Spatial Patterns of Resource Subsidies in Great Lakes Tributaries from Migratory Fishes

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TRENT UNIVERSITY
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Michael McKenzie
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Abstract

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Michael McKenzie

Migratory fish can influence the rivers where they spawn by depositing nutrients and organic matter which increase primary and secondary production. Past research in the Laurentian Great Lakes has focused on individual tributaries, accordingly, the spatial extent of subsidies and how environmental factors influence subsidies are not clear. To determine which tributaries received subsidies, I compared stable carbon isotope values ($\delta^{13}C$) of resident stream fishes above and below 54 barriers in 37 tributaries. Subsidies were found in found across 43 of the barriers. The subsidy magnitude varied among the lakes, with Lake Superior having significantly larger subsidies. Correspondence analysis of environmental factors showed that large differences in $\delta^{13}C$ were associated with steeper river channels on the Canadian Shield with little agricultural land-use. Migratory fish supply resource subsidies to rivers across the Great Lakes basin, though their magnitude is contextually dependent.

Keywords: Resource subsidies, Great Lakes, stable isotopes, migratory fish, barriers, resident stream fish, stream characteristics

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Chapter 1. General Introduction

Few animals remain completely static for the entirety of their lives, but instead move between separate home ranges in search of resources. Migrations have been observed in birds (Thorup et al., 2017), mammals (Bohrer et al., 2014), fish (Bilby et al., 1996; Jorgensen et al., 2010), and many invertebrate species (Inamine et al., 2016; O'Malley et al., 2018) and can range from thousands of individuals travelling hundreds of kilometres to single individuals moving less than a kilometre(Bohrer et al., 2014; Inamine et al., 2016; Jorgensen et al., 2010; O'Malley et al., 2018; Thorup et al., 2017). Episodic changes in resource abundance and quality necessitate individuals to leave their home range in search of ecosystems with higher quantity or quality resources. Organisms that can migrate along resource gradients are likely to be more ecologically fit, though migration provides its own set of risks for individuals compared to resident individuals that choose to remain static year-round (Gnanadesikan et al., 2017). In this way, the circumstances and limitations imposed by the ecosystem shape the lives of organisms and drive the development of their migrations.

In turn, migrants can shape their surroundings, altering ecosystem functions by physically changing the environment, called a process subsidy, or directly donating nutrients, known as a material or resource, subsidy (Bauer and Hoye, 2014). Resource subsidies involve the direct transport of nutrients across an ecosystem boundary, often from a nutrient-rich ecosystem to an oligotrophic one, where they can potentially influence local productivity (Polis et al., 1997). In the simplest form, a resource subsidy can come via natural, abiotic forces moving allochthonous Resources, such as ocean upwelling bringing up nutrients (Polis et al., 1997), wind distributing volcanic ash (Arnalds et al., 2013), or waves depositing wrack on a beach (Richardson and Wipfli, 2016). For systems where there is no physical force to move material, however, or where the ecosystems are separated by too great a distance, such transport of resources must rely on the movements of migratory animals.

Migrants connect separate ecosystems, crossing boundaries and integrating food webs that would otherwise be isolated from one another. Having spent much of their year feeding, growing, and incorporating nutrients into their tissues in one environment, such migrants cross an ecosystem boundary to new, potentially less productive environments, where they donate a resource subsidy that can be consumed by locals (Bauer and Hoye, 2014; Flecker et al., 2010). Most often, these subsidies come in the form of carcasses, excretion, or in the case of breeding migrations, eggs, and other reproductive material (Tsipoura and Burger, 1999). For consumer populations in the recipient ecosystem, whose numbers may be low due to a lack of resources, decoupling themselves from the productivity of their local prey through feeding on subsidies can boost their body mass (Tsipoura and Burger, 1999), abundance (Buckner et al., 2018; Hawn et al., 2018), and density (Nowlin et al., 2007). The most substantial subsidy effects occur when several key requirements are fulfilled; the ratio of migrant biomass to recipient ecosystem size is large, the recipient ecosystem is nutrient poor, and the subsidy is retained, not washed away, so that its nutrients enter the ecosystem (Flecker et al., 2010).

The importance of subsidies is most evident in the oligotrophic rivers and streams of North America's west coast, which each year receive large migrations of Pacific salmon in the form of eggs, excrement and carcasses that are left to decompose in the streams and in the riparian zone. Research into these migrations has clearly demonstrated that salmon are the primary source of nitrogen and other nutrients and lead to increases primary productivity and invertebrate populations (Hocking et al., 2013; Janetski et al., 2009; Kline et al., 1990). Through predation of these invertebrates, or through the direct consumption of the subsidy, the resource subsidy also increases the abundance and condition factor of stream fish including the juveniles of the parental migrants (Bilby et al., 1998). Stable isotope analysis (SIA) in these studies further identified the presence of resource subsidies by detecting elevated $\delta^{13}C$ and $\delta^{15}N$ in tissues from fish and invertebrates below barriers and comparing them to organisms above the barriers (Bilby et al., 1998; Kline et al., 1990).

Compared to the Pacific Coast, little research has been conducted on resource subsidies in the Great Lakes basin. Most studies have focused on individual rivers so the geographic extent of subsidies in Great Lakes tributaries is not known. Research has identified rivers where resource subsidies led to increases in dissolved nutrients (Collins et al., 2011), primary production (Childress et al., 2014), and growth of juvenile salmonids (Hermann et al., 2020). In addition, this work demonstrated that migratory iteroparous fish can contribute large nutrient donations in rivers despite not leaving carcasses to decompose (Childress and McIntyre, 2016; Jones and Mackereth, 2016). In addition to its geographic extent, it is not clear how stream characteristics at the regional (e.g., geologic) and local level (e.g., riparian cover) influence resource subsidies (Cederholm et al., 1999; Polis et al., 1997; Rand et al., 1992).

Moreover, the rivers of the Great Lakes region have been heavily fragmented through a combination of hydroelectric dams, small private dams, road culverts, legacy mill dams, and low-head lamprey weirs. In addition to the well documented damage these barriers cause to the reproductive ability of migratory fishes, such dams restrict resource potential subsidies from reaching ecosystems that may have previously benefited on them (Freeman et al., 2003; Greathouse et al., 2006). Even partial barriers, such as lamprey weirs, which allows jumping salmonids to pass, prevents non-jumping fish and the large subsidy they have been shown to provide (Harford and McLaughlin, 2007; Jones and Mackereth, 2016; Klingler et al., 2003). Through comparisons of stable isotopes this study seeks to determine where in the Great Lakes basin are resource subsidies occurring and how factors such as barrier types, land-use, or local stream characteristics play a role.

Chapter 2. Spatial Patterns of Resource Subsidies in Great Lakes Tributaries from Migratory Fishes

Introduction

The movement of energy across ecosystem boundaries is referred to as resource subsidies and contributes to a wide variety of food webs (Duda et al., 2020; Leroux and Loreau, 2008; Polis et al., 1997). Many migratory animals act as vectors of energy as they regularly traverse between ecosystems, incorporating energy in one region and then enriching the area at their destination (Flecker et al., 2010; Gnanadesikan et al., 2017). Some migrants, like sea birds and hippos, subsidize via their excrement (Subalusky et al., 2015; Vizzini et al., 2016); some, such as sea turtles, leave behind eggs or other reproductive materials (Bouchard and Bjorndal, 2000), while species like whales die in the new environment and leave behind a nutritious carcass for residents (Onishi et al., 2020).

Migratory Pacific salmon are a classic example of resources subsidies which have been studied for decades; these semelparous species donate large quantities of nutrients to rivers, streams, and riparian forests through all three of these methods (Bilby et al., 1996; Flecker et al., 2010). Having grown large in the ocean, adults return to their natal stream to spawn and die, leaving behind highly energetic eggs and carcasses that contain 11 kJ/g and 5.3 kJ/g respectively (Gende et al., 2004). A comparison of river sections that receive subsidies to sections that do not receive such subsidies demonstrates increases in the survival and biomass of stream fish (Hocking et al., 2013), benthic invertebrate productivity (Wipfli et al., 2003, 1998), and greater recruitment of juvenile salmonids (Wipfli et al., 1998). The decomposition of these tissues, in addition to the direct donation of excrements, produces a spike in dissolved nitrogen and phosphorous that leads to increases in primary production, biofilm growth and microbial stimulated nitrification rates (Janetski et al., 2009; Levi et al., 2013; Wipfli et al., 1998). Using stable isotope analysis (SIA), marine-derived nutrients can be tracked moving through stream food webs, identifying which organisms were feeding on the subsidy. This techniques reveals the different pathways through which subsidies are incorporated and highlights how salmon subsidies crossed a second habitat boundary and fertilized riparian forests (Bilby et al., 1998; Kiffney et al., 2018; Kline et al., 1990; Reimchen, 2017).

While there are numerous studies on the importance of Pacific salmon nutrient subsidies, this has not been studied nearly as much in the freshwater Laurentian Great Lakes. Though it has long been known that fish migrations occur in Great Lake tributaries it has been unclear if they result in resource subsidies (Flecker et al., 2010). A few studies, mostly on individual tributaries, have noted that resource subsidies occur (Collins et al., 2011; Rand et al., 1992), as these studies found increases in primary productivity (Childress and McIntyre, 2016; Jones and Mackereth, 2016), benthic invertebrate abundance (Childress and McIntyre, 2015; Ivan et al., 2011; Jones and Mackereth, 2016), and stream fish growth following migration events (Ivan et al., 2011). In much of the Great Lakes, however, fish migrations are dominated not by salmonids but by iteroparous species such as the walleye (*Sander vitreus*), lake sturgeon (*Acipenser fulvescens*), and white sucker (*Catostomus commersonii*). While the Pacific Salmon species die in the river after spawning, leaving behind carcasses, these other species return to the lake to spawn again in the future (Childress and McIntyre, 2015; Flecker et al., 2010). Though they do not leave behind carcasses, research has shown that they can donate large quantities of resources. Jones and Mackereth (2016) calculated that white and longnose suckers deposited an estimated 5635 kg of eggs and 2025 kg of milt, representing 84% and 78% of the annual subsidies of N and P, or 212 and 14 kg respectively in a 165km^2 oligotrophic tributary. This strongly suggests that fishes other than salmon can provide large subsidies in the Great Lakes (Childress and McIntyre, 2016; Jones and Mackereth, 2016).

