaine inondable constitue une extension fonctionnelle du cours d'eau principal. Son inondation périodique entraîne un transfert de nutriments et de matière organique (Junk et al., 1989; Tockner et al., 2000), stimule la productivité primaire et crée une mosaïque d'habitats offrant refuges (King et al., 2003), ressources alimentaires et sites de reproduction pour de nombreuses espèces aquatiques (Bouloy et al., 2024). Le régime hydrologique pulsé, ou « floodpulse », conditionne la fréquence, l'ampleur et la durée de ces connexions entre le cours d'eau et sa plaine. Ce processus contrôle ainsi la disponibilité temporelle des habitats et la circulation des organismes et des ressources entre compartiments (Junk et al., 1989). Le *floodpulse* a cependant était conceptualisé dans les systèmes tropicaux et non dans les systèmes avec plaine inondable en milieu tempéré où la durée et l'intensité de l'inondation n'est pas aussi forte. En effet, l'inondation en milieu tempéré est plus prévisible puisqu'elle est causée par les pluies printanières et la fonte des neiges à la différence des autres climats où l'inondation est plus irrégulière et imprévisible dans le temps (Torre Zaffaroni et al., 2023). Ces conditions environnementales spécifiques aux milieux tempérés doivent favoriser seulement les espèces qui ont intérêt à coupler ces habitats.

Cette connexion entre lac et plaine s'inscrit dans le cadre plus large de la théorie des méta-écosystèmes, développée au début des années 2000 pour décrire les flux de matière, d'énergie et d'organismes entre habitats distincts mais connectés (Loreau et al., 2003). Selon cette théorie, la dynamique d'une communauté locale dépend en partie des échanges avec des habitats voisins. L'application de ce cadre conceptuel aux systèmes fluvio-lacustres souligne l'importance des plaines inondables comme zones de transit et de transformation des flux biologiques et trophiques (Figure 1). Dans ce contexte, les poissons, en tant qu'organismes mobiles, jouent un rôle dans le couplage des macrohabitats en exploitant les ressources de la plaine, transportant ainsi l'énergie et les nutriments allochtones. De plus la diversité d'habitats offerts par la plaine d'inondation crée des opportunités pour des espèces aux traits fonctionnels variés. Ce cadre théorique permet donc de mieux appréhender comment la dynamique saisonnière influence la distribution des espèces, leurs interactions trophiques, et *in fine*, le fonctionnement global de l'écosystème.

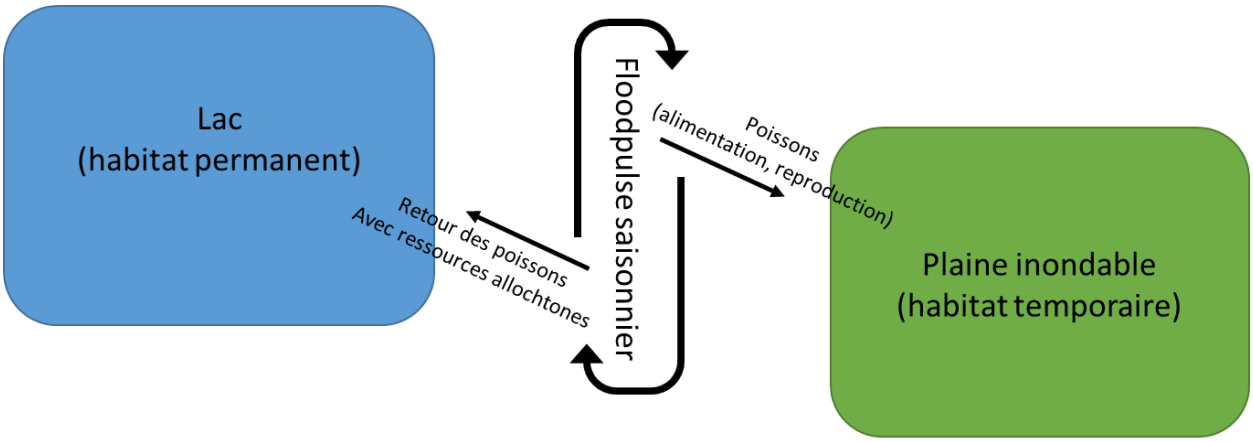


Figure 1. Schéma conceptuel illustrant le couplage fonctionnel entre un lac (habitat permanent) et sa plaine inondable (habitat temporaire). Pendant la crue printanière, la plaine inondable devient accessible aux poissons, qui y trouvent des habitats favorables à la reproduction et l'alimentation. Ce processus de connectivité hydrologique et trophique illustre le rôle de ces habitats dans le fonctionnement écologique de ce méta-écosystème.

Cependant, les caractéristiques du *floodpulse* varient selon les systèmes et peuvent être altérées par les activités humaines, ce qui pose des défis pour comprendre et préserver leur rôle écologique maintenant l'équilibre du système. Dans ce contexte, il devient nécessaire de mieux identifier les mécanismes qui déterminent l'accès et l'utilisation de la plaine par les poissons, la nature des flux trophiques qui en résultent, et l'empreinte que ces processus laissent dans la structure des communautés.

Ayant établi que les plaines innondables jouent un rôle clé dans la productivité des écosystèmes inondables tempérés, nous nous intéressons maintenant à la manière dont les mécanismes de couplage entre ces habitats peuvent être étudiés. Pour ce faire, nous mobilisons trois approches complémentaires qui forment le cadre conceptuel de cette thèse.

Cadre conceptuel

L'étude des interactions écologiques entre lac et plaine inondable peut être abordée à travers différents prismes complémentaires. Dans cette thèse, trois approches conceptuelles sont mobilisées pour éclairer les mécanismes de couplage qui composent les trois chapitres de ma thèse : les traits fonctionnels, la signature isotopique et la distribution en taille de la communauté.

Les traits fonctionnels décrivent les caractéristiques mesurables des espèces qui influencent leur fitness, leur écologie et leur rôle dans les écosystèmes (Mcgill et al., 2006). Dans le cas des poissons, des traits tels que la taille maximale, le mode et l'habitat de reproduction, la tolérance thermique ou encore la position de la bouche peuvent déterminer leur capacité à occuper différents habitats et à répondre aux contraintes de l'environnement (Blanchet et al., 2013). En considérant la plaine inondable comme un habitat temporaire soumis à des fluctuations hydrologiques, ces traits pourraient expliquer pourquoi certaines espèces parviennent à exploiter ce système.

Le second angle d'analyse concerne les flux trophiques qui relient la plaine au lac. L'inondation saisonnière ne se traduit pas seulement par un élargissement de l'espace disponible, mais aussi par un accès à des ressources alimentaires d'origine allochtone (invertébrés et nutriments provenant de la plaine inondable) (Górski et al., 2011, 2013). Les poissons qui fréquentent la plaine peuvent ainsi incorporer dans leur régime des proies issues de cet habitat temporaire, ressources qui peuvent ensuite être transférées vers le lac lors du retour des poissons (Farly et al., 2019). L'analyse des signatures isotopiques ($\delta^{13}C$ et $\delta^{15}N$) permet de quantifier la contribution relative de ces ressources et d'identifier les espèces et les habitats qui jouent un rôle dans ce couplage trophique (Fry, 2006).

Enfin, la taille corporelle constitue une caractéristique structurante des communautés ichtyologiques, car elle influence à la fois les besoins énergétiques (Brown et al., 2004), les interactions trophiques (Elton, 1927) et les stratégies d'occupation spatiale (Petchey et al., 2008). L'analyse de la distribution des tailles au sein d'une communauté, à travers les spectres de taille, offre une représentation synthétique de la structure trophique et la dynamique énergétique d'un système (Blanchard et al., 2009; White et al., 2007). Dans le contexte d'un *floodpulse*, ces spectres peuvent révéler l'empreinte laissée par la plaine inondable sur la croissance et la survie des individus, ainsi que sur la composition globale de la communauté.

Pris ensemble, ces trois angles : traits fonctionnels, ressources alimentaires et spectre de taille, permettent d'aborder le couplage lac-plaine sous des perspectives complémentaires : prédire quelles espèces se retrouvent dans les différents habitats, quantifier la part des ressources issues de la plaine, et détecter les signatures intégrées de ces processus dans le structure de taille des communautés. Ce cadre conceptuel, que nous définissons comme l'articulation de plusieurs dimensions écologiques en un ensemble cohérent permettant de formuler des prédictions et de

structurer les analyses, guide la progression de la thèse. Ce cadre établit un lien direct entre les mécanismes écologiques étudiés et leurs manifestations observables à différentes échelles (Figure 2).

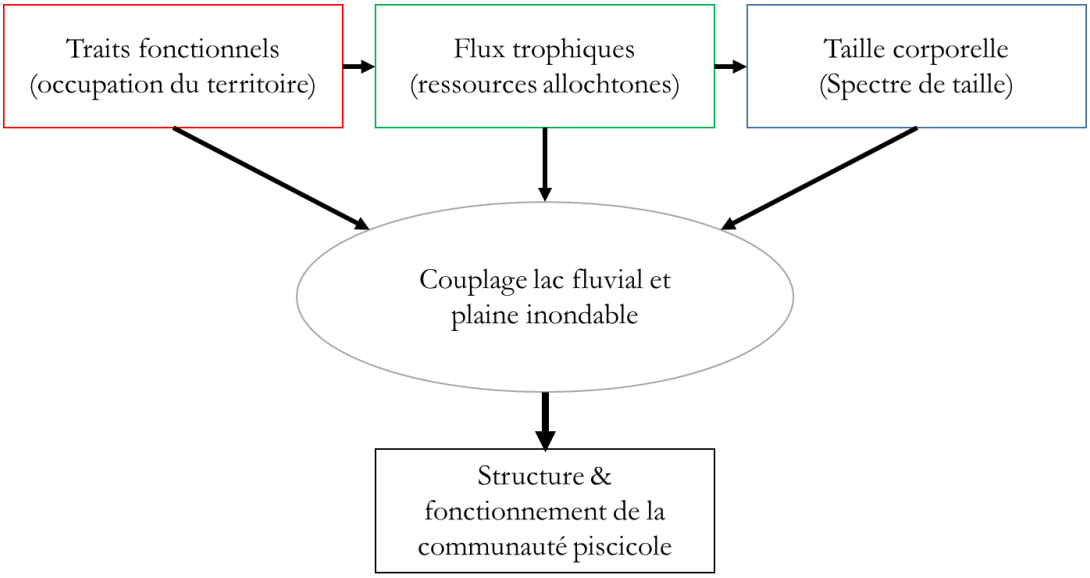


Figure 2. Schéma conceptuel illustrant les liens entre les trois axes de recherche abordés dans la thèse. Les trois encadrés supérieurs représentent les différents volets d'analyse : (1) la distribution spatiale entre le lac et la plaine inondable des espèces et leurs traits fonctionnels (rouge), (2) l'exploitation des ressources allochtones issues de la plaine (vert) et (3) la structure de taille des communautés de poissons du lac Saint-Pierre (bleu). Ces trois volets ont pour but d'expliquer les origines du couplage entre un lac et sa plaine inondable à l'échelle individuelle, populationnelle et communautaire. Cette approche vise à fournir un cadre généralisable pour l'étude d'autres systèmes soumis à des dynamiques hydrologiques comparables.

Système d'étude

Le lac Saint-Pierre (LSP), situé entre Montréal et Trois-Rivières, Québec, constitue le plus vaste lac fluvial du fleuve St-Laurent. Avec une superficie de plus de 300 km^2 et une profondeur moyenne de 3 m, il est caractérisé par un vaste archipel et par une plaine inondable d'environ 540 km^2 (La Violette, 2004; Langlois et al., 1992). Cette configuration en fait un système hydrologique et

écologique singulier, à la fois lacustre et fluvial, où les échanges avec la plaine inondable sont au cœur du fonctionnement des communautés biologiques.

Le LSP est un haut lieu de biodiversité aquatique et riveraine, notamment en raison de la biodiversité de ses habitats : herbiers aquatiques, marais, forêts riveraines, prairies humides et chenaux secondaires. Ces milieux jouent un rôle crucial pour de nombreuses espèces de poissons, dont plusieurs utilisent la plaine comme aire de reproduction et de croissance des juvéniles (grand brochet, perchaude, cyprinidés) (Bailly et al., 2008). Le site a d'ailleurs reçu la désignation Ramsar en 1998 (site Ramsar No. 949) et a été inscrit au réseau des réserves de la biosphère de l'UNESCO en 2001 (La Violette 2004).

Cependant, l'écosystème du LSP a subi d'importantes transformations au cours du XX^{e} siècle. Les travaux de régulation du fleuve Saint-Laurent, l'expansion et le changement des pratiques agricoles dans les basses terres ont modifié la dynamique hydrologique et l'occupation du sol dans la plaine inondable. Entre 1950 et 1997 une large proportion des milieux naturels de la plaine a été convertie en terres agricoles ou en infrastructures (prairie naturelle en culture intensive maïs ou soya), entraînant une réduction de l'habitat disponible pour les poissons (Dauphin & Jobin, 2015). Ces changements d'usage du sol se sont combinés à une intensification des apports en nutriments et en sédiments issus des bassins versants agricoles, modifiant la qualité de l'eau et les conditions de lumière nécessaires à la croissance des herbiers aquatiques. De tels changements ont également contribué à altérer la connectivité hydrologique entre le lac et sa plaine inondable, un processus essentiel au maintien des flux de matière et d'énergie dans ce type de système (Zhang et al., 2022).

La végétation aquatique submergée, en particulier la valisnérie d'Amérique (*Vallisneria americana*), a connu un déclin marqué au cours des dernières décennies, principalement attribué à

l'augmentation de la turbidité et aux apports de nutriments (Laporte et al., 2023). La raréfaction de ces herbiers a entraîné une simplification des habitats et réduit la disponibilité de refuges pour les poissons juvéniles, ce qui a contribué au déclin d'espèces emblématiques comme la perchaude (*Perca flavescens*) (Laporte et al., 2025).

Aujourd'hui, le LSP se trouve à la croisée des enjeux de conservation et d'utilisation humaine. D'un côté, il constitue un laboratoire naturel pour comprendre le rôle des plaines inondables tempérées dans le fonctionnement des communautés aquatiques. De l'autre, il est soumis à des pressions anthropiques intenses, liées à l'agriculture intensive, aux aménagements fluviaux, à la pêche professionnelle et de loisir, les espèces invasives et aux changements climatiques. C'est ce double caractère, à la fois système modèle et territoire fragilisé, qui confère au LSP un intérêt scientifique et sociétal majeur.

Problématique et lacunes

Les plaines inondables ont été largement étudiées dans les régions tropicales (Baldwin & Mitchell, 2000; Jardine et al., 2012; Robertson et al., 2001; Thoms, 2003), où le concept de *floodpulse* a permis de mettre en évidence leur rôle central dans la productivité et la dynamique des communautés aquatiques. Ces travaux s'inscrivent plus largement dans le cadre de la théorie des métaécosystèmes, selon laquelle les écosystèmes connectés par des échanges et flux de matières et d'énergie véhiculés par les organismes, ne peuvent pas être compris indépendamment les uns des autres (Loreau et al., 2003 ; Gounand et al., 2018). En revanche, dans les écosystèmes tempérés, la compréhension de ces processus reste plus fragmentaire (Bayley, 1995; Petsch et al., 2023). Les systèmes nord-américains, tels que le LSP, par les subsides qu'apporte sa plaine inondable, offrent une occasion de documenter le rôle des plaines inondables dans le fonctionnement des réseaux

trophiques en milieu tempéré dans un contexte soumis à une forte variabilité hydrologique et à des pressions anthropiques marquées.

Des lacunes importantes persistent dans notre compréhension du couplage lac-plaine en milieu tempéré. Premièrement, même si de nombreuses études se sont intéressées aux espèces de poissons présentes dans la plaine inondable en milieu tempéré (ex., (King et al., 2003; Sullivan & Watzin, 2009; Humphries et al., 2014; Farly et al., 2019, 2021)), il reste difficile de prédire quelles espèces exploitent à la fois le lac et la plaine, et selon quels déterminants écologiques. Une approche basée sur les traits fonctionnels pourrait permettre d'éclairer ce processus, mais elle demeure encore peu appliquée dans les plaines inondables tempérées.

Deuxièmement, bien que l'importance des apports trophiques allochtones soit reconnue dans de nombreux écosystèmes (ex., (Farly et al., 2019; Perkins et al., 2018)), leur contribution réelle au régime alimentaire des poissons en contexte lac-plaine reste mal quantifiée. Le rapport des isotopes stables constitue un outil privilégié pour tracer l'origine des ressources et la structure des réseaux trophiques. L'étude de Fry (2006) a établi les bases conceptuelles et leur utilisation, montrant que les signatures isotopiques (notamment $\delta^{13}C$ et $\delta^{15}N$) permettent de distinguer les sources de production et de positionner les organismes dans la chaîne trophique. Si ces méthodes ont été largement mobilisées dans les systèmes marins et fluviaux (Stasko et al., 2016; B. C. Stock et al., 2018), leur application à l'étude du couplage trophique en milieu lac-plaine demeure limitée (Bertrand et al., 2011).

Troisièmement, la plupart des études sur le *floodpulse* se sont concentrées sur la composition spécifique des communautés, laissant en arrière-plan des approches plus intégratives. Or, la taille corporelle constitue un indicateur central des processus écologiques, car elle influence, entre autres,

les relations trophiques, la dynamique de croissance et la survie (Blanchard et al., 2009; Hildrew et al., 2007; Peters, 1986a). L'utilisation des spectres de taille pourrait fournir une empreinte intégrée des effets de la plaine inondable sur les communautés de poissons, mais cette approche reste encore peu développée dans ce contexte.

Enfin, le « Generalist Module Hypothesis » (GMH) (McMeans et al., 2016) offre un cadre théorique pour comprendre le fonctionnement des réseaux trophiques soumis à des fluctuations saisonnières. Selon cette hypothèse, les communautés aquatiques sont structurées par des caractéristiques écologiques clés, telles que la taille corporelle et la plasticité alimentaire, qui déterminent la manière dont les espèces utilisent différents habitats et redistribuent les flux d'énergie. La résilience des réseaux trophiques dépendrait ainsi de la capacité des espèces à coupler plusieurs provenances de ressources et à ajuster leurs interactions face aux variations environnementales. Bien que prometteuse, la pertinence de cette hypothèse a été peu évaluée dans un contexte de couplage lac-plaine inondable en milieu tempéré, ce qui justifie de la tester dans ce contexte d'étude.

En résumé, il manque encore une compréhension globale de la manière dont les espèces de poissons exploitent conjointement un lac et une plaine inondable, notamment de la part de ressources allochtones qu'elles exploitent et de comment cette utilisation se répercute sur la structure de la communauté. Cette lacune justifie une approche combinée, mobilisant les traits fonctionnels, l'analyse de la signature isotopique et les spectres de taille, afin de tester la GMH et de mieux saisir les mécanismes du couplage lac-plaine dans les écosystèmes tempérés. Alors que la GMH a été testé dans les lacs du bouclier canadien (MccMeans et al., 2016), son application à un système fluvio lacustre tempéré comme le LSP, caractérisé par une dynamique hydrologique pulsée et une forte occupation anthropique de la plaine, offre une opportunité unique d'évaluer sa généralisation.

Objectifs et hypothèses

L'objectif général de cette thèse est d'évaluer dans quelle mesure les plaines inondables tempérées, à travers leur connexion saisonnière avec leurs milieux permanents, influencent la structure et le fonctionnement des communautés de poissons. Cette recherche s'inscrit dans le cadre de la GMH. Cette hypothèse avance que les espèces de grande taille, caractérisées comme plus mobiles, et de haut niveau trophique sont les plus aptes à relier différents milieux par les échanges de matières qu'elles véhiculent. Cette hypothèse a été évaluée initialement dans les lacs du bouclier canadien avec les touladi (*Salvelinus namaycush*) qui sont les grands organismes à l'origine du couplage entre la zone littorale et pélagique des lacs (McMeans et al., 2016). Toutefois, la GMH n'a pas encore été appliquée dans des systèmes caractérisés par une forte dynamique hydrologique temporelle et spatiale. La présente thèse propose donc d'explorer la pertinence de la GMH dans ce contexte particulier. En parallèle de cette hypothèse, la thèse explorera également si d'autres caractéristiques morphologiques, comportementales ou évolutives permettent d'expliquer le couplage entre un lac et se plaine inondable.

Le premier volet porte sur le rôle des traits fonctionnels dans l'occupation conjointe de la plaine inondable et du milieu principal, le LSP. Plusieurs traits sont considérés (niveau trophique, période de reproduction, position de la bouche, préférence d'habitats et la taille maximale), mais une attention particulière est accordée à la taille corporelle et au niveau trophique, car ces traits représentent des axes majeurs de différenciation écologique chez les poissons (Keppeler et al., 2020). Nos hypothèses sont : qu'une espèce de grande taille, de haut niveau trophique, avec une position de bouche médiane, phytophile et dont la période de reproduction coïncide avec la phase d'inondation de la plaine, devrait avoir une probabilité accrue d'exploiter les habitats temporaires de la plaine.

Le second volet explore, à l'aide des signatures isotopiques, la contribution des ressources allochtones au régime alimentaire des poissons. Notre hypothèse suppose ici que la part des ressources alimentaires provenant de la plaine est déterminée par la taille des consommateurs, leur niveau trophique et leur préférence pour un habitat riche en végétation. En effet, ces traits pourraient conditionner l'accès et l'assimilation des ressources de la plaine par les consommateurs.

Enfin, le troisième volet s'intéresse à l'effet de l'exploitation de la plaine inondable sur la distribution en taille de la communauté. La plaine inondable fournit des ressources allochtones abondantes et énergétiquement riches (Tockner et al., 2000). Ces apports profitent particulièrement aux poissons de grande taille, dont les besoins métaboliques et la mobilité incitent à exploiter ces ressources (Vander Zanden & Vadeboncoeur, 2002). Un tel enrichissement en organismes de grande taille devrait se traduire par une pente moins négative du spectre de taille, indiquant une augmentation relative de l'abondance des grands individus (Andersen & Beyer, 2006a; Jennings & Mackinson, 2003).

Le regroupement de ces trois approches complémentaires dans ce travail de recherche permet d'articuler différents niveaux d'analyse afin d'évaluer la pertinence de la GMH dans un méta-écosystème composé d'un lac fluvial associé à sa plaine inondable. Cette démarche vise à améliorer la compréhension et la connaissance du rôle écologique des plaines inondables dans le fonctionnement et la structure des communautés aquatiques.

