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CHAPITRE I

RÉSUMÉ SUBSTANTIEL

1.1 Introduction

1.1.1 Migration

Les poissons d'eaux vives, « angl. : stream fish », démontrent une très grande variation de taille au cours de leur vie. Cette variation complique leur cycle vital ainsi que leurs patrons d'utilisation des différents habitats (Schlosser, 1991). Les multiples ressources nécessaires à leurs besoins (nourriture, site de fraie, refuge) tendent à avoir une distribution éparse et inégale, en plus d'être variables qualitativement et quantitativement (Townsend, 1989). Durbec *et al.* (2010a) ont répertorié trois activités d'importance biologique, soit la reproduction (Hobson et Wassenaar, 1997), l'alimentation (Ciancio *et al.,* 2008) et l'hivernation (Wocher et Rosch, 2006), qui incitent les animaux à entamer ces mouvements entre divers habitats. Les organismes doivent donc réaliser un grand éventail de mouvements ou de migrations (longitudinaux, horizontaux et verticaux) afin d'accéder aux ressources et ainsi répondre à leurs demandes biologiques (Schlosser, 1995; Jungwirth *et al*., 1998; Hohausova *et al*., 2003). Schlosser (1995) présente un schéma conceptuel (Figure 1.1) répertoriant les mouvements entre les différents habitats du cycle annuel d'un poisson.

Lors du cycle annuel, les poissons sexuellement matures migrent vers les sites de fraie afin de trouver des zones regroupant les caractéristiques environnementales répondant à leurs besoins pour la reproduction (ex., substrat, vitesse de courant, température) (Schlosser, 1991). Par exemple, l'esturgeon jaune (*Acipenser fulvescens*) entreprend une migration longitudinale vers l'amont de la rivière afin d'atteindre un site de fraie (Auer, 1996). Généralement, les caractéristiques environnementales des sites de fraie diffèrent de celles retrouvées aux sites d'hivernage et d'alimentation.

Les différences des caractéristiques environnementales entre les multiples habitats utilisés au cours de l'ontogénèse ont été étudiées chez plusieurs espèces, tel l'esturgeon jaune (McKinley *et al.*, 1998) et la perchaude (*Perca flavescens*) (Radabaugh *et al.*, 2010). En étudiant les déplacements des populations de doré jaune (*Sander vitreus)* du lac Érié, Wang *et al.* (2007) ont démontré que les populations migratrices ont tendance à avoir une biomasse plus élevée ainsi qu'un taux de reproduction supérieur à celui des populations dites sédentaires. Ceci pourrait s'expliquer par le fait que les individus migrateurs exploitent des habitats supportant des conditions optimales (ex. : température, abondance de proies) qui maximisent le développement des individus. Cette stratégie de changer d'habitats spécifiques afin d'optimiser la croissance est répandue chez plusieurs espèces (Schlosser, 1995). De plus, lorsque la température de l'eau chute à l'automne et au début de l'hiver, les poissons entament une migration vers les refuges hivernaux (Schlosser, 1995; Lucas et Baras, 2001). Ces refuges se caractérisent par leur capacité à atténuer les fluctuations de température ainsi que les changements brusques et extrêmes du niveau d'eau, réduisant de ce fait le stress physiologique des poissons (Schlosser, 1991).

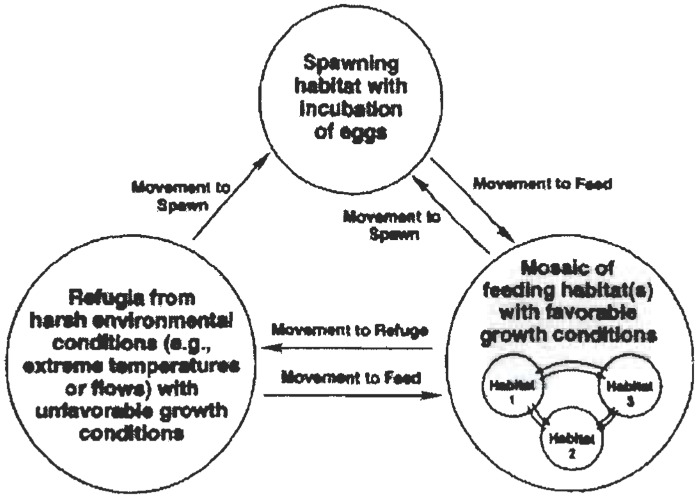

Figure 1.1 Schéma des patrons d'utilisation des habitats et des mouvements effectués lors du cycle vital des poissons d'eau douce de rivière. (Tirée de Schlosser, 1995.)

1.1.2 Migration partielle

Il est toutefois possible qu'une espèce démontre des variations au sein de sa stratégie de migration (Newton, 2008). Lorsqu'il y a présence de plusieurs stratégies de migration au sein d'une même population génétique, nous sommes en présence de migration partielle (Berthold, 2001, Kerr *et al.*, 2010; Chapman *et al.*, 2012). Chaque sous-groupe associé à une stratégie de migration au sein d'une population partiellement migratrice est appelé un contingent (Secor, 1999; Chapman *et al.*, 2012). Les populations sont généralement divisées en deux contingents : migrateur et résident. Le contingent migrateur est composé d'individus se déplaçant entre les habitats pour exploiter les ressources, tandis que les individus du contingent résident sont sédentaires, exploitant les ressources d'un seul habitat. Shaw et Levin (2011) décrivent trois types de migration partielle soit la migration partielle non-reproductive, reproductive et reproductive alternée (Figure 1.2). La migration partielle non-reproductive se produit lorsque les deux contingents, migrateur et résident, vivent dans des habitats différents, mais que le contingent migrateur migre dans l'habitat du contingent résident pour se reproduire. À l'opposé, la migration partielle reproductive implique que les deux contingents vivent au sein du même habitat, mais se reproduisent dans des habitats distincts. La migration partielle reproductive alternée se produit lorsque les individus d'une population ne se reproduisent pas toutes les années. Le contingent migrateur est composé d'individus en reproduction et le contingent résident est formé d'individus ne se reproduisant pas cette année. Le contingent résident ne se reproduisant pas n'a pas à se déplacer pour accéder à un habitat propice à la reproduction.

Les contingents ayant des stratégies de vie distinctes peuvent développer des caractéristiques différentes. Par exemple, les contingents de certaines espèces de salmonidés démontrent un polymorphisme en relation avec leur stratégie de migration (Jonsson et Jonsson, 1993). De plus, les résultats obtenus par Kerr *et al.* (2010) montrent que les contingents composant une population diffèrent en stabilité, productivité et résilience face aux changements environnementaux. Il est donc pertinent d'étudier les populations au niveau des contingents afin d'établir des stratégies de conservation adéquates. Bien que la migration partielle soit bien documentée pour certaines familles de poisson, comme les cyprinidés et les salmonidés (Brodersen *et al.*, 2008, Chapman *et al*,. 2013), il y a un manque de connaissances pour la majorité des familles taxonomiques.

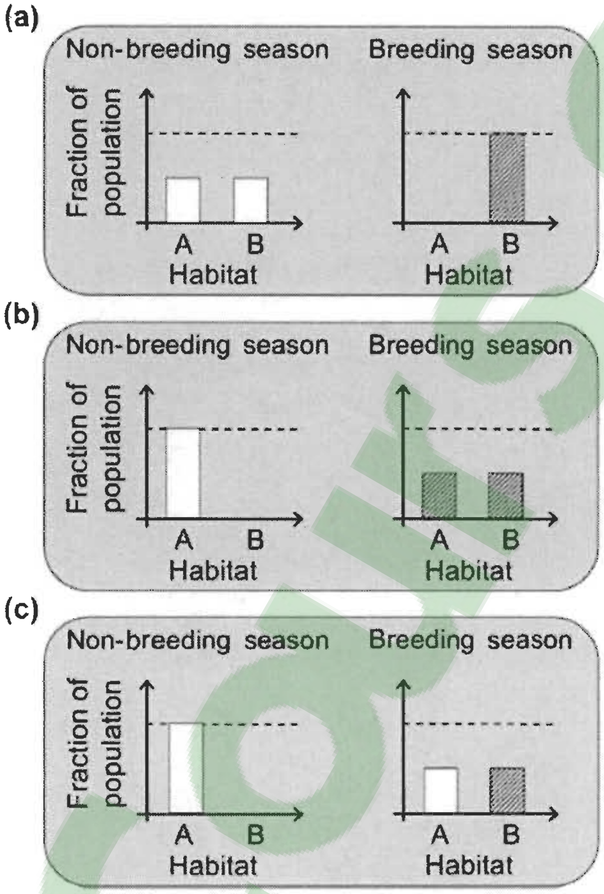

Figure 1.2 Schéma des trois types de migration partielle : (a) migration partielle non-reproductive; (b) migration partielle reproductive et (c) migration partielle reproductive alternée.

Chaque panneau montre la fraction de la population dans chacun des deux habitats (A et B) pendant chacune des saisons (non-reproductive : « angl. : non-breeding » et reproductive : « angl. : breeding »). Les barres ombragées représentent les individus en reproduction. (Tirée de Shaw et Levin, 2001.)

1.1.3 Connectivité

La connectivité est un concept fondamental que l'on retrouve dans plusieurs branches de l'écologie (ex. : biologie des métapopulations, écologie du paysage) (Pringle, 2003). On définit la connectivité comme étant « le degré auquel le paysage facilite ou entrave les mouvements d'un organisme entre différentes ressources » (Taylor *et al.*, 1993). La connectivité influence le déplacement des poissons et par le fait même, leur accès aux ressources. Depuis plusieurs années, la connectivité ainsi que plusieurs autres principes tirés de l'écologie du paysage sont incorporés dans les recherches sur l'écologie des rivières. L'incorporation de ces principes donna naissance à une nouvelle discipline, « angl. : riverscape ecology » qui sera traduit dans ce travail par l'écologie du paysage fluviale (Schlosser, 1991; Ward *et al.*, 2002). La notion de variabilité hydrologique annuelle est très importante dans l'écologie du paysage riverain. Elle agit sur le niveau de connectivité entre différents habitats ainsi que sur la taille des habitats. Ces variations sont principalement causées par les fluctuations du niveau d'eau reliées aux périodes d'inondation et de sécheresse (Taylor et Warren, 2001). Plusieurs espèces de poissons synchronisent donc leur migration entre les multiples habitats avec une période de forte connectivité. Par exemple, la perchaude migre horizontalement vers les herbiers au printemps afin de déposer ses œufs lorsque le niveau de l'eau est élevé, ce qui génère ainsi une plus grande connectivité entre ces deux habitats (Scott et Crossman, 1974; Radabaugh *et al.*, 2010).

1.1.4 Isotopes stables

Au cours des dernières décennies, l'analyse des isotopes stables s'est avérée être un outil de recherche puissant en écologie, entre autres pour l'étude des patrons de déplacement (Hobson et Wassenaar, 1999; Cunjak *et al.*, 2005). Les isotopes stables sont souvent utilisés comme marqueurs intrinsèques pour étudier les déplacements. L'utilisation des isotopes contrairement à celle des marqueurs dits conventionnels de capture-marquage-recapture ne nécessite pas le marquage des individus (Hobson *et al.*, 1999). De plus, cette approche peut donner des résultats fiables lors des recherches sur les mouvements des poissons d'eau douce, tout en réduisant le temps, l'argent et le travail requis pour recapturer les individus marqués (Blamart *et al.*, 2002; Hobson, 2002; Durbec *et al.*, 2010a, 2010b). Cependant, l'approche isotopique peut être utilisée seulement si les habitats entre lesquelles l'animal se déplace sont isotopiquement distincts.