Many of these iteroparous migrants are not able to jump and so are blocked by small barriers that do not halt migrant salmonids (i.e., partial barriers) (Klingler et al., 2003). Such semi-permeable barriers include dams with fish ladders, waterfalls that are passable during high flows, and hundreds of low-head weirs meant to stop invasive sea lampreys. Fragmentation of rivers impacts a wide range of ecosystem processes, such reducing biodiversity (Zwick, 1992) and inhibiting nutrient transfers (Freeman et al., 2003) and has been linked with the extirpation of many migratory species (Pringle et al., 2000). Comparisons between stream reaches above and below barriers showed differences in primary productivity, ecosystem respiration and fish growth in downstream sections following a spawning migration, suggesting these benefits would be present in the upper reaches had the barrier not been present (Childress and McIntyre, 2016; Hicks et al., 2005; Schuldt and Hershey, 1995).

Although they prevent migrants from spawning in their preferred location, dams around the Great Lakes provide a simple way to study resource subsidies as they allow the comparison stable isotopes below and above barriers to migration (Bilby et al., 1998; Chaloner et al., 2002). Great Lakes fish are typically more enriched in $\delta^{13}C$ than stream fish in tributaries (Jones and Mackereth, 2016; Robillard et al., 2011). This likely relates to the differences in rates of $\delta^{13}C$ discrimination by the primary producers that form the basis of lacustrine, riverine, or terrestrial (for which stream food webs are heavily reliant on) environments (Michener and Lajtha, 2007). Therefore, if a stream fish feeds on lake-derived tissues, including indirectly via feeding on benthic invertebrates that consumed periphyton that absorbed migrant excrement, its $\delta^{13}C$ signature will be altered. Their tissues can then be compared to stream fish from above complete barriers, which do not have access to lake-derived tissues, to determine if resource subsidization has occurred (Robillard et al., 2011; Schuldt and Hershey, 1995).

As noted by Subalusky and Post (2019), resource subsidy input is translated through the lens of the recipient ecosystem's characteristics. This includes both abiotic and consumer characteristics that define the quantity, quality, timing, and duration of inputs. Flecker et al (2010) suggested that three factors influence the success of resource subsidies: magnitude of migrant biomass, the nutrient status of recipient ecosystem, and the efficiency of retention and incorporation of the subsidy. Retention and incorporation could relate to whether the subsidy is in a form that can easily be consumed by residents (e.g., small fish eggs) (Flecker et al., 2010) but can also relate to factors that regulate metabolism and primary productivity, such as temperature (Allen and Gillooly, 2009) and canopy cover (Warren et al., 2013), or factors that determine how the subsidy could persist in the ecosystem before being washed downstream, such as stream slope (Paudel et al., 2015) or riverbed substrate (Roseman et al., 2011).

To date, most studies on resource subsidies in the Great Lakes have focused on individual river systems that host fish migrations, often with introduced salmonid species. This study used stable isotope analysis to identify resource subsidies in tributaries of the Great Lakes in Canada (Superior, Huron, Erie, Ontario). In rivers that received a nutrient subsidy I predict there would be higher (i.e., less negative) values of $\delta^{13}C$ in fish below barriers than above. I also expect subsidization would be influenced by the level of passability of the barriers, with larger differences in $\delta^{13}C$ across completely impermeable barriers than semi-permeable partial barriers. In addition, I expect that stream characteristics including local (e.g., riparian cover, substrate size, channel slope) and regional (e.g., land use, geology) may be associated with the differences in $\delta^{13}C$ that might further explain patterns of subsidies across the Great lakes. Streams with larger differences of $\delta^{13}C$ above and below barriers may have favourable characteristics that lead to greater incorporation of subsidies. To investigate these hypotheses, I sampled 37 river systems that drain into the Great Lakes and compared the stable isotope ratios from above and below barriers on each stream.

Methods

Stream and Site Selection

The comparison of stable isotopes (SI) between stream fish that have and have not benefited from lake-derived resource subsidies required river systems that were fragmented by a barrier. This provided a classic upstream-downstream comparison to evaluate differences (Green 1979). Rivers from each of Ontario's four Great Lakes were used for this study, ranging from the Moira River (18T 309666 4891700) in Lake Ontario's Bay of Quinte to the Pine River (16U 313014 5324066), a tributary of Lake Superior (Figure 2.1). Additionally, one barrier-free Lake Ontario tributary, Wilmot Creek (17T 693065 4863409), was sampled to examine the SI signature of an unfragmented system.

Potential rivers were selected through a combination of prior knowledge of barriers, searching Google Earth for evidence of barriers, waterfall tourism websites (e.g., Waterfalls of Ontario, https://waterfallsofontario.com/) and the Great Lakes Fishery Commission's Sea Lamprey Control Map (http://data.glfc.org/) for the location of lamprey weirs. Additionally, I communicated with local Conservation Authorities and Ontario Parks staff to determine the location and accessibility of barriers as well to assess if potential rivers hosted large migrations of salmonids, white suckers, or other species. Some rivers had one barrier near the mouth whereas others had two or more.

Barriers with significant lakes or reservoirs immediately upstream were avoided when possible as the primary productivity in the lake water can alter the $\delta^{13}C$ in downstream organisms. Plankton in a reservoir accrue heavy δ^{13}C and are washed downriver, where they subsidize stream food webs for several kilometres (Doi et al., 2008). This enrichment may obscure the presence of resource subsidies from migratory fish.

In total, 37 river systems were selected (Figure 2.1). All rivers flowed directly into their respective Great Lake, except for the Little Thessalon River, Beaver Creek, and Venison Creek, which converged with larger tributaries before entering a Great Lake.

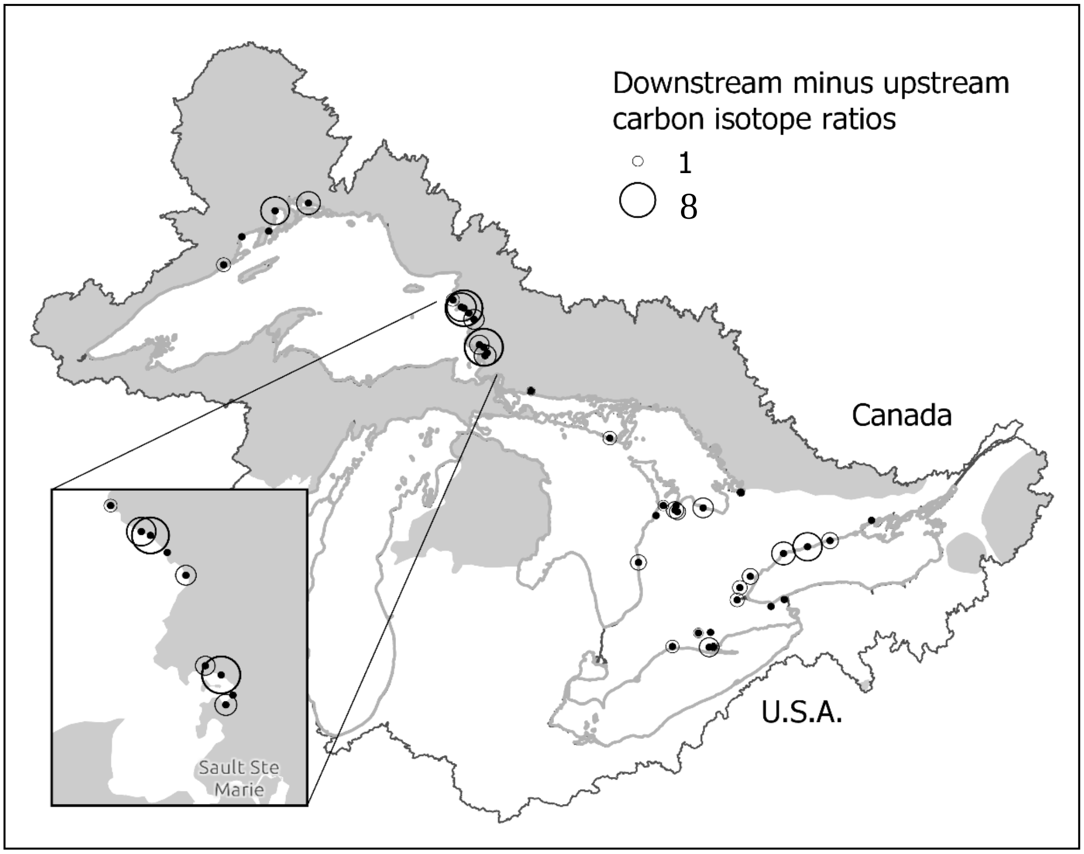

Figure 2.1. Location of sampling sites along 37 Ontario rivers across the Great Lakes. Fourteen rivers drained areas on the Canadian Shield (grey area) and 23 rivers drained areas of the Great Lakes – St. Lawrence lowlands. Circle size relates to the magnitude of the difference in δ13C between the downstream and upstream sample sites. Negative values are represented by a dot.

Proposed sampling locations along the rivers were pinpointed through use of Google Earth and local knowledge. Ideally, sites within tributaries were as close to barriers and as close together as possible as the natural gradient of SI longitudinally along the river can yield differences between sites approximately as little as 4 kilometres apart (Costas and Pardo, 2015). The precise location of sampling sites along each river was chosen by the sampling crew while on the stream. Sites were numbered with Site 1 being closest to the lake and increasing in number farther inland.

Field Methods

Choice of Study Species

For consistency across the Great lakes, longnose dace, *Rhinichthys cataractae*, and two ecologically similar sculpin species, slimy sculpin, *Cottus cognatus*, and mottled sculpin, *C. bairdii*, were chosen for study. These species are widespread and abundant in the Great Lakes basin (Holm et al., 2021; Hubbs and Lagler, 2004). These species prefer cold-water systems but can also be found in warmer streams in the watersheds of each of Ontario's four Great Lakes, living along the bottom streams, feeding benthically on invertebrates, algae, and fish eggs when available (Burridge et al., 2022; Hubbs and Lagler, 2004). In turn, they are consumed by larger predatory stream fish such as juvenile salmonids, passing energy and nutrients up the food web (Petrosky and Waters, 1975). Despite the widespread range of these study species, they were absent in some rivers or could be found only on one side of a barrier. In these situations, substitute species belonging to the same feeding guild were used.

Fish Collection

Sampling began in June of 2017 and continued until August of that year. The timing of sampling was based on the estimated rate of incorporation of $\delta^{13}C$. As demonstrated by Thomas and Crowther (2015), who utilized water temperature and approximate body masses. Fish in this region require approximately 24 days for 50% of their stable isotope value to be replaced by that of a subsidy and 95-119 days to be fully replaced. Based on this calculation, plus previously conducted laboratory experiments, fish collection occurred approximately two months after the spring spawning run (N. E. Jones, unpubl. data). Due to Lake Superior remaining cooler for longer, this replacement may take extra time, so these sites were sampled later in the summer.