Chapitre 1

Testing the generalist module hypothesis in a lake-floodplain meta-ecosystem

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Abstract

Meta-ecosystems comprising distinct macrohabitats can be coupled through the active or passive movement of species. The Generalist Module Hypothesis (GMH) in food web ecology advances that body size is a key predictor of which species drive coupling and energy exchange in a meta-ecosystem, with larger organisms contributing more to coupling than smaller organisms due to their greater mobility and niche breadth. The GMH initially emphasized pelagic-littoral coupling in lacustrine ecosystems, but remains largely untested in other systems. In lake-floodplain meta-ecosystems, other functional traits (e.g., reproductive timing, diet, and habitat preferences) might influence the use of lake and floodplain habitats, and their trophic coupling, by fish species. To examine the applicability of the GMH to a lake-floodplain system, we sampled fish communities in fluvial Lake Saint Pierre (Quebec, Canada) and its floodplain over two years and across seasonal flooding stages. We used a joint species distribution model to identify which fish species or functional groups might provide coupling between habitats. We also examined how fish community structure differs between macrohabitats (floodplain vs. lake), and whether occupancy of these macrohabitats could be predicted by functional traits. Contrary to the GMH, we found that smaller species were more likely to occupy both the lake and floodplain macrohabitats than larger species, reflecting greater mobility of small species between these macrohabitats. Environmental conditions in the floodplain might offer refuge from predation and a high concentration of food resources for planktivorous species, thus favoring smaller species. The observed discrepancy with the GMH suggests that functional traits other than body size can mediate habitat coupling through animal movement in meta-ecosystems.

Keywords: animal movement, fish, fluvial lake, food webs, functional traits

Introduction

While ecology has traditionally viewed ecosystems as spatially distinct units operating mostly in isolation, the more recent notion of "meta-ecosystem" stipulates that neighboring ecosystems exchange matter and energy, thus forming a set of connected ecosystems (Loreau et al., 2003). Connection and exchanges between different ecosystems can be achieved through the movement of organisms within the meta-ecosystem (Gounand et al., 2018). To predict these exchanges, organisms potentially coupling two ecosystems can be characterized according to functional traits associated with mobility. For example, the generalist module hypothesis (GMH; McMeans et al. 2016) states that animal mobility, diet breadth, and trophic level all tend to increase with body size. Thus, animals higher up in the food chain should spatially couple larger habitat components than animals at lower trophic levels, with such couplings promoting food web stability (McMeans et al., 2016). For example, lake trout (*Salvelinus namaycush*) are large mobile predators which enable the exchange of material and energy between the littoral and pelagic zones of boreal lakes (McMeans et al., 2016). Likewise, large organisms such as the double-crested crocodile (*Crocodylus porosus*) can account for the majority of material and energy exchanges between tropical rivers and their floodplains (Jardine et al., 2017).

The GMH has been studied in temperate environments, but never in the context of a fluvial lake coupled to a floodplain through exchanges of water, nutrients, and mobile organisms such as fish. The dynamics of these coupled ecosystems are strongly influenced by lateral transfers associated with seasonal flooding, which modulates the interactions and productivity of floodplain organisms (Junk et al. 1989). Floodplains often show high productivity due to the varied nature of energy inputs (Thoms, 2003). Allochthonous resources from the terrestrial, flooded habitat (e.g., coarse detritus, dissolved organic carbon, methane) can fuel primary and secondary production of floodplains through detrital energy pathways (Farly et al., 2019). Fish moving from the floodplain to

the open waters of a lake after having assimilated allochthonous terrestrial resources from the floodplain represent an energy subsidy that couples these two macrohabitats. However, the characteristics of the species or functional guilds ensuring this coupling remains unknown. The GMH predicts that larger, more mobile generalist fish species are those most likely to colonize the seasonal floodplain, thus favouring the coupling between lake and floodplain macrohabitats.

However, in some cases, mobility may not be a good predictor of a fish species' ability to occupy a floodplain. This habitat are often rich in submerged vegetation and deadwood that provide favorable spawning habitats, which may lead phytophilic species to occupy this environment as a refuge, spawning ground, or nursery (Leyer, 2006; Bailly et al., 2008; Copp, 1989). Furthermore, species whose reproduction also coincides with seasonal flooding have an interest in entering the floodplain if their mobility allows them to do so, for the refuge that this environment offers (Jardine et al., 2012). High turbidity and hypoxia in floodplains can be environmental stressors for certain fish species (Whittier & Hughes, 1998). Species differences in stress tolerance and abiotic niches can be barriers to coupling among habitats that differ in abiotic conditions, as has been shown for brook trout (*Salvelinus fontinalis*) and lake trout (*Salvelinus namaycush*), whose oligotrophic lake use is restricted by oxythermal conditions between central deep basin and the rest of the lake (Ridgway et al., 2023). Prey resources can also differ between floodplain and lake habitats. Thus, species diets, stress tolerance, and reproductive traits could better reflect their ability to colonize the floodplain than their mobility or size.

Our main objective was to examine the applicability of the GMH to the coupling of a temperate fluvial lake and its floodplain. We sampled fish communities over two seasonal flood cycles from spring to summer over two years. We then used a joint species distribution model to identify species that occur in both floodplain and lake habitats, a prerequisite for contributing to

coupling within the meta-ecosystem. We further identified the functional traits of species that occur in both habitats. Based on the GMH, we predicted that larger fish species would have a higher probability of occupying both macrohabitats due to their greater mobility. We also evaluated the alternative hypotheses that reproductive or trophic traits may better explain the presence of species in both macrohabitats.

Methods

Study system

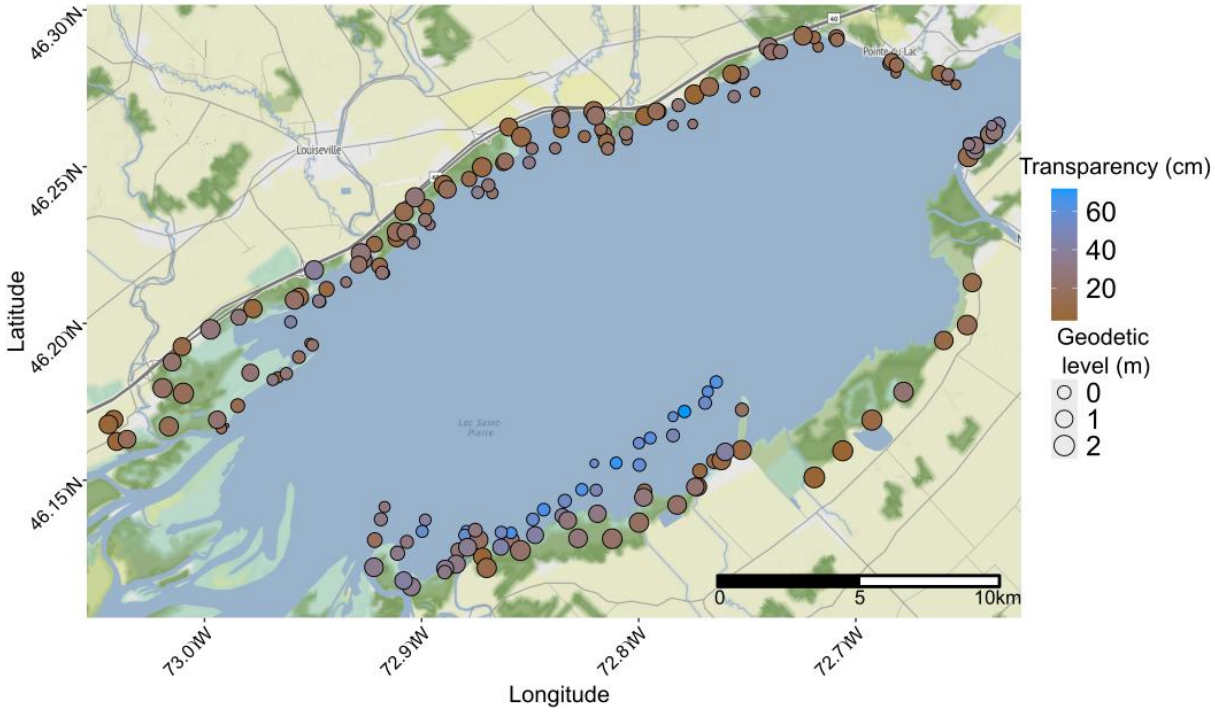
This study focuses on Lake Saint Pierre (LSP), a fluvial lake in the Saint Lawrence River upstream of Trois-Rivières, Quebec, Canada. The lake is approximately 25.6 km long and 12.8 km wide, with a mean depth of 2.7 m, excluding a human-made navigation channel that runs along the river thalweg (La Violette, 2004). Seasonal changes in water level (mean: 1.8 m) arise from varying discharge of the Saint Lawrence and Ottawa Rivers, and of several smaller tributaries (Hudon et al., 2017). Seasonal variation in discharge, coupled with a shallow topographical relief, have led to the development of a large floodplain. The 2-year flood recurrence zone covers ≈210 km^2; peak floods occur during a period of 5 to 9 weeks between April and June (Lessard, 1991). The LSP floodplain represents more than 20% of the total wetland surface in the Saint Lawrence River watershed (Langlois et al., 1992) and is classified as a RAMSAR wetland of international importance. Biodiversity in the lake is high and includes 79 species of fish (Laporte et al., 2025) The floodplain macrohabitat contributes to fish production by providing spawning grounds and abundant prey resources for early life stages of fish (Górski et al., 2011; Massicotte et al., 2015).

Sampling sites were selected at approximately equidistant intervals along the lake perimeter, every 2.5 km along the north shore and every 1.5 km along the south shore (Fig. 1). No samples

were collected along the easternmost part of the south shore, which is a military zone with restricted access. Sampling took place in April, June, and August of 2021 and 2022, with approximately 30 sites sampled per period. A total of 184 sites were sampled over two years; 103 sites on the north shore and 81 on the south shore.

Figure 1. Map showing the sampling stations (circles) and their water transparency (color) and geodetic level (symbol size).

Field sampling



At each site, fish were caught with a seine net (2 m high by 25 m long, with the central 6-m pouch having a 2 mm mesh). All fish were counted, measured and identified to species using Scott and Crossman (1974) and Massé et al. (2008). Environmental features were also measured at each site. Water transparency was measured using a Snell tube. We included transparency as a covariate because of its influence on floodplain fish communities (Laplante-Albert et al., 2010; M. A.

Rodríguez & Lewis Jr., 1997; Tejerina-Garro et al., 1998). Geodetic lake depth, measured as water depth minus the lake level relative to a fixed International Great Lakes low-water datum (Schmidt et al. 2015), was calculated for each location and sampling date. Geodetic depth, a proxy measure of the relative elevation of a station, is linked to potential determinants of fish abundance. These include patterns of current flow, influence from terrestrial inputs, and duration of flood period (Schmidt and Rodríguez 2011). Daily water levels used to calculate geodetic depth were obtained from the Fisheries and Oceans Canada gauging station at Sorel (46.047N, -73.116W; https://www.tides.gc.ca/en/stations/15930).

Species functional traits

Five functional traits were gathered for all LSP fish species to determine the characteristics of species that occur only in the lake, only in the floodplain, or in both macrohabitats. To test the GMH, we compiled maximum body size reached by the species and trophic position (Frimpong & Angermeier, 2009; Su et al., 2021). We used mouth orientation (ratio between mouth and head heights) as a measure of diet type (benthic diets have values near 0; surface diets have values near 1) (Dumay et al., 2004). Maximum size and mouth orientation were obtained from Su et al. (2021). We used preference for macrophyte-rich or macrophyte-poor habitats as a functional trait reflecting increased floodplain use by more phytophilic species (La Violette et al., 2003). Finally, some species such as northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*), use floodplain habitats for reproduction. The mean spawning month (coded from 1 to 12) was calculated for each species using "JAN-DEC" from the FishTraits database (Frimpong & Angermeier, 2009).

Quantitative analyses

We modelled species occurrences using a joint species distribution model (JSDM). Specifically, we used the 'Hierarchical model of species communities' (HMSC) framework (Ovaskainen et al., 2017; Tikhonov et al., 2020), a multivariate generalized linear mixed model which can integrate four types of information: fish species occurrences (Y), environmental gradients (X), species functional traits (T), and phylogenetic relationships (C), while simultaneously accounting for structured spatial and temporal dependencies in the sampling design. Data on species occurrences (Y) across sites were linked to environmental covariates and trait values. We used spatial and temporal random effects to control for non-independence among sampling units arising from our nested sampling design. Variation in the linear predictor was partitioned into components attributable to environmental filtering (two covariates) and latent residual structure (random effects). We excluded alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), which are migratory species that arrive in LSP in late spring or summer and thus should not contribute to floodplain-lake coupling irrespective of their traits. The phylogenetic matrix (C) encodes evolutionary distances among species, so that closely related taxa can be modelled as having more similar ecological responses than distant ones, thereby correcting for the non-independence associated with shared ancestry. This matrix was obtained using the fishtree R package (Chang et al., 2019). Analyses were done using the Hmsc package (v. 3.0-13) in R (v. 4.3.3) (R Core Team, 2020).

We used the geographic coordinates of each sampling site (longitude and latitude) to construct a spatial random effect. This effect was defined using a nearest-neighbor Gaussian process with ten neighboring sites, to approximate spatial covariance while maintaining computational efficiency (Datta et al., 2016). We formulated the temporal random effect as an autocorrelated process of order 1, so that correlation between samples decayed exponentially with time. We used the default priors of the Hmsc package for all parameters except for the spatial autocorrelation

parameter (ρ), to which we assigned a uniform distribution. The posterior distribution was obtained using Markov Chain Monte Carlo (MCMC) sampling. Four chains were run over 400,000 iterations each; the first 200,000 iterations were discarded as burn-in, and then 1 out of 200 samples were retained to obtain a total of 4,000 samples (1,000 per chain). The posterior means and 95% credible intervals of the parameters representing the effects of environmental variables on species' probabilities of occurrence, and of functional traits on species' responses to environmental factors, were extracted for interpretation.

Results

Of the 47 fish species captured, three showed a positive relationship between occurrence and geodetic level: the central mudminnow (*Umbra limi*), the banded killifish (*Fundulus diaphanus*) and the blackchin shiner (*Notropis heterodon*), had a greater probability of occurrence deep within the floodplain (Fig. 2). Occurrence was negatively related to geodetic level in 25 species, which were more likely to occur in the lake than on the floodplain. The remaining 19 species showed no clear association between occurrence and geodetic level, meaning their occurrence was not influenced by their position relative to the lake or floodplain. These results suggest that most species were generally less present in the floodplain than in the lake.

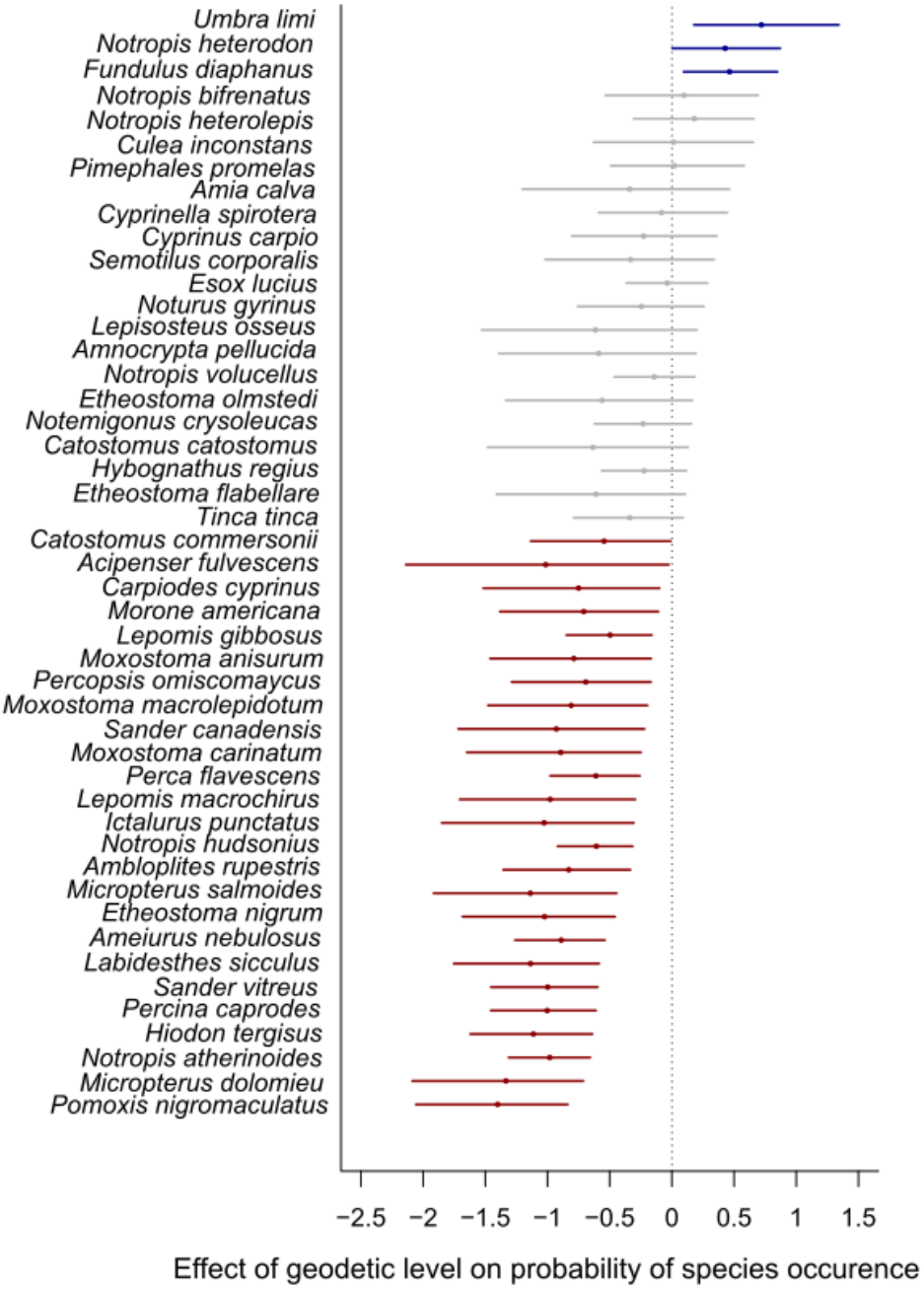


Figure 2. Summary of posterior distributions of regression coefficients for the effect of geodetic level on the probability of occurrence of individual species (mean and 95% credible intervals). Colors refer to the direction of the effect. Blue: greater occurrence in the floodplain; red: greater occurrence in the lake; gray: no preference.

Water transparency had little influence on the probability of occurrence of most species (Fig. S1). The banded killifish, the central mudminnow, and the blackchin shinner were the only species positively associated with water transparency, in part because they mostly occurred near the south shore of the lake where transparency is generally higher. Eight species were negatively associated with transparency, and the remaining species showed no association with transparency. Variation partitioning assigned 18.4% of the variance in the linear predictor to transparency, 45.9% to geodetic level, 12.8% to the temporal random variable, and 22.9% to the spatially-structured random variable (Fig. S2). Among the functional traits, only body size and habitat preference were associated with geodetic level, with smaller and phytophilic species found farther into the floodplain. Breeding season, trophic level, and mouth position showed no association with geodetic level (Fig. 3).

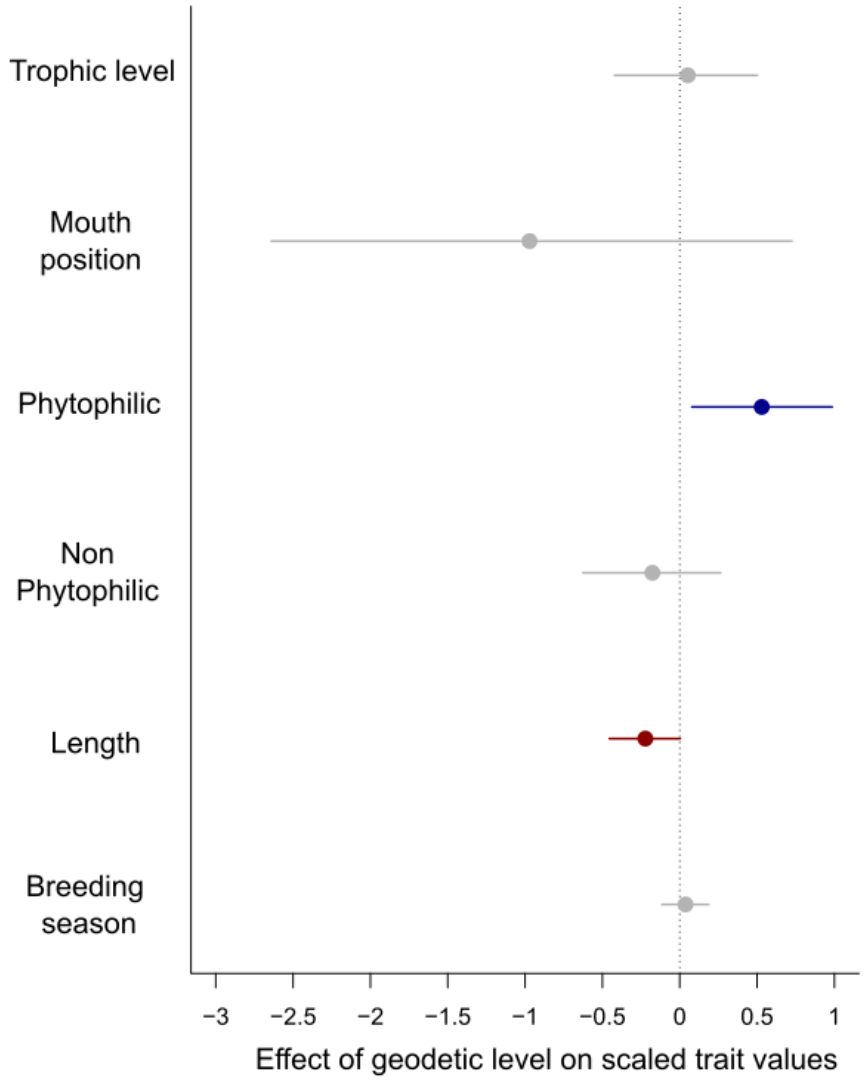


Figure 3. Summary of posterior distributions of regression coefficients for the effect of geodetic level on functional traits (mean and 95% credible interval). Colors refer to the direction of the effect as in Fig. 2

Discussion

We aimed to test the generalist module hypothesis (GMH) in a lake-floodplain metaecosystem, sampling fish communities over two flooding cycles and using various functional traits to predict occurrence in the two macrohabitats. Although the majority of species had greater occurrence in the lake than in the floodplain, there was substantial inter-species variation in the probability of occurrence in the floodplain. Contrary to the GMH, it was the smaller species that were found more frequently in the floodplain. Species with a preference for vegetation-rich habitats (phytophilic species) also had a greater probability of occurrence in the floodplain. We discuss these main findings in relation to the GMH and patterns found in other metaecosystems.