L'utilisation des isotopes stables pour l'analyse des mouvements est fondée sur le principe selon lequel la valeur isotopique du tissu d'un organisme procure de l'information sur la composition du régime alimentaire ainsi que sur sa provenance (Hobson, 1999). Les valeurs isotopiques du carbone ($\delta^{13}C$) des tissus d'un organisme sont principalement déterminées par la valeur isotopique de son régime alimentaire (Fry et Arnold, 1982; Tieszen *et al.*, 1983). Il est donc possible en principe de retracer l'origine de la migration des organismes, puisque la valeur isotopique du tissu reflètera la signature isotopique du réseau trophique dans lequel il se nourrit, et plus précisément celle de ses proies (DeNiro et Epstein, 1978; Peterson et Fry, 1987). Lorsqu'un animal se déplace entre deux systèmes ayant des signatures isotopiques distinctes, ses tissus retiennent l'information isotopique de leurs précédents sites d'alimentation (Hobson et Clark, 1992; O'Reilly *et al.*, 2002). Toutefois, la différence isotopique entre les deux sites d'alimentation doit être assez importante pour permettre de discriminer les signaux des deux sources (Hobson et Clark, 1992).

1.1.5 Renouvellement isotopique

Le changement isotopique n'est pas immédiat lors d'un changement de source nutritionnel; un décalage survient avant que la signature de l'animal soit isotopiquement à l'équilibre avec sa nouvelle source (Hesslein *et al.*, 1993; MacAvoy *et al.*, 2001; Maruyama *et al.*, 2001). Le temps de rétention de l'information isotopique, et par le fait même, l'importance du décalage temporel sont directement reliés au taux de renouvellement du tissu considéré (Hobson et Clark, 1992; Sakano *et al.*, 2005). Ce taux de renouvellement est déterminé par l'addition de nouveau matériel (la croissance) et le remplacement métabolique des tissus (Fry et Arnold, 1982; Hesslein *et al.*, 1993; MacAvoy *et al.*, 2001; Maruyama *et al.*, 2001). Cependant, les tissus n'ont pas tous le même taux de renouvellement (Tieszen *et al.*, 1983). La différence entre ces taux est principalement reliée au taux de renouvellement des protéines du tissu (renouvellement métabolique). Les tissus splanchniques, comme le foie, l'estomac et le tube digestif ont un taux de renouvellement des protéines très rapide en comparaison aux tissus structuraux comme les muscles (Carleton *et al.*, 2008). Pour cette raison, le foie a un taux de renouvellement isotopique plus rapide que le muscle (revue par Wolf *et al.*, 2009). De plus, Carleton et Martinez del Rio (2010) ont trouvé que le temps de résidence des isotopes dans le foie était plus court que celui du muscle, menant ainsi à un renouvellement isotopique plus rapide dans le foie.

1.1.6 Isotopes du carbone (^{13}C et ^{12}C)

Les isotopes stables utilisés varient selon le type de recherche ainsi que les conditions géochimiques des systèmes étudiés. Les isotopes stables du carbone (^{13}C et ^{12}C), de l'azote (^{15}N et ^{14}N), de l'oxygène (^{18}O et ^{16}O), pour ne nommer que ceux-ci, ont été grandement étudiés et utilisés dans les recherches concernant les mouvements d'organismes. Pour l'étude des déplacements, le ^{13}C est préféré par rapport à ceux d'autres éléments, car il n'y a pas ou peu de fractionnement entre les niveaux trophiques ($\Delta\delta^{13}C = 0.05\pm0.63$ ‰) (Peterson et Fry, 1987; Vander Zanden et Rasmussen, 2001), ce qui laisse la signature de la source pratiquement intacte dans les tissus (Figure 1.3).

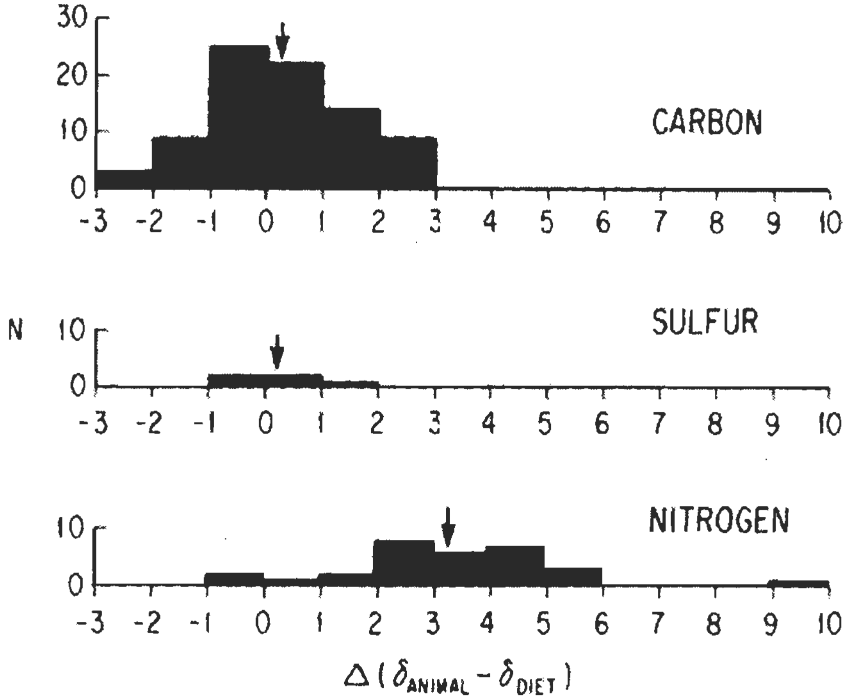

Figure 1.3 Relation entre la composition isotopique d'un animal et celle de son régime alimentaire pour les isotopes stables du carbone, du soufre et de l'azote. (Tirée de Peterson et Fry, 1987.)

Le fractionnement (Δδ) est déterminé par la différence de la signature isotopique entre le consommateur (δc) et son régime alimentaire (δr) : (Δδ = δc - δr). Ce fractionnement est produit lors des processus physiologiques, tels la synthèse de composés métaboliques (Dufour et Gerdeaux, 2001; Rubenstein et Hobson, 2004). De plus, la signature du muscle est entièrement dérivée du régime alimentaire (Grey, 2001); par conséquent, aucune autre source ne peut faire varier la valeur isotopique de ce tissu. Pour ces raisons, le ^{13}C est un indicateur idéal pour déterminer la source de l'alimentation et ainsi révéler les patrons de mouvements (Harrigan *et al.*, 1989).

Un point très important dans les études utilisant l'approche isotopique est la détermination d'une valeur de référence isotopique moyenne, « angl. : baseline », pour chaque source. La différence entre les valeurs de référence isotopique moyenne des sources confirmera la faisabilité de l'étude, car une différence élevée facilitera l'interprétation des résultats (Rubenstein et Hobson, 2004; Durbec *et al.*, 2010a).

Cabana et Rasmussen (1996) ont proposé l'utilisation de la signature isotopique d'unionidés comme valeurs de référence, car ces organismes se situent à la base de la chaîne alimentaire et leur longévité les rend moins susceptibles aux variations isotopiques saisonnières. Post (2002) confirme que les moules et les escargots intègrent les variations isotopiques dans le temps, appuyant ainsi leur utilisation comme valeur de référence (Figure 1.4).

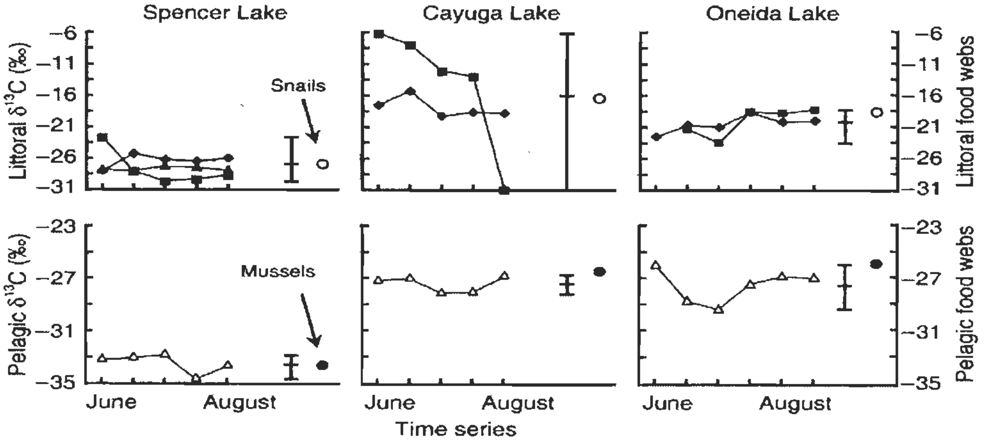

Figure 1.4 Variabilité temporelle de différentes sources (littorale : périphyton et détritus; pélagique : zooplancton herbivore) et l'intégration temporelle du signal isotopique à la base de la chaîne alimentaire des escargots et des moules dans trois lacs. (Tirée de Post, 2002.)

1.2 Problématique

Dans les systèmes aquatiques d'eau douce, les tributaires offrent des ressources essentielles à la communauté ichthyenne des rivières majeures (Matthews, 1998; Pracheil *et al.*, 2009) et les individus de plusieurs espèces migrent dans les tributaires afin d'exploiter ces ressources (p. ex., barbue de rivière, *Ictalurus punctatus* : Dames *et al.*, 1989; esturgeon jaune, *Acipenser fulvescens* : Fortin *et al.*, 1993; barbeau commun, *Barbus barbus* : Lucas et Batley, 1996; omble à tête plate, *Salvelinus confluentus* : Swanberg, 1997; blageon, *Leuciscus souffia souffia* et ablette spirlin, *Alburnoides bipunctatus* : Durbec *et al.*, 2010b). De plus, les déplacements d'une partie de la communauté ichtyenne vers un tributaire font augmenter la diversité de ce dernier

(Ward, 1998; Schaeffer et Kerfoot, 2004). La taille des habitats et les patrons de connectivité entre les habitats et le cours d'eau principal auront donc une influence marquée sur la structure de la communauté du tributaire (Osborne et Wiley, 1992; Taylor, 1997; Magnuson *et al.*, 1998; Pfister, 1998). La connectivité représente donc une caractéristique très importante des écosystèmes aquatiques, car elle permet l'accès aux ressources se trouvant dans des habitats distincts (Schlosser, 1991) nécessaires au maintien des populations de poissons.

Afin de mieux comprendre l'écologie, l'évolution et les stratégies utilisées durant l'ontogénèse chez les poissons d'eau douce, il est important d'étudier leurs patrons de déplacement (Webster *et al.*, 2002; Sellick *et al.*, 2009). Puisque les mouvements jouent un rôle si important, il est essentiel de bien établir ces patrons de migration afin de concevoir des plans de conservation adéquats et efficaces (Hobson *et al.*, 1999; Rubenstein et Hobson, 2004; Wocher et Rosch, 2006). Cependant, les connaissances reliées aux déplacements dans les tributaires sont limitées pour un grand nombre d'espèces. De plus, les études portant sur la migration et plus particulièrement la migration partielle chez les poissons ne portent généralement que sur un petit nombre d'espèces à la fois.

La présente recherche vise à répondre à différentes questions relatives aux déplacements et aux usages des différents habitats pour plusieurs espèces. À l'aide d'un modèle de mélange isotopique ancré dans un cadre bayésien, nous examinons les variations inter- et intra-spécifiques des patrons de déplacements des poissons transitant entre le fleuve Saint-Laurent (FSL) et l'un de ses tributaires, la rivière Saint-Maurice (RSM). De plus, en mettant en relation les sorties du modèle de mélange avec les dates et sites de capture ainsi que le stade de développement des gonades des individus, nous avons déterminé les ressources exploitées par les spécimens capturés dans la RSM.