Fish were collected using a backpack electrofisher, and a crew with one to three netters. The crew walked upstream, consistently shocking at a rate of approximately 7 seconds per square metre. Based on the conductivity of the stream, the electrofisher settings were calibrated before each site, dictating the proper voltage, frequency, and duty cycle to attract but not injure fish. Twelve longnose dace and sculpins were kept from each site for stable isotope analysis. Even after additional sampling, substitute species were required in nine river systems as target fish could not be found (Appendix 1). Samplers chose the replacement species from the limited local fauna but took care to only choose fish that also feed benthically. Western blacknose dace, *Rhinichthys obtusus*, white sucker, *Catostomus commersonii*, and round goby, *Neogobius melanostomus*, were each collected from three river systems; rainbow darters, *Etheostoma caeruleum*, were collected in two systems, while creek chub, *Semotilus atromaculatus*, and hornyhead chubs, *Nocomis biguttatus,* were each found only once. A minimum fish size of 50 mm total length was chosen in order to exclude potential young-of-year (YOY) which likely either would not have hatched in time to feed on the subsidy or whose small size, and thus mouth gape limitation, would reduce their ability to eat fish eggs. Additionally, fish under 50 mm in length would likely still be young enough to reflect the isotopic signature of their parents, as they would have been feeding on their egg yolk. Fish were euthanized by placing them in a bucket of tricaine methanesulfonate (MS-222), diluted to a concentration of 250 mg/L for several minutes. Fish were rinsed with clean water and placed in whirlpacks, labelled with the river name, site ID and fish species. In total, 1,412 fish were kept for analyses (Appendix, Table 4.1). These were placed on ice in coolers until they could be transferred to freezers for storage.

Simultaneous to the collection of stream fish, kick nets (400 µm mesh) were used to collect benthic invertebrates. Rather than sample for a set amount of time, the kick and sweep was conducted until enough invertebrates had been collected to fill a 100-ml whirlpack. As when collecting stream fish, no large individuals were kept (e.g., crayfish).

Stream Characteristics

Quantitative information regarding water characteristics were gathered using a portable hand-held Hanna meter for pH, temperature (°C) and total dissolved solids (mg/L; Appendix ii). A LaMotte turbidity meter measured the streams turbidity (measured in standard Nephelometric Turbidity Units, NTU) and a third, separate probe measured the conductivity of the stream (µS/cm). Canopy cover over the site was determined with a densiometer, a curved mirror that reflects an image of the sky when held parallel to the ground and displays the canopy in on a grid of 24 squares. The four canopy cover estimates derived from facing each direction with the densiometer were averaged together to reach a single value for each site. The substrate of the streambed was determined by visually examining the area where the electrofishing occurred and recording the proportions of different substrate types. The seven categories of substrate included clay/silt (<0.06 mm), sand (0.06-2 mm), small gravel (2-32 mm), large gravel (33-64 mm), cobble (65-256 mm), boulder and bedrock (>256 mm).

Landscape-scale stream characteristics were gathered using the Ontario Flow Assessment Tool (OFAT), a GIS tool hosted by the Ontario Ministry of Natural Resources and Forestry that allows displays topographic information at the watershed level. From these shapefiles the total watershed area, percent agriculture, upstream channel length and elevations were recorded for each stream. Comparing the channel lengths at each sampling site yielded values for the distance between sites and the distance to the river mouth. While the OFAT did provide data for channel slope, I decided this is not reflective of the true local-scale stream slope. I instead calculated a new slope value using the change channel length and the change in elevation for the section of stream below the barrier.

Barrier Classification

Through a combination of online research, communication with local conservation authorities, and direct observation in the field, each barrier was classified into different barrier classes including complete barriers, human-intervened barriers, partial barriers, and unknown barriers. Complete barriers were tall dams or waterfalls not passible by any fish. Partial barriers were those passable by jumping fishes (e.g., trout and salmon) and not passable by non-jumping fishes (e.g., suckers). Additional barrier types included those with fish ladders or where fish were lifted over a complete barrier via human intervention and unknown barriers that may stop fish in some circumstances but likely would not stop all fish, such as during high flow events.

Laboratory Methods

Before beginning tissue removal for SIA, each fish was weighed (g) and measured (total length mm). These measurements were needed for later analysis to determine if fish size was a confounding variable that could influence spatial patterns found in stable isotopes. Sculpins were confirmed as either Mottled or Slimy sculpin by counting the number of rays in the pelvic fins (Hubbs and Lagler, 2004).

Muscle was harvested consistent with other studies by dissecting tissue from the fish's left side, behind the dorsal fin, and above the lateral line. Studies using SIA typically use white muscle tissue as it tends to have less variable stable isotope ratios than other tissue types and is more likely to resemble its environmental signature (Michener and Lajtha, 2007). In addition, white muscle has a relatively low lipid content which has made white muscle the preferred method for most stream fish studies (Jardine et al., 2005). At least 0.15 g of white muscle tissue was dissected from each fish, though more was taken from elsewhere when needed. The tissue was then weighed and stored in a labelled vial and freezer box. Individual macroinvertebrates were too small to provide an adequate sample on their own; thus, samples were composed of whole-body tissues from most or all individuals collected at each site. The invertebrates were cleaned of sand and placed in the vial, with care being taken to not preferentially take all from the same species; these samples were then weighed.

To prevent contamination of the stable isotopes, technicians wore gloves, and all weighing, and dissecting was conducted on fresh pieces of "weigh paper." Scalpels, forceps, and all other tools were cleaned with 95% ethanol between the processing of each fish. Samples were dried for approximately 48 hours in a freeze dryer at -49 °C and a pressure of 0.1 mm HG. After 36 hours, the ten largest samples were weighted every 12 hours until they were a constant weight, implying all moisture had been removed. At this point, weights of all samples were recorded. After freeze drying, samples were individually homogenized using a mortar and pestle until each sample was a fine, well-mixed powder. This ensures the small amount of sample used in the stable isotope analysis is representative of the entire tissue. The process was similar for invertebrates which, having been dried, needed to be homogenized so that samples were representative of the entire benthic community, rather than of a single individual. Equipment was wiped clean with a fresh paper tissue and sanitized with ethanol between each sample. Powder tissue was encapsulated into a tin cup for combustion in the mass spectrometer. The sample was weighed, and sample was added or subtracted until it weighed approximately 0.45 mg (+/- 0.05 mg). An analytical balance accurate to 0.05 mg was used to weight samples. The tin cup was flattened using flat-tipped forceps, and repeatedly folded over itself until it was a sphere, completely sealing in the sample. The balled sample was placed into a well of a 100-well tray. In between samples all associated tools, the scale and the work bench were cleaned of potential isotope contaminant using 95% ethanol. For benthic invertebrates three balled samples were created from each site's homogenized collection. This decreased the likelihood of an individual invertebrate or species making up the entire sample, and thus increased the likelihood of the final average representing the site.

To assess and maintain the accuracy of the results of the mass spectrometer, duplicates of every tenth fish were included in the tray. Comparison of the results from each duplicate alerted the technician to any drift by the machine away from the true stable isotope value, allowing for it to be calibrated before too many samples were burned.

Although 12 samples were collected from each site for each species, I assessed how many samples were needed to estimate the mean for a site. This analysis potentially saves time and resources if the sample sizes can be reduced. Two trays, totalling 169 unique fish samples were sent for stable isotope analysis. Only rivers where 12 longnose dace and 12 sculpins were caught at both the top and bottom sites were used, with rivers chosen from multiple Great Lakes to avoid bias. The $\delta^{13}C$ of each fish species in each river system were then assessed using bootstrap analysis. This process involved repeatedly calculating the average stable isotope value using a random selection of the fish, at first using only two fish but progressively including more fish until all possible combinations had been computed and 95% confidence intervals generated. Based on the bootstrapping analysis I concluded that only eight fish were required for an accurate estimate of the mean with confidence. Following this result, I began preparing no more than eight fish samples per site, per species, excluding the necessary duplicates.

Stable Isotope Analysis

Samples were processed at the Chemical Tracers Lab at the Great Lakes Institute for Environmental Research (GLIER) in the University of Windsor. Each capsule was burned in an elemental analyzer-isotope ratio mass spectrometer (EA-IRMS), producing gases such as CO_2, containing either the heavy or light isotope, that were then ionized and accelerated through a magnetic field, separating them by their weight. In this way, the ratio of heavy isotope to the lighter isotope (i.e., ^{13}C to ^{12}C) in the sample was determined. The isotope ratio from the sample was compared with the isotope ratio in standard reference materials (bovine liver and a series of four secondary standards) using the formula:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] * 1000$$

with R_{sample} representing the ratio of ^{13}C ions to ^{12}C ions in the sample, and R_{standard} representing the same in the standard (Jardine and Cunjak, 2003). For each sample the GLIER lab returned values for $\delta^{13}C$ and $\delta^{15}N$, as well as the carbon to nitrogen ratio (C:N) in the sample.

Data Preparation

Due to differences in the carbon content of various biological macromolecules, lipids tend to contain less $\delta^{13}C$ than proteins or carbohydrates, obscuring the true stable isotope content (Post et al., 2007). Traditionally, tissue samples that are high in lipids would undergo additional steps to have the lipids chemically removed. Recently it has become possible to achieve the same end result using an arithmetic formula, based on the relationship between the species-specific ratio of carbon and nitrogen of lipid-free sample

($C{:}N_{\text{lipid free}}$), the species specific discrimination between lipids and proteins ($\Delta\delta^{13}C_{\text{lipid}}$) and the $\delta^{13}C$ content and carbon-nitrogen ratio of the bulk (original) samples (Hoffman et al., 2015):

$$\Delta\delta^{13}C_{\text{lipid free}} = \delta^{13}C_{\text{bulk}} + (\Delta\delta^{13}C_{\text{lipid}} *(C{:}N_{\text{lipid free}} - C{:}N_{\text{bulk}}))/ C{:}N_{\text{bulk}}$$

The specific values of $C{:}N_{\text{lipid free}}$ and $\Delta\delta^{13}C_{\text{lipid}}$ needed were gathered from the literature. Though values specific to the species used in this study were not available, approximate values could be estimated from multiple analyses of similar species. I decided to use $C{:}N_{\text{lipid free}}$ and $\Delta\delta^{13}C_{\text{lipid}}$ values of 3.5 and -6.5 for fish respectively, and 4.2 and -6.3 for invertebrates, respectfully (Hoffman et al., 2015; Hoffman and Sutton, 2010; Kiljunen et al., 2006; Logan et al., 2008; Smyntek et al., 2007). This process was recommended for datasets that contained samples with C:N greater than 4 (Hoffman et al., 2015). I found that 32% of my samples contained C:N > 4.

Preliminary analysis of the data revealed outliers that were potentially obscuring trends, especially at the scale of single rivers. These values could have been the result of measurement error or mistakes during sample preparation and analysis. Samples that were identified as greater than two standard deviations away from the mean for their site were removed. For sites that I had previously only had eight of its fish fully processed for SIA I analysed an additional sample. For sites that had already had all twelve fish processed and included I removed the outlier with no additional steps taken. In total, 36 outliers out of 1160 samples (3%) were replaced with new samples.