Lake food webs are spatially structured, as there are different communities occupying different habitats and varying in terms of traits (Borrelli & Relyea, 2022) and degree of coupling between habitats (Dolson et al., 2009). The GMH posits that body size reflects species mobility and therefore indicates the species' ability to couple increasingly distant habitats as body size increases (McMeans et al., 2016). However, our results show that body size instead correlates negatively with the presence of a species on the floodplain. High body size therefore does not appear to be a determining factor in the ability to occupy the LSP floodplain and couple it to the lake. Large species known to be mobile, such as white sucker (*Catostomus commersoni*) and smallmouth bass (*Micropterus dolomieu*) (Cuerrier, 1943; Geen et al., 1966), were not found on the floodplain, even though they were frequently found along the lake shoreline. Moreover, the species most frequently found on the floodplain were small forage species considered to be less mobile, such as golden shiner (*Notemigonus crysoleucas*) and blackchin shiner (*Notropis heterodon*). Thus, the mobility of fish species may not limit their ability to occupy seasonal floodplains, unlike the pelagic-littoral systems which have been highlighted by the GMH.

Smaller fish species may be more tolerant than larger species to the specific environmental conditions of the floodplain, notably higher turbidity (Clermont et al., 2023) and lower dissolved oxygen (Bayley, 1995). However, higher turbidity can lead to better juvenile survival and lower predation in smaller species (Miranda & Dembkowski, 2024). Turbid water reduces the ability of visual predators to locate prey and reduces their foraging efficiency (Pekcan-Hekim et al., 2010; Pekcan-Hekim & Lappalainen, 2006). Walleye (*Sander vitreum*) and sauger (*Sander canadensis*) have adaptations that improve visual acuity, such as the *tapetum lucidum*, a reflective layer that improves vision at low light levels (Zyznar & Ali, 1975). However, these species are not found frequently in the floodplain. In addition to high turbidity, prey species using the floodplain may encounter lower levels of dissolved oxygen. Two species found more frequently on the floodplain than in the lake, central mudminnow (*Umbra limi*) and banded killifish (*Fundulus diaphanus*), have a high tolerance of hypoxia (Livingstone, 1953; Peckham & Dineen, 1957). However, channel catfish (*Ictalurus punctatus*) and lake sturgeon (*Acipenser fulvescens*), two large species that tolerate hypoxia (Magnin, 1963; Magnin et al., 1966), are not found on the floodplain. The potentially more stressful environmental conditions of the floodplain do not therefore seem to be the only limitation to species occurrence.

Species that use the floodplain are potentially those that find a greater abundance of their preferred prey, such as zooplankton, in this habitat (Pratt et al., 2023a). The small fish species found on the LSP floodplain consume mainly zooplankton, particularly cladocerans (Keast, 1965; Keast & Webb, 1966). Cladoceran abundance and diversity could be greater on the floodplain than in the main waterbody (Górski et al., 2013), due to nutrient inputs from flooded soils and terrestrial and aquatic vegetation in the floodplain (Junk et al., 1989; Humphries et al., 2014). The occurrence of fish in the floodplain is closely linked to the search for food resources, at least for planktivorous fish species (Pratt et al., 2023a). While trophic level and mouth position, a morphological correlate of diet, were not linked to floodplain occupancy in this dataset, a more detailed analysis of prey density

and fish diet (e.g. with stomach content analysis) across both habitats would be useful to determine if food availability if an important factor at play here.

We also hypothesized that reproductive timing would predict floodplain occupancy but this prediction was not supported. Species that spawn in the floodplain, such as northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*), select this environment to provide their offspring with favourable conditions for rapid development and protection from predation (Bailly et al., 2008). Neither of these species had positive associations with geodetic level. Because eggs and larvae have limited mobility, spawning may not be concentrated at higher elevations near the periphery of the floodplain, where flood duration is short. Instead, spawners may select zones where the flood duration is long enough to ensure successful incubation and early juvenile development (Bailly et al., 2008). This strategy may also be influenced by the swimming capacity of larvae at low temperatures (Herbing, 2002) and by current speed (Bertolo et al., 2012). Thus, while spring spawners might colonize the floodplain habitat, they may not venture deep into it.

Our results show that occupation of floodplains in this temperate system is not primarily determined by greater body size or trophic position, two traits expected to facilitate habitat coupling according to the GMH (McMeans et al., 2016). Instead, the species found most frequently in the floodplain were those favouring macrophyte-rich environments. So habitat preference can potentially outweigh mobility in determining which species effectively exploit floodplain resources and habitat coupling. Similar patterns have been reported in other floodplain environments, where vegetation-rich habitats selectively favour phytophilic species, thereby shaping fish assemblages independently of mobility-related traits (Petr, 2000; Petry et al., 2003). These findings highlight the need to reconsider which functional mechanisms drive floodplain-lake coupling at temperate

latitudes. Future research should examine whether this pattern also influences trophic pathways and energy transfer across the floodplain-lake interface.

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Author contributions

TT, MAR, and VF designed the research. TT, MAR, and VF analyzed the data, TT made figures and wrote the manuscript with significant inputs from MAR. and VF.

Conflict of interest statement

The authors declare that they have no competing interests.

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Supplementary material for: testing the generalist module hypothesis in a lake-floodplain meta-ecosystem

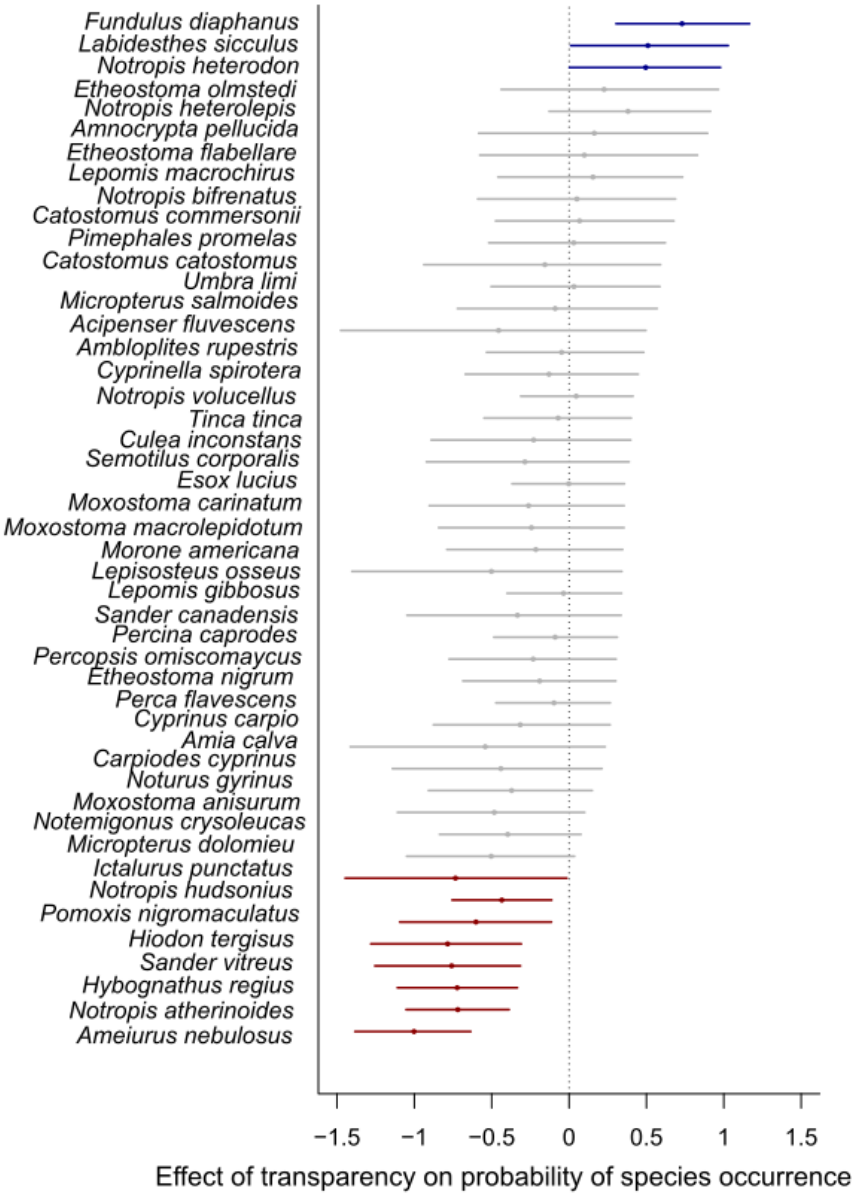


Figure S1. Summary of posterior distributions of regression coefficients of the effect of transparency on the probability of occurrence of each species (mean and 95% credible interval). A credible interval overlapping the vertical zero line indicates no apparent relationship between occurrence and

transparency. Colors indicate whether the probability of occurrence increases (blue), decreases (red), or shows no relationship (grey) with transparency.

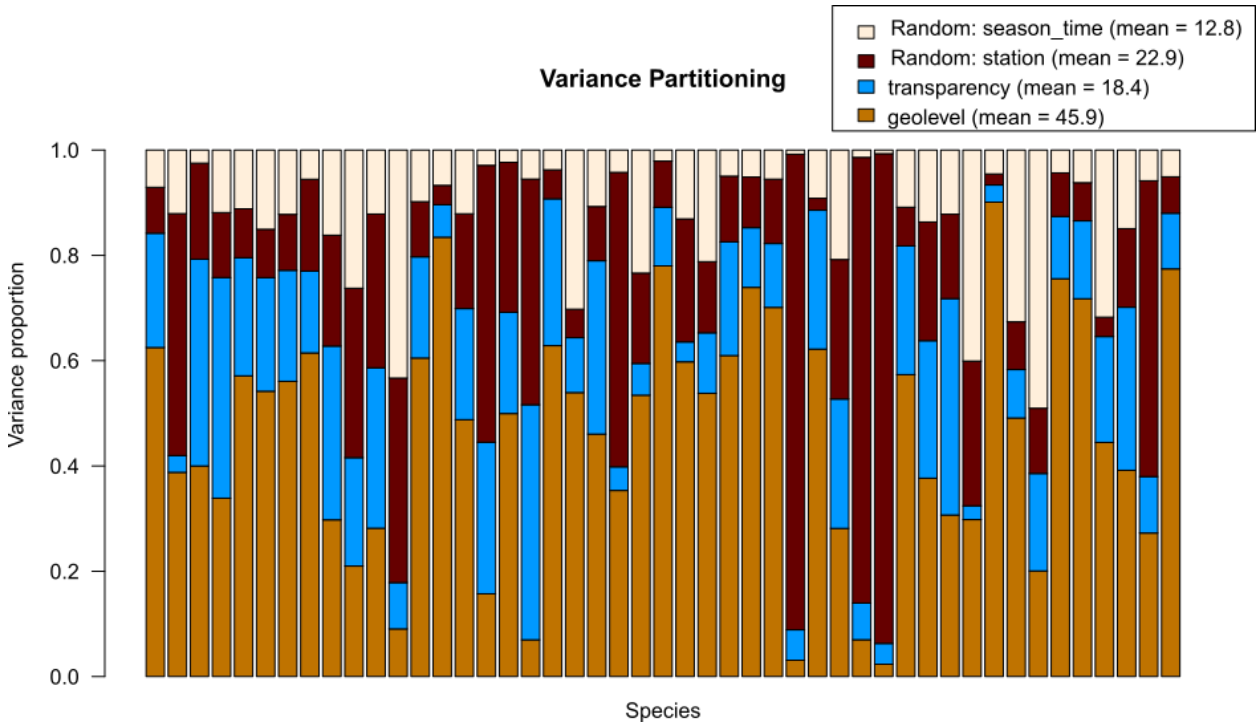


Figure S2. Partitioning of the variance into components associated with fixed and random effects, by species.

Chapitre 2

A trait-based analysis of habitat coupling by fish in a lake-floodplain metaecosystem

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Abstract

Understanding how organisms mediate resource flows across ecosystem boundaries is a central question in metaecosystem ecology. In aquatic ecosystems, fish can act as key vectors of energy transfer between macrohabitats, but the functional traits that determine how individual species contribute to the trophic coupling of macrohabitats remain poorly defined. This study investigates which functional traits of fish are associated with the use of allochthonous floodplain resources in a large temperate lake-floodplain metaecosystem. After an extensive sampling of both floodplain and lake communities over two years, we used stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) and a Bayesian mixing model to estimate the contribution of floodplain-derived resources to the diet of 43 fish species. We then assembled a trait matrix and used a phylogenetic generalized linear mixed model to identify which functional traits predict floodplain use. Approximately one-third of the fish species showed a clear tendency to incorporate floodplain resources into their diet. Species that use floodplain-derived resources had a high trophic position and a preference for macrophyte-rich habitats. Contrary to our hypotheses, traits such as body size, thermal preference, or reproductive timing did not predict floodplain resource use. These findings suggest that species feeding at higher trophic levels and commonly found in vegetated habitats play a key role linking habitats in lake-floodplain metaecosystems. Comparisons of our results with the synthetic IsoFresh database confirmed the generality of this pattern, with phytophilic species showing a more negative $\delta^{13}C$ signature, indicative of allochthonous (detritus-based) resource use. Our results highlight how traits can mediate the role of consumers in metaecosystem connectivity in dynamic environments such as floodplains, with potential implications for biodiversity conservation and ecosystem management.

Keywords: isotopic mixing models, mobility traits, phylogenetic GLMM, trophic subsidies, temperate fluvial lake

Introduction

Understanding how ecosystems are connected through flows of energy and matter is a central question in meta-ecosystem ecology. In aquatic ecosystems, these exchanges are often driven by mobile organisms that mediate the transfer of resources across habitats (Gounand et al., 2018). Although the role of animals in coupling ecosystems is well established, it remains unclear whether specific functional characteristics can predict the contribution of mobile consumers to ecosystem coupling. The generalist module hypothesis (GMH) proposes that species with high mobility and broad diets play a key role in transfer and energy across spatially distinct habitats (McMeans et al., 2016). This hypothesis provides a useful framework for identifying traits associated with coupling, but it may overlook other relevant traits in ecosystems where exploitation of multiple habitats is favoured by a different set of traits. Trait-based approaches offer a promising avenue to test and extend the GMH by linking species functional traits to their contribution to ecosystem dynamics (Carlucci et al., 2020; Green et al., 2022; Levine, 2016). While widely used in terrestrial plant communities, trait-based studies remain less common in aquatic ecosystems, especially for mobile consumers such as fish (Martini et al., 2021).

To our knowledge, the GMH has not been previously assessed in floodplain ecosystems. Floodplain can be viewed as metaecosystems shaped by strong spatial and temporal variability, particularly due to seasonal flooding (Junk et al., 1989; Humpries et al., 2014). During floods, lateral exchanges of energy and matter between floodplains and their associated main waterbody, such as a river or fluvial lake intensify and allow, for transfers of organic matter and mineral nutrients that sustain high biological productivity (Humphries et al., 2014). However, access to food resources in the floodplain could be limited by environmental filters, e.g. greater turbidity or hypoxic conditions (Tockner et al., 2000; Wantzen & Junk, 2000). Such conditions impose physiological constraints that only species with suitable functional traits may overcome. Oxygen concentration is linked to water

temperature (Walczyńska & Sobczyk, 2017), just as water turbidity influences primary production and therefore the abundance of aquatic plants (Austin et al., 2017). Thus, in order to predict which fish species can use temporary floodplain habitats and contribute to habitat coupling in lake-floodplain systems, other traits such as thermal guild, and habitat preference could be informative in addition to traits invoked by the GMH. However, the most significant stress factor affecting the survival, development and presence of fish in flood zones remains the fluctuating flood period in these areas (Bouloy et al., 2024; Górski et al., 2011).

Previous studies have examined at the functional traits possessed by fish species that colonize seasonal floodplains. For example, in tropical floodplains species' functional traits, including habitat preferences and life-history characteristics, can interact with predation, floodplain vegetation structure, and hydrology to determine their biomass distribution across the floodplain system (Rodríguez and Lewis 1994; Espirito-Santo et al. 2013; Arantes et al., 2019). In European lowland rivers the fish species benefiting most from floodplain reconnection following restoration have traits which allow them to exploit increased habitats heterogeneity and stay in more stagnant water (non-rheophilic species) (Stoffers et al., 2022). Finally, in temperate river-floodplain systems fish assemblages in floodplain lakes are structured by functional traits linked to turbidity, depth, and oxygen conditions, which mediate species' capacities to use temporary habitats (Lubinski et al., 2008). However, it remains unknown whether the functional traits that predict floodplain resource use are also those that predict species' reliance on energy pathways originating with allochthonous or autochthonous organic matter resulting from the flood pulse. The incorporation of such resources is a prerequisite for habitat coupling by fish that move between floodplain habitats and connected, permanent water bodies.

In this study, we aim to identify which functional traits predict the use of food resources originating in the floodplain by fish in metaecosystem comprising fluvial lake and floodplain

macrohabitats. To that end, we used stable isotope analyses ($\delta^{13}C$ and $\delta^{15}N$) to estimate the relative contribution of floodplain-derived resources to fish diets. These isotopic estimates were then related to species' functional traits to identify which traits were most strongly associated with exploitation of allochthonous resources. We hypothesized that traits related to mobility (e.g. body size) and trophic ecology (e.g. trophic level, thermal guild and habitat preference) influence access to floodplain-derived resources, under the challenging environmental conditions of early spring floods, characterized by low water temperature, high turbidity, and reduced dissolved oxygen levels (Dumay et al., 2004; Lefcheck et al., 2014; McMeans et al., 2016, 2019; Stiling et al., 2023). Since the capacity to benefit from floodplain trophic subsidies is constrained by the ability to reach, tolerate, and exploit floodplain habitats, we tested hypotheses linking isotopic signatures to functional traits associated with movement capacity, trophic position, habitat preference, and synchronization of reproduction with peak flooding. Trophic position is chosen to predict a core of the GMH, which proposes that species occupying higher trophic positions are more likely to couple distinct habitats by linking energy pathways between floodplain and permanent waters due to a more generalist feeding regime (i.e., both fish and invertebrate prey, as opposed to only invertebrates for species at lower trophic level). The floodplain provides habitats conducive to phytophilic fish species due to its wide variety of submerged aquatic vegetation (Laporte et al., 2023). Thus, species that reproduce early and prefer substrates rich in macrophytes are more likely to use the floodplain. Finally, to evaluate the generality of our results at a boarder spatial scale, we assessed whether the relationships between traits and allochthonous resources use identified in our system were consistent across temperate systems, using IsoFresh (Boulêtreau et al., 2025), a synthetic dataset of stable isotopes in aquatic systems.

Methods

Study system

Lake St Pierre (LSP) is a large fluvial lake in the St. Lawrence River watershed upstream of Trois-Rivières, Québec, Canada. The lake is approximately 25.6 km long and 12.8 km wide, with a mean depth of 2.7 m, excluding a human-made navigation channel that runs along the river thalweg (La Violette, 2004). Seasonal changes in water level (mean: 1.8 m) arise from varying discharge of the Saint Lawrence and Ottawa Rivers, and of several smaller tributaries (Hudon et al., 2017). Each spring, the floodplain is inundated following snowmelt and increased precipitation in the St. Lawrence River watershed. The flood period generally begins in April and last up to two months, with flood magnitude and duration varying interannually depending on hydrological conditions but for reference the 2-year recurrence zone covers ≈210 km² (Langlois et al., 1992). We use water levels recorded at the Sorel gauging station, located at the upstream end of LSP (46.047, -73.116, https://www.tides.gc.ca/en/stations/15930), to determine the timing and extent of floodplain inundation during sampling periods. LSP has high species richness (79 species, Laporte et al., 2025). Submerged aquatic vegetation plays a critical role in supporting larval fish abundance in this system (Massicotte et al., 2015). A pronounced deterioration of littoral and spawning habitats, linked to vegetation loss, turbidity increase and changing hydrological conditions has occurred the past decades (Laporte et al., 2025). These habitat changes have been associated with shifts in fish community composition and declines in the quality of nursery areas (Giacomazzo et al., 2023; Laporte et al., 2023).

We used carbon and nitrogen isotopes to determine the origin of basal resources supporting fish consumers. Lake and floodplain habitats in LSP differ in environmental conditions ans isotopic baselines. The shallow lake favors autochtonous primary production, whereas the floodplain receives greater allochthonous carbon inputs processed through microbial pathways, resulting in more

negative $\delta^{13}C$ values in floodplain waters and biota (Hélie et al., 2002; Zeug & Winemiller, 2008; Brett et al., 2017). Higher turbidity in the floodplain further limits light availability can enhance $\delta^{13}C$ depletion in periphyton (Paris et al., 2016). Consequently, more negative $\delta^{13}C$ values in consumers indicate greater reliance on floodplain-derived resources (Farly et al., 2019, 2021).

Field sampling

Field sampling was conducted in 2021 and 2022 over the months of April, June and August, for a total of 6 field campaigns covering two flood cycles. Sites were distributed every 2.5 km along the northern shoreline of the lake and every 1.5 km on the southern shoreline. We did not sample along easternmost part of the south shores, there are a military zone with restricted access. The same sampling design was used for the 6 campaigns, totaling 169 sampling locations, but sites were located progressively closer to the center of the lake, as floodwaters receded. Sampling was therefore conducted mostly in the floodplain in April, and in the lake littoral in June and August.