Nous nous attendions à ce que le phénomène de migration partielle soit présent chez plusieurs espèces à l'étude. Différents contingents (migrateur et résident) étaient donc susceptibles d'être capturés dans la RSM lors de l'étude. Nous croyions que le contingent migrateur de plusieurs espèces provenant du FSL migrait dans la RSM au printemps, lors de la période de fraie (Scott et Crossman, 1974). Les individus migrateurs des différentes espèces capturées dans la RSM en période de fraie devaient avoir une contribution isotopique très forte en provenance de la source FSL. Toutefois, les ressources exploitées dans le tributaire par ces individus migrateurs étaient variables. Par exemple, plusieurs espèces, telles l'esturgeon jaune, le meunier noir (*Catostomus commersoni*) et le meunier rouge (*Catostomus catostomus*) quittent généralement les tributaires rapidement suite à la fraie n'exploitant que les habitats de reproduction de ceux-ci (Auer, 1999; Doherty *et al.,* 2010; Boase *et al.*, 2011). Bien que d'autres espèces (ex. : achigan à petite bouche, *Micropterus dolomieu*) migrent vers l'amont des tributaires au printemps, leur temps de résidence peut s'étirer jusqu'au début de l'hiver, ceux-ci utilisant donc ainsi les ressources alimentaires en plus des habitats de reproduction (Barthel *et al.*, 2010). Une autre migration d'envergure, toutefois moins importante que la migration printanière, était attendue à la fin de l'automne afin que les individus rejoignent les habitats d'hivernage présents dans le fleuve (Schlosser, 1995; Lucas et Baras, 2001).

CHAPITRE II

CARBON ISOTOPES REVEAL COMPLEX VARIATION IN FISH MIGRATORY STRATEGIES NEAR THE CONFLUENCE OF TWO LARGE RIVERS

Article en attente de soumission à
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Abstract

1. Animal migration results from the need to access multiple resources distributed among different locations. Connectivity between those locations can be variable among populations and species, which can lead to inter- and intra-specific variation in migration patterns. Variation in migratory strategies within a population ("partial migration") is believed to be widespread, but individual studies typically focus on a small number of species. Characterizing the migration patterns of multiple species between the river mainstem and its tributaries is essential to understanding the importance of connectivity at the community level.

2. We present an approach to identify annual migration patterns of multiple fish species between a major river and one of its main tributaries. We analyzed the carbon isotope signature ($\delta^{13}C$) of muscle tissue of fish caught in the St. Lawrence River (SLR: $\delta^{13}C \approx$ -20‰) and the St. Maurice River (SMR: $\delta^{13}C \approx$ -30‰) over a one-year period. We used a stable isotope mixing model fitted in a Bayesian framework to determine the contribution of each source (SLR and SMR) to the diets of individuals.

3. Stable isotope analysis of 556 fish from nine species identified three general migration patterns: residency (*Ambloplites rupestris*, *Micropterus dolomieu*, and *Moxostoma macrolepidotum*), spawning migration (*Acipenser fulvescens*, *Catostomus catostomus*, and *Sander vitreus*), and trophic migration associated with a transient strategy (*Esox lucius, Hiodon tergisus,* and *Ictalurus punctatus*). Resident and migrant species showed marked intra-specific homogeneity in their movement behaviours. However, movement patterns of transient species were highly variable intra- and inter-specifically. Partial migration was found in six of the nine species. Among the six partially migrating species, only channel catfish showed differences in body condition among contingents.

4. The elucidation of species-specific migration patterns by stable isotope analysis showed that mainstem fish species exploit resources (spawning and feeding grounds) in the tributary. Moreover, the general migration pattern of a species (residency, migratory,

or transient) seems related to the type of resources exploited in the tributary. This finding highlights the ecological role of tributary-mainstem connectivity for the mainstem fish community.

Key words

δ^{13}C, fish movement, habitat use, partial migration, river connectivity, stable isotope mixing model

Introduction

Connectivity is a fundamental concept in landscape ecology (Pringle 2003). Landscape connectivity is defined as the degree to which a landscape facilitates or impedes movement of organisms among different resource patches (Taylor *et al*. 1993). This dependence on landscape structure and on animals' ability to move makes connectivity species- and landscape-specific (Tischendorf and Farhig 2000). To fulfill their life history requirements, animals must move between patches of resources (feeding, spawning and refuge habitats; Schlosser 1991) that exhibit spatial and temporal variation in quantity and quality (Towsend 1989; Schlosser 1995). Therefore, by affecting movement between vital resource patches, connectivity plays a crucial role in an animal's life cycle. In river systems, tributaries provide essential resources to the mainstem fish community (Osborne & Wiley 1992; Fernandes, Podos & Lundberg, 2004; Pracheil, Pegg & Mestl, 2009) and fish of many species enter tributaries to exploit those resources (e.g., channel catfish, *Ictalurus punctatus*: Dames, Coon & Robinson 1989; lake sturgeon, *Acipenser fulvescens*: Fortin *et al*. 1993; barbel, *Barbus barbus*: Lucas & Batley 1996; bull trout, *Salvelinus confluentus*: Swanberg 1997; soufie, *Leuciscus souffia souffia* and spirlin, *Albutnoides bupunctatus*: Durbec *et al*. 2010). Spatial and temporal variation can contribute to interspecific differences in resource use in a heterogeneous landscape (Bentley *et al*. 2015). Species may either exploit the same resources at different times, or exploit different resources (Lucas & Baras 2000; Klemetsen *et al*. 2003). Moreover, distances between exploited resource patches can vary from a few meters in sedentary species to hundreds of kilometers in more mobile species, contributing to inter-specific variation of migration strategies. Furthermore, many species show intraspecific variation in their migratory strategies (Newton 2008). When multiple migratory strategies are present in the same genetic population, the population is known as partially migrating (Kerr, Secor & Piccoli 2009; Chapman *et al.* 2012b). Each subgroup associated with a distinct migratory strategy within a partially migrating population is known as a contingent (Secor 1999; Chapman *et al.* 2012b). A recent literature review pointed to differences in length, mass, or body condition between contingents as potential drivers of partial migration in fishes (Chapman *et al.* 2012a). Many non-exclusive hypotheses may explain the relationship between body size and migration behaviour. One of the hypotheses postulates a tradeoff between predation risk and growth potential, such that fish with a high vulnerability to predation risk also have a high probability of migration (Brönmark *et al.* 2008, Skov *et al.* 2011). Intra-specific competition can also play a role in driving partial migration by forcing competitively inferior individuals to pay the cost of migration for foraging (the "competitive release hypothesis": Chapman *et al.*, 2011). Although partial migration is well documented for some fish families, such as cyprinids and salmonids (Brodersen *et al.* 2008, Chapman *et al.* 2013), it is less well understood in a wide range of fish taxa. Migratory contingents can differ in stability, productivity, and resilience, and these differences must be understood to efficiently manage a partially migrating population (Kerr, Cadrin & Secor 2010, Wang *et al.* 2007).

Stable isotopes are useful natural tracers to distinguish contingents of partially migrating populations (Durbec *et al.* 2010) and to study animal migration patterns across a range of spatial scales (continental: Hobson 1999, Rubenstein & Hobson 2004; a few kilometers: Cunjak *et al.* 2005, Durbec *et al.* 2010, Bertrand *et al.* 2011). The carbon stable isotope ratio (^{13}C:^{12}C) of an organism is primarily derived from its diet (DeNiro & Epstein 1978). Diet switching experiments have shown that the isotopic signature of an organism changes gradually through time, yielding information about past as well as current diet (Hesslein, Hallard & Ramlal. 1993). Therefore, the $\delta^{13}C$ signature of an organism can be used to track its movement between areas providing isotopically distinct food sources (Peterson & Fry 1987). Tissues with relatively slow turnover rate, such as muscle, retain past diet information for a long time, and are thus useful to study annual migration patterns (Hesslein, Hallard & Ramlal. 1993; Logan *et al.* 2006). Stable isotope analyses of riverine fish migration generally focus on a single species or on a few species (Cunjak *et al.* 2005; Durbec *et al.* 2010). However, multispecific analyses are required whenever the goal is to understand interspecific variation in migration patterns, to determine the importance of connectivity between the mainstem and its tributaries at the community level, or to ascertain the ecological services provided by tributaries.

Here, we use stable isotope analyses to characterize the intra- and inter-specific variation in migratory patterns of nine species of freshwater fish, and to link these patterns to differences in the exploitation of tributary and mainstem resources. Moreover, we test whether partial migration is associated with differences in body condition among individuals of different contingents. To this end, we collected fish over a one-year period, along a spatial gradient running from a tributary to the river mainstem. We used an isotopic mixing model set in a Bayesian framework to assess, for each individual, the trophic contribution of the tributary and to relate this contribution to the time and location of capture. We used information on individual migratory patterns and gonadal development to assign both individuals and species to three contingents associated with contrasting migratory strategies: resident, transient, and migrant, and to identify the resources exploited by each contingent.

Methods

Study system

Migration patterns were studied near the confluence of the St. Maurice River (SMR) and St. Lawrence River (SLR) in Québec, Canada (Fig. 1). The SLR is 3 060 km in length, drains an area of 1.34 million km^2 and has a mean discharge of 12 100 m^3s^{-1}. The catchment area geology is dominated by silicate rocks of the Canadian Shield (Precambrian Shield) in the upper portion of the basin, and by carbonates of the

Paleozoic lowlands in the lower portion of the basin. The SMR drains an area of 43 250 km^2 and runs from its source at the Gouin Reservoir in the Canadian Shield to its confluence with the SLR (46°21'N, 72°30'W). SMR runoff has a high concentration of humic materials and a relatively negative $\delta^{13}C$ signature of dissolved inorganic carbon (DIC) (Galimov 2006). The SMR is dammed at 10 different locations, the most downstream of which (Gabelle Dam; 46°27'55.9" N, 72°46'0.7" W) is located 22.8 km upstream from the confluence with the SLR. The lower four km of the SMR near its confluence with the SLR (hereafter labelled "transition zone") comprise a small internal delta that differs from the main channel of the SMR by the presence of three small islands (< 0.6 km^2), six islets (< 0.03 km^2) and a juxtaposition of swamps, marshes, and other slow-flowing habitats. The isotopic signature of dissolved inorganic carbon ($\delta^{13}C_{DIC}$) differs markedly between the two rivers (SMR ≈ -16.5‰, SLR ≈ -3.7‰; Yang *et al.* 1996). This difference in $\delta^{13}C$ signature is incorporated into food chains (~ 10‰ difference between baseline values for the two rivers; G. Cabana: unpublished data) and is large enough (Philips & Eldridge 2006) to render $\delta^{13}C$ useful as a tracer of fish movements between the SMR and SLR rivers.

Field sampling

We focused on nine fish species: channel catfish, lake sturgeon, longnose sucker (*Catostomus catostomus*), mooneye (*Hiodon tergisus*), northern pike (*Esox lucius*), rock bass (*Ambloplites rupestris*), shorthead redhorse (*Moxostoma macrolepidotum*), smallmouth bass (*Micropterus dolomieu*), and walleye (*Sander vitreus*). These species were selected because they are abundant in the SMR and SLR and encompass a broad range of life history traits. We established 6 gillnet stations and 5 seine stations in the SLR between Lake St. Pierre (46°20'N, 72°85'W) and the Batiscan River (46°30'N, 72°13'W) and 12 gillnet stations and 11 seine stations along the SMR (Fig. 1). We established an additional 3 gillnet and 2 seine stations upstream of the Gabelle Dam. Fish were collected during four surveys conducted between August 2012 and June 2013 (August-September 2012, November 2012, May 2013, and June 2013). From April to August 2013, light casting (fishing rod and lures) was used to supplement the sampling of some species. Fish were also collected in Lake St. Pierre during surveys conducted by G. Cabana in 2009 and the Ministère des Forêts, de la Faune et des Parcs (MFFP) in September and October 2013.