In addition to the data collected in the field, my dataset was augmented with data from the literature and unpublished data from colleagues. Stable isotope data taken from above and below the barrier on the Cypress River, collected by Jones and Mackereth (2016) as part of the study that acted as a proof of concept for this thesis, were included in the dataset alongside my own, filling in a section of western Lake Superior I did not sample. Data needed for the creation of mixing models, in particular the stable isotope values of the eggs of lake fish (e.g., migratory sucker, salmon, trout) was provided as unpublished data by Tom Johnston and Tim Johnson from the Ontario Ministry of Natural Resources and Forestry. Because these datasets did not include samples for each lake, more reference data points were collected from the literature (Table 2.1). Only one literature source provided SI values of eggs specific to a Great Lake, Jones and Mackereth (2016), so egg values were instead approximated. For this estimation, I lowered the average value of lake fish muscle tissue by 2.2 for $\delta^{13}C$ which represented the average difference between the adult fish (muscle) and their eggs, as estimated from donated data which included both muscle and gonad tissues from the same adult individual.

Table 2.1. Stable isotope values of lake fish muscle tissue gathered from the literature. In addition to donated, unpublished data and collected benthic invertebrate data, these values were entered into a MixSIAR mixing model to determine the percent diet composition of stream fish.

Reference	Lake	Species	$\delta^{13}C$	$\delta^{15}N$	n
Yuille et al., 2015	Ontario	Coho Salmon	-22.34	15.82	20
	Ontario	Chinook Salmon	-22.07	15.61	121
	Ontario	Rainbow Trout	-22.00	15.32	33
	Ontario	Brown Trout	-21.90	16.98	71
Campbell et al., 2009	Erie	Rainbow Trout	-21.6	13.8	3
	Erie	White Sucker	-20.9	13.5	10
Gerig et al., 2019	Huron	Atlantic Salmon	-23.3	10.4	40
	Huron	Chinook Salmon	-23.4	11.8	43
	Huron	Coho Salmon	-23.4	10	10
Paterson et al., 2020	Huron	Smelt	-22.5	9.6	59
Paterson et al., 2016	Huron	Smelt	-22.6	9.8	129
Keough et al., 1996	Superior	Longnose Sucker	-24.8	8.4	6
	Superior	Rainbow Trout	-24.4	8.3	3
Jones and Mackereth, 2016	Superior	Brook Trout	-21.3	9.5	3
Robillard et al., 2011	Superior	Brook Trout	-20	8.3	10
	Superior	Rainbow Trout	-22.7	9	1
Harvey and Kitchell, 2000	Superior	Chinook Salmon	-24.73	8.04	6
	Superior	Coho Salmon	-24.86	6.89	3

Statistical Analysis

Preliminary Tests for Difference Amongst Great Lakes, Fish Species and Fish Size

Before hypothesis testing, it was necessary to identify any potential differences in the data that could obscure understanding patterns in resource subsidies. Potential geographic patterns in stable isotope signatures among the different Great Lakes could confound interpretations of subsidy patterns. Next, it was unclear if stream fish size was linked to differences in SI values, as potentially small individuals would be gape limited and not able to eat the subsidy. Finally, even though the variety of fish species caught were all from the same feeding guild (benthivorous), implying their stable isotope signatures should all be similar, it was imperative to determine if species had inherent differences in stable isotope values.

To assess if there was a geographic pattern in the stable isotope signatures among the Great Lakes I used a linear mixed (LME) model, using and the R package *nlme* in R Studio version 1.0.153 (R Development Core Team, 2017)(Pinheiro, J and Bates D, 2000). For these tests, only fish (n=314) from each river's uppermost site, above the barrier, were used because these fish should receive much less of a lake-derived subsidy than fish inhabiting downstream sections. This test used species as a random factor, controlling for its variance so that fish species did not obscure the effect of the lakes. A Tukey test, performed using *emmeans*, was subsequently used to further determine which lakes differed from the others (Lenth, 2021).

To test the potential for fish size influencing stable isotope values, a linear regression was used to compare δ^{13}C values with the length and mass for fish 314 unsubsidized sections. Smaller fish, due to their gape-limitation, may not be able to access the resource subsidy as readily as larger individuals, potentially creating a relationship between fish size and δ^{13}C. Additionally, to determine if fish size was distributed randomly across the sites, or if larger fish tended to be found more often on one side of a barrier, a paired t-test compared the difference in average length and average mass on either side of each barrier for each species. This was important because if fish size was distributed randomly across the barriers, then even if there was a relationship between size and δ^{13}C values, size would not bias the above/below SI comparisons. The results of these tests determined if fish size would need to be considered as part of subsequent analyses.

To assess if fish species influenced stable isotope values, a paired t-test compared the seven upstream sites where both longnose dace and sculpins were collected. These sites were the Sydenham River, the Manitou River, the Little Thessalon River, the Batchawana River, the Coldwater Creek, the Baldhead River, and the Wolf River. By using only paired sites where the target species were found, I avoided potential regional patterns in fish δ^{13}C values that could prevent the analysis of species differences.

In addition to sculpin and longnose dace, I examined stable isotope values of other fish species using an ANOVA and a Tukey's test. This test used all fish species from all upstream sites, as the sample size for each species within each lake was too small to run each lake separately (N=314). The results of these tests were used to determine if future analyses could be run on all species simultaneously or if they must be conducted on each species individually. As a result, sites where goby and rainbow darter were collected were excluded from further tests.

Subsidy Magnitude Among the Great Lakes

To investigate how resource subsidies vary across the Great Lakes, a linear mixed model was created to compare the difference in the magnitude of stable isotope change across barriers (upstream vs. downstream), using the *nlme* package (Pinheiro, J and Bates D, 2000). The difference in stable carbon isotope values across a barrier, created by subtracting the average SI value of the top site from the average value of the bottom site, can be used as a proxy for the magnitude of the subsidy. This simple calculation was performed across every sampled barrier, using each species. Additionally, this mixed model was used to determine if barrier type played a role in subsidy magnitude. The test was run once using the classification system with two barrier-types (complete barriers and partial barriers) and run a second time using the system with four barrier-types (complete barriers, human-intervened barriers, partial barriers, and unknown barriers). This linear mixed model tested two variables, Great Lake, and barrier type, as well as a random factor, fish species. The mixed model controls the variance caused it by the random factor, so that the influence of the lake and the barrier type on the subsidy is not obscured by the fish species. To appropriately run this test, the dataset was first tested to determine whether it met all assumptions of homogenous variance with a Levene median test, using the R package *car* in R Studio version 1.0.153 (Fox and Weisberg, 2019). Then the mixed model and associated ANOVA were run. Finally, two Tukey's tests were applied to determine which of the lakes significantly differed from each other, and which barrier type significantly differed from each other. An additional variance extraction function was performed to extract the amount of variance related to the random factor.

Subsidy Magnitude at Individual Rivers

To determine which rivers were significantly subsidised and where along the rivers subsidise were occurring, I applied a series of t-tests and Mann-Whitney U test using an $\alpha = 0.05$. Using the Lilliefors test all sites were tested for normality using the package *nortest*, of which several failed due to too small a sample size (Gross and Ligges, 2015). Adjacent sites were not tested if no barrier lay between them. Additionally, Cohen's d effect sizes were calculated to assess the magnitude of the differences across each barrier. The absolute magnitude of the d-values from each lake were then averaged together.

Diet Analyses based on Mixing Models

To further investigate the presence of lake-derived resource subsidies, the R package MixSIAR, as well as packages *gWidgets*, and *RGtk2*, were used in R Studio version 1.0.153 to develop a Bayesian mixing model that compares the SI values of a consumer and the SI values of its various prey sources (Lawrence and Lang, 2010; Stock et al., 2018; Verzani, 2019). Such a model determines how much each prey source, such as benthic invertebrates or migrant fish eggs, contributed to the diet of a consumer, such as longnose dace or sculpins. Both the $\delta^{13}C$ and $\delta^{15}N$ values of each consumer fish were input into MixSIAR, along with the carbon and nitrogen values for the invertebrates at each bottom site and the value of eggs from migrant fishes. Due to the natural differences in SI values between the Great Lakes, separate egg SI values were estimated for each lake using a combination of salmonid muscle samples and sucker muscle samples (Table 2.1). The discrimination factor is a measure of how much fractionation or isotopic enrichment occurs after a tissue is consumed and incorporated into the consumer. This value was taken from the literature as 0.8 for carbon and 3.4 for nitrogen (Vander Zanden and Rasmussen, 2001). Each river and species were run separately in each Great Lake to determine relative proportions of eggs and invertebrates in the diet.

Relationships between stream characteristics and the magnitude of resource subsidies

To examine the role of stream characteristics in the incorporation and function of resource subsidies, a correspondence analysis was performed, using the R package *FactoMineR* (Lê et al., 2008). I examined the relationship between the magnitude of the subsidy (up vs downstream δ13C values) and local factors (canopy cover, substrate type, stream reach slope, watershed area, distance from the river mouth) and regional factors (percentage of the watershed area that is agriculture land, and whether the watershed was on the Canadian Shield). A value for coarse substrate was calculated by combining the values out of 100 for large gravel, cobble, and boulders to yield a single value, as these larger substrates are more likely to capture and retain subsidies (e.g., eggs, carcasses). Each stream characteristic was normalized, to prevent larger values from dominating the regression, using the formula:

$$X_{\text{normalized}} = (X_{\text{raw}} - \text{minimum})/(\text{maximum} - \text{minimum})$$

The resulting dimensions from the correspondence analysis were plotted in a biplot and visually compared to the magnitude of SI difference above and below barriers.

Results

Fish size and species in relation to stable isotope values

The total length of fish was not associated with $\delta^{13}C$ values (ANOVA, $F_{1,312}$=3.019 R^2= 0.0095, P = 0.083); however, there was a significant relationship between $\delta^{13}C$ and the logarithmically transformed fish mass (ANOVA, $F_{1,312}$=13.567**,** R^2= 0.04167, P < 0.001), a**s** $\delta^{13}C$ became more enriched with increasing mass but this relationship was weak. There was no significant difference in fish length (paired t-test, d.f.= 47**,** P = 0.5605**)** or mass (paired t-test, d.f.= 47, P = 0.2328**)** from above and below barriers for the species**.** There were no significant differences in $\delta^{13}C$ between longnose dace (mean -29.14 ‰, SD= 3.09) and sculpin species (mean -28.82 ‰, SD= 2.29) collected from seven streams where both species were present (Paired t-test, d.f. = 47, P=0.5887). There were significant differences in $\delta^{13}C$ values among all species collected from each upstream site (ANOVA, $F_{5,308}$=4.49, P < 0.001). Tukey's test indicated that longnose dace and sculpins did not significantly differ (P=0.64) and were not significantly different from blacknose dace or white suckers (P>0.5), however, goby and rainbow darters were significantly different. The Tukey test found rainbow darter's $\delta^{13}C$ values differed from all other species (P<0.03) and goby $\delta^{13}C$ values differed from longnose dace and blacknose dace (P<0.10). These species were found only in one tributary of Lake Huron and one tributary of Lake Ontario, respectively.