Fish were collected at daytime using a seine net (25 meters long and 2 meters high, with the central 6 meters having a 2mm mesh), attempting to sample an area of approximately 250 m^2 per site. All captured fish were measured and identified to species level in the field. For isotope analyses, we retained a maximum of two individuals per species per site, usually near the extremes of range of body sizes observed at the site. All retained fish were immediately euthanized with an overdose of clove oil before further processing. All procedures were approved by the UQTR Animal Care Committee and by Ministère de l'Environnement de la Lutte contre les Changement Climatique Faune et Parcs (permits N° 2022 03 15 027 04 S P and 2021 03 10 007 04 S P). A total of 1129 individuals from 43 different species were retained for isotopic analyses (Fig. 1). Macroinvertebrates, used as basal resources, were collected using a kick net (500-µm mesh) and then live-sorted on site

in a tray to separate them from submerged vegetation. We captured representatives of fourteen different families (Fig. S1), five of which were widely distributed across many sites: Gammaridae, Unionidae, Lymnaeidae, Physidae and Corixidae. Gammaridae and Lymnaeidae appear to act primarly as grazers feeding on periphyton (Hadicke et al., 2017; Nelson, 2011), which leads to an isotopic signature associated with carbon derived from autochthonous primary production (weakly negative $\delta^{13}C$). However, as Gammaridae can also function as detritivores relying heavily on allochthonous organic matter in other contexts (Nelson, 2011). The Corixidae and Physidae are detritivores in LSP, which leads to more negative $\delta^{13}C$ values (Bertrand et al., 2011; Li et al., 2018). To simplify interpretation, and following common practice (Post 2002), we retained only two taxa, the Gammaridae and Corixidae as basal sources in the analyses, due to their ubiquitous spatial and temporal distribution across sites and sampling dates and their contrasting $\delta^{13}C$ signatures (Fig. S2). Geodetic lake depth was calculated for each sampling site and date as the difference between the measured water depth and the lake level relative to a fixed reference level of the international Great Lakes (Schmidt et al., 2015). This measurement represents an approximation of the relative elevation of each station and is associated with key factors influencing fish abundance, including current velocity patterns, degree of terrestrial influence, and duration of flood exposure (Schmidt & Rodríguez, 2011). The daily water level data used to calculate the geodetic depth were obtained from the Fisheries and Oceans Canada gauging station at Sorel.

Isotope analyses

We took a sample of dorsal muscle from each fish, dried it at 55 °C for 48h (drying oven SMI6E Shel Lab), and then ground it to a powder for isotope analysis using a mixer mill (Retsch MM300). The same procedure was used for macroinvertebrates but we used whole organisms

instead. Samples were weighed to 1±0.15 mg (Mettler-Toledo XP6 balance, 0.001 mg accuracy) and encapsulated in tin combustion cups for C and N isotope measurements. Samples were analyzed using an Elementar Pyrocube elemental analyzer connected to a Delta V Plus Isotope Ratio Mass Spectrometer (IRMS). The isotopic ratio, denoted with the symbol δ and expressed in ‰, represents a deviation from a standard following the equation below (with C as an example):

$$\delta^{13}C=\left[\frac{\left(\frac{^{13}C}{^{12}C}\right)_{sample}}{\left(\frac{^{13}C}{^{12}C}\right)_{standard}}-1\right]\times 1000$$ (Bromley et al., 1982)

Replicate analyses of isotopic standard reference materials USGS 40 ($\delta^{13}C$ = –26.39‰; $\delta^{15}N$ = –4.52‰), USGS 41 ($\delta^{13}C$ = 37.63‰; $\delta^{15}N$ = 47.57‰) and T67 (brook trout) ($\delta^{13}C$ -37.02‰ $\delta^{15}N$ 8.63‰) were used to normalize isotopic values of working standards to the Air ($\delta^{15}N$) and Vienna Pee Dee Belemnite ($\delta^{13}C$) scales (Farly et al., 2019). Working standards were analyzed after every 10 samples to monitor instrument performance and check data normalization. The precision of the laboratory standards was within ±0.3‰ of the target values for both carbon and nitrogen. This protocol is consistent with other, recent studies of C-N stable isotopes in freshwater fish and their invertebrate prey items (e.g., González et al., 2025). It is important to note that $\delta^{15}N$ signature of water bodies can vary spatially and temporally due to differences in nitrogen sources and microbial processes (Diebel et al., 2009). In LSP, the floodplain and the main lake may exhibit distinct $\delta^{15}N$ baselines, which could influence the isotopic signatures of fish independently of their diet. While we accounted for the baseline variability by including two distinct basal sources in our model, residual variability in water $\delta^{15}N$ could introduce uncertainty in our estimates of floodplain resource use. Future studies could address this limitation by directly measuring $\delta^{15}N$ dissolved inorganic nitrogen across habitats and sampling periods to better constrain isotopic baselines.

Trait database

To identify the characteristics that best predict the exploitation of floodplain resources, we compiled a species-level trait database for all fish species included in the isotope analyses. Functional traits were selected for their relevance to mobility, phenology, habitat preference, and tolerance to environmental variation, all of which were hypothesized to influence a species' ability to occupy the floodplain habitat and thus its use of floodplain-derived resources. Maximum body length, an indicator of individual mobility, was extracted from Su et al. (2021). Larger species are expected to exhibit greater movement capacity, which may facilitate the exploitation of distant or transient habitats such as floodplains (McMeans et al., 2016, 2019). This trait therefore may confirm the hypothesis that species with greater mobility have enhanced access to allochthonous resources during the flood pulse. Trophic level, obtained from FishTraits (Frimpong & Angermeier, 2009) and estimated as the average diet-based position of each species in the food web, was used as a proxy for feeding strategy and energy acquisition pathways. Thermal guild information was extracted from Giacomazzo et al. (2023) and used as a proxy for physiological tolerance to temperature. To simplify our interpretation of the results, we merged the thermal guilds to retain only two categories: cold-water species and other warm-cool species. We hypothesized that species characterized by a preference for cold water would be better able to exploit floodplain habitats, as warm-water species might be less active during spring floods when water temperature is low (Guzzo et al., 2017; Amat-Trigo et al., 2023) (Fig. S2). Habitat preference, obtained from Giacomazzo et al. (2023), was grouped into three categories reflecting spawning behavior and preferred substrate for egg deposition: phytophilic (vegetation-dependent), non-phytophilic (egg-laying on mineral substrates), and facultative (species using multiple habitat types, which do not have a specific laying substrate). We expected that phytophilic species would rely more heavily on floodplain-derived resources. Finally, the spawning period (mean months of reproduction) was calculated from FishTraits

database using "JAN-DEC" (Frimpong & Angermeier, 2009). Species reproducing earlier in the year (April, May), when floodplain inundation peaks, were hypothesized to benefit more from allochthonous resources available during the flood pulse. Together, these chosen traits provide complementary information on species' ecological strategies and can potentially explain exploitation of floodplain-derived resources within Lake Saint Pierre. Functional traits characterised as explanatory of a resource exploitation strategy will also be selected to confirm the generality of these mechanisms on a larger scale through analysis of the IsoFresh database (see below).

Quantitative analyses

We used a Bayesian mixture model implemented in the MixSIAR package (v. 3.1.12) (B. Stock et al., 2018) in R (v. 4.3.3) (R Core Team, 2020).In this model, the mixture corresponds to the isotopic signatures of fish consumers at the community level, assumed to result from a combination of the defined basal sources. This model can accommodate up to two fixed or random effects to explain part of the variability in isotopic signature within the fish community. Each consumer isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) is expressed as a combination of potential food sources, weighted by their proportional contribution to the diet. The model estimates these proportional contributions using Bayesian inference, accounting for uncertainty in source signatures, trophic discrimination, and within-source variability (Stock et al., 2018). The likelihood of the mixture is then expressed as:

$$Y_{ij} \sim N\left(\sum_k p_{ik}\mu^s_{jk}, \sum_k p^2_{ik}\omega^2_{jk} \times \xi_j\right)$$

With p_{ik} the proportion of the contribution of the k sources to the i mixtures, μ^s_{jk} is the average of each source by j tracers. ω^2_{jk} is the weighted variance of the combination of the k sources for each tracer and finally ξ_j is a multiplicative factor allowing for a residual error (Stock & Semmens, 2016).

The model requires data from consumers (Fig. S3) and basal sources, which we measured empirically, and trophic discrimination factors, which were assigned values of 2.1 for $\delta^{13}C$ and 3.1 for $\delta^{15}N$ for all species (Canseco et al., 2022).

We used floodplain resource use (%) as the response variable in trait-based models. Floodplain resource use is quantified as species-level mean estimates derived from MixSIAR along with their associated uncertainties (standard deviation). We modelled these data using a phylogenetic linear mixed model (PGLMM) implemented in the MCMCglmm R package (Hadfield, 2010). This model allows for the inclusion of a phylogenetic correlation structure to account for non-independence among species arising from shared evolutionary history (Ives & Helmus, 2011; Gallinat & Pearse, 2021). Functional traits were included as fixed effects and comprised trophic position (standardized), maximum body size (log-transformed and standardized), average breeding period (standardized), habitat preference, and thermal guild. Phylogenetic relationships between species were taken into account to reflect the non-independence of ecological responses resulting from a shared evolutionary history, by modelling the random effect at the species level using a covariance matrix derived from a phylogenetic tree constructed with the fishtree R package (Chang et al., 2019). Importantly, uncertainty associated with species-level estimates of floodplain resource use was explicitly represented in the model as measurement error variance. The PGLMM propagates this uncertainty from the isotope mixing model into the trait-based comparative analysis, rather than treating estimated species means as error-free observations. We ran three MCMC chains with 1,000,000 iterations each, with the first 500,000 iterations discarded as burn-in and samples thinned every 100 iterations. Model checking included inspection of trace plots and assessment of effective samples size (ESS > 1000).

Comparison of LSP results with the IsoFresh database

To determine whether results obtained in our system are generalizable to a larger scale, we carried out a comparative analysis using the IsoFresh database (Boulêtreau et al., 2025). This dataset compiles isotopic signatures ($\delta^{13}C$ and $\delta^{15}N$) of aquatic organisms including more than 1 300 fish species distributed across ≥700 different studies. We used this dataset to: 1) assess whether the $\delta^{13}C$ signature of fish differs depending on the type of aquatic ecosystem and 2) confirm that the species and functional groups identified as "allochthonous users" also generally have lower $\delta^{13}C$ at other localities with similar species pools. To adress the first objective, we split observations by ecosystem type (lotic vs. lentic), considering that lotic ecosystems generally receive more allochthonous resource subsidies than lentic systems, and thus that fish $\delta^{13}C$ signatures should be more negative in lotic systems (Eglite et al., 2024).

To assess differences in fish $\delta^{13}C$ signatures between lotic and lentic ecosystems, we fitted a linear mixed model using the brms R package (Nalborczyk et al., 2018). We first filtered the IsoFresh dataset to retain only observations from lotic and lentic ecosystems. Ecosystem type was included as a fixed effect, whereas species was specified as a random effect to account for repeated measurements across species. To address the second objective (fish $\delta^{13}C$ signatures explained by functional traits), we merged the IsoFresh data with only fish species for which we had compiled trait data. We then fitted a second linear mixed model, with trophic level and habitat preference. We included species and study ID as random effects to account for non-independence of observations due to repeated measurments of the same species across multiple sites/studies, and to control for unmeasured site or study-specific variability that could otherwise bias fixed effect estimates. The two model were run with three MCMC chains of 4000 iterations each (1000 warm-up), using a Gaussian

family and weakly informative priors. Convergence was verified using the $\hat{R}$ statistic (all < 1.01) and effective sample sizes (ESS > 1000).

Results

The $\delta^{13}C$ signature was consistently more negative for Corixidae than for Gammaridae (Fig. S3). For Gammaridae, $\delta^{13}C$ was more negative earlier in spring than in summer (Fig. S3), presumably reflecting the development of in-lake primary production during the growing season.

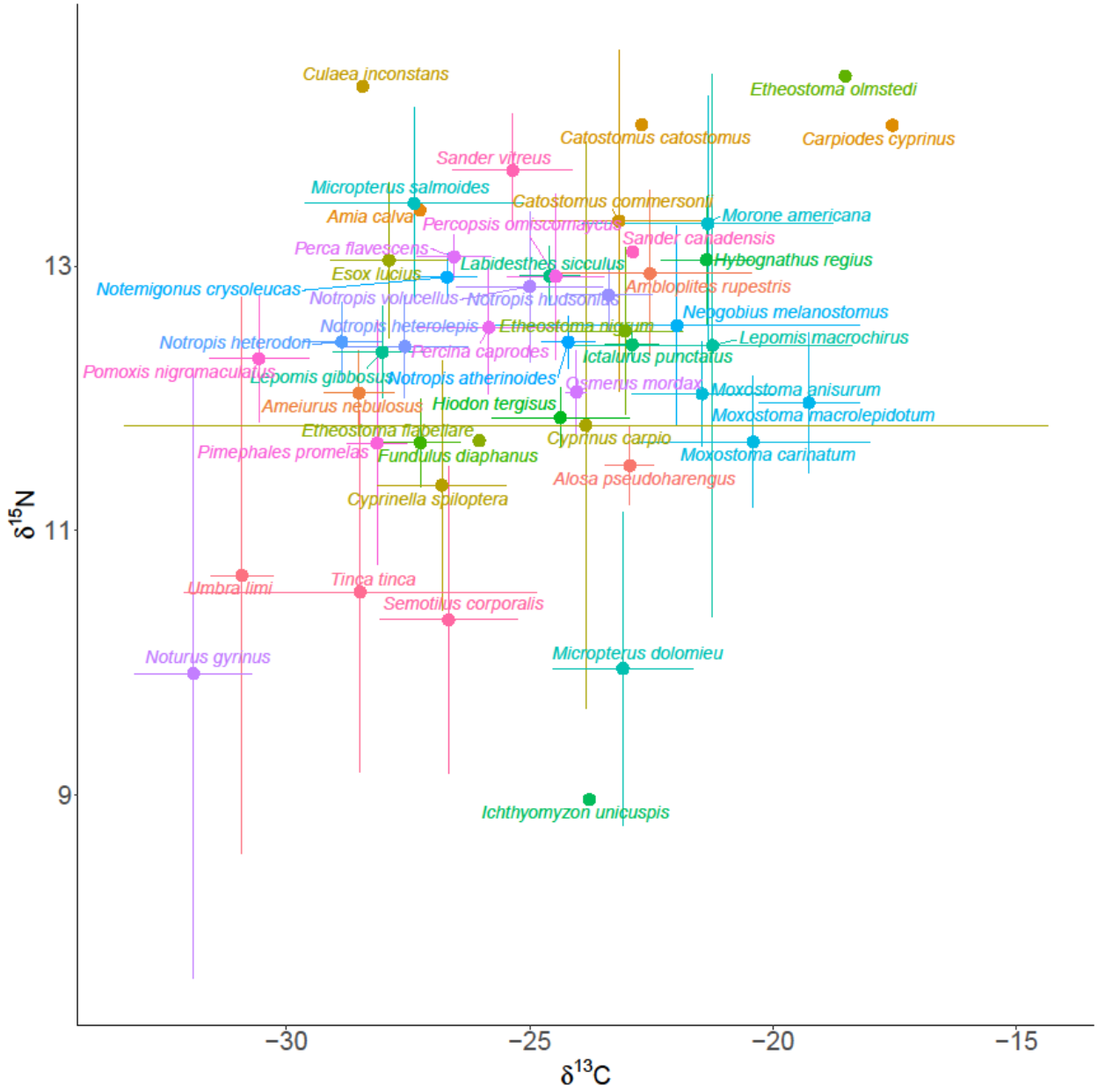


Figure 1. Summary of isotopic signatures (δ13C and δ15N), by fish species. Means (dots) and standard deviations (horizontal and vertical lines) are shown for $\delta^{13}C$ and $\delta^{15}N$.

The mixing model revealed that 14 species had a greater proportion of their diet coming from the floodplain (Fig. 2). The three species with the greatest contribution from the floodplain were tadpole madtom (*Noturus gyrinus*), northern pike (*Esox lucius*) and central mudminnow (*Umbra*

limi). Nine species are characterized by a greater contribution from less negative $\delta^{13}C$ sources ('lake' resources), emerald shiner (*Notropis atherinoides*), spottail shiner (*Notropis hudsonius*), mooneye (*Hiodon tergisus*), rock bass (*Ambloplites rupestris*), bluegill *(Lepomis macrochirus*), smallmouth bass (*Micropterus dolomieu*), river redhorse (*Moxostoma carinatum*), shorthead redhorse (*Moxostoma macrolepidotum*) and eastern silvery minnow (*Hybognathus regius*). The remaining twenty species do not tend to exploit floodplain-derived resources more than lake-derived ones, and thus have weakly negative $\delta^{13}C$ values.

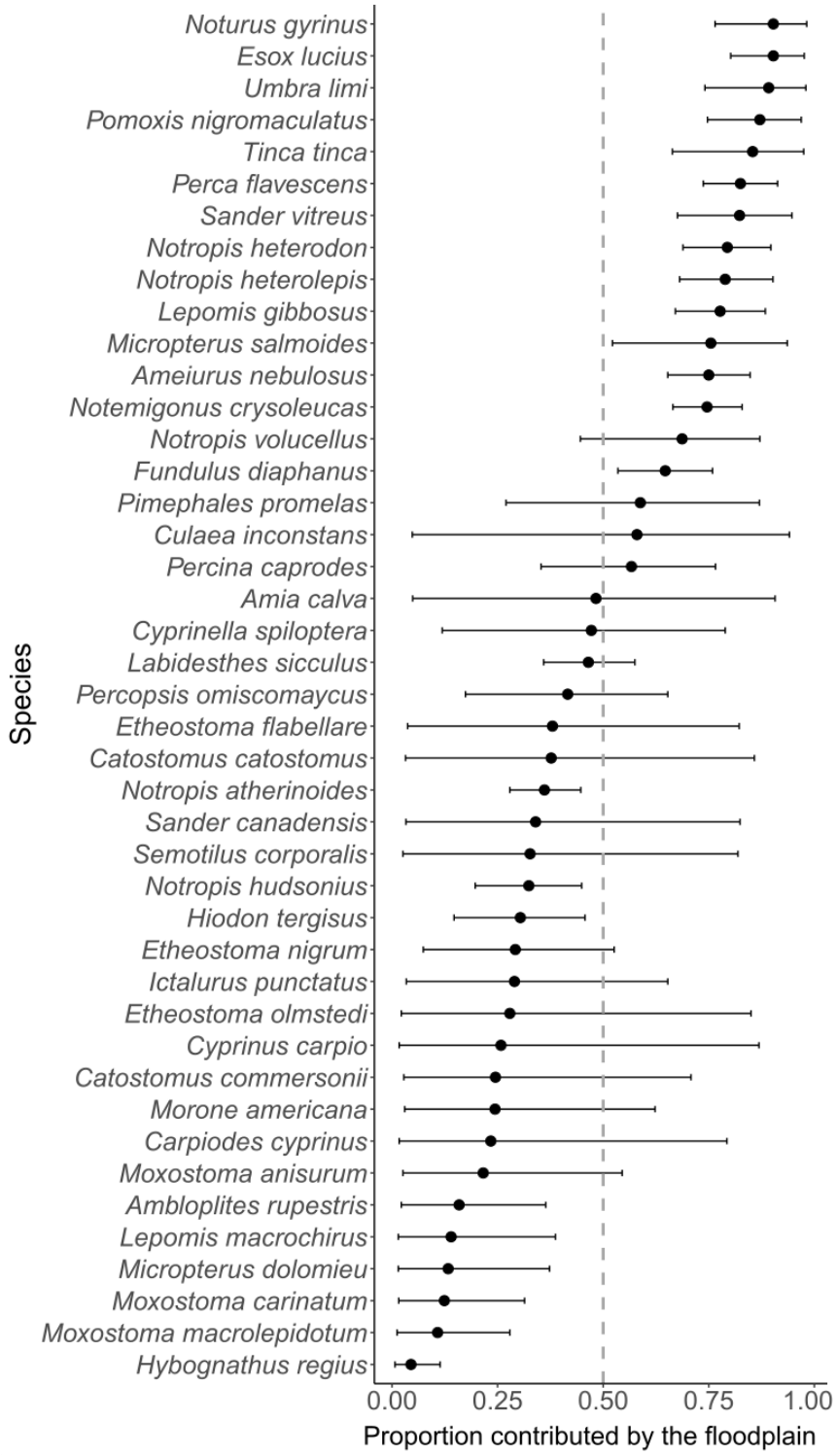


Figure 2. Summary of estimates of the resource contribution from the floodplain by species (mean and 95% credible interval). Credible intervals straddling the dashed vertical line indicate no clear preference for floodplain or lake resources.

When using functional traits to predict the floodplain's contribution to diet, only trophic level and a preference for vegetation-rich habitats were linked to floodplain resource use (Fig. 3A). Species with a higher trophic level tended to show greater reliance on floodplain resources (Fig. 3B). Similarly, phytophilic species exhibited higher floodplain contribution values compared to non-phytophilic and facultative species (Fig. 3C). Contrary to our hypothesis, breeding season, body size, and thermal guild were not linked to floodplain resource use.