At each gillnet station, we set two gillnets separated by a distance of 20 m. Each gillnet (60.8 x 1.8 m) comprised eight panels of different mesh sizes (25, 38, 51, 64, 76, 102, 124, and 152 mm). Gillnets were installed parallel to the river flow at depths of 1.8 to 3.5 m and were deployed for 18 to 24 hours. At each seine station, one haul was made from the shoreline with a 12.5 x 4.0 m seine (mesh size = 3 mm). Captured fish were rapidly anesthetized in a mix of clove oil and river water (1 ml oil / 25 l water), killed by cervical dislocation, and immediately put on ice. At the end of the day, fish were frozen at -20 °C at the Centre de Recherche sur les Interactions Bassins Versant-Écosystèmes Aquatiques (RIVE), Université du Québec à Trois-Rivières, until further analysis. For two species, lake sturgeon (individuals > 300 mm only) and walleye, tissue samples were collected using a non-lethal technique during the spawning period. In spring 2013, lake sturgeons and walleyes were anesthetized as above and muscle tissue was sampled with a biopsy punch (True-Cut, 6 mm; Robbins Instruments) behind the dorsal fin. Individuals were weighted (weight, W; nearest g), measured (fork length, FL, and total length, TL; nearest mm), and classified as ripe (gametes extruded following light pressure on the abdomen) or undetermined (no extrusion of gametes).Scales and skin were removed with scissors and muscle tissue was placed in a glass vial and put on ice. To prevent infection, the incision was covered with a liquid topical adhesive (Nexaband). Fish were placed in a plastic holding tank filled with river water until they recovered their balance, and were then released.

Water temperature, pH, dissolved oxygen, and conductivity were measured at each station at a depth of 1 m with a multiparameter water quality meter (Yellow Springs Instruments 650MDS) which was calibrated weekly.

Laboratory analyses

Fish were identified to species, measured (fork length, FL, and total length, TL; nearest mm), weighed (frozen weight; nearest g), sexed, and assigned a maturity stage using the following scale: 1 = immature, 2 = latent, 3 = developing, 4 = mature, 5 = ripe (Nikolsky 1963). We quantified body condition by means of Fulton's index ($100000\ W\ /\ TL^3$; where W is fresh or frozen weight). Samples of dorsal muscle tissue, cleared of any remaining skin, scales, or bone, were wrapped in foil paper and stored in a freezer at -20 °C.

We conducted stable isotope analyses of muscle tissue for 556 fish from the nine study species (Appendix 1). Tissue samples were placed in a glass vial, dried at 60 °C for at least 48 hours and ground to a fine powder with a mortar and pestle. Powder samples (0.9 to 1.2 mg) were packed into a tin aliquot (8 x 5 mm; Bn 202723: ISOMASS). All analyses were run on a continuous-flow isotope ratio mass spectrometer (Delta V Plus; Thermo Scientific) at the RIVE laboratory. Carbon isotope ratios were expressed in delta (δ) notation, defined as the deviation from an international standard material (Vienna Pee Dee Belemite) in parts per thousand (‰). The working standard was USGS40 (L-glutamic acid: $\delta^{13}C$ mean ± SD = -26.389 ± 0.09) from the International Atomic Energy Agency (IAEA). Two internal standards from muscle of two specimens of brook trout (*Salvelinus fontinalis:* mean ± SD = -34.83 ± 0.06‰ and -25.09 ± 0.06‰) were used to correct for instrument drift during analysis.

Mixing model

Two distinct potential food sources, SMR and SLR, are present in our study system. We used a mixing model fitted in a Bayesian framework to estimate the proportional contribution of the SMR source (C_{SMR}) to the diet of each individual. We first estimated the $\delta^{13}C$ signature (mean and SD) of the SLR and SMR sources separately for each species, as follows. The $\delta^{13}C$ signature of the SLR source was estimated from the individuals caught in the SLR between Lake St. Pierre and the Batiscan River (Fig. 1). The $\delta^{13}C$ signature of the SMR source was estimated from fish caught upstream of

Gabelle Dam, because the dam completely blocks upstream and downstream movements in this system. Fish captured upstream of the dam must therefore have derived their signature entirely from the SMR source. For the four species captured upstream of the dam (longnose sucker, rock bass, smallmouth bass, and walleye) mean and SD was calculated separately for each species. For the five species that were not found upstream of Gabelle Dam (channel catfish, lake sturgeon, mooneye, northern pike, and shorthead redhorse), we estimated the isotopic signature of the SMR source by means of a linear mixed-effects model which yielded an overall mean and SD of isotopic signatures from the species captured upstream of the dam.

We obtained the posterior probability distribution for the dietary proportion contributed by the SMR source using the package SIAR (Stable Isotope Analysis in R; Parnell *et al.* 2008) in R (R Development Core Team 2014). The mean and SD of the signature sources were used together with the $\delta^{13}C$ signature of individual fish as input for SIAR. A vague Beta(1,1) prior distribution for the mixing proportion was used to allow the results to be influenced primarily by the data (Parnell *et al.*, 2010). The Markov chain Monte Carlo algorithm was run for 500000 iterations following an initial run of 50000 iterations (burnin) which were discarded.

Assignment of individuals to migratory contingents

We assigned each individual to one of three possible migration contingents (resident, transient, or migrant), based on the capture site and the estimated contribution of the SMR source (C_{SMR}) to the diet of the individual (Fig. 2). Assignment to contingents was determined by examining the position of the 95% credible interval (CI) for C_{SMR} relative to the midpoint value of 0.5 that indicates an equal contribution of the SLR and SMR sources to the individual's isotopic signature (Fig. 2). We assumed that the primary source used by an individual can be clearly identified when the 95% CI is entirely below (SLR) or above (SMR) the midpoint. The site of capture was then used to determine whether the location of capture matched the main source. Individuals were classified as resident if their site of capture corresponded to the main source, and as migrant otherwise. Individuals whose 95% CI overlapped the midpoint could not be assigned unambiguously to either source and were classified as transients. Additionally, we classified each species as predominantly resident, migrant, or transient based on the proportional representation of each contingent among individuals caught in the SMR downstream of Gabelle Dam.

Turnover rate and projected isotopic signature

To determine whether migrant individuals captured in the SMR could attain isotopic values corresponding to a SMR resident over a single growing season, we calculated the change expected in isotopic signature based on the mixing model of Hesslein, Hallard & Ramlal (1993). Four species (lake sturgeon, longnose sucker, walleye, and channel catfish) were selected based on the capture of migrant individuals before and during the spawning period and resident individuals at the end of the summer. We first estimated the muscle turnover rates (λ_i) for migrant individuals of these four species captured in the SMR before and during the spawning period, using the equation proposed by Weidel *et al.* (2011):

$$\ln(\lambda_i) = -3.65 - 0.2\ln(W_i)$$

where λ_i is the turnover rate and Wi is the fresh or frozen weight (g) of individual i. We then used the estimated λ_i in the equation proposed by Hesslein, Hallard & Ramlal (1993) to project the change in the isotopic signature from the moment of capture to November 26th (day of the year 330) 10 days after the last specimen was caught:

$$\delta^{13}C_t = \delta^{13}C_i\, e^{-\lambda i\ t} + \delta^{13}C_{SMR}{}^{(1 - e^{-\lambda i\ t})}$$

Where t varies from 0 to T_i, the number of days elapsed from capture until November 26th (day of the year 330), $\delta^{13}C_t$ is the isotopic signature of individual at time t, $\delta^{13}C_i$ is the isotopic signature of individual i at capture, and $\delta^{13}C_{SMR}$ is the SMR baseline.

Results

Intra- and inter-specific variation in migratory behavior

Only four of the study species (longnose sucker, rock bass, smallmouth bass, and walleye) were found in the SMR upstream of Gabelle Dam (a total of 57 fish; $\delta^{13}C$ mean ± SD =-28.9 ± 1.1‰; Appendix 1). All nine species were found in the three other study sectors (Appendix 1). A total of 252 fish were collected from the SMR downstream of Gabelle Dam, including the transition zone ($\delta^{13}C$ mean ± SD = -25.5 ± 4.3‰) and 247 fish were collected from the SLR ($\delta^{13}C$ mean ± SD = -20.9 ± 2.1‰; Appendix 1). The proportional representation of each migratory contingent in species caught in the SMR downstream of Gabelle Dam is summarized in a ternary plot (Fig. 3). In this plot, positions near to a triangle vertex reveal limited variation in migratory strategy; they reflect homogeneous populations comprising mostly resident, migrant, or transient individuals, whereas positions near the triangle centroid reflect heterogeneous populations comprising approximately one third of each contingent. Species classified as predominantly resident (rock bass, shorthead redhorse, and smallmouth bass) comprised mainly (> 85%) individuals from the resident contingent in the SMR (Fig. 3).

Species classified as predominantly migrant (lake sturgeon, longnose sucker, and walleye) comprised mainly (> 68%) individuals from the SLR migrant contingent (Fig. 3). Species classified as predominantly transient (channel catfish, mooneye, and northern pike) showed greater compositional heterogeneity than those in the migrant and resident contingents, as shown by the distances among resident species relative to those among resident or migratory species in Fig. 3. As well, channel catfish and mooneye showed marked within-species compositional heterogeneity, as seen by their distance from the apex denoting “pure” transients (top of the triangle in Fig. 3). Channel catfish comprised similar proportions of transients, residents, and migrants, whereas for mooneye 45% of individuals were in the transient contingent (Fig. 3). Northern pike comprised mostly (92%) transient individuals. Among the predominantly transient species, individual body condition appeared to differ among contingents only for channel catfish, which showed better condition for transient and migrant individuals than for resident individuals (Table 2).

Migratory behaviour in relation to site of capture

Resident individuals for all nine species were found in both the SLR and the SMR with the exception of the northern pike, for which resident individuals were absent in the SMR (Fig. 4). Migrant individuals were only captured in the SMR, and there was no evidence of movements from the SMR to the SLR for any species (Fig. 4). Transient individuals (95% CI overlapping the $C_{SMR} = 0.5$ line), could not be assigned to a predominant source on the basis of their isotopic signatures, suggesting that they move freely between the SLR and SMR and exploit food resources from both sources (Fig. 4). In our system, the C_{SMR} variability change spatially (Fig. 4). The C_{SMR} variability in relation to the distance from the dam follows a species specific pattern (Fig. 4). For predominantly resident species (rock bass, shorthead redhorse and smallmouth bass) the C_{SMR} shows a greater variability as we approach the mouth of the river (distance from the dam > 13.5 km), suggesting more movement of individuals between the SMR and SLR occurring near the confluence for these three species (Fig. 4). However for predominantly migrant (lake sturgeon, longnose sucker and walleye) and transient (channel catfish, mooneye and northern pike) species, the C_{SMR} seems highly variable along the SMR due to the wide spatial distribution of multiple contingents (Fig. 4). This suggests that migrant and transient individuals from those six species can migrate and exploit resources in the SMR from the mouth of the river (22.8 km) to almost the Gabelle Dam (0 km).

Migratory behavior in relation to the spawning period

The C_{SMR} temporal pattern in the SMR seems to vary with the species (Fig. 5). For predominantly resident species the C_{SMR} remain relatively constant in relation to the date of capture (Fig. 5), suggesting that predominantly resident species use the SMR year round. For predominantly migrant species, we observed that the C_{SMR} varies in relation to the spawning periods (Fig. 5). During the spawning period the C_{SMR} is generally low and become higher after the spawning period (Fig. 5). Most migrant individuals captured during the spawning period had sexually mature gonads (Table 2), suggesting that they enter the SMR for reproduction purposes. For predominantly transient species, the C_{SMR} is highly variable through the year (Fig. 5). This pattern can be related to the exploitation of isotopically distinct trophic sources (transient contingent) and the presence of multiple contingents. The gonad development of migrant individuals from predominantly transient species, before and during the spawning period seems species specific (Table 2).