Regional differences

There were significant differences in $\delta^{13}C$ values of fish sampled from above barriers (no to little subsidy) among streams of the four Great Lakes (ANOVA, $F_{3,294}=39.41$, $P < 0.001$). Fish from Lake Superior and Lake Erie rivers did not significantly differ ($P=0.8153$) but had higher $\delta^{13}C$ values, less negative, than fish from the tributaries of Lake Ontario and Lake Huron ($P < 0.001$, Figure 2.2). Fish from Lake Erie tributaries also averaged significantly higher $\delta^{13}C$ values than fish from Lake Ontario and Lake Huron ($P < 0.001$). Fish taken from Lake Huron tributaries were significantly depleted in $\delta^{13}C$ relative to Lake Ontario fish ($P < 0.001$, Figure 2.2).

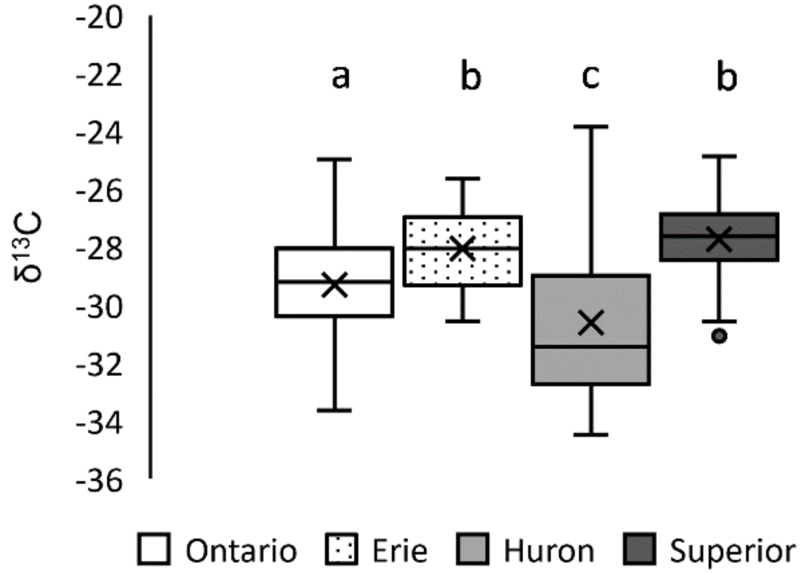

Figure 2.2. $\delta^{13}C$ values of all fish species from the uppermost site (no migrant subsidy) on each river grouped by Great Lake. Each box represents the range between the data's first and third quartiles, the line marks the median value, and the X marks the mean value. The whiskers show the minimum and maximum values in the set and outliers are marked by a dot placed beyond the whiskers. Letters above each box denote which groups were statistically similar.

The magnitude of the differences in δ^{13}C values from above and below all barriers pairs significantly differed among lakes (mixed model ANOVA, $F_{3,43}$=6.73, P = 0.008; Figure 2.3). Rivers flowing into Lake Superior tended to have downstream sites significantly more enriched in δ^{13}C relative to their upstream sites, more than the rivers flowing into Lake Ontario (P=0.0075), Lake Erie (P=0.0026) or Lake Huron (P=0.061). Lakes Huron, Erie, and Ontario were not significantly different from each other (Figure 2.3).

There were no significant differences in the magnitude of enrichment between complete and partial barrier types (mixed model $F_{1,43}$=0.31, P = 0.5782, Figure 2.4a). There was no interaction between the barrier type and which Great Lake the river flowed into ($F_{3,40}$=0.65, P = 0.586). There were also no differences among the four types of barriers (partial, unknown, ladder, complete) (mixed model $F_{3,43}$=2.00, P = 0.1276, Figure 2.4b).

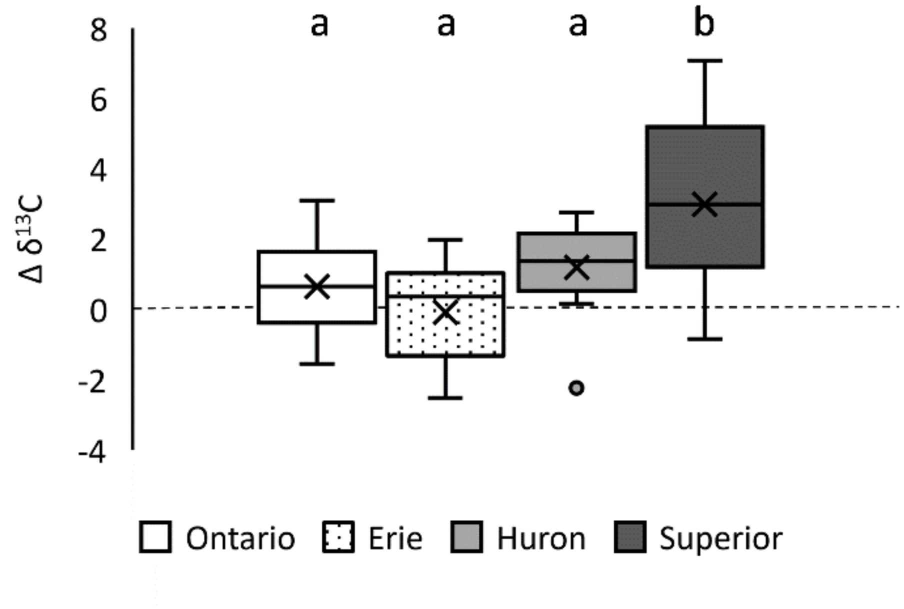

Figure 2.3. The magnitude of the subsidy for each barrier grouped by Great Lake. Differences calculated by subtracting the average δ^{13}C value at the site above the barrier from the site below the barrier. Positive values imply relative enrichment of δ^{13}C at the downstream site. Each box represents the range between first and third quartiles, the line marks the median value, and the X marks the mean value. The whiskers show the minimum and maximum values in the set and outliers are marked by a dot placed beyond the whiskers. Letters above each box denote which groups were statistically similar.

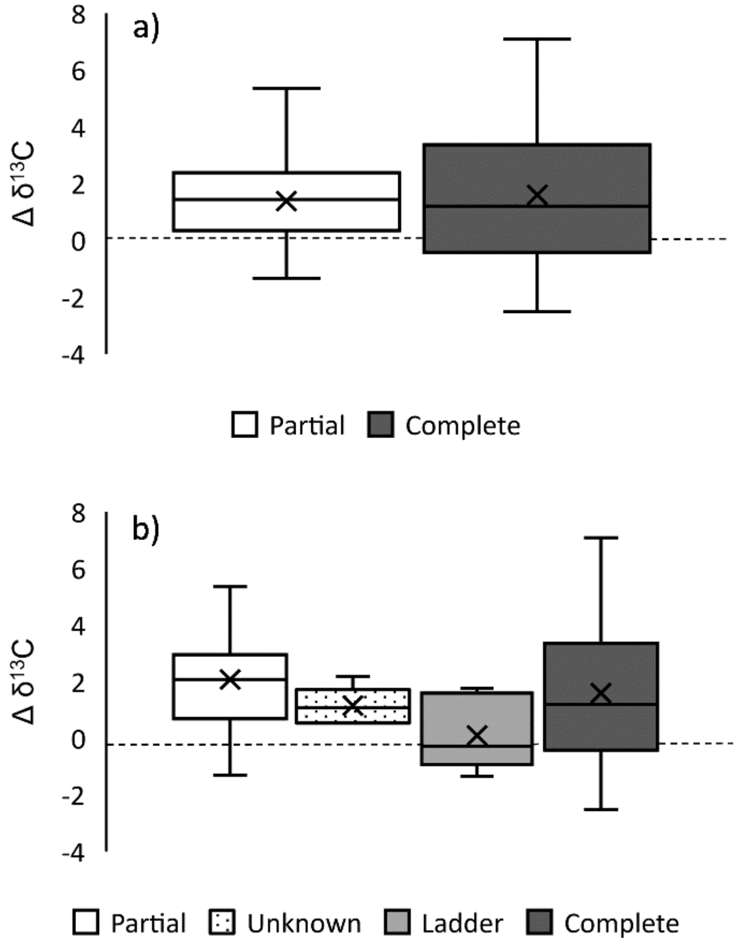

Figure 2.4. The magnitude of the subsidy for each barrier grouped by barrier type a) the two-barrier or b) the four-barrier classification system. Magnitude is calculated by subtracting the average $\delta^{13}C$ value at the site above the barrier from the site below the barrier. Each box represents the range between the first and third quartiles, the line marks the median value, and the X marks the mean value. The whiskers show the minimum and maximum values in the set.

Visual interpretation of $\delta^{13}C$ values

Visual examination of the of the average $\delta^{13}C$ value at each site yielded patterns that highlight the presence and distribution of lake-derived resource subsidies in Great Lake tributaries (Figure 2.5). Many of the sampled rivers had higher $\delta^{13}C$ values below barriers than above barriers. The largest and most frequent differences occurred in the Lake Superior basin and in rivers with complete barriers. In rivers with multiple barriers, the most significant difference in $\delta^{13}C$ tended to be across the first barrier. Some of the rivers with partial barriers (e.g., Manitou River) had higher $\delta^{13}C$ values on each side of the barrier suggesting enrichment by subsidies on both sides. Wilmot Creek, which has no barriers to fish passage, had elevated $\delta^{13}C$ values throughout its lower reaches and less enrichment at the sites closer to the headwaters (Figure 2.5).