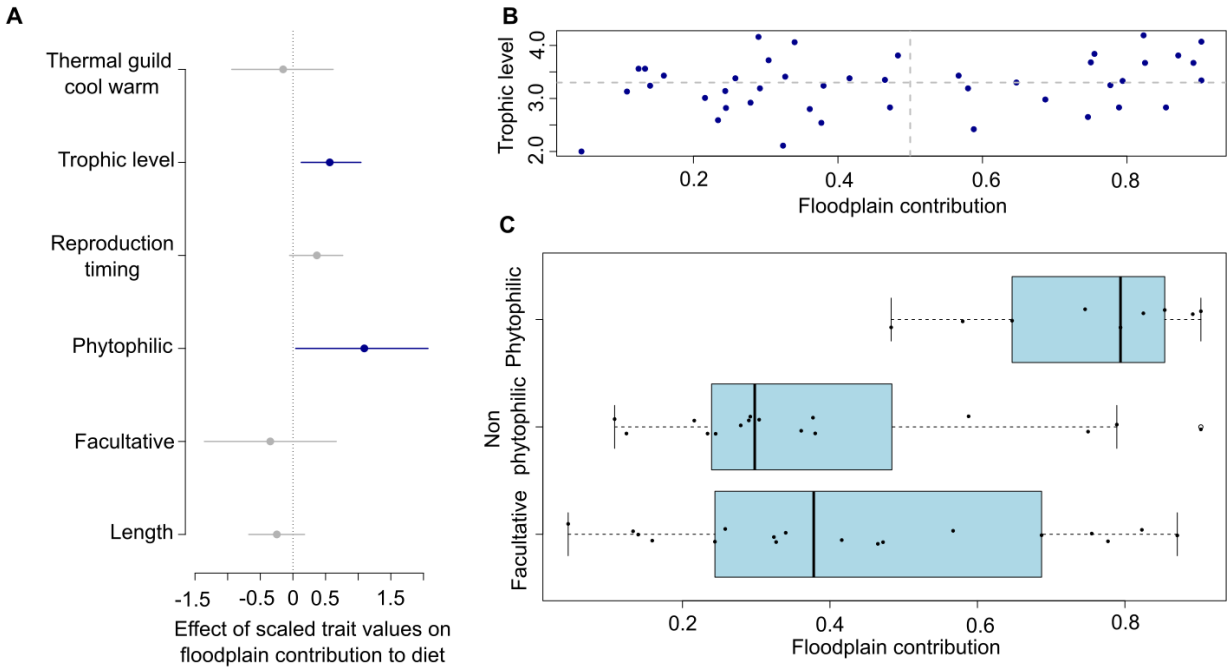


Figure 3. (A) Summary of posterior distributions of regression coefficients for the effect of floodplain resource contribution on functional traits (mean and 95% credible interval). The two credible intervals excluding zero indicate greater reliance on floodplain resources (blue). (B) Scatterplot showing the relationship between trophic level and floodplain contribution for each species. Horizontal dashed line: median trophic level across all species. Vertical dashed line: equal contribution from lake and floodplain. (C) Boxplot showing the distribution of floodplain contribution values for phytophilic, non-phytophilic, and facultative species.

Analysis of the IsoFresh dataset (Boulêtreau et al., 2025) revealed a clear distinction in $\delta^{13}C$ values between ecosystem types: fish from lotic systems exhibited lower $\delta^{13}C$ signatures than those from lentic systems (Fig. 4A), consistent with stronger access to allochthonous inputs in more hydrologically dynamic environments. To evaluate whether traits indicative of floodplain resource use in LSP also influence $\delta^{13}C$ signatures at other sites where the same fish species occur, we tested the effect of trophic level and macrophyte habitat affinity on $\delta^{13}C$ values in the IsoFresh database (Fig. 4B). We found that phytophilic fish species exhibited $\delta^{13}C$ values below the community mean, whereas trophic level was not correlated to $\delta^{13}C$ signature, as it did not differ from the average value for the fish community.

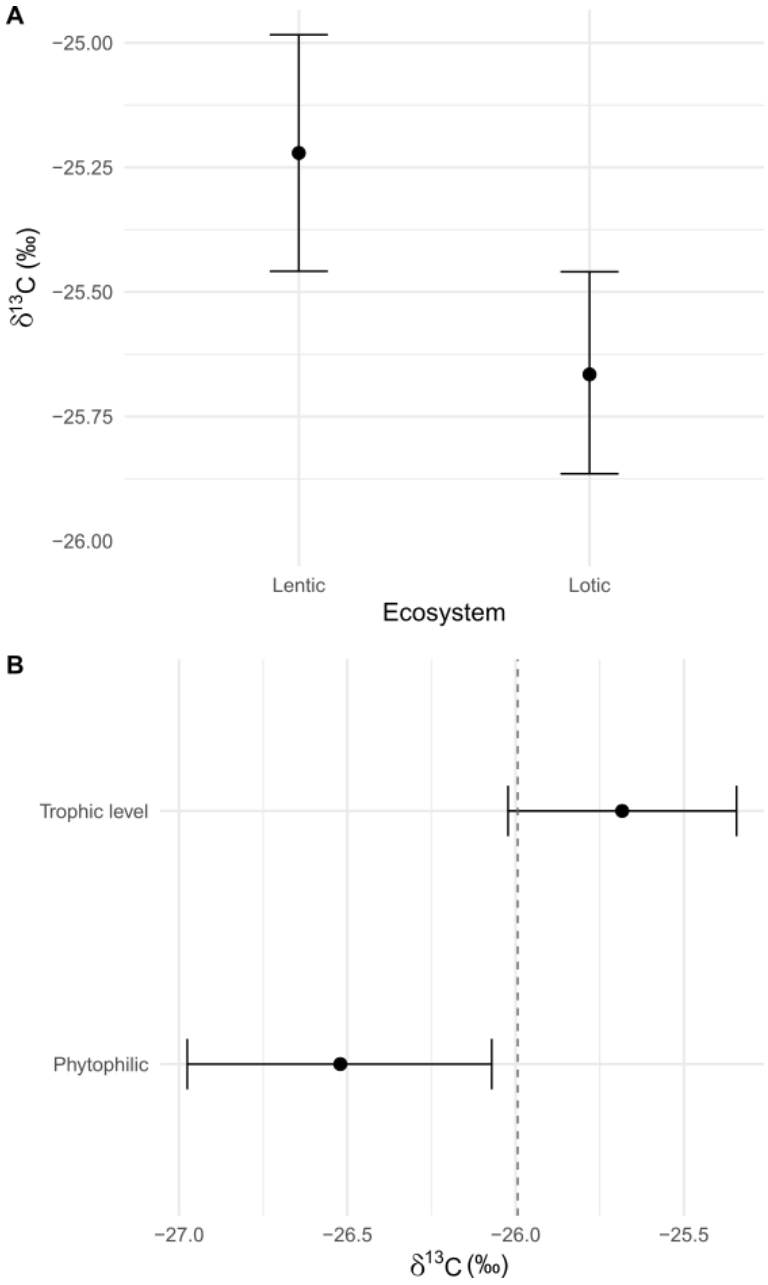


Figure 4. (A) Mean $\delta^{13}C$ values (with 95% credible intervals) of fish communities in lentic and lotic freshwater systems from the IsoFresh database. Points represent the estimated group means for each ecosystem type. (B) Estimated effects of trophic level and preference for vegetated habitats on fish $\delta^{13}C$ values, using data from all localities within the IsoFresh database and the trait matrix from LSP (so only species found also in LSP). Points represent the posterior mean effect of each trait; horizontal lines indicate

95% credible intervals. The vertical dash line represent the mean values of $\delta^{13}C$ in the fish community from IsoFresh database.

Discussion

We examined the applicability of the GMH (McMeans et al., 2016) in a fluvial lake-floodplain metaecosystem. We hypothesized that traits other than body size and trophic level could predict macrohabitat coupling by fish that exploit both macrohabitats. Sampling fish and their invertebrate prey items across seasons over two years, we found that nearly a third of the fish species showed a tendency to exploit resources from the floodplain, demonstrating the importance of the floodplain to trophic flows. Exploitation of allochthonous resources by fish did not appear to be linked to body size. Instead, trophic level and preference for vegetation-rich habitats best predicted $\delta^{13}C$ values indicative of floodplain-derived inputs.

Floodplain exploitation by fish depends, among other abiotic factors, on hydrological timing and temperature regime (Górski et al., 2011). We hypothesized that in temperate floodplains such as LSP, cold-water fish species that are active or breeding during spring floods would more readily exploit floodplain resources. However, our results do not support the notion that temperature preference impacts floodplain resource use. For example, walleye (*Sander vitreus*), a cool-water species (Bozek et al., 2011) and pumpkinseed (*Lepomis gibbosus*), a warm-water species, were both found to exploit floodplain resources. Similarly, redhorses and suckers were among the most $\delta^{13}C$-rich species, indicating low reliance on floodplain resources use despite their preference for cool water (Bayley, 1995). Floodplains are highly heterogeneous habitats that show great diversity and variability in temperature and resources (Tonolla et al., 2010). We found that fish species with varied temperature affinities and diets can colonize the floodplain.

Our results suggest that two functional dimensions, trophic position and affinity for macrophytes, play a major role in determining which species effectively exploit floodplain-derived resources. The floodplain delivers episodic pulses of energetic opportunity, via enriched primary and secondary production during inundation (Petsch et al., 2023), which may favor higher trophic level species capable of integrating heterogenous, temporally variable food sources (Høberg et al., 2002; Stoffers et al., 2022; Rossi et al., 2024). In parallel, we observed a strong association between phytophilic species and the use of allochthonous resources, suggesting that habitat preference acts as an ecological filter: vegetated floodplain habitats provide both trophic subsidies and structural refuge, benefiting species adapted to a macrophyte-rich environment (Lubinski et al., 2008; Glińska-Lewczuk et al., 2016; Giacomazzo et al., 2023). Yellow perch (*Perca fluvescens*) and northern pike (*Esox lucius*), two abundant species in LSP, exemplify the tendency for species of high trophic level and preference for macrophyte-rich habitats to exploit floodplain resources. Our findings highlight that floodplain exploitation may emerge from the interplay between habitat association and trophic ecology rather than from any single trait alone (Angulo- Valencia et al., 2022). Such a mechanism could partly explain why certain species consistently benefit from floodplain subsidies despite hydrological variability, whereas others appear to rely primarily on lake-derived resources. Floodplain accessibility is also shaped by landscape configuration and anthropogenic activity (e.g., transportation and agriculture). Human activity can interrupt the connection between a floodplain and its main waterbody, curtailing the transfer of energy and matter between these macrohabitats (Thoms et al., 2005).

Comparisons with the IsoFresh global database allowed us to place our findings in a broader context and test their generalizability to other freshwater ecosystems. Overall, fish from lotic systems exhibited substantially lower $\delta^{13}C$ signatures than those from lentic systems in the global database, supporting the notion that lotic environments promote the exploitation of allochthonous

resources. This finding is consistent with the River Wave Concept (Humphries et al., 2014), which emphasizes the role of flood pulses and lateral exchanges in structuring aquatic food webs (Junk et al., 1989).

The global analysis revealed a pattern consistent with our local findings: phytophilous LSP species had lower $\delta^{13}C$ values across localities in the IsoFresh database, suggesting that this pattern is consistent across systems. In contrast, trophic level did not show a consistent relationship with $\delta^{13}C$ signatures, confirming that the use of allochthonous resources is not strictly a function of food web position (McMeans et al., 2019). This discrepancy suggests that although trophic position can be informative in LSP, where floodplain habitats are highly productive, isotopically distinct, and readily accessible (Farly et al., 2019, 2021), it does not more generally predict allochthonous resources use across diverse freshwater ecosystems. In more heterogeneous systems, differences in hydrological connectivity, habitat structure, and baseline isotopic gradients likely decouple trophic level from carbon source, making habitat affinity a more robust indicator of floodplain resource exploitation than food-web position alone.

Our findings align with patterns documented in other floodplain river systems. Spatial gradients in $\delta^{13}C$ and $\delta^{15}N$ have been shown to reliably reflect fish habitat use when isotopic contrasts among habitats are sufficiently strong, allowing inference on habitat integration and movement at relevant spatial scales (Winter et al., 2021). In this lowland river context, the isotopic differentiation observed between lake and floodplain habitats within LSP is comparable to spatial isotope patterns reported in other lowland river systems. Hydrological connectivity has repeatedly been identified as a key driver regulating fish access to floodplain-derived resources. In floodpulse systems, seasonal inundation promotes increased trophic niche breadth and plasticity by enabling fishes to exploit a wider diversity of food sources available in floodplain habitats (Pool et al., 2017). These results emphasize that temporal variation in connectivity strongly influences the degree to

which fishes integrate floodplain resources into their diet. In LSP, previous isotope-based studies have demonstrated that the floodplain constitutes a substantial and seasonally variable trophic subsidy for fish communities. Using mixing models, Farly et al. (2019) showed that floodplain-derived carbon can contribute substantially to fish diet during periods of high connectivity, highlighting the functional role of floodplains as feeding habitats beyond their importance for reproduction or refuge. More broadly, a weak global relationship between morphological traits and isotopic niches indicates that morphology alone is not a consistent predictor of resource use in dynamic environments (Olden et al., 2025).

In conclusion, our analyses show that two functional traits, trophic level and affinity for macrophytes, are useful in predicting the origin of food resources used by fish in floodplain ecosystems. Thus, species contributing most to habitat coupling in river-floodplain metaecosystems would be phytophilous species instead of large, high-trophic level species, a finding that departs from the GMH developed in boreal lakes with presumably smaller floodplains and a weaker reliance on allochthonous carbon sources. Future research could expand this analysis at the intraspecific level, to better understand how individual-level trait variation shapes the strength and dynamics of coupling in floodplain systems.

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Author contributions

TT, MAR, and VF designed the research, analyzed the data, TT made figures, and wrote the manuscript with significant inputs from MAR and VF.

Conflict of interest statement

The authors declare that they have no competing interests.

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Supplementary material for: A trait-based analysis of habitat coupling by fish in a lake-floodplain metaecosystem

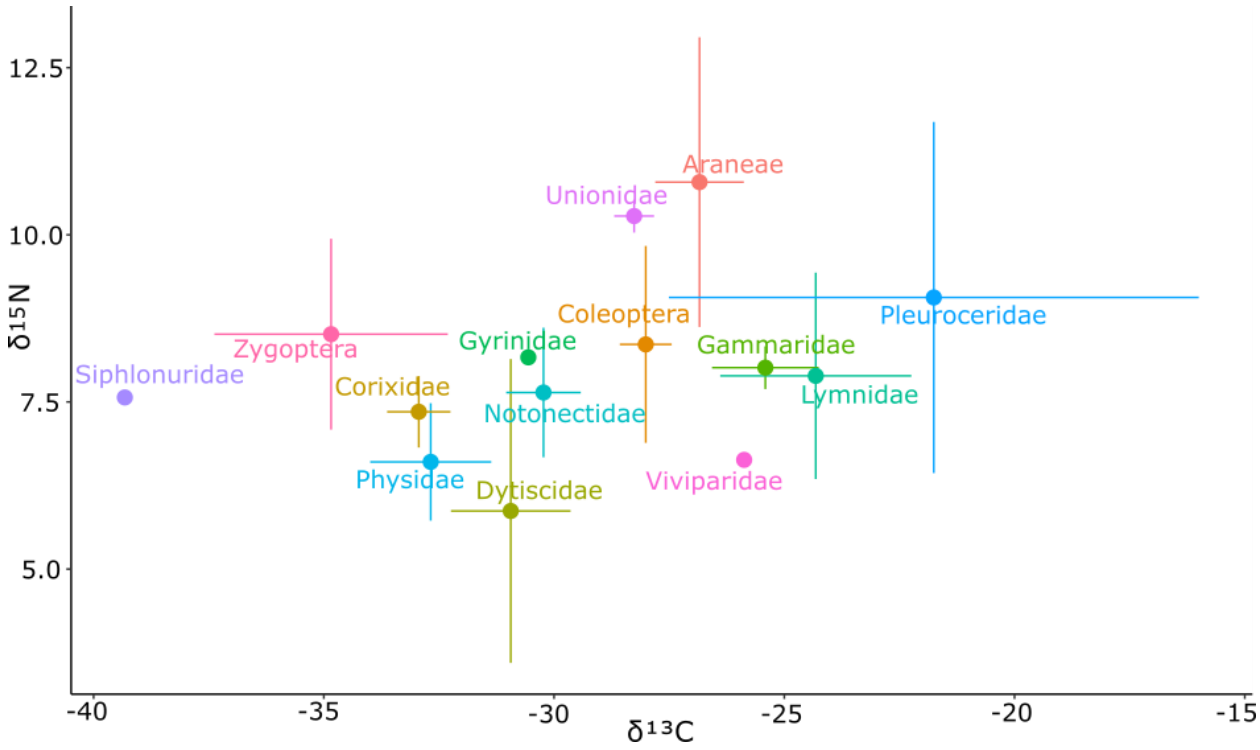


Figure S1. Mean isotopic signature ($\delta^{13}C$ and $\delta^{15}N$) of baseline invertebrate taxa collected. Each point represents the mean value for a taxa, with horizontal and vertical error bars indicating standard deviation for $\delta^{13}C$ and $\delta^{15}N$, respectively.

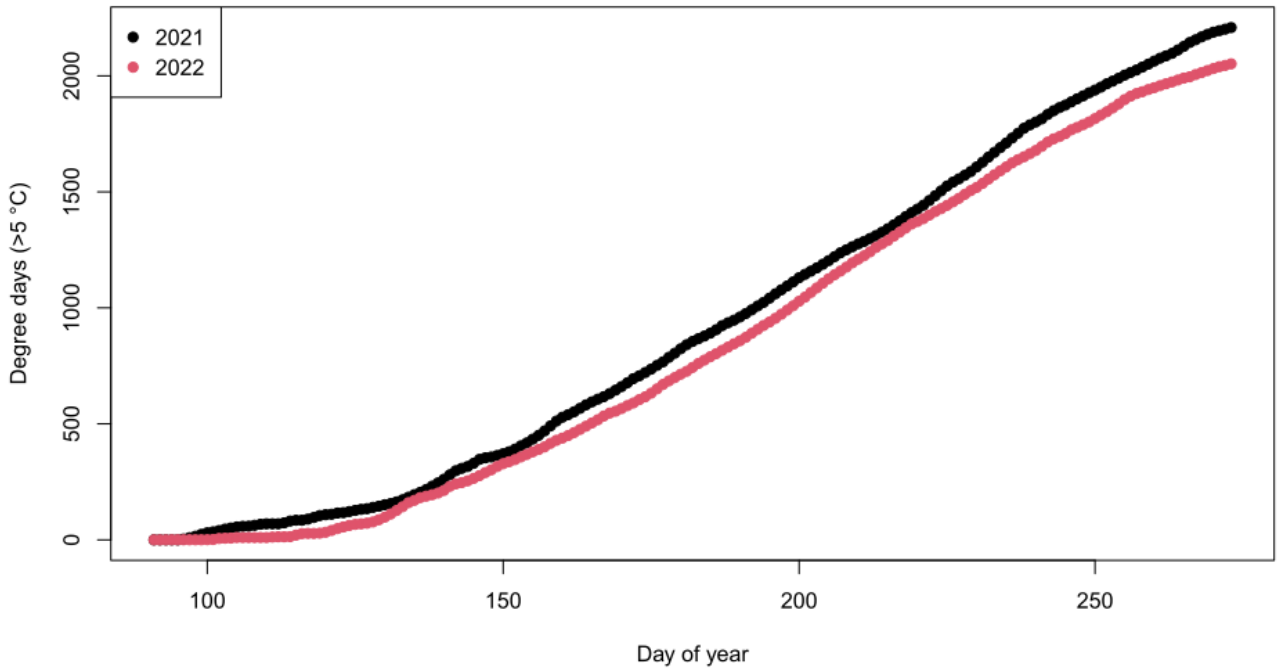


Figure S2. Evolution of degree day (above 5 °C) during time for 2021 (black) and 2022 (red) campaign.

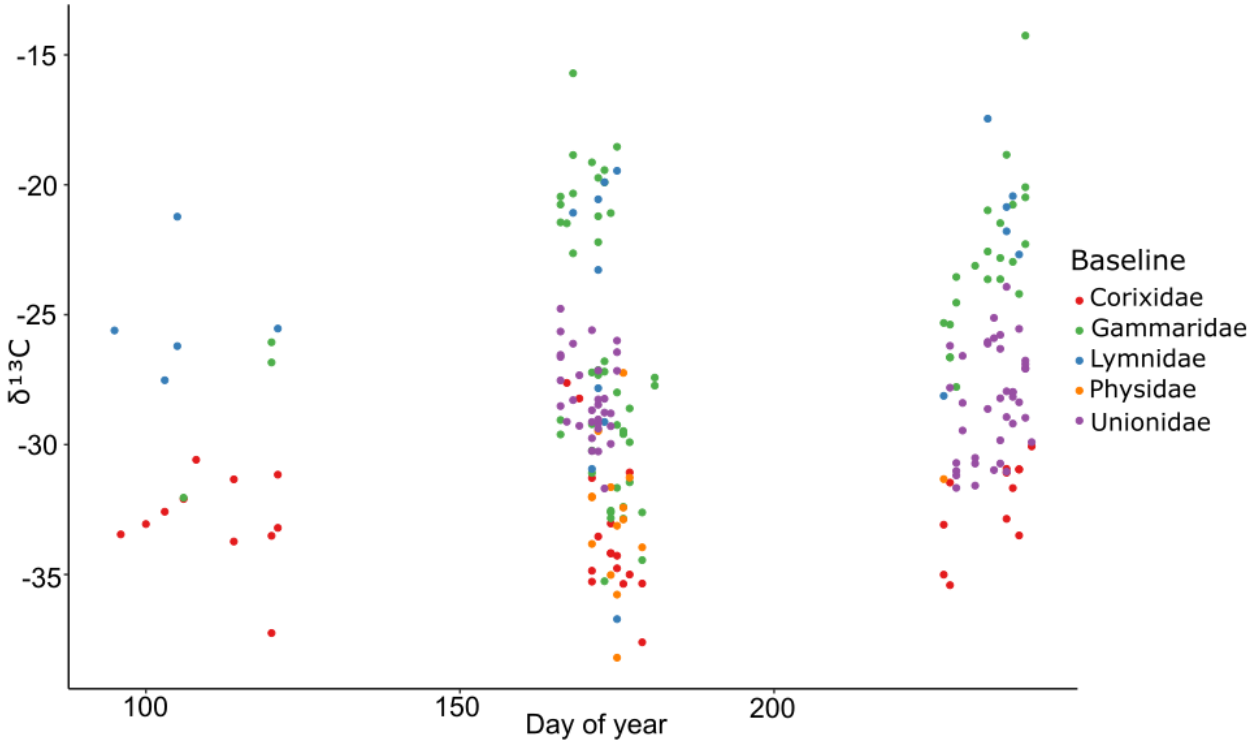


Figure S3. Temporal distribution of the $\delta^{13}C$ isotopic signature of invertebrates at the base of the food web.

Chapitre 3

Seasonal patterns in the size spectrum of a fluvial fish community linked to floodplain-derived subsidies and juvenile recruitment

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Abstract

Floodplains play an essential role in shaping fish communities by temporarily enhancing habitat connectivity, trophic subsidies, and recruitment. However, their influence on the size structure of communities, a key indicator of trophic functioning, remains poorly documented. We investigated temporal shifts in the size spectrum of a fish community in a system with marked seasonal variation: Lake Saint Pierre (LSP), a large fluvial lake in Québec (Canada) which has extensive floodplain development during spring floods. We used a model of individual size distribution to analyze seasonal variation in fish size spectra from standardized nearshore sampling conducted over two flooding cycles. The results revealed a size-spectrum slope consistently less negative than expectations from size spectrum theory, indicating an over-representation of large individuals possibly driven by floodplain subsidies. This pattern was disrupted in June, when a sharp influx of recruits led to a temporary steepening of the slope. Comparing our results with a global dataset of size spectra in aquatic systems, we found that few other studies had been conducted in floodplain environments, especially during seasonal floods. Our results illustrate how size spectra can detect subtle, system-specific signal. Our findings also highlight the need for more research on floodplains and the value of preserving natural flood regimes and lateral connectivity in these systems, with size-based indicators offering potential to monitor functional responses to hydrological variation.