Turnover rate and isotopic signature projection

The estimated turnover rates for each species are found in Table 3. Projection of isotopic signature trajectories for the three predominantly migrant species (lake sturgeon, longnose sucker, and walleye) and for the channel catfish showed that the isotopic signature of migrant individuals captured in the SMR during the spawning period would not have changed rapidly enough for them to be classified as resident individuals at the end of the summer (Fig. 6). For channel catfish, the projections overlap the values of transient individuals at the end of the summer suggesting that migrant individuals could attain the signal of transient individuals by the end of the summer (Fig. 6).

Discussion

Our results provide insights into the spatial and temporal migration patterns of nine abundant and taxonomically diverse fish species between a tributary and the mainstem. The stable isotope analyses identified three general migration patterns, each represented by three species: residency, spawning migration, and trophic migration associated with a transient strategy. Partial migration was found in all six of the non-resident species, but differences in body condition among contingents were found in only one of them (channel catfish), suggesting that body condition is not the main driver of partial migration in our system.

Connectivity between mainstem and tributary

Many studies have investigated the effect of connectivity between tributaries and the river mainstem on fish communities. Connectivity can influence tributary fish community structure near the mouth of the tributaries through its effect on fish movement (Osborne & Willey 1992). The contingent composition in the SMR showed variability through the year. Migrant contingents from predominantly migrant species (lake sturgeon, longnose sucker, and walleye) are present in the tributary only during the spawning period (Fig. 5). For predominantly transient species (channel catfish, mooneye and northern pike), the transient individuals were only present in the SMR during the summer (growth period). These results suggest that the effect of movement of mainstem individuals into the tributary on fish community structure in the tributary varies throughout the year.

Moreover, connectivity also impacts the mainstem fish species by providing them with access to needed resources present in tributaries. Paddlefish (Polyodon spathula) in the Missouri River (Nevada, USA) used a tributary to access specific spawning habitats that were not available in the mainstem (Pracheil, Pegg & Mestl 2009). We found that the SMR provided spawning grounds (lake sturgeon, longnose sucker, walleye, and possibly channel catfish) as well as food resources (channel catfish, mooneye, and northern pike) to individuals migrating from the SLR.

Partial migration

Divergent migratory responses found among a population are sometime related to body condition (Näslund *et al.* 1993, Brodersen *et al.* 2008). In a population of Arctic charr (Salvelinus alpinus), individuals that migrate into a stream to exploit food resources had lower condition than lake residents (Näslund *et al.* 1993). However, in a roach population (Rutilus rutilus), migrating individuals exploiting winter refuge showed the opposite trend (Brodersen *et al.* 2008). Among the six partially migrating species in our study, only channel catfish showed differences in condition among contingents. Migrant and transient channel catfish had better condition compared to resident individuals, as observed in the two contingents (resident and migrant) roach population by Brodersen *et al.* (2008). The other five partially migrating species did not show difference in body condition related to their contingent. Another partially migrating roach population composed of a resident and a migrant contingent also showed no differences in body condition among migratory contingents (Brodersen *et al.* 2014). The lack of difference in body condition between contingent of five out of partially migrating species suggests that differences in body condition are not the main driver of partial migration in our system.

Resident species

For species classified as predominantly resident (rock bass, shorthead redhorse, and smallmouth bass), multiple contingents were present only in or near the transition zone (Fig. 4). This pattern suggests that resident fish make short-distance movements between the SMR and SLR and feed on multiple isotopically distinct food sources, leading to increased variability of C_{SMR}. Increased variability in C_{SMR} could also result if residents of the transition zone feed on migrating prey entering the SMR from the SLR (Wocher & Rösch 2006; Chapman *et al.* 2013).

Rock bass is a relatively sedentary species (Lucas & Baras, 2001), a behaviour consistent with the residency pattern we observed in the SMR. However, the resident behaviour of shorthead redhorse and smallmouth bass in the SMR contrasts with findings in other riverine systems, in which these species have been identified as spawning migrants (Robbins & MacCrimmon 1977; Lucas & Baras 2001; Barthel *et al.* 2008). Shorthead redhorse use tributaries for spawning in a neighboring system, the Richelieu River (Reid 2006; Hatry *et al.* 2014). However, the Richelieu River has a more natural flow regime than the SMR, in which strong daily variation of water discharge is induced by the Gabelle Dam during the spawning period of shorthead redhorse (Chen *et al.* 2015). Variation in discharge may therefore curtail entry into the tributary of redhorse spawners from the SLR. Smallmouth bass nests are highly vulnerable to rapid changes in water level (Scott & Crossman 1974), which might also inhibit spawning migration into the tributary for this species. These results suggest that the migration patterns of shorthead redhorse and smallmouth bass may be river-specific. Individuals of the resident species in this study seemingly remain year-round in a single macrohabitat (SLR or SMR), potentially resulting in distinct populations in the mainstem and tributary.

Migrant species

For species classified as predominantly migrant (lake sturgeon, longnose sucker, and walleye) almost all individuals from the migrant contingent were caught during the spawning period (Fig. 5). The seasonal timing of migration and gonad development of these individuals (Table 2) suggest that they migrate from the SLR to the SMR to reproduce. Studies using other tracking techniques also have concluded that lake sturgeon (Fortin *et al.* 1993; Auer 1999; Gerig *et al.* 2011), longnose sucker (Lucas & Baras 2001), and walleye (Pritt *et al.* 2013; Hayden *et al.* 2014) migrate into tributaries to exploit spawning habitat. The absence of the migrant contingent after the spawning period can be explained by two alternative hypotheses. The first is that migrants return rapidly to the mainstem following the spawning period, and do not exploit trophic resources in the tributary. The second is that after spawning, migrants exploit trophic resources in the tributary over the summer and undergo changes in isotopic signature that shift them into the resident contingent by the end of the summer. The second hypothesis seems unlikely given the estimated turnover rates (Table 3) and projected isotopic trajectories of migrant individuals (Fig. 6). Furthermore, rapid return to the mainstem following the spawning period has been shown for lake sturgeon (Auer 1996) and walleye (Hayden *et al.* 2014). Moreover, lake sturgeon do not feed in tributaries during spawning migrations (Houston 1987), which also supports the hypothesis of rapid migration out of the tributary after reproduction.

Transient species

Channel catfish, mooneye, and northern pike were classified as predominantly transient species. It seems likely that transient individuals from these species move between the SLR and SMR to exploit different food resources in the two systems. Channel catfish can use tributaries for reproduction (Gerhardt & Hubert 1990; Pellett, Van Dyck & Adams 1998) and sometimes undertake major migrations into tributaries during the spawning period (Butler & Wahl 2011). In other river systems, channel catfish move into tributaries in spring to feed over the summer and return to the main river at the end of summer or in autumn, to overwinter there (Dames, Coon & Robinson 1989; Pellett, Van Dyck & Adams 1998; Butler & Wahl 2011). The migration pattern described above suggests a migration into the tributary for reproduction purposes following by a period of residency in the tributary for trophic exploitation during the growth period (summer). This migratory pattern is consistent with our results. The SMR provides habitats corresponding to the channel catfish requirements for spawning habitat (holes in banks, in between rocks or large woody debris; Scott & Crossman 1974). Furthermore, most migrant individuals capture in the SMR during the spawning period had ripe gonads (Table 2). Therefore, it is coherent that channel catfish migrate into the SMR to reproduce. The fact that CSMR still shows high variability at the end of the summer suggests trophic exploitation of multiple distinct isotopic trophic sources. Moreover, projections found in Fig. 6 for the channel catfish suggest that migrant individuals exploiting the trophic resources can attain an isotopic signature to be classified in the transient contingent. Then it is coherent to conclude that channel catfish exploit food resource in the SMR during the summer (Fig. 5).

Mooneye can reproduce in tributaries such as the Des Prairies River, a tributary of the SLR (D'Amours, Thibodeau & Fortin 2001). However, we captured too few migrant or transient mooneyes (2) during the spawning period to determine whether mooneye migrate into the SMR to reproduce (Table 2). High variability of the SMR at the end of the summer (Fig 5.) suggests that some individuals feed on one (resident or migrant individuals) or both (transient individuals) trophic sources (SLR and SMR).

We sampled the SMR after the northern pike spawning period and therefore cannot tell whether northern pike used the tributary for spawning. However, the SMR does not offer suitable spawning habitat for northern pike (floodplain with high vegetation density, river bay, swamp; Scott & Crossman 1974). Therefore, northern pike probably do not migrate from the SLR to spawn in the SMR. Northern pike tend to show less migratory activity from May to November (Pauwels *et al.* 2014). Northern pikes were caught in the SMR only during summer, and more than 90% of these individuals were classified as transient (Fig. 5), suggesting that they spend the growing period feeding in the SMR. Transient individuals might feed on isotopically distinct food sources while migrating between overwintering and growth habitats (Winfield, Fletcher & James 2012; Pauwels *et al.* 2014) or may be resident of the SMR but feed on migrating prey from the SLR. However, we cannot determine whether it is the prey or the predator that move.

Species-specific migration patterns reflected inter-specific differences in resource exploitation strategies. Both intra- and inter-specific variation in movement behaviours were related to the spatial distribution and temporal availability of the resources exploited in the tributary and the mainstem. Individuals of predominantly resident species seemingly remain in and use resources from a single macrohabitat (SLR or SMR). Individuals of predominantly transient species move into the tributary to feed, whereas those of predominantly migrant species move into the tributary primarily to exploit spawning habitats. Use of the tributary by transient and migrant species appears to be strongly seasonal, which implies that migration dynamics can have temporally varying impacts on population structure both in the tributary and the mainstem. Further efforts to understand the factors underlying intra- and inter-specific variation in migration patterns will likely yield valuable insight into the ecological role of tributary/mainstem connectivity and its importance for metacommunity dynamics.

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Tables

Table 1. Body condition of individuals, by migratory contingent, for the predominantly transient species (channel catfish, mooneye, and northern pike) captured in the SMR downstream of Gabelle Dam. The number of individuals (n), mean condition factor, associated 95% confidence interval, and p value from a one-way anova testing for difference in condition factor among contingents are shown.

Species	Resident			Transient			Migrant			*p*
	n	Mean	95% CI	n	Mean	95% CI	n	Mean	95% CI	
Channel catfish	21	0.896	(0.804, 0.987)	21	1.012	(0.923, 1.101)	24	1.071	(0.970, 1.172)	0.027
Mooneye	9	1.035	(0.977, 1.093)	11	1.065	(0.998, 1.132)	2	1.002	(0.826, 1.179)	0.562
Northern pike	0			11	0.559	(0.515, 0.602)	1	0.553		

Table 2. Number of individuals captured in the SMR downstream of the Gabelle Dam, by reproductive period (before and during spawning; after spawning) contingent (resident, transient, migrant), maturity (M: stage 4 or 5; T: not mature; U: undetermined), and species.