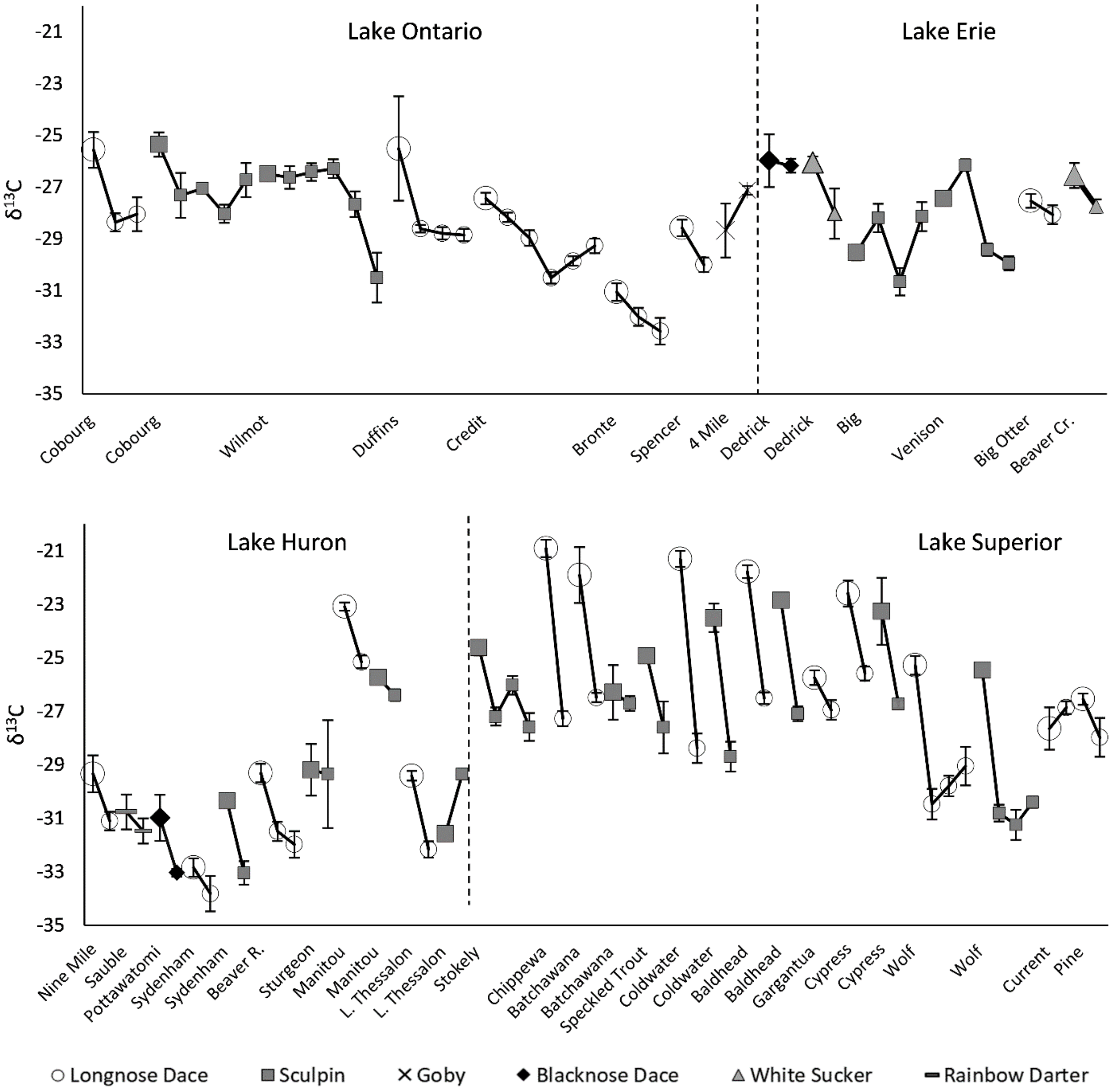

Figure 2.5. Average δ^{13}C at each site for six fish species; bars represent 95% confidence intervals. Sites along the same river are connected by a line, with the leftmost point on each line representing the site closest to the lake and the rightmost point representing the site highest in the watershed. Sites with a greater enrichment of δ^{13}C are more elevated on the y-axis. The vertical, dotted lines differentiate the Great Lake watersheds (Ontario, Erie, Huron and Superior, respectfully).

Differences in carbon isotopes at individual tributaries

Of the 54 comparisons from above and below barriers, 36 were significantly greater (enriched) downstream (t- and Mann-Whitney tests, $P < 0.05$, Figure 2.6). 9 were significantly lower downstream, and 9 were not statistically different. The average Cohen's d-value was 1.97 for Lake Ontario, 2.01 for Lake Erie, 2.56 for Lake Huron, and 3.71 for Lake Superior, with larger values representing greater effect sizes. Individual d-values for each barrier comparison can be found in Table 4.2 in Appendix II. To summarize, six of seven Lake Ontario rivers, four of five Lake Erie rivers, six of eight Lake Huron rivers, and ten of eleven Lake Superior rivers showed greater $\delta^{13}C$ values downstream than upstream across at least one barrier on the river. In contrast, Four Mile Creek gobies, and Big Creek and Little Thessalon sculpins were significantly more enriched in $\delta^{13}C$ at the upstream sites than the downstream.

Nine rivers had multiple barriers (i.e., 2-3) limiting movement of migrating fishes totalling 20 comparisons. Significant differences in $\delta^{13}C$ were found across all of the barriers though only thirteen of these comparisons found the downstream site to be enriched in $\delta^{13}C$. Nine of the eleven (82%) of first barriers showed significant enrichment downstream. Four of ten (40%) of second barriers had significant enrichment. Two rivers, Cobourg Creek and the Credit River, had a third barrier upstream that were more enriched upstream.

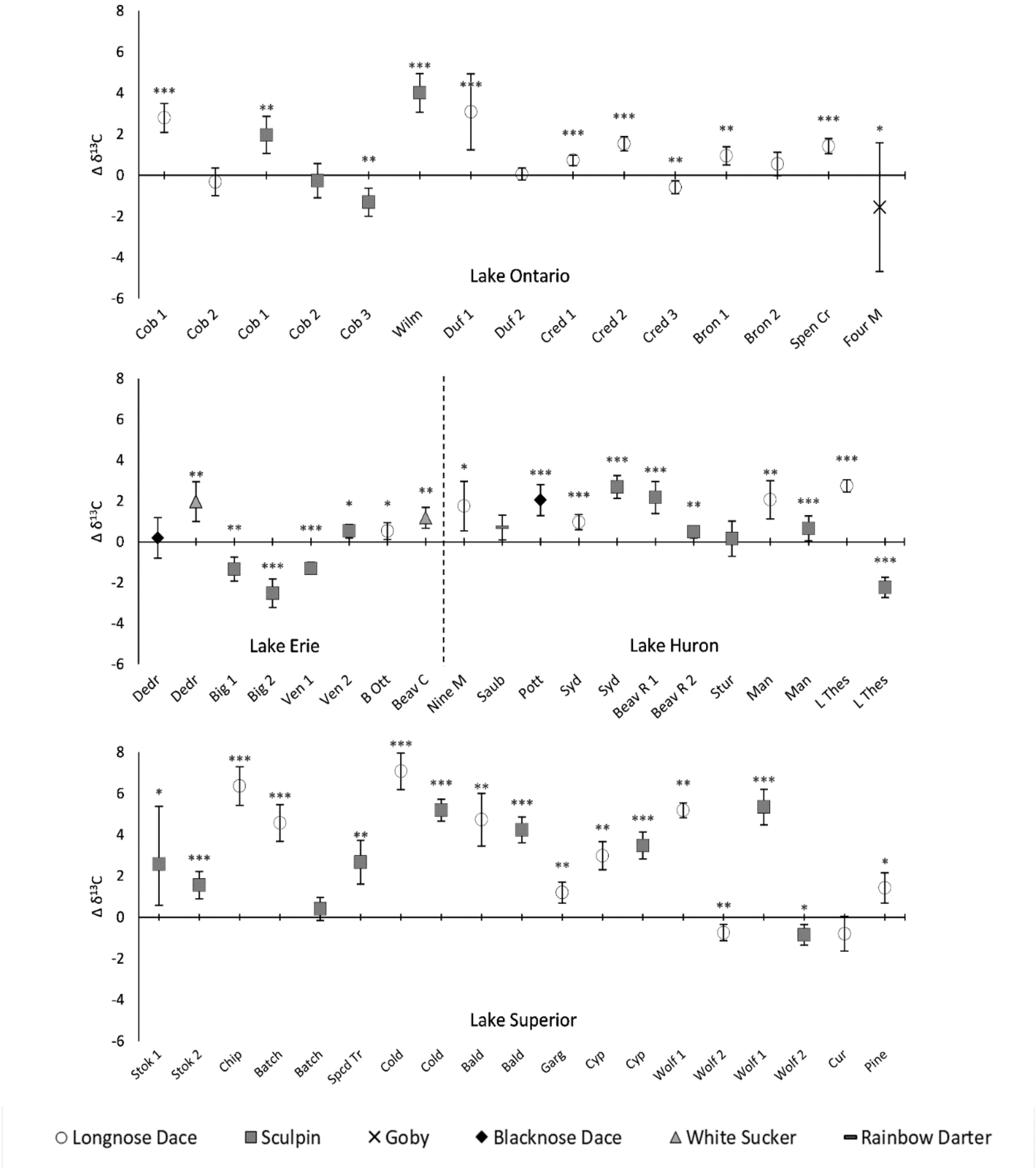

Figure 2.6. The magnitude of the subsidy for each river by species, 95% confidence intervals (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). A positive difference implies a relative enrichment of $\delta^{13}C$ at the downstream site. The very top and bottom sites of Wilmot Creek were also compared and shown here despite the river containing no barriers to fish passage. Full river names can be found in Appendix II.

Diet analyses based on mixing models

Mixing models estimated that the diets of fish in Great Lake tributaries partially included lake-derived subsidies. The proportion of the diet represented by the eggs or carcasses of migrant fishes varied among rivers (range 5-90%, Figure 2.7). Lake subsidies, mainly eggs, in the diet of stream fishes represented on average 13% for Lake Ontario, 6% for Lake Erie, and 9% for Lake Huron. Lake Superior was the only lake where egg subsidies represented most of the diet of stream fish (average 52%). Benthic invertebrates are therefore still the primary food source for stream fish in Lake Huron, Lake Erie, and Lake Ontario (Figure 2.7).