Key words: fish community, functional ecology, habitat coupling, individual size distribution, trophic subsidies

Introduction

Aquatic ecosystems are structured by complex interactions between abiotic conditions (e.g., seasonal hydrology regime, substrate, temperature) and biotic dynamics (e.g., competition, predation, reproduction) (Davies & Jackson, 2006; Dunson & Travis, 1991). In these systems, fish communities play a fundamental role in food webs, ensuring the transfer of energy between primary producers and higher trophic levels (Mihalitsis et al., 2021). To understand aquatic food webs, the functional trait approach offers a relevant framework for going beyond simple taxonomy (Villéger et al., 2017). For example, body size is a fundamental functional trait: it influences metabolism (Andersen et al., 2016; Kooijman, 2010), mobility (Ware, 1978), trophic interactions (Barnes et al., 2008), survival (Pepin, 1991; Graeb et al., 2004), and reproductive success (Barneche et al., 2018). As such, it is a key element to understanding individual performance and life history strategies (Peters, 1986). At the community level, body size structures trophic interactions, notably though the predator-prey mass ratio (PPMR; (Arino et al., 2004; Nakazawa, 2017)) i.e., the relative size of prey consumed by predators. Predators tend to select prey within specific size ranges, and this size preference leads to non-random patterns of energy transfer (Brose et al., 2006). Importantly, the PPMR is not fixed, but varies with ecological context (Benoît & Rochet, 2004; Tsai et al., 2016), which makes size a useful proxy for examining food web structure and dynamics.

By aggregating individual sizes independently of species, the size spectrum represents the distribution of biomass or abundance as a function of individual body size within a community. Size spectra reflect underlying trophic processes (Andersen & Beyer, 2006). For example, according to the metabolic theory of ecology (Brown et al., 2004), the energy consumed by organisms is constant across size classes: smaller individuals are more numerous but metabolically less demanding, while

larger individuals are rarer but have greater consumption in absolute terms (Elton, 1927). According to size spectrum trophic theory, the balance between growth, predation mortality, and energy transfer leads to a stable abundance-mass relationship, whereby the shape and parameters of size spectra follow predictable patterns related to energy transfer efficiency across trophic levels (Andersen & Beyer, 2006). Trophic theory predicts that only a small fraction of the energy consumed at one trophic level (10%) is transferred to the next level, the remainder being lost through respiration, excretion, and unassimilated production (Lindeman, 1942; Pauly & Christensen, 1995). This progressive loss of energy constrains the biomass that can be supported at larger body sizes and underpins the emergence of a power-law size spectrum with a theoretical slope to -2 (Andersen & Beyer, 2006).

Historically, the size spectrum approach aimed to describe the structure of aquatic planktonic communities based solely on body size distributions (Sheldon et al., 1972, 1977). This framework has since been applied across a wide range of ecosystems and size (Blanchard et al., 2017), from small high-altitude lakes (Rodríguez et al., 1990) to open oceans (Reum et al., 2015; Edwards et al., 2020), illustrating its robustness and flexibility. Because it relies exclusively on individual size, the size spectrum approach bypasses the need for taxonomic identification and allows for functional comparisons across communities with distinct species compositions. Its relative methodological simplicity and modest data requirements have further contributed to its widespread use, particularly in large scale or long-term monitoring contexts (Guiet et al., 2016).

In addition to its theoretical interest, the size spectrum approach has established itself as a practical tool for ecological assessment. For example, size spectra can be used to identify breaks in the trophic chain (Benejam et al., 2018), detect the effects of anthropogenic pressures such as overfishing or eutrophication (Jennings & Blanchard, 2004; Shin et al., 2005), and assess an

ecosystem's resilience or trophic mechanism (Stasko et al., 2016). In the context of environmental management, size spectra offer an integrative approach capable of revealing functional changes even in the absence of major taxonomic modifications (Cattaneo, 1993). Several factors can influence the slope of the spectrum. For example, changes in the PPMR, directly influence the transfer of energy between trophic levels. When predators consume much smaller prey (high PPMR), the structure of the spectrum flattens (Coghlan et al., 2022), reflecting increased trophic efficiency or an accumulation of larger individuals. Deviations from a theoretical slope may therefore signal functional variations in the food web (Sprules & Barth, 2016).

Hydrological dynamics may also affect community size structure in aquatic ecosystems such as floodplains (Humphries et al., 2014). Flooding and temporary enlargement of water bodies can offer temporary access to resource-rich habitats favorable to fish recruitment, growth, and survival. This underlies the floodpulse concept (Junk et al., 1989), which postulates that seasonal alternation between floods and ebbs enhances productivity and biological diversity in fluvial ecosystems. Floodplains are indeed recognized as important spawning and nursery areas for multiple fish species, and local flooding and connectivity processes may scale up to influence river-wide population dynamics (Foubert et al., 2019). However, the effect of hydrological dynamics on the size structure of fish communities remains poorly studied in floodplains. Seasonal flooding could, for example, lead to flatter size spectrum slopes due to terrestrial-derived subsidies producing an overabundance of large-bodied consumers. Indeed, allochthonous inputs have been shown to alter size spectra in forest soil community (Hocking et al., 2013), UK streams community (Perkins et al., 2018), and fish community living in subtidal kelp forest (Gartenstein et al., 2024), resulting in a contribution to a specific size class of the community. While the impact of allochthonous resource subsidies and seasonal recruitment on fish community size spectra have been tested in other systems, these patterns have not been evaluated in floodplains (Miranda & Dembkowski, 2024).

This study aims to fill this gap by analyzing the size structure of a fish community in a fluvial lake connected to a floodplain. Using a recent approach based on a hierarchical size-spectrum model (Wesner et al., 2024), we examine how seasonal flooding modifies the distribution of body size within floodplain fish community. Then, to evaluate more broadly whether seasonal variation in size spectra represent a general feature of temperate aquatic ecosystems, we also draw on a recent global meta-analysis by Ersoy et al. (2025), which compiled over 8,000 size spectra from diverse aquatic environments, including freshwater, estuarine, and marine systems. This extensive dataset provides a unique opportunity to examine whether seasonal shifts in size structure, potentially driven by recruitment, growth dynamics, or energy flow changes, are consistent across temperate ecosystems. First, we predicted that our system, through both energetic subsidies and access to productive temporary habitats, promotes the growth and persistence of large, mobile species (fish), resulting in a shallower community size spectrum slope. We also hypothesized that seasonal steepening of the community size spectrum may result from pulses of recruitment, whereby the influx of small-bodied individuals following reproduction temporarily increases the relative abundance of small size classes, leading to steeper size-spectrum slopes. Then, we expected the size spectrum slope of fish community to vary seasonally, reflecting life-cycle processes such as recruitment and growth that are amplified by seasonal floodplain connectivity (steep in recruitment period). Finally, we hypothesized that these temporal and trophic patterns are not unique to our system, but can also be detected in other temperate aquatic systems.

Methods

Study system

This research was carried out in Lake Saint Pierre (LSP) and its fringing floodplain. LSP is a fluvial lake of the Saint Lawrence River in Quebec, Canada. The lake measures approximately 25.6 by 12.8 km, and has an average depth of 2.7 m (La Violette, 2004). The lake hosts a high fish biodiversity for a temperate system, with 79 recorded species (Laporte et al., 2025). Yearly variation in water level averages 1.8 m, and is driven mainly by fluctuating inputs from the Saint Lawrence River and its watershed (70%), the Outaouais River (20%), and other minor tributaries (10%) (Hudon et al., 2017; Morin & Bouchard, 2001). Seasonal flooding generally occurs between April and June and lasts 5 to 9 weeks (Lessard, 1991). These hydrological fluctuations and the flat topography in surrounding areas generate a vast floodplain (210 km² within the 2-year recurrence zone) which form the largest wetland complex along the Saint Lawrence River. Indeed, the LSP floodplain accounts for over 20% of all the wetlands in the Saint Lawrence River watershed (Langlois et al., 1992) and is designated as a RAMSAR wetland site.

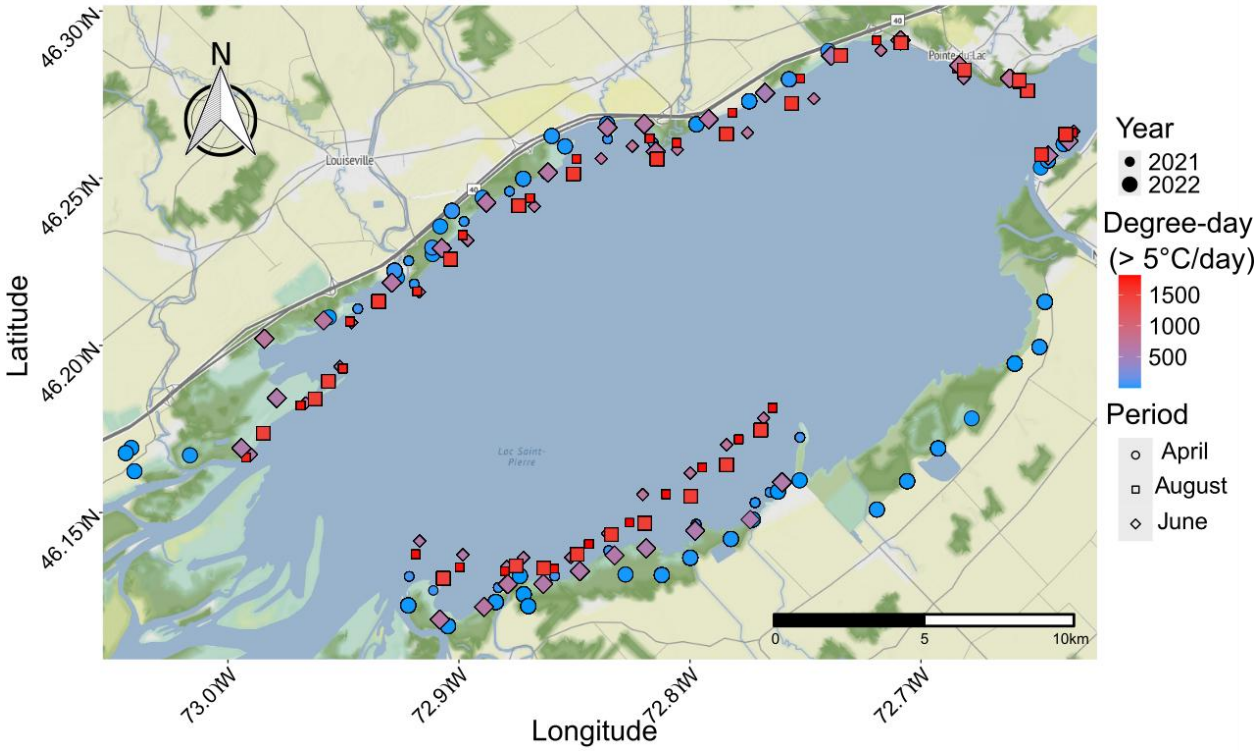


Figure 1. Map of sampling sites around Lake Saint Pierre for the years 2021 and 2022. Each dot represents a site, coloured according to the sum of cumulative degree-days (in °C above 5°C). The shape of the symbols indicates the sampling period (circle: April; diamond: June; square: August), whereas the size of the symbols indicates the year (small: 2021; large: 2022).

Field sampling

Sampling was conducted every ~2.5 km along the shoreline on the north shore and ~1.5 km on the south shore, except for a military zone in the southeastern sector of the lake, which had restricted access. Data collection took place in April, June, and August of 2021 and 2022, with approximately 30 sites sampled per period, totaling 172 sampled sites across two flooding cycles (93 sites on the north shore and 79 on the south shore) (Fig. 1). Sampling was carried out using a 25-metre-long seine net (height: 2 m; mesh size of net wings: 1 cm; mesh size of central 6-m bag: 2 mm). The net sampled an area of roughly 25 by 25 meters. Water depth ranged from 50 to 120 cm. All collected fish larger than 20 mm in total length were enumerated, identified to the species level and measured to the nearest millimeter in the field. Individual fish mass m was calculated from measured length L as:

$$m=a \times L^b$$

Where the a and b coefficients for each species were obtained from FishBase (https://www.fishbase.de/). To avoid underestimation of the number of small fish arising from sampling bias (Jennings et al., 2009; Sprules & Barth, 2016; Edwards et al., 2017), only fish with a body mass greater than 0.35 g were kept for analysis (Fig. S1). The fraction of fish retained for analysis represented 97% of the total biomass of captured fish.

Quantitative analyses

We evaluated how seasonality affects the size structure of the LSP fish community by comparing the slope of size spectra across sampling dates. The relationship between the abundance of individuals and their body size generally follows a power law (White et al., 2008) of the form:

$$N(m) \propto m^{\lambda}$$

With N(m), the density of individuals of mass m, is proportional to m^{λ}, where $\lambda<0$, so that small organisms are abundant while large ones are rare. This relationship becomes linear on a logarithmic scale:

$$logN(m) = \lambda \times log(m)$$

The slope of the size spectrum (λ) is a key indicator of the trophic and energetic structure of an ecosystem (Blanchard et al., 2017; Sprules, 2022). Higher values of λ indicate stronger dominance of small individuals, whereas smaller magnitudes reflect a more equitable size distribution in the community. This type of power law, conceptually close to the Pareto distribution, reflects the operation of energy constraints, mortality rates, and trophic dynamics in shaping the size distribution in aquatic communities (Wesner et al., 2024).

Several formulations of the size spectrum are possible depending on the method used to measure abundance. Thus, for a spectrum describing the density of individuals per size class, the theoretical slope from size spectrum theory is equal to -2 (Andersen et al., 2009, 2016; Andersen & Beyer, 2006). This slope reflects the fact that, to maintain an energy balance in an ecosystem, larger organisms must be proportionally less numerous in terms of their energy demand (Brown et al.,

2004). However, when the size spectrum is expressed in terms of biomass per size class, abundance is multiplied by mass, giving the relationship:

$$B(m) \propto mN(m) \propto m^{(\lambda+1)}$$

In this case, the expected theoretical slope of the biomass spectrum is -1, indicating that biomass is evenly distributed among size classes (Sheldon et al., 1972, 1977). Different theoretical slopes of a size spectrum can be derived based on ecological and thermodynamic principles (Scott et al., 2014). The expected slope can be based on a combination of allometric laws and the efficiency of trophic transfers (Andersen et al., 2009). First, available energy declines with each trophic transfer, i.e., an efficiency of around 10% (Brown et al., 2004), which limits the number of large individuals that depend on small producers. Second, metabolic rates increase allometrically with body mass according to the relationship:

$$B \propto m^{\frac{3}{4}}$$

Indicating that a large individual needs proportionally more energy to maintain itself. Finally, predator-prey relationships are constrained by body size, predators being limited to a maximum prey size by their morphology (Trebilco et al., 2013, 2016). Combining these explanations, the number of individuals decreases in proportion to the square of their size, reflecting a hierarchical organization of a food web's energy flow (Lindeman, 1942). In this study, we calculated biomass size spectra for LSP, which we compared to a theoretical slope of -2.

We quantified size spectra using truncated Pareto distributions (Wesner et al., 2024). The Pareto distribution of an individual size spectrum model is described by a probability density function of the form:

$$C=\begin{cases} \frac{\lambda+1}{x_{max}^{\lambda+1}-x_{min}^{\lambda+1}}, \lambda \neq -1 \\ \frac{1}{logx_{max}-logx_{min}}, \lambda=-1 \end{cases},$$

where C is a constant, x_{max} is the maximum individual mass of an organism, x_{min} is the smallest individual mass and λ is the slope of a size spectrum, which can be modeled as a function of explanatory covariates (Wesner et al., 2024). Here, we evaluate the effects of seasonality (April, June, and August, three months representing different phases of the annual flooding cycle), sampling year (2021 and 2022), and the season by year interaction, on the slope of the biomass spectrum, while controlling for a random effect (sampling site):

$$w_i \mid c_i, x_{max}, x_{min} \sim Truncated\text{-}Pareto(\lambda_i, x_{max}, x_{min})$$

$$\lambda_i=\beta_0+\beta_s \times Season+\beta_y \times Year+\beta_{sy}(Season \times Year)+u_{sampling\ sites}$$

$$u_{sampling\ sites} \sim N(0, \sigma^2_{sampling\ sites})$$

Where for the truncated-Pareto λ_i is a shape parameter indicating the slope, x_{max} and x_{min} lower and upper bounds of the distribution. The equation describes the distribution of fish individual weight w_i across all samples. The Pareto shape parameter is represented by a linear model where β_0 is the intercept, β_s, β_y, β_{sy} are the estimated coefficients for season, year, and their interaction, and $u_{sampling\ sites}$ is the random effect for sampling sites, which is assigned a normal prior distribution. The random effect accounts for the nesting of individual fish within sites. This hierarchical approach makes it possible to explicitly incorporate the sampling structure while modelling individual fish mass, which improves the precision of estimates and the robustness of inferences about ecological mechanisms underlying size structure in an ecosystem (Wesner et al., 2024). We used the 'isdbayes' package in R (Wesner et al., 2024), which implements an individual size spectrum model based on a truncated Pareto distribution. Analyses were carried in R version 4.3.3. (R Core Team, 2020).

Comparison with other aquatic systems

To evaluate whether the temporal variation in size spectrum slopes observed at LSP reflects a broader ecological pattern, we extended our analysis across multiple temperate freshwater ecosystems. Specifically, we assessed whether freshwater fish communities tend to exhibit seasonal changes in size structure. We also examined whether previous studies of aquatic size spectra had been conducted in floodplains during seasonal floods. To this end, we leveraged the freshwater subset of the GLOSSAQUA database (Ersoy et al., 2025), which compiles size spectrum slopes from a wide array of aquatic studies. The freshwater subset comprises a total of 8459 slopes calculated for lakes, rivers, and reservoirs sampled primarily across North America and Europe. We focus on fish size spectra from these systems (total of 4290 slopes). From this subset of the dataset, we extracted slope values from studies in which both the sampling month and spectrum estimation method were available. The slope estimation methods used in the studies included in GLOSSAQUA are diverse. They include normalized abundance spectra, biomass spectra, linear regression on size classes, and approaches focusing on statistical distributions, such as Pareto modeling. To assess the distribution of methodological approaches across ecosystem types, we compiled a summary table that cross-references sampling month and habitat categories (Table 1). After filtering, the final dataset comprised 1425 slopes from 1346 distinct sites and 4 distinct studies, covering periods from June to November. Each slope was associated with a sampling month and a study identifier, enabling us to analyze within- and between-study variation in seasonal dynamics.

To test for a general temporal trend in the spectrum slopes across freshwater ecosystems, we fit a multilevel model using the brms package in R (Nalborczyk et al., 2018). The model was specified as:

$$Slope \sim Student_{\nu}(\mu_i, \sigma_e)$$

$$\mu_i = \beta \times SamplingMonth_i + \alpha_0 + \varepsilon_{Study_i} + \varepsilon_{Site_i}$$

Where the response variable $Slope$ represents the normalized slope of the biomass spectrum, which follows a Student distribution with location μ_i, scale σ_e, and degrees of freedom ν. The assumption of Student residuals provides more robustness to outliers than the usual assumption of normality. β is the coefficient of the fixed effect estimating the change in slope per unit time (month), α_0 is the intercept, ε_{Study_i} is the random effect for study, and ε_{site_i} is the random effect for site. In this model, month is treated as a categorical fixed effect, whereas the study and site IDs type are modeled as random effects to account for within-group correlations. This framework allowed us to assess whether seasonal variation in the slope of the size spectrum pointed to a common functional signal of recruitment or growth patterns across freshwater fish communities.

Table 1. Number of individual size spectrum slopes included in the GLOSSAQUA freshwater subset, categorized by ecosystem type and sampling month. Ecosystem types include natural lake, artificial reservoirs and streams, with lakes occasionally reported without further classification (denoted as "Lake"). The values correspond to slope estimates derived using various methods.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Lake	0	0	0	0	0	0	45	12	3	1	0
Natural lake	0	0	0	0	0	4	657	25	60	8	0
Reservoir	0	0	0	0	0	44	36	47	68	22	0
Stream	7	4	0	7	1	405	667	500	1053	35	4

Results

Estimates of the slope of the LSP fish community size spectrum did not appear to differ between sampling years (Fig. 2, left panel). However, for both years, the slope was less negative than the expected theoretical value of -2. Slopes varied seasonally; the slope value was near -2 in June at the end of the annual flood, but shallower slopes were observed in April (during the spring flood) and August (at the end of the growing season), reflecting a surplus of large individuals compared to the expected theoretical distribution in those months (Fig. 2, right panel). The steep slope observed in June reflects the recruitment of small fish (≤2 g), primarily yellow perch (*Perca flavescens*), which represented more than 80% of total abundance (Table S1).

Most studies in freshwater in the GLOSSAQUA dataset fitting our inclusion criteria focused on summer months (Table 1). Slopes of size spectra in that dataset showed no consistent directional trend over time, with monthly means remaining relatively stable throughout the sampling period (Fig. 3). In contrast, for LSP the slope in June displayed a marked decrease compared to April and August, and was closely aligned with the theoretical value of -2 (Fig. 3). Thus, the distinctive feature of LSP relative to the global dataset is a strong seasonal structuring of size-spectrum slopes, which in June become relatively steep compared to April and August in LSP, and to samples from April to October for other temperate freshwater systems.