Species	Before and during spawning period			After spawning period		
	Resident M/T (U)	Transient M/T (U)	Migrant M/T (U)	Resident M/T (U)	Transient M/T (U)	Migrant M/T (U)
Channel catfish	0/5 (1)	4/5 (0)	10/3 (1)	0/12 (3)	1/11 (0)	0/10(0)
Lake sturgeon	0/0 (0)	2/0 (1)	7/0 (6)	0/0 (2)	0/0 (0)	0/0 (0)
Longnose sucker	0/2 (2)	0/0 (0)	6/3 (4)	0/0 (2)	0/0 (0)	0/0 (0)
Mooneye	1/6 (0)	1/0 (0)	1/0 (0)	1/1 (0)	3/7 (0)	0/1 (0)
Northern pike	0/0 (0)	0/0 (0)	0/0 (0)	0/0 (0)	0/11 (0)	0/1 (0)
Rock bass	2/2 (0)	0/1 (0)	0/0 (0)	0/20 (0)	0/0 (0)	0/0 (0)
Shorthead redhorse	0/7 (1)	0/1 (0)	0/0 (0)	0/4 (1)	0/0 (1)	0/0 (0)
Smallmouth bass	1/0 (0)	0/0 (0)	1/0 (0)	0/33 (0)	0/4 (0)	0/0 (0)
Walleye	0/0 (0)	0/1 (0)	21/5 (0)	0/6 (0)	0/2 (0)	1/0 (0)

Table 3. Mean of estimated turnover rate (λm) and their standard deviation (SD) for migrant individuals captured before and during the spawning period of four species. These four species were selected because migrant individuals were captured before and during the spawning period in the SMR and resident individuals were captured at the end of the summer in the SMR. Turnover rates were estimated from the equation proposed by Weidel *et al.* (2011). Due to missing data for some individuals, we were not able to estimate the λ for each migrant individual. Therefore, N represents the number of individuals with an estimated turnover rate.

Species	λ_m	SD	N
Lake sturgeon	0.0045	0.0002	9
Longnose sucker	0.0074	0.0005	12
Walleye	0.0071	0.0007	22
Channel catfish	0.0062	0.0011	14

Figure captions

Figure 1. Study area showing the St. Maurice (SMR) and St. Lawrence (SLR) Rivers, Québec, Canada, and the transition zone near their confluence. Gabelle Dam, an impassable barrier in the SMR, is also shown.

Figure 2. Criteria for classification of individuals into migration contingents. Individuals were assigned to a contingent according to their capture site and the 95% credible interval for their CSMR value. Medians (symbols) and 95% CI (vertical lines) for CSMR are shown. Black circles: resident individuals; empty circles: migrant individuals; empty squares: transient individuals. Horizontal dotted line: equal trophic contribution from the two sources (SLR and SMR). Grey area: transition zone between the SMR and SLR (18.8 < River km < 22.8). See text for details.

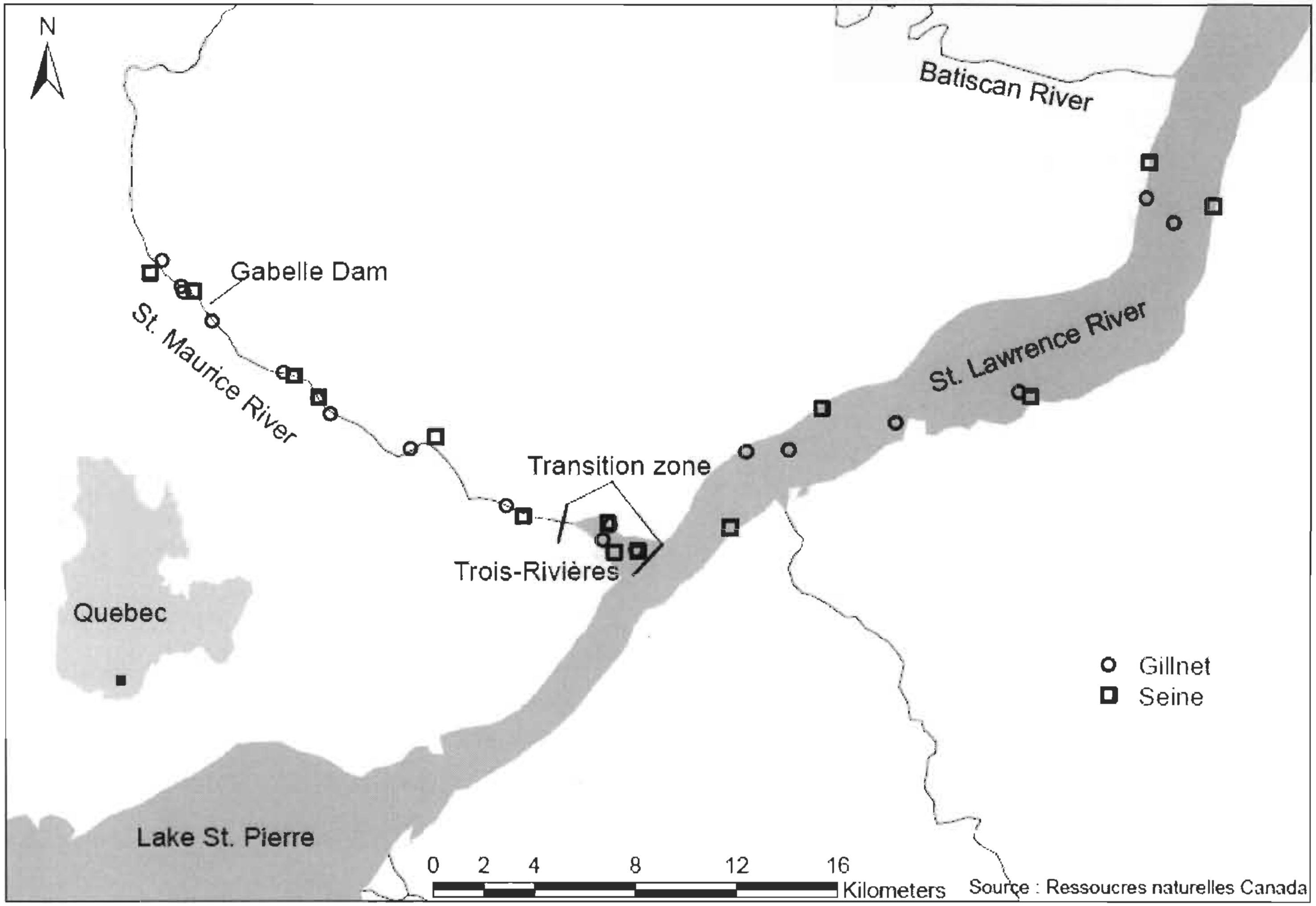
Figure 3. Ternary plot showing the positioning of the nine study species along the resident-migrant-transient continuum, based on individuals caught in the SMR downstream of Gabelle Dam (0 < River km < 22.8). Circles: resident; Triangles: migrant; Squares: transient.

Figure 4. Proportional contribution of the SMR to individual diets (CSMR) as a function of the site of capture (river km measured as distance from Gabelle Dam), by species. Medians (symbols) and 95% CI (vertical lines) for CSMR are shown. Black circles: resident individuals; empty circles: migrant individuals; empty squares: transient individuals. Horizontal dotted lines: equal contribution from the two sources (SLR and SMR). Crosses indicate the location of sampling stations: upstream of Gabelle Dam (river km = 0), downstream of Gabelle Dam (0 < river km < 22.8), and SLR (river km > 22.8). Grey area: transition zone between the SMR and SLR (18.8 < river km < 22.8).

Figure 5. Proportional contribution of the SMR to individual diets (CSMR) as a function of the date of capture, for individuals caught in the SMR downstream of Gabelle Dam (0 < river km < 22.8), by species. Medians (circles) and 95% CI (vertical lines) for CSMR are shown. Black circles: resident individuals; empty circles: migrant individuals; empty squares: transient individuals. Crosses: sampling dates. Horizontal dotted lines: equal trophic contribution from the two sources (SLR and SMR). Grey area: spawning period.

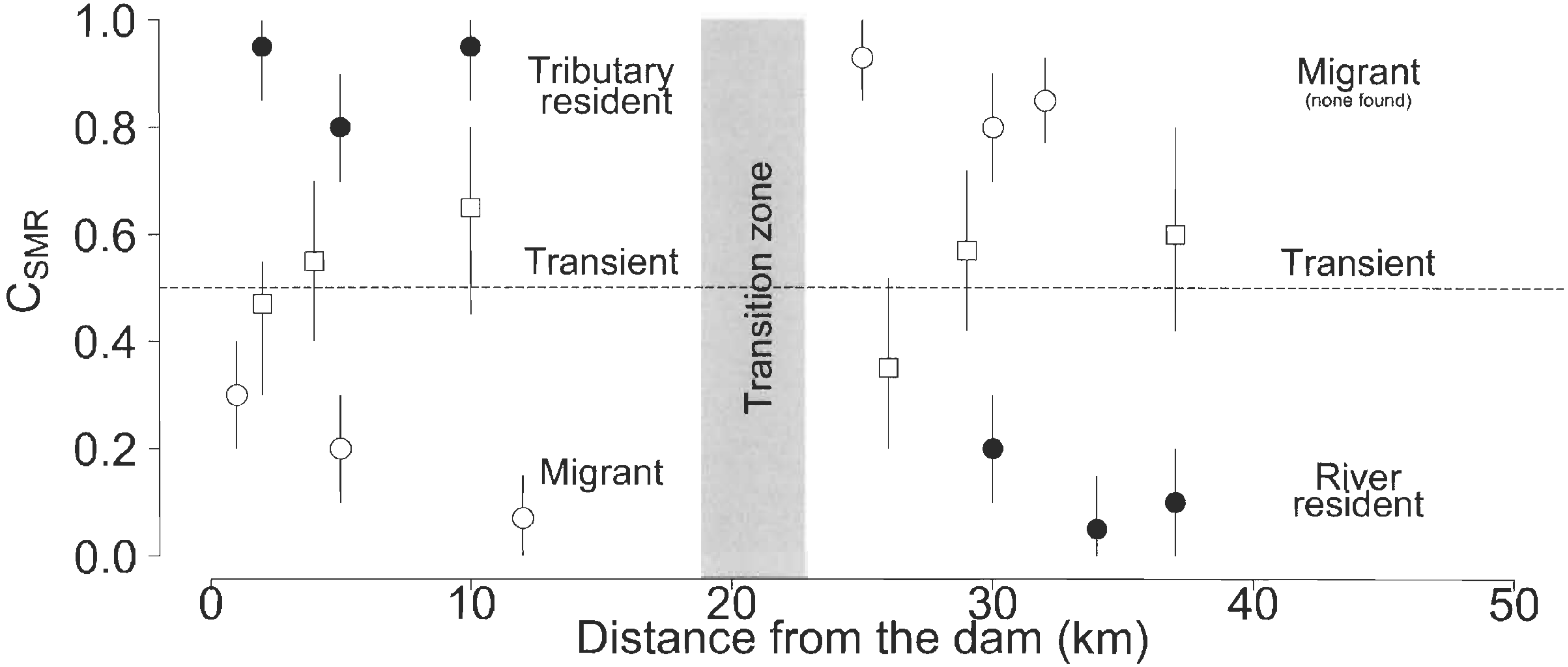
Figure 6. Isotopic signature projections ($\delta^{13}C$) of migrant individuals from four species captured in the SMR before and during the spawning period. From all studied species, these four were selected to do the projection because migrant individuals were captured before and during the spawning period and resident individuals were captured at the end of the summer. Therefore, we wanted to know if the resident individuals captured at the end of the summer were year round resident individuals or migrant individuals that have changed their isotopic signature through the summer to attain the isotopic signature of a resident individual. Lines represent the projection of the isotopic signature from the equation found in Hesslein, Hallard & Ramlal (1993). The turnover rate (λ) used in the previous equation was estimated from Weidel et al (2011). Due to missing data for some individuals, we were not able to estimate the λ for each migrant individual. Black circles: resident individuals; empty circles: migrant individuals; empty squares: transient individuals. Horizontal dotted lines: SMR and SLR $\delta^{13}C$ baseline. Grey area: spawning period. The Y axis was inverted to be consistent with Fig. 5.