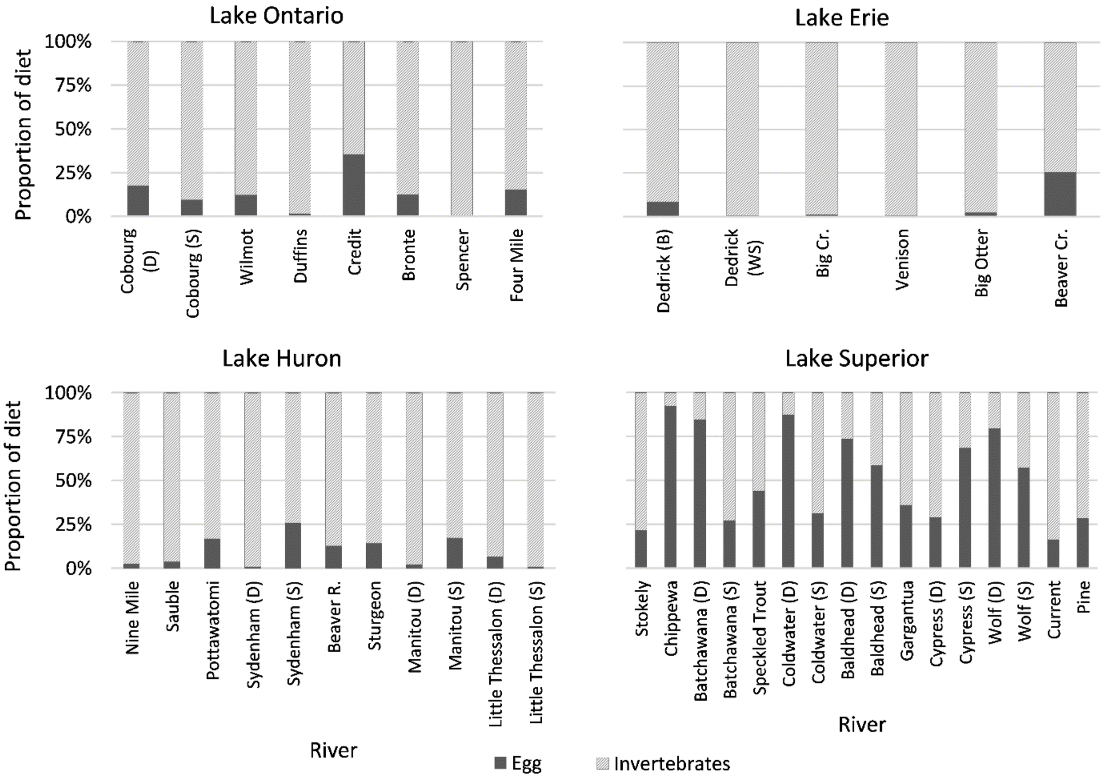

Figure 2.7. Dietary proportions of eggs and invertebrates of stream fishes (D – longnose dace, S – sculpins) based on a Bayesian mixing model (MixSIAR). Eggs are from migratory fishes (e.g., trout, salmon, suckers) and represent part of the resource subsidy.

Relationship between stream characteristics and the magnitude of carbon enrichment

Correspondence analysis showed relationships among regional and local-stream characteristics and the magnitude of enrichment (difference between $\delta^{13}C$ values above and below barriers) (Figure 2.8). The first CA axis explained 55.5% of the variation and was positively correlated with streams on the Canadian Shield and negatively correlated with increasing temperature and agriculture lands. This places Lake Superior tributaries on the positive side of the first axis; these tributaries had the largest differences in $\delta^{13}C$

values up- and down-stream suggesting a large carbon enrichment. The second axis explained 17.1% of the variation and was positively correlated with watershed area and negatively correlated with slope and coarse substrate (large gravel, cobble, and boulders). Canopy cover did not appear to meaningfully contribute to this model. The third axis (not shown) explained only 11.8% of the variation.

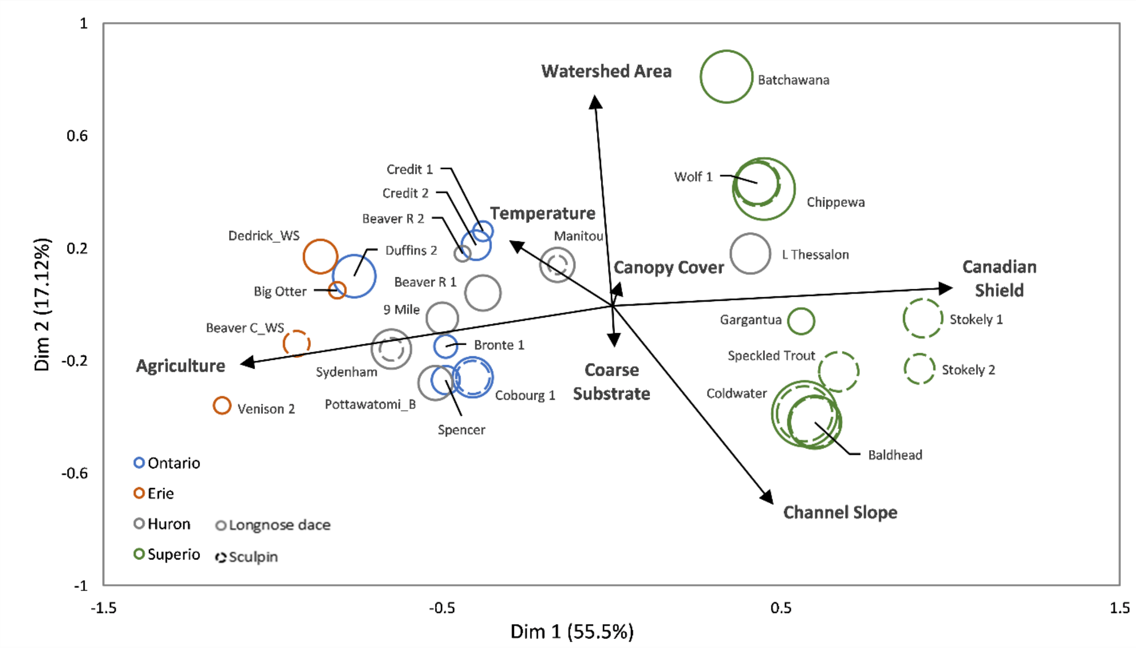

Figure 2.8. Correspondence analysis biplot of stream characteristics (vectors) measured downstream of the first barrier and the $\Delta\ \delta^{13}$C values at the barrier (upstream minus downstream δ^{13}C value). The size of each circle is proportional to the $\Delta\ \delta^{13}$C. Fish species other than the primary two (sculpin and longnose dace) are included in the stream label: G – goby WS – white sucker, BND – blacknose dace, R – rainbow darter. The numbers in parentheses represent the percentage of variance explained by each axis.

Discussion

This study supports the hypothesis that that many Great Lakes tributaries have enriched levels of $\delta^{13}C$ downstream of barriers relative to upstream reaches. These differences are likely due to resources subsidies (i.e., eggs, excrement, and carcases) from spawning migratory fishes (e.g., Salmonidae, Castostomidae) from the Great Lakes. The magnitude of enrichment of $\delta^{13}C$ varied among the Great Lakes, with the largest enrichment in Lake Superior rivers and smaller up- and down-stream differences in Lake Ontario, Lake Huron, and especially Lake Erie. Some environmental factors appeared to influence the enrichment, including stream slope which had a positive relationship with $\delta^{13}C$ differences and agricultural land-use having a negative relationship. The type of barrier that migrants encountered, and at times crossed, did not have an apparent influence on the magnitude of the enrichment, however the classification of barrier type was imperfect.

Resource subsidies because of migratory spawning fishes occur in rivers throughout the Great Lakes basin, as evidenced by the enriched levels of $\delta^{13}C$ below barriers. Higher levels of $\delta^{13}C$ below barriers is consistent with other studies of tributaries of the Great Lakes (Childress and McIntyre, 2016; Jones and Mackereth, 2016; Rand et al., 1992; Sarica et al., 2004; Schuldt and Hershey, 1995). For example, Childress et al. (2014) and Jones and Mackereth (2016) used SIA to identify that stream invertebrates and fish were enriched with lake-derived carbon and nitrogen following spawning migrations, compared to upstream reaches. Schuldt and Hershey (1995) and Sarica *et al.* (2004)

identified resource subsidies in Great Lake tributaries by detecting the associated increases in NH_4, dissolved organic carbon (DOC), and phosphorous, a different but complementary methodology to $\delta^{13}C$ SIA. Others concluded that migratory fish subsidies do not affect invertebrate density (Ivan et al., 2011), fish density (Burtner et al., 2011), or primary productivity, but suggest that local agricultural activity increases nutrient concentrations and likely negates the potential benefits from migratory fish subsidies (Rand et al., 1992).

Based on MixSIAR mixing models, the diets of stream fishes (cottids and leuciscids) below barriers were between 1-35% originated from lake subsidies for lakes Ontario, Erie, and Huron, but represented on average 52% of the diet of fish from Lake Superior tributaries. This finding is consistent with previous studies that also examined fish diets, such as Joy *et al.* (2020) who recorded between 0-40% assimilation of tissues following a spring salmon migration in Alaska, and Jones and Mackereth (2016) that showed that lake-derived subsidies accounted for 30-58% of stream fishes' diets in a Lake Superior tributary. This shows that resident stream fish incorporate nutrients from resource subsidies into their new tissues, taking advantage of surges in food resources and consuming seasonally available eggs laid by migrants. Gorging is an energetically costly feeding strategy, requiring the development of robust digestive tract which typically cannot be maintained for extended periods of time. Instead, many fish species such as Dolly Varden increase the size of their digestive system in response to pulses in subsidies, allowing them to maximize intake of available food (Armstrong and Bond, 2013; Armstrong and Schindler, 2011). Great Lake stream fishes likely also exhibit gorging behaviour following spring and fall spawning migrations, although in the current study any effect of fall subsidies would have dissipated by the time fishes were sampled. Sampling throughout the year could better quantify the linkages between the lake and its tributaries (Joy et al., 2020).

While the MixSIAR mixing model can estimate the proportion of the diet that was lake-derived versus stream-derived, it can not determine whether the heavy isotopes were accumulated directly or indirectly – that is, through direct consumption of migrant eggs or indirectly from aquatic invertebrates that fed on the tissues of migratory fishes or via nutrients excreted from fishes that increased primary productivity. Post-subsidy boosts in primary production have been linked to increases in, or δ^{13}C enrichment of, benthic invertebrates, suggesting invertebrates are feeding on the enriched algae or biofilms and that they represent a secondary path for resident fish to benefit from the donation (Childress et al., 2014; Jones and Mackereth, 2016; Wipfli et al., 1998). Additionally, instead of gonad δ^{13}C values from migrants entering each river, the food source data used in the MixSIAR model came from individuals caught in each Great Lake and at different times of the year. This potentially introduced bias into the comparison, over- or under-emphasizing the importance of eggs in stream fish diets. More specific data, such as δ^{13}C values that are acquired from region- or river- specific migrants and their eggs, may more accurately quantify the proportion of stream fish diet that comes from subsidies.

The magnitude of the subsidy in each stream was estimated by subtracting the average downstream δ^{13}C from the average upstream δ^{13}C value, a method which relies on the assumption that the upstream values are unsubsidized (Bilby et al., 1998; Kline et al., 1990). This is not necessarily true for all comparisons because jumping fish species can cross and spawn above partial barriers, leading to increased δ^{13}C values in the upstream reach. This scenario results in the difference across the barrier appearing minimal or nonexistent, as both upstream and downstream fish are enriched at similar rates and so the tissue δ^{13}C values do not appear different, despite a resource subsidy occurring. Without a complete barrier upstream, there is no true control to compare the subsidized reaches. For example, Lake Huron's Manitou River has only modest δ^{13}C differences between above and below the partial barrier, but both sections of river appear to have elevated δ^{13}C values compared to the unsubsidized upstream reaches of neighbouring streams. Examination of nearby streams that do not receive any migrants and could serve as a baseline could confirm such above-barrier enrichment.