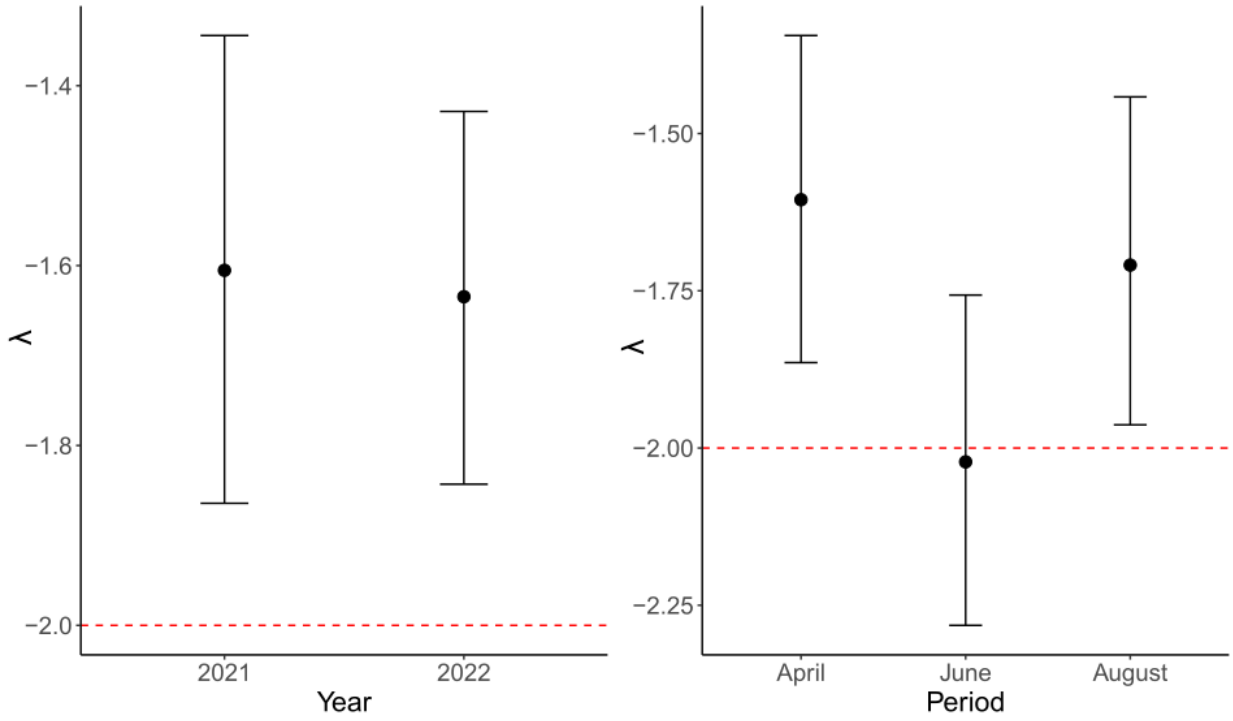


Figure 2. Estimates of size spectrum parameter λ by year (left) and sampling period (right). Dots represent posterior means and vertical bars 95% credibility intervals. The red dotted line indicates the expected value for a size distribution following a theoretical power law from size-spectrum theory.

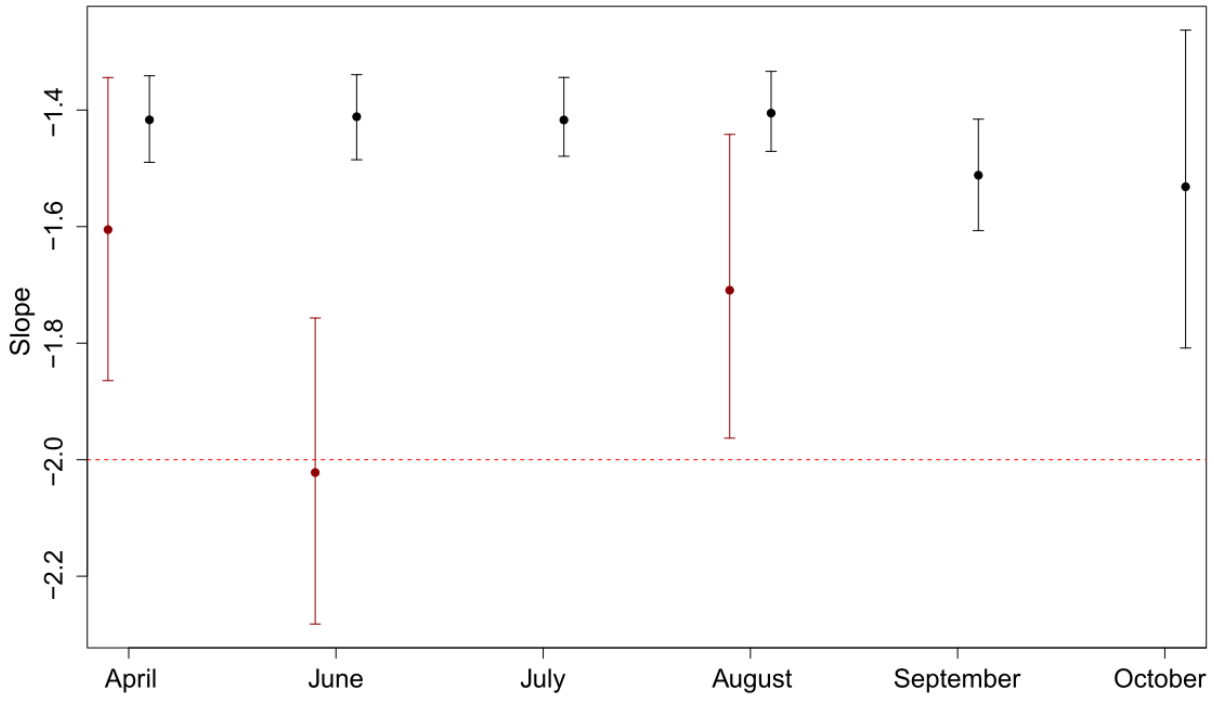


Figure 3. Monthly variation in size spectrum slopes across temperate freshwater fish communities and in Lake Saint Pierre. Distributions of monthly slope values are summarized as means (dots) and 95% credible intervals (vertical bars) for the GLOSSAQUA (black) and LSP (red) data. The red dotted line indicates the expected value for a size distribution following a theoretical power law from size-spectrum theory.

Discussion

To assess how floodplain subsidies may alter the community size structure of a fluvial lake, we sampled littoral fish communities along the shore of LSP during the flood period (April), and in early and late summer (June and August) over two successive years (2021 and 2022). We found that in April and August the overall slope of the size spectrum was less negative than expected based on

predictions from size-spectrum theory, indicating an over-representation of large individuals in the community. This pattern may suggests a higher level of production or efficiency in terms of energy transfer to higher trophic levels (Trebilco et al., 2013), which in turn may reflect a substantial contribution of the floodplain to fish growth (Baber et al., 2002; Hashemi et al., 2015). Temporary access to habitats rich in resources (e.g., insects, macroinvertebrates, organic matter) and less subject to predation could enable individuals to grow more rapidly (Pratt et al., 2023). The mobility of species and their ability to efficiently exploit these temporarily accessible habitats play a key role in accessing resources in flooded areas (Jardine et al., 2017). Some large species, such as carp (*Cyprinus carpio*), occupy relatively low trophic levels while having a large size relative to their prey. Large fish that occupy comparatively low trophic positions can contribute to a shallower size-spectrum slope by weakening the relationship between body size and trophic level (Trebilco et al., 2013). The LSP floodplain provides substantial energetic subsidies to the fish community, increasing resource availability during the flooding period (Farly et al., 2019). In addition to enhanced foraging opportunities, the floodplain offers structurally complex habitats that improve reproduction and survival conditions for several fish species (Foubert et al., 2019). The combination of high resource input and favorable habitat characteristics during flood period (low predation) may therefore promote a transient accumulation of large-bodied individuals in the community, ultimately contributing to a flatter size-spectrum slope.

Comparable shifts in size structure have been observed in other floodplain systems, driven by ecological mechanisms unrelated to those operating in LSP (Miranda & Dembkowski, 2024). Human land use and the introduction of non-native species can lead to a profound reorganization of fish communities, with large-bodied native fishes progressively replaced by large-bodied exotic taxa (Moi et al., 2025). Introduced species can dominate the upper end of the size distribution, illustrating how external pressures can reshape the contribution of large individuals to the community size-

spectrum (Moi et al., 2025). Although example differs from the dynamics associated with seasonal flooding in our system, the comparison embodies a general principle: alterations in habitat accessibility can modify the abundance and identity of large-bodied fishes, ultimately influencing the slope of the size-spectrum.

LSP undergoes a marked intra-annual change in community size structure. In June, the slope of the size spectrum steepened and approached theoretical expectations, which deviates from other systems represented in the GLOSSAQUA dataset, in which slopes remained approximately constant and well above the expected theoretical value. The steeper slope observed in LSP in June is likely due to a large influx of recruits following the reproductive season. This seasonal change suggests that size structure is shaped not only by floodplain-driven growth, but also by recruitment pulses that shift the size distribution. The concept of floodpulse (Junk et al., 1989) describes seasonal floods as key events promoting intense energetic exchanges between the floodplain and the main channel. The floods temporarily allow access to favorable breeding habitats for certain species. Yellow perch, for example, enter the LSP in spring to spawn in shallow, vegetated areas as early as April (Dabrowski et al., 1996). However, most species, including many cyprinids, reproduce later, mainly in June, when the waters warm up (Mongeau, 1985; Ross & Matthews, 2014). The reproductive pulse leads to a marked increase in the proportion of smaller individuals in the community, temporarily diluting the trophic signal inherited from the flood. This seasonal dynamic reflects the importance of reproductive cycles in the temporal structuring of the size spectrum (Boudreau & Dickie, 1992). Contrary to the classical view of the floodpulse (Junk et al., 1989; Tockner et al., 2000), which emphasizes enrichment primarily at the base of the trophic chain through increased primary production, our results indicate that the floodplain also functions as a growth engine for individuals present in the lake prior to inundation, due to the subsidies and the protection from predation provided by the floodplain. In this sense, the benefits of the floodpulse

extend beyond the promotion of recruitment and include enhanced growth performance at later life stages, for the species or individuals capable of efficiently exploiting flooded habitats. This perspective reinforces the idea that floodplains should not be regarded solely as spawning or nursery areas, but also as functionally important trophic habitats for post spawning and adult fish, contributing directly to individual growth and condition (Vuić et al., 2024).

While these results highlight how seasonal signals can strongly modify the size structure of communities at the local scale, it remains unclear whether this pattern is widespread across freshwater ecosystems. Contrary to the marked seasonal shift in slope of the size spectrum at the local scale (in LSP), our comparative analysis using the GLOSSAQUA dataset did not reveal any consistent temporal trend in the slope values in other systems. In this dataset, the distribution of slope estimates remained relatively stable across months, with no evident steepening or flattening from spring to autumn. Several non-exclusive explanations may account for the absence of a clear temporal signal in the global dataset. First, although the analysis was restricted to freshwater systems in temperate regions, these systems still encompass a wide spectrum of ecological contexts and community compositions shaped by biogeographic and climatic gradients (Bower & Winemiller, 2019; Sánchez-Hernández et al., 2021). This ecological heterogeneity likely contributes to the absence of a consistent temporal signal in a slope values across studies. Second, the timing of the reproductive and recruitment events likely varies among systems (Blanck et al., 2007; Winemiller, 1989), depending on species composition and the local thermal and hydrological regimes. Such variability in biological cycles may hinder the detection of consistent seasonal trends. Third, while lotic systems are generally more likely to be associated with floodplains, the GLOSSAQUA dataset does not specify whether any given stream or river is connected to an active floodplain. As a result, it is impossible to isolate and evaluate the specific influence of floodplain dynamics on seasonal patterns in size structure within these systems. The lack of detailed hydrological context in the

GLOSSAQUA dataset may partly explain why no consistent variation was detected. Direct quantitative comparisons between the absolute values of the size spectrum slope between the LSP and the systems included in the GLOSSAQUA dataset are nevertheless limited by methodological differences between studies, including variations in fishing gear, size selectivity, spatial coverage, and slope estimation procedures. Consequently, our comparison deliberately focuses on relative and temporal trends rather than absolute slope values. However, regardless of the heterogeneous nature of the GLOSSAQUA dataset, we note that no slope estimates approached the steep values recorded for LSP in June, which confirms the unusual nature of the LSP community size spectrum in this setting.

Notably, while the global GLOSSAQUA dataset reveals that size-spectrum slopes tend to be consistently shallower than theoretical predictions without a clear seasonal trend, the pattern observed in the LSP system deviates from this generality. In LSP, the size-spectrum slope in June approaches the theoretical expectation (slope = -2), coinciding with a pronounced recruitment pulse of juvenile fish, particularly yellow perch, whose reproduction primarily occurs in the floodplain earlier in the season. This strong seasonal shift in slope reflects a distinct seasonal re-structuring of size distribution directly linked to floodplain reproduction dynamics, a phenomenon not apparent in most systems represented in GLOSSAQUA. To our knowledge, relatively few study studies have focused specifically on the size structure of fish communities in floodplain environments. Previous work in floodplain lakes of the Mississippi River has focused on environmental drivers of size structure in floodplain contexts but not addressed seasonal dynamics (Miranda & Dembkowski, 2024). Changes in the size structure of fish communities that have shifted from native to exotic species have also been studied in floodplains, but the role of the environment in shaping the size structure of fish communities has not been clearly defined (Moi et al., 2025). Such scarcity of research underscores the unique ecological insights provided by examining size spectra in seasonal

floodplain ecosystems such as LSP, and suggests that temporal variability in size structure linked to seasonal reproduction and connectivity between macrohabitats may be underrepresented in broader freshwater ecological syntheses.

It is also worth noting that global data like GLOSSAQUA are often dominated by marine or large lacustrine systems, which may not fully capture the dynamics of shallow fluvial lakes like LSP. For instance, the dataset may underestimate the role of lateral connectivity in shaping size spectra, as such processes are less pronounced in the systems studied in the dataset.

The differences between local and global patterns of seasonal change in size spectrum slopes highlights the importance of context-dependent drivers in shaping size structure. It also suggests that temporal variation in size spectra may not emerge unless certain ecological conditions are met, such as floodplain connectivity, synchronized reproduction in highly seasonal systems, or strong seasonal productivity gradients (Junk et al., 1989; Humphries et al., 2014). Taken together, these results emphasize the potential of size spectra as a integrative tool to detect subtle ecological dynamics and the signals of seasonal events such as flood pulses (Sprules & Barth, 2016). The observation of floodplain effects on size spectra also calls for a re-evaluation of the classic productivity indicators used in the assessment of aquatic ecosystems. Traditional approaches often rely on snapshot measurements of species richness, community composition, or individual abundance (Bain et al., 2000). Although relevant for other biological event (such as invasive species arriving), these metrics may be relatively insensitive to the cumulative and delayed effects of hydrological events such as seasonal flooding. Importantly, this limitation does not imply that traditional community metrics fail to capture ecological responses to flood pulses. Rather, these metrics and size-based approaches describe different, complementary dimensions of community structure. For example, taxonomic approaches are well suited to detecting changes in population-

level responses (Lindenmayer & Likens, 2010). In contrast, the size spectrum is a powerful integrative indicator, as it reflects the structure of the whole community by taking into account the distribution of body sizes, and thus indirectly trophic processes, growth, and energy transfer within the trophic network (Blanchard et al., 2017; Guiet et al., 2016; Sprules, 2022). Size spectra thus allow for the detection of lasting signatures of floodpulses after water recession, and of effects that may not be amenable to detection by methods focused on particular taxonomic groups.

Overall, our results indicate that the most consistent and robust signal emerging from the size spectrum analysis is the predominant influence of energy subsidies from floodplains on community size structure. Despite pronounced seasonal fluctuations associated with recruitment peaks, the overall slope of the size spectrum remained consistently lower than theoretical predictions, indicating a consistent overrepresentation of large individuals. This pattern suggests that floodplain connectivity not only modulates short-term demographic processes, but also exerts a lasting influence on energy transfer and biomass accumulation in larger size classes. In fact, LSP and its floodplain along the Saint Lawrence River comprise key spawning and nursery habitats for multiple fish species, with seasonal flooding creating connected shallow wetland areas used for reproduction beyond the lake itself and into the downstream river corridor (Foubert et al., 2020). In this sense, the LSP floodplain functions as a long-term energy subsidy that shapes community structure beyond transient seasonal dynamics (Trebilco et al., 2013; Jardine et al., 2017). From an applied perspective, the littoral wetlands of lakes provide valuable ecosystem services. For example, in the Great Lakes, fish species that use wetlands close to shores account for up to half of the fish biomass and are of great value to both commercial and recreational fisheries (Trebitz & Hoffman, 2015). Our results underscore the crucial importance of preserving littoral wetlands, natural flood cycles, and lateral connectivity between rivers and their alluvial plains. Our results also highlight the need for future studies to explicitly investigate how floodplain connectivity shapes community size

structure. The size-spectrum dynamics of floodplain fish communities remains poorly documented in the literature, as evidenced by the underrepresentation of floodplain systems in global syntheses such as GLOSSAQUA and the sparsity of size-spectrum studies in tropical floodplains of the Southern Hemisphere and Asia (Ersoy et al., 2025).

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Author contributions

TT, MAR, and VF designed the research. TT, MAR, and VF analyzed the data, TT made figures and wrote the manuscript with significant inputs from MAR and VF.

Conflict of interest statement

The authors declare that they have no competing interests.

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Supplementary material for: Seasonal patterns in the size spectrum of a fluvial fish community linked to floodplain-derived subsidies and juvenile recruitment

Table S1. Number and proportion of catches by weight class and period. The last column focuses on the number of yellow perch.

Period	Weight (g)	n	Total proportion (%)	n yellow perch
April 2021	≤2	1363	66.72	0
April 2021	2-4	288	14.1	31
April 2021	4-8	250	12.24	45
April 2021	8-16	57	2.79	8
April 2021	16-32	20	0.98	9
April 2021	32-64	11	0.54	5
April 2021	64-128	8	0.39	1
April 2021	128-256	33	1.62	2
April 2021	256-512	4	0.2	0
April 2021	≥512	9	0.44	0
June 2021	≤2	2893	83.32	2319
June 2021	2-4	157	4.52	73
June 2021	4-8	172	4.95	147

June 2021	8-16	47	1.35	18
June 2021	16-32	20	0.58	8
June 2021	32-64	109	3.14	9
June 2021	64-128	46	1.32	12
June 2021	128-256	16	0.46	2
June 2021	256-512	4	0.12	0
June 2021	≥512	8	0.23	0
August 2021	≤2	2374	61.79	2
August 2021	2-4	463	12.05	71
August 2021	4-8	755	19.65	108
August 2021	8-16	174	4.53	24
August 2021	16-32	36	0.94	12
August 2021	32-64	16	0.42	9
August 2021	64-128	14	0.36	3
August 2021	128-256	6	0.16	0
August 2021	256-512	3	0.08	0
August 2021	≥512	1	0.03	0
April 2022	≤2	2039	72.56	0

April 2022	2-4	317	11.28	1
April 2022	4-8	350	12.46	28
April 2022	8-16	67	2.38	10
April 2022	16-32	11	0.39	4
April 2022	32-64	5	0.18	1
April 2022	64-128	7	0.25	3
April 2022	128-256	6	0.21	3
April 2022	256-512	4	0.14	0
April 2022	≥512	4	0.14	0
June 2022	≤2	5147	85.93	3767
June 2022	2-4	567	9.47	1
June 2022	4-8	165	2.75	0
June 2022	8-16	65	1.09	35
June 2022	16-32	33	0.55	24
June 2022	32-64	8	0.13	7
June 2022	128-256	1	0.02	0
June 2022	256-512	1	0.02	0
June 2022	≥512	3	0.05	0

August 2022	≤2	4257	71.46	30
August 2022	2-4	886	14.87	68
August 2022	4-8	554	9.3	2
August 2022	8-16	192	3.22	25
August 2022	16-32	54	0.91	26
August 2022	32-64	5	0.08	1
August 2022	64-128	6	0.1	0
August 2022	128-256	2	0.03	0
August 2022	≥512	1	0.02	0

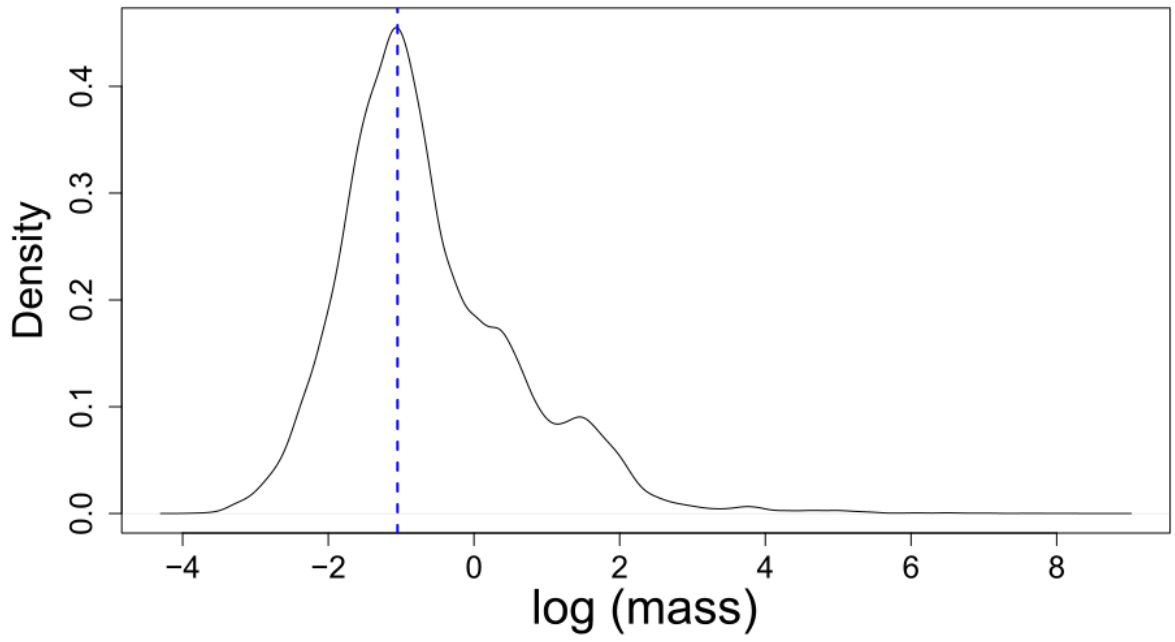


Figure S1. Empirical density estimate for the logarithm of fish mass (black curve). The cutoff threshold (-1.05) used for individual mass is also shown (blue).