Fig. 1



N
Batiscan River
Gabelle Dam
St. Maurice River
St. Lawrence River
Transition zone
Trois-Rivières
Quebec
Lake St. Pierre
○ Gillnet
□ Seine
0 2 4 8 12 16
Kilometers
Source : Ressoucres naturelles Canada

Fig. 2



1.0
0.8
0.6
0.4
0.2
0.0
C_{SMR}
Tributary resident
Transient
Migrant
Transition zone
Migrant
(none found)
Transient
River resident
0
10
20
30
40
50
Distance from the dam (km)

Fig. 3

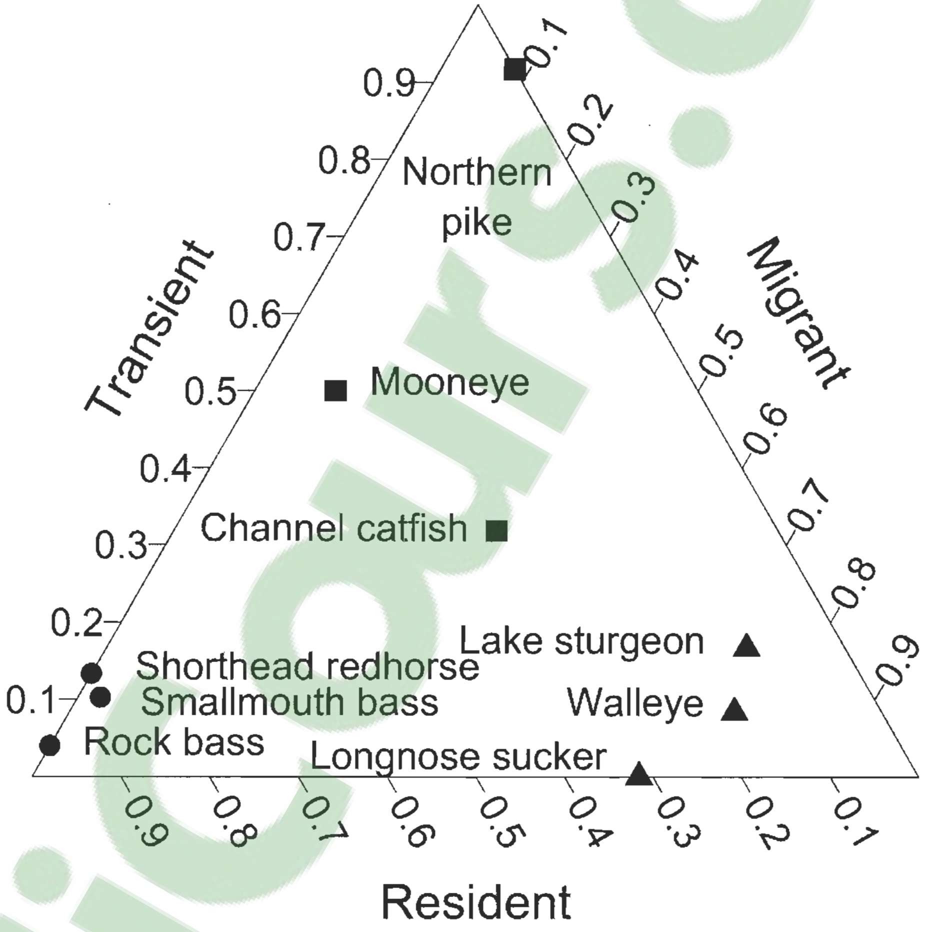

Transient
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Migrant
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Resident
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Northern pike
Mooneye
Channel catfish
Lake sturgeon
Walleye
Longnose sucker
Shorthead redhorse
Smallmouth bass
Rock bass

Fig. 4

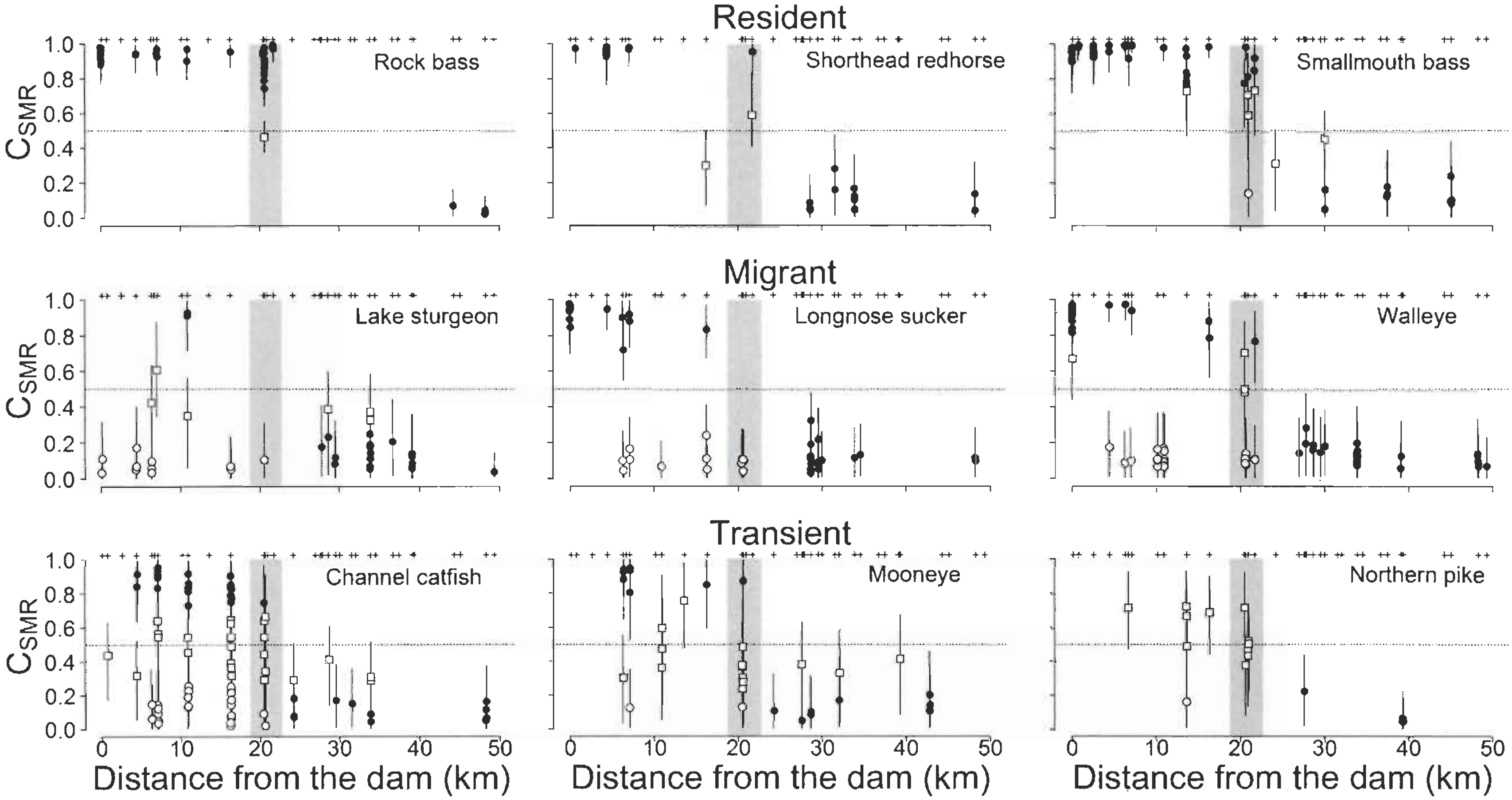
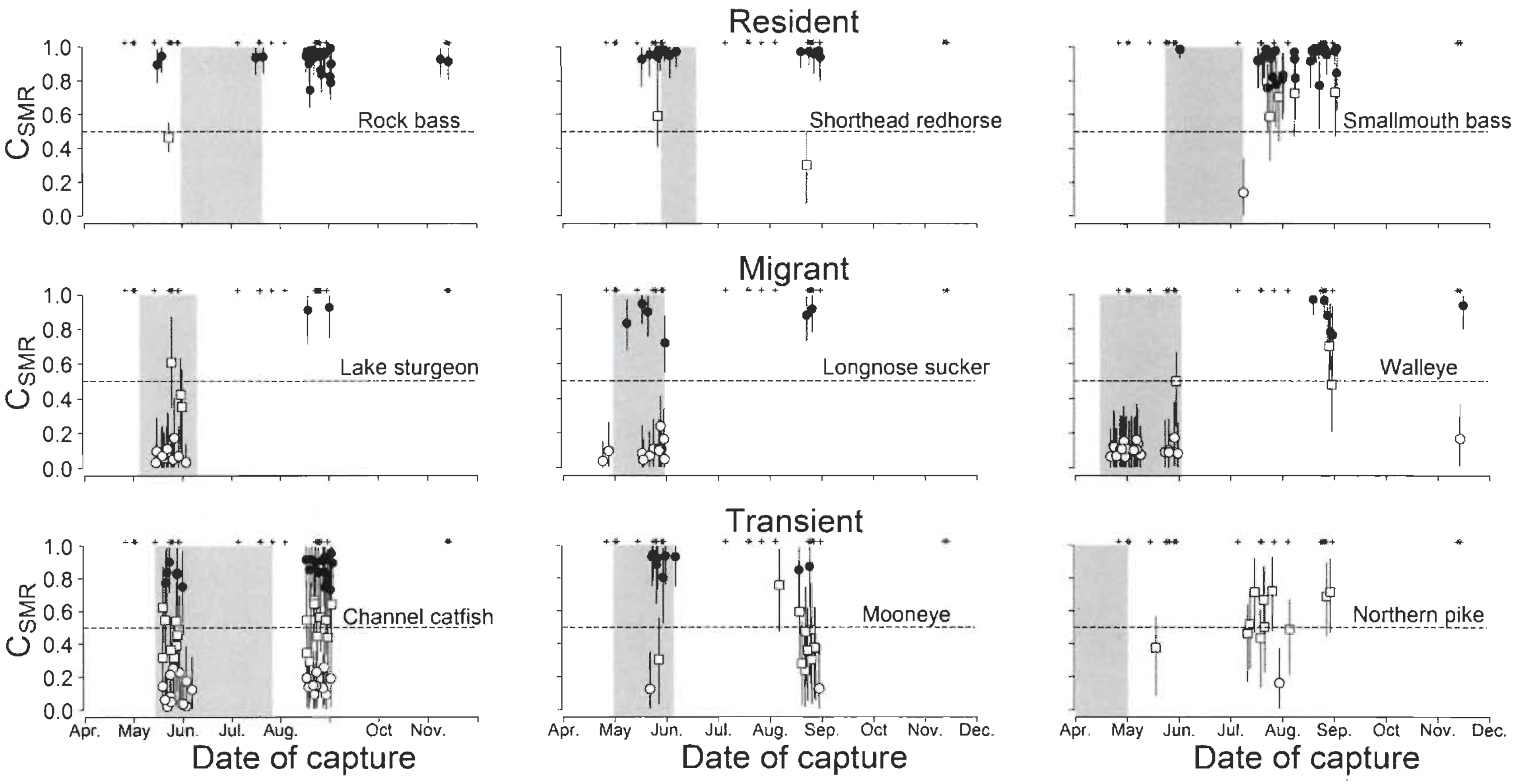
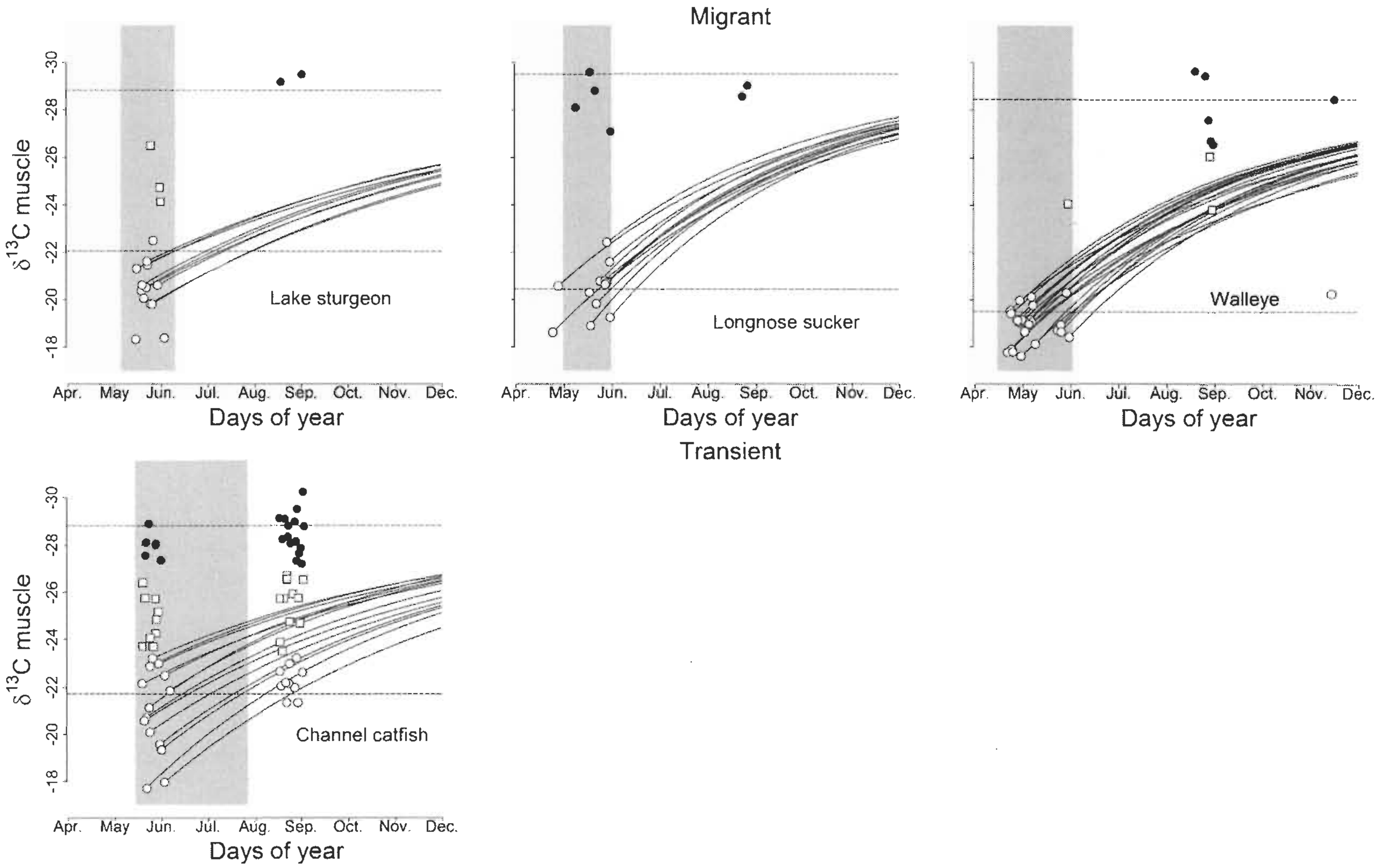