Additionally, some of the barriers that I judged to be complete barriers that could be used as a true control may not have 100% effective at stopping fish, especially during high flows. The classification system was created using site visits and local knowledge, but this was unavailable for some sites and may have been misleading. Future studies may choose to use barriers whose permeability is more certain. Alternatively, stable isotope analysis may be a useful tool to determine and classify the permeability of barriers by comparing above-below barrier δ^{13}C values.

Wilmot Creek provides an example of spatial patterns of enrichment in a river system without barriers. Enrichment levels were high for the first four sites or 10km upstream from the lake. Based on δ^{13}C values the remaining 18 km had lower subsidies. The two sites not heavily enriched were small headwater stream not typically used by chinook (*Oncorhynchus tshawytscha*), the most abundant migrant salmonid in the river, coho (*Oncorhynchus kisutch*), and steelhead (*Oncorhynchus mykiss*) (Sarica et al., 2004). This is consistent with our understanding of salmonid spawning behaviour as some species (e.g., Chinook salmon) spawn lower in the watershed (Clark et al., 2015). Wilmot Creek also highlights how the addition of a complete barrier lower in the drainage could limit lake-derived subsidies, originally destined for the upstream reaches, and the benefits to the production of fishes subsidies provide. However, it also demonstrates that the higher in the watershed that a barrier is constructed, the smaller its effect on subsidies however this may have other consequences related to habitat fragmentation (Fausch et al., 2009). Future studies may wish to examine the relationship between resource subsidies and distance a barrier is from the river's mouth.

δ^{13}C enrichment varied among the Great Lakes, with the greatest differences occurring in Lake Superior tributaries, suggesting environmental factors may be influencing the incorporation of the subsidy. The correspondence analysis in this study illustrated that there is an association between enrichment and regional factors such as agricultural land-use and the Canadian Shield. These regional-scale environmental factors may be the cause behind the differences between the lakes as the nutrient status of rivers is influenced by the surficial geology and land-use in the watershed (Marcarelli et al., 2019). As Flecker *et al.* (2010) outlined, the background nutrient status of a recipient ecosystem can modulate the effect of a resource subsidy. Agriculture areas surrounding Lake Erie, southern Lake Huron, and Lake Ontario tend to have higher nutrient run off due to naturally nutrient-rich soil and use of fertilizers (Robertson and Saad, 2011). While these nutrients do not directly affect stable isotope values, they can reduce the impact of resource subsidies, as nutrients may not represent the limiting factor in these streams, due to their abundance. Rand et al. (1992) suggested that instead in these streams light penetration through riparian canopy is likely the limiting factor affecting primary productivity. This means a nutrient addition from migrant fish would not substantially augment primary productivity in the stream (Lee et al., 2018; Robertson and Saad, 2011; Subalusky and Post, 2019). However, even when the surrounding land-use obscures a resource subsidy from contributing through mechanisms of primary productivity, the subsidy can still benefit an ecosystem through the direct consumption of tissues (e.g., eggs), as this provides nutrients directly to the consumers**.** In contrast, streams located on the Canadian Shield tend to be oligotrophic due to surficial geology and poor soil development (Marcarelli et al., 2019). In these streams, nutrients are likely limiting primary productivity and so they respond to a resource subsidy (i.e., excrement and decomposing carcasses) by increasing primary productivity. Many studies have detected an increase in primary production following a migration of fishes into nutrient-poor streams, as well as enrichment of macroinvertebrates through pathways other than direct tissue consumption (Childress et al., 2014; Robertson and Saad, 2011; Zhang et al., 2003). The injection of nutrients into oligotrophic streams by resource subsidies provides an opportunity for increased primary production which in turn can feed the invertebrates and resident fish, producing a characteristic $\delta^{13}C$ signature.

In addition to regional-scale factors, the effects of resource subsidies can also be influenced by local-scale factors such as channel structure, substrate type, and woody debris (Cederholm et al., 1999; Minakawa and Gara, 2005; Roseman et al., 2011) that influence retention of materials (e.g., eggs, carcasses). As Flecker *et al.* 2010 proposed, for a resource subsidy to influence the stream ecosystem it must be present long enough to be incorporated and not simply washed away. Large substrate sizes and woody debris in conjunction with more slowly flowing mesohabitat areas (e.g., pools) are important elements in the retention of subsidies in streams as they help retain subsidy materials and increasing the likelihood that nutrients are incorporated (Minakawa and Gara, 2005). Resident fish consume eggs while migrant carcasses and excrement are retained to decay and release nutrients for primary productivity (Cederholm et al., 1999; Roseman et al., 2011). Streams with simplified channels will not retain subsidies very well as removal of woody debris, sand riverbed and straightened channels tend to wash nutrients away (Ito et al., 2005). In my study, I found no apparent association between substrate type and subsidy magnitude in this study; however, I did find steeper slopes tended to have increased resource subsidies. In such steeper sloped streams, subsidies can be held by successive step pools, a physical structure that is common in streams with steep gradients (Mccabe et al., 2010). It is also possible that steeper channel slopes are just a spurious association because tributaries flowing into Lake Superior are heavily enriched relative to other Great Lakes and generally these northern rivers have steep channel slopes.

Canopy cover can alter a subsidy’s ability to boost a stream’s primary productivity because heavy canopy cover prevents sunlight reaching the water (Warren et al., 2013). Interestingly, there was no association between the magnitude of the subsidy and canopy cover in this study. My findings are different than previous studies as Rand et al. 1992 suggested that light availability controlled primary production in agricultural tributaries of Lake Ontario, implying that a nutrient addition to a shaded stream would not be as meaningful to primary production as nutrient addition to a stream without canopy cover. Similarly, (Ambrose et al., 2004) found that nutrients from resource subsidies were absorbed and useful to the ecosystem only when the stream was exposed to sunlight. These conflicting findings may indicate that direct consumption of fish eggs may have more consistent influence on productivity than excrement and carcass consumption via primary productivity.

The number of migrant fishes and/or their biomass is likely the most influential factor on the magnitude of the subsidy, however, information was generally not available on run size, biomass, or species composition. More numerous migrants provide a larger subsidy which may mask the effect of other environmental factors. A river system with "poor" environmental factors but receiving a large number of migrants may result in a greater δ^{13}C difference than a river with more favourable environmental factors but a small migration. The area in which spawning fish use in each stream, and how differences in stream length and width below barriers also play roles in the detection of resource subsidies. For example, a run with many migrant fishes in a small stream would lead to a high density of nutrients and stronger δ^{13}C enrichment per unit area, compared to the same run size in a larger stream, as the nutrients would be dispersed over a larger area (Hocking and Reimchen, 2009). Additionally, a small number of migrant fishes is unlikely to provide much of a subsidy even if the river has favourable stream conditions such as being nutrient-poor and capable of retaining subsidy materials (Flecker et al., 2010). Thus, it is difficult to compare the influence of environmental factors, and barrier type on the magnitude of the subsidy without quantitative data on the density or biomass of fishes spawning in the streams.

Future research into resource subsidies in the Great Lakes should consider the animal vector characteristics, such as the number of individuals migrating into the rivers as well as the species composition of the migration. Understanding which species migrate into the river would allow for greater resolution in comparisons of barrier types, as only some species can jump above partial barriers. This study focused on the impacts of spring migration events, yet large fall migrations do occur (e.g., pink salmon, *Oncorhynchus gorbuscha*) and likely contribute a resource subsidy capable of influencing stream productivity that is worth considering in future research (Jones and Mackereth, 2016). Researchers wishing to further investigate Great Lake resource subsidies can use the findings of this study to direct their study and refine hypotheses. They may choose to have stricter control over which regions they study or to focus on tributaries of a specific Great Lake as each lake has significantly different magnitudes of enrichment.

This study demonstrated that resource subsidies are occurring in many Great Lake tributaries and is the first examination of stream characteristics that may influence the magnitude of the subsidy. These findings are generally consistent with predictions about resource subsidies in aquatic ecosystems (Flecker et al., 2010). As studies demonstrate, the fragmentation of stream networks has several harmful and long lasting effects on stream ecosystems and their inhabitants: preventing access to spawning areas (Fuller et al., 2015; Novak et al., 2015; Perkin et al., 2013), restricting gene flow (Fuller et al., 2015; Pavlova et al., 2017), and increasing mortality risk for individuals crossing the barrier through increased energy expenditure or injury (Roscoe et al., 2011). As my study demonstrates, barriers also prevent resources subsidies from contributing to ecosystems above some barriers which may limit stream productivity and consequently the growth, survival, and recruitment, of young migrant and resident fishes (Bilby et al., 1998; Freeman et al., 2003; Jardine et al., 2008). This fact is highlighted by Wilmot Creek, a river without barriers, where migrating fishes spawned in the whole watershed. Intuitively, barriers to fish, and their subsidies, have the most impact on lower mainstem reaches that block access to entire watersheds (Cote et al., 2009). Partial barriers, those that limit non-jumping fishes (e.g., sea lamprey weirs), limit potential resource subsidies of non-jumping fishes that would benefit both the juveniles of the jumping migratory fish and resident stream fish (Jones and Mackereth, 2016). The presence of barrier on many other tributaries to the Great Lakes are likely limiting the production of stream fishes and migratory fishes that depend on streams for juvenile production. The importance of resource subsidies should be considered when decisions are made about the fate of existing and the construction of new barriers that might result in reduced stream productive capacity.

CHAPTER 3. GENERAL CONCLUSIONS

This thesis demonstrates that resource subsidies from migratory lake fish occur across the Great Lakes watershed. Lake Superior had the largest subsidies, as evidenced by the greater enrichment of its rivers, while Lake Erie had the smallest resource subsidies. These differences imply that there are other factors that influence the relative importance of resource subsidies, such as regional and local environmental factors like catchment productivity, agricultural land-use, stream substrate size, and channel slope. Regional factors such as agricultural land use and whether the river was on the Canadian Shield were associated with larger differences in $\delta^{13}C$ across barriers and show the context dependency of animal resource subsidies. These factors play roles in controlling the primary productivity of a stream and therefore can influence to what extent nutrients from excrement or decomposing tissues can be incorporated into the food chain via primary producers and consumers. Local factors such as the channel slope were also associated with large $\delta^{13}C$ differences. High stream channel slopes tend to include step-pool structures that can capture and retain tissues, thus extending the time available to be consumed by residents before being washed away. There was, however, no apparent association found between differences of $\delta^{13}C$ and substrate size and canopy cover. Nevertheless, as demonstrated in other areas, large substrate sizes can also provide settling areas in crevasses