Discussion Générale

Discussion générale

Objectifs et synthèse des résultats

L'objectif général de cette thèse était d'évaluer comment les plaines inondables tempérées, par leur connexion saisonnière avec leurs milieux permanents, influencent la structure et le fonctionnement des communautés de poissons. Cette démarche s'inscrit dans le cadre du « Generalist Module Hypothesis » (GMH) (McMeans et al., 2016), qui avance que les espèces de grande taille et de haut niveau trophique sont les plus à même de coupler différents habitats en intégrant et redistribuant les flux de ressources. Ici, cette hypothèse a été examinée dans un système caractérisé par une dynamique hydrologique marquée, où la dimension temporelle des crues joue un rôle central dans l'organisation des communautés.

Le premier axe de ma thèse visait à identifier les traits fonctionnels qui définissent les poissons aptes à occuper la plaine inondable. L'objectif n'était pas de dresser une liste d'espèces, mais de déterminer quels traits écologiques permettent de généraliser le profil des poissons capables d'occuper cet habitat temporaire. Les résultats montrent que les espèces occupant la plaine se caractérisent par des plus petites tailles et une affinité pour les habitats riches en macrophytes (Figure 1), qui leur offrent à la fois nourriture, protection et site de reproduction lors des crues. Ces résultats vont ainsi à l'encontre de la GMH. Cette approche par les traits permet ainsi d'identifier les mécanismes fonctionnels qui conditionnent l'accès et l'utilisation de la plaine inondable, et qui pourraient s'appliquer à d'autres systèmes soumis à des régimes hydrologiques similaires.

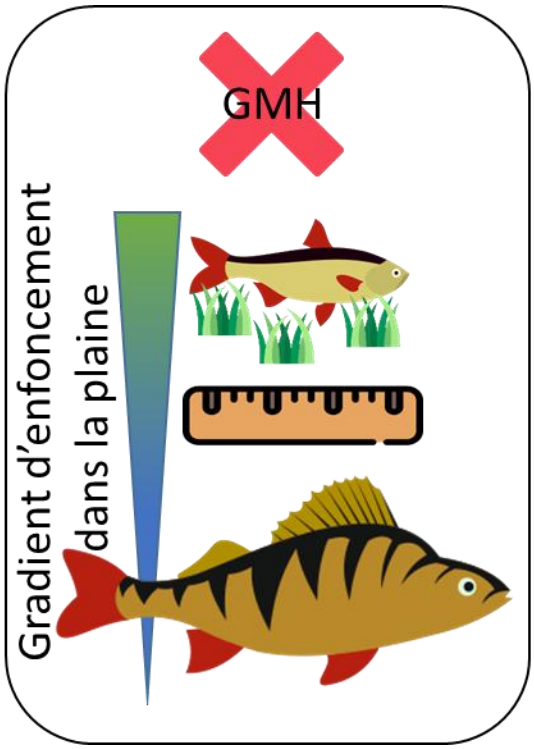


Figure1. Schéma conceptuel illustrant l'occupation des habitats du lac selon un gradient d'enfoncement, depuis le littoral jusqu'aux secteurs les plus éloignés dans la plaine inondable. Les espèces avec la plus forte probabilité d'être retrouvées loin dans la plaine inondable sont de petite taille et phytophiles.

Le deuxième axe de ma thèse a porté sur l'analyse des transferts trophiques liés à l'apport de subsides allochtones provenant de la plaine inondable, en utilisant les isotopes stables pour quantifier leur intégration dans le régime alimentaire des poissons. Les résultats montrent que ce sont principalement les espèces de haut niveau trophique, en accord cette fois avec la GMH, qui incorporent une proportion importante de ces ressources (Figure 2). Ces espèces présentent elles aussi une affinité pour les habitats riches en macrophytes, confirmant le rôle de ces zones comme points d'entrée privilégiés des flux énergétiques issus de la plaine. Ces résultats contrastent donc avec ceux du premier axe, suggérant que le couplage lac-plaine ne repose pas sur un seul profil fonctionnel, mais sur des mécanismes complémentaires : d'un côté l'occupation spatiale par des

petites espèces adaptées aux habitats temporaires, de l'autre l'intégration des subsides allochtones par des espèces situées plus haut dans le réseau trophique. Afin d'évaluer la portée générale de ces mécanismes, une analyse complémentaire a ensuite été réalisée à l'échelle de la base de données IsoFresh (Boulêtreau et al., 2025), en testant spécifiquement les traits identifiés somme significatifs dans le lac Saint-Pierre (LSP). Les résultats confirment que le rôle des espèces phytophiles se retrouve dans une diversité de systèmes lotiques (plus susceptibles d'avoir une zone inondable), renforçant la robustesse et la généralité de ces observations.

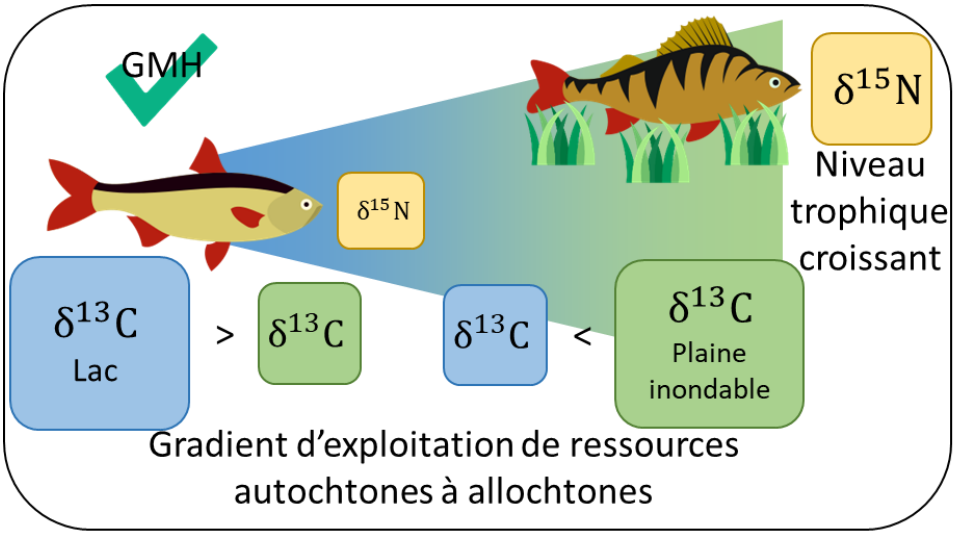


Figure 2. Schéma conceptuel concernant l'exploitation des ressources disponibles dans le système du lac Saint-Pierre. La signature isotopique du carbone et de l'azote ($\delta^{13}C$, $\delta^{15}N$) montraient que les espèces présentant les valeurs les plus associées à des ressources provenant de la plaine sont de haut niveau trophique et phytophiles.

Le troisième axe a exploré la manière dont la structure de la communauté reflète l'exploitation de la plaine inondable, à travers l'analyse des spectres de taille. Les résultats montrent d'abord que la plaine apporte des subsides énergétiques qui bénéficient en particulier aux organismes de grande taille, confirmant leur rôle central dans l'intégration de ces ressources. Ils révèlent

également une dynamique intra-annuelle, marquée par un recrutement massif qui accentue la pente du spectre en juin par rapport aux autres périodes (Figure 3). Toutefois, lorsque cette approche a été élargie par l'ajout d'une méta-analyse (Ersoy et al., 2025), ces tendances n'ont pas été retrouvées à plus large échelle, ce qui suggère soit une spécificité des dynamiques propres au LSP, soit un manque de travaux explicitement consacrés à ce sujet. En effet, la pente douce du spectre de taille retrouvée au LSP n'est pas généralisable par manque de données concernant ce type de système (lac-plaine inondable) et en intégrant un suivi printanier. L'empreinte laissée par la plaine inondable sur la structure de taille de la communauté suggère ainsi que ce type d'indicateur (pente du spectre de taille) intègre à la fois l'effet des subsides énergétiques et la dynamique démographique saisonnière, offrant une mesure synthétique des mécanismes mis en évidence dans les trois chapitres. Ainsi, la pente du spectre de taille au LSP est plus douce

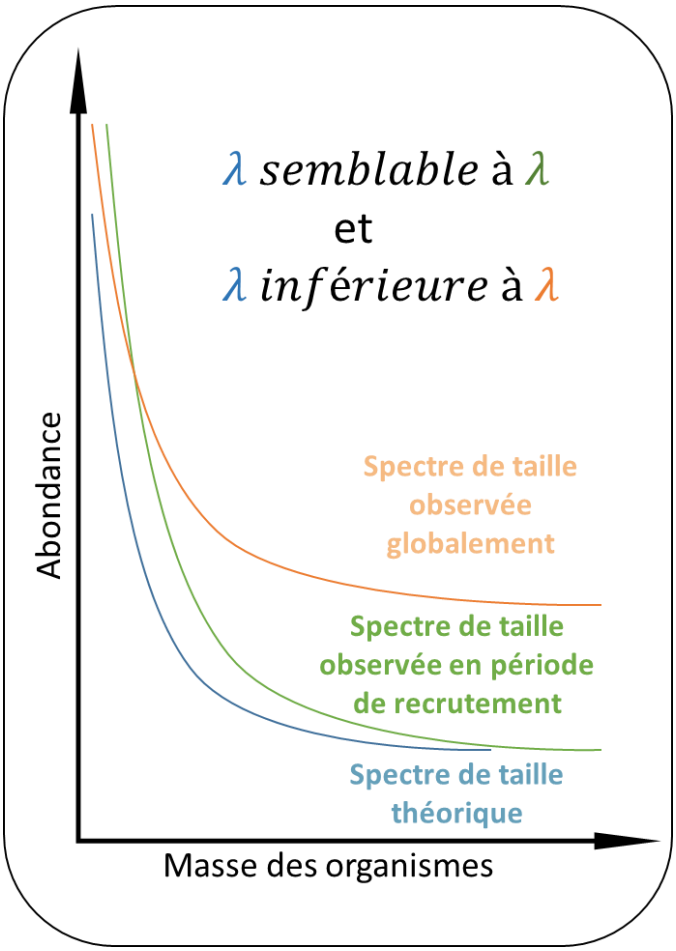


Figure 3. Schéma conceptuel présentant la comparaison entre un spectre de taille théorique attendu selon Andersen et Beyer (2006) (spectre bleu) dans un système aquatique avec celles observées au LSP durant une période spécifique du cycle annuel. Le LSP une surreprésentation d'organismes de grande taille (spectre orange) soutenue par un recrutement de jeunes petits poissons durant l'année (spectre vert).

Réunis, ces trois volets mettent en évidence que le couplage entre une plaine inondable et son milieu permanent est assuré par une combinaison de mécanismes complémentaires : l'occupation spatiale par des petites espèces phytophiles, l'intégration des subsides allochtones par des espèces de haut niveau trophique, et une structuration communautaire qui porte la trace de ce couplage. L'approche conjointe fondée sur les traits, les isotopes et la taille corporelle a permis ainsi

de mieux comprendre comment la dynamique hydrologique saisonnière module la résilience des communautés ichtyologiques dans ce système lac-plaine tempéré.

Apports conceptuels et théoriques

Les résultats de cette thèse offrent plusieurs apports conceptuels en lien avec les théories existantes sur le fonctionnement des réseaux trophiques aquatiques. Le premier concerne la GMH (McMeans et al., 2016). Cette hypothèse, testée sur des lacs tempérés, avance que les organismes de grande taille et de haut niveau trophique sont les principaux vecteurs du couplage entre habitats, car leur mobilité leur permet d'intégrer et de redistribuer des flux de ressources. Nos résultats montrent toutefois une réalité plus nuancée. Le premier chapitre révèle que l'occupation de la plaine inondable repose avant tout sur des espèces phytophiles et de petite taille ; cela constitue un résultat en contradiction avec les prédictions initiales de la GMH. En revanche, le deuxième chapitre confirme que les espèces de haut niveau trophique intègrent effectivement une part importante des subsides provenant de la plaine, conformément aux attentes de la GMH. Le troisième chapitre quant à lui nous apprend que la reproduction et donc le recrutement en juvéniles, contribue au maintien d'une surreprésentation d'organismes de grande taille par rapport à la théorie des spectres de taille. Pris ensemble, ces résultats indiquent que la GMH ne peut rendre compte à elle seule de la complexité des systèmes dynamiques lac-plaine inondable : le couplage ne dépend pas seulement de la mobilité des grands prédateurs, mais aussi de la capacité des espèces à occuper l'espace temporaire de la plaine et à relier ainsi les habitats.

Un second apport concerne la théorie du *floodpulse* et du concept de méta-écosystèmes (Gounand et al., 2018; Junk et al., 1989; Loreau et al., 2003; Tockner et al., 2000). La thèse confirme que le cycle saisonnier des crues constitue un moteur fondamental de la structuration des communautés aquatiques, mais en mettant en lumière les mécanismes fins qui sous-tendent cette

influence ; traits fonctionnels, transferts de matière et d'énergie et modifications de la structure de la communauté. Elle rejoint par ailleurs la perspective des méta-écosystèmes en montrant que les flux de matière et d'énergie entre milieux ne sont pas homogènes, mais qu'ils dépendent à la fois de la dynamique hydrologique et des caractéristiques des espèces qui exploitent conjointement les deux habitats.

Enfin, un troisième apport tient à la mise en relation de trois approches rarement combinées dans ce type de système. Plusieurs travaux ont déjà rapproché analyse isotopique et spectre de taille pour caractériser la structure trophique des communautés (Jennings & Mackinson, 2003; Layman et al., 2007; Romanuk et al., 2011). Ces études ont notamment montré que la distribution des tailles reflète, au moins en partie, la structure des relations trophiques dérivées des isotopes stables, permettant d'évaluer la diversité trophique et la longueur des chaînes alimentaire à l'échelle des communautés (Layman et al., 2007). D'autres travaux, en particulier dans les systèmes fluviaux, ont révélé l'importance des apports allochtones pour soutenir la production piscicole, tout en soulignant la variabilité spatiale et temporelle de cette contribution (Zeug & Winemiller, 2008). Toutefois, l'intégration d'autres traits fonctionnels reste à explorer, et d'autant plus dans des systèmes lac-plaine dont la connectivité est dépendante de la variabilité hydrologique (Larsen et al., 2019; Tull et al., 2024). La convergence des résultats souligne le rôle central de la taille corporelle comme fil conducteur reliant les trois approches. De plus, l'utilisation des spectres de taille a permis de révéler non seulement l'effet global de l'utilisation de la plaine sur la structure de la communauté, mais aussi une dynamique intra-annuelle. Cette combinaison d'approches offre ainsi un cadre original pour évaluer la pertinence des hypothèses théoriques dans des systèmes dynamiques, et ouvre la voie à une utilisation élargie des spectres de taille comme indicateurs intégrateurs de l'exploitation des plaines inondables.

Portée, implications et limites pour la gestion

L'ensemble des analyses menées dans cette thèse met en lumière un rôle écologique important des plaines inondables tempérées dans le fonctionnement des communautés ichtyologiques. En favorisant le recrutement de certaines espèces, en fournissant des habitats structurés et en apportant des subsides énergétiques à la communauté, ces zones assurent des fonctions essentielles pour la biodiversité et la productivité halieutique (Dembkowski & Miranda, 2012; Farly et al., 2019). La reconnaissance de cette importance dépasse le cadre du Lac Saint-Pierre et soutient l'idée de préserver les plaines inondables tempérées pour leur rôles écologique, souvent sous-estimées par rapport à leurs équivalents tropicaux plus emblématiques (Schramm & Eggleton, 2006).

Au LSP, les observations soulignent des enjeux de gestion très concrets. Le déclin de la végétation aquatique submergée (Laporte et al., 2023) affecte directement les espèces phytophiles identifiées comme principales occupantes de la plaine. La conservation et la restauration des habitats végétalisés apparaissent ainsi comme des priorités pour maintenir les mécanismes de couplage identifiés entre la plaine et le milieu permanent. Ces préoccupations sont cohérentes avec les initiatives récentes menées en collaboration avec les agriculteurs du littoral pour tester des pratiques agricoles favorisant la cohabitation entre production et conservation (MAPAQ 2025). Les aménagements prévus ont montré des impacts positifs sur la biodiversité, c'est le cas des bandes végétalisées (Birnbeck et al., 2025). Ces programmes d'aménagement sont regroupés et dirigés par l'union des producteurs agricoles avec le projet, en action pour le lac Saint-Pierre. Ces projets participatifs montrent qu'une gestion concentrée des terres inondables peut contribuer à restaurer la qualité des habitats tout en maintenant l'activité agricole (UPA 2023). De même, la préservation de la connectivité hydrologique conditionne, par la variabilité naturelle des crues, à la fois l'accès aux

habitats temporaires et à l'intégration des subsides allochtones (Tull et al., 2024). Ces considérations rejoignent aussi les préoccupations liées aux pêcheries, notamment pour des espèces d'intérêt culturel et économique comme le doré jaune (*Sander vitreus*), dont la dynamique dépend en partie des habitats de reproduction et d'alimentation liés à la plaine (Marcogliese et al., 2001).

Ce travail de thèse doit toutefois être interprété en prenant compte de certaines limites méthodologiques. L'approche isotopique, bien qu'informative, intègre les régimes alimentaires sur des périodes variables et reste sensible aux incertitudes dans l'estimation des contributions des sources (Fry, 2006). L'analyse par les traits fonctionnels repose sur une simplification des caractéristiques écologiques, qui ne tient pas pleinement compte de la variabilité intra-spécifique. Enfin, les spectres de taille offrent une vue d'ensemble de l'organisation des communautés, mais leur interprétation peut être influencée par l'agrégation des données et par la superposition de plusieurs signaux écologiques (Blanchard et al., 2017; Guiet et al., 2016; Sprules, 2022). Malgré ces limites, la complémentarité des approches mobilisées renforce la robustesse des conclusions, en montrant de manière convergente que la plaine inondable façonne à la fois l'occupation spatiale, l'exploitation des ressources et la structure de la communauté.

Au-delà du LSP, les travaux présentés ici portent un message plus général : les plaines inondables tempérées doivent être reconnues comme des éléments structurants des réseaux trophiques aquatiques, et non comme de simples annexes saisonnières. Leur conservation constitue une condition essentielle pour maintenir la biodiversité, la productivité halieutique et la résilience des écosystèmes soumis à des pressions anthropiques croissantes, qu'il s'agisse de l'eutrophisation, de la régulation hydrologique ou de la fragmentation des habitats (Jakubínský et al., 2021; Opperman et al., 2010). Cette thèse souligne ainsi la nécessité d'intégrer les plaines inondables dans les stratégies de gestion et de conservation, au même titre que d'autres habitats clés des écosystèmes aquatiques.

Perspectives de recherche

Cette thèse ouvre plusieurs pistes de recherche pour approfondir la compréhension du rôle des plaines inondables dans la structuration des communautés de poissons. Une première perspective consisterait à étendre les analyses à d'autres systèmes lac-plaine présentant des dynamiques hydrologiques comparables. De telles comparaisons permettraient de vérifier si les mécanismes mis en évidence au LSP se retrouvent ailleurs ou relèvent de particularités locales. Ces études contribueraient à préciser le degré de généralité des prédictions de la GMH dans des systèmes caractérisés par une forte variabilité temporelle et spatiale.

Une seconde perspective concerne le raffinement et la diversité des traits fonctionnels mobilisés. Les analyses menées ici reposaient sur un ensemble de traits écologiques essentiels, mais relativement généraux. Il serait pertinent d'intégrer des traits plus précis et encore peu documentés, tels que la température critique ou la tolérance à l'hypoxie, qui conditionnent la tolérance à un milieu tel que la plaine avec ses contraintes environnementales abiotiques (Beitinger et al., 2000; Sunday et al., 2012). Un tel élargissement permettrait de mieux comprendre les contraintes qui pèsent sur l'occupation des habitats temporaires.

Une troisième perspective pourrait être l'intégration d'autres variables environnementales potentiellement importantes dans l'analyse du couplage entre les milieux. Parmi celles-ci, la concentration en oxygène dissous dans l'eau peut être déterminante pour l'écologie des poissons et pour leur occupation des habitats de la plaine inondable (Rogers et al., 2016). Bien que cette variable n'ait pu être exploitée dans ce travail en raison de contraintes techniques, elle constitue une piste prometteuse pour de futurs suivis. L'articulation entre traits physiologiques et conditions environnementales locales pourrait ainsi éclairer de nouveaux mécanismes dans l'organisation des communautés de poissons.

Une dernière perspective concerne l'amélioration des approches statistiques employées. Dans ce travail, le modèle HMSC a été appliqué à des données d'occurrence pour des raisons de convergence du modèle, ce qui a permis d'identifier des patrons robustes mais qui a en même temps limité l'interprétation quantitative : un modèle basé sur l'abondance aurait pu palier à cette limite. De même, le modèle de mélange isotopique utilisé ici, efficace pour estimer des contributions moyennes de sources, reste peu adapté à l'intégration simultanée de covariables spatiales et temporelles ou environnementales sur des jeux de données aussi vastes et hétérogènes. Rendre ces modèles hiérarchiques et capables d'accueillir des effets aléatoires et prédicteurs explicatifs exigerait cependant un important travail de développement méthodologique et informatique.

Conclusion générale

Cette thèse avait pour objectifs d'évaluer dans quelle mesure les plaines inondables tempérées, à travers leur connexion saisonnière avec leurs milieux permanents, influencent la structure et le fonctionnement des communautés de poissons. En mobilisant trois approches complémentaires : l'analyse de traits fonctionnels, la caractérisation des flux de ressources allochtones par la signature isotopique et l'étude de la structure de taille de la communauté, cette thèse a permis d'examiner la pertinence et les limites de la GMH dans un système soumis à une forte variabilité hydrologique. L'association de ces résultats souligne que la GMH, bien qu'elle apporte des éléments de réponse sur certaines caractéristique fonctionnelles à l'origine du couplage entre habitats, doit être élargie pour tenir compte de la diversité des traits fonctionnels et des contraintes environnementales propres aux systèmes lac-plaine.

Au-delà de leurs apports conceptuels, ces résultats rappellent l'importance des plaines inondables tempérées pour la biodiversité et le fonctionnement des réseaux trophiques aquatiques. Leur rôle dans le recrutement, la fourniture de subsides énergétiques et le maintien de la structure

des communautés souligne la nécessité de préserver la connectivité hydrologique et les habitats composent le système plaine-lac, dans un contexte de pressions anthropiques croissantes. En ce sens, cette thèse plaide pour une reconnaissance accrue des plaines inondables tempérées comme éléments structurants des écosystèmes aquatiques et comme des priorités de gestion et de conservation.

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