Resident
Rock bass
Shorthead redhorse
Smallmouth bass
Migrant
Lake sturgeon
Longnose sucker
Walleye
Transient
Channel catfish
Mooneye
Northern pike
C_{SMR}
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
Distance from the dam (km)

Fig. 5



Resident
Migrant
Transient
Rock bass
Shorthead redhorse
Smallmouth bass
Lake sturgeon
Longnose sucker
Walleye
Channel catfish
Mooneye
Northern pike
C_{SMR}
1.0
0.8
0.6
0.4
0.2
0.0
Apr.
May
Jun.
Jul.
Aug.
Sep.
Oct
Nov.
Dec.
Date of capture

Fig. 6


Migrant
Lake sturgeon
Longnose sucker
Walleye
Transient
Channel catfish
δ^{13}C muscle
-30
-28
-26
-24
-22
-20
-18
Apr.
May
Jun.
Jul.
Aug.
Sep.
Oct.
Nov.
Dec.
Days of year

Appendix

Number of individuals in stable isotope analyses, by species and capture site.

Species	Capture site			
	SMR upstream of Gabelle Dam	SMR downstream of Gabelle Dam	SMR transition zone	SLR
Channel catfish	0	57	9	24
Lake sturgeon	0	17	1	25
Longnose sucker	10	14	5	18
Mooneye	0	14	8	12
Northern pike	0	6	6	48
Rock bass	12	8	17	3
Shorthead redhorse	0	13	2	12
Smallmouth bass	7	30	9	12
Walleye	28	22	14	93

CHAPITRE III

CONCLUSION GÉNÉRALE

3.1 Contextualisation

L'objectif général de ce projet de maîtrise était de caractériser les variations inter- et intra-spécifique des patrons de migration de différentes espèces de poissons entre une rivière majeure et l'un de ses tributaires et d'identifier les ressources exploitées dans le tributaire.

3.2 Résultats principaux

Au total, nous avons analysé la signature isotopique du muscle de 556 individus de neuf espèces. Chacun des individus a été classé dans l'un des trois contingents que l'on pouvait identifier selon des critères préétablis (voir Table 1, Chapitre II). Suite à l'identification du contingent pour chaque individu (voir Figure 2, Chapitre II), nous avons classifié les espèces en 3 groupes (espèce résidente, espèce migratrice et espèce transitoire) selon l'importance des contingents retrouvés dans la RSM en aval du barrage de la Gabelle (voir Figure 3, Chapitre II). Les espèces résidentes et migratrices ont démontré une grande homogénéité dans leur comportement migratoire. Toutefois, les espèces transitoires ont démontré une grande variabilité intra- et inter-spécifique dans la composition de leur population. Parmi les six espèces migratrices et transitoires, seulement la barbue de rivière a montré des différences de condition de corps entre les différents contingents retrouvés dans la SMR en aval du barrage.

3.2.1 Espèces résidentes

L'achigan à petite bouche, le chevalier rouge et le crapet de roche ont été classés comme espèces résidentes. Le contingent résident compose à plus de 85 % des captures pour ces espèces dans la RSM en aval du barrage de la Gabelle. Les individus des contingents migrateurs et transitoires sont localisés dans les quatre derniers kilomètres de la RSM près de l'embouchure (voir Figure 4, Chapitre II). Cette section diffère du reste du système par la présence d'îles et d'habitats composés de végétation submergées offrant un milieu diversifié à la communauté ichthyenne. La présence de différents contingents ne semble pas être relié ni à la date de capture, ni à la période de fraie des espèces (voir Figure 5, Chapitre II). Nos résultats supportent l'idée que ces espèces vivent dans la RSM à l'année exploitant toutes les ressources nécessaires dans la même rivière.

3.2.2 Espèces migratrices

Le doré jaune, l'esturgeon jaune et le meunier rouge ont été classés comme espèces migratrices dans notre système. Dans la RSM, les individus du contingent migrateur en provenance du FSL composent plus de 65 % des captures pour ces espèces. Les contingents migrateurs et transitoires se retrouvent du barrage de la Gabelle à l'embouchure de la rivière (voir Figure 4, Chapitre II). La présence des individus des contingents en provenance du FSL, ont été capturés principalement en période de fraie (voir Figure 5, Chapitre II). Le fait que les gonades des individus migrateurs capturés en période de frai étaient matures supporte l'hypothèse que ces individus aient migré dans la RSM pour exploiter les habitats de reproduction qui y sont présents. De plus, les individus des contingents migrateur et transitant n'ont pas été capturés durant le reste de l'année, indiquant que ces individus retournent rapidement au FSL suite à la reproduction. Cette hypothèse est supportée par le fait que le renouvellement isotopique est trop lent pour que les individus changent leur signature isotopique à un point qu'il serait classifié comme individus résidents à la fin de l'été (Fig. 6, Chapitre II). Ceci supporte que ces individus n'exploitent pas ou très peu les ressources alimentaires de la RSM.

3.2.3 Espèces transitoires

La barbue de rivière, le grand brochet et la laquaiche argentée sont des espèces dites transitoires. Le contingent transitoire compose plus du tiers des captures dans la RSM en aval du barrage de la Gabelle. Les trois contingents présents dans la RSM ont été capturés tout au long de la rivière en aval du barrage (voir Figure 4, Chapitre II). Toutefois, pour la barbue de rivière et la laquaiche argentées, les captures ont été faites principalement à la fin mai et fin août (voir Figure 5, Chapitre II). Pour la barbue de rivière, plus de 60 % des individus migrateurs et transitoires capturés en mai étaient prêts à la reproduction. Ceci supporte l'idée que cette espèce entre dans les tributaires afin de se reproduire. Toutefois ce scénario ne s'applique pas pour la laquaiche argentée car seulement 2 individus des contingents migrateurs et transitoires ont été capturés lors de la période de fraie (voir Figure 5, Chapitre II). La présence à la fin de l'été des contingents migrateurs et transitoires pour la barbue de rivière et la laquaiche argentée, nous indique une exploitation de la ressource alimentaire dans la RSM et un retour potentiel au FSL pour atteindre les habitats d'hivernage présent dans le fleuve. La majorité des captures du grand brochet ont été faites à la ligne durant l'été. Plus de 90 % des individus capturés dans la RSM ont été classés dans le contingent transitoire nous indiquant que cette espèce a changé de source alimentaire au cours de l'été. Puisqu'aucune capture n'a été faite en période de fraie pour le grand brochet dû au fait que nous étions absents en ces dates, nous ne pouvons tirer aucune conclusion sur l'exploitation des habitats de reproduction dans la RSM. Ces trois espèces semblent migrer dans le tributaire pour utiliser principalement les ressources alimentaires durant l'été et retourne au fleuve à l'automne afin d'atteindre les habitats d'hivernage.

3.3 Conclusion

Le phénomène de migration partielle est présent chez six des neuf espèces étudiées. Le fait que seulement une espèce partiellement migratrice montre des différences physiques entre les contingents supporte l'idée que la condition du corps n'est pas la principale force évolutive ayant mené à la présence de la migration partielle dans notre système. Nos résultats montrent qu'un grand nombre d'espèces migre d'une rivière majeure à un tributaire afin d'exploiter différentes ressources. Les patrons de migration semblent être fortement reliés aux ressources exploitées dans le tributaire. De plus, les espèces étudiées démontrent une grande variabilité inter- et intra-spécifique dans leur patron de migration. L'homogénéité intra et inter-spécifique des patrons de migration semble être liée à la distribution spatiale des ressources exploitées ainsi qu'à la disponibilité temporelle de celles-ci. De plus, le mouvement de contingent spécifique (migrateur et transient) à des périodes précises de l'année change la structure des populations du tributaire. La connectivité entre le RSM et le FSL donne un accès à ces ressources biologiques importantes situées dans le tributaire pour les individus provenant du FSL. La connectivité joue donc un rôle important afin de rendre accessible les services écosystémiques du tributaires à la communauté de poisson du fleuve. En somme, cette étude démontre que la connectivité entre les tributaires et la rivière majeure à un impact sur la communauté de poissons de la rivière majeure en rendant accessible les services écosystémiques offerts par les tributaires ainsi que sur la structure de la communauté des tributaires.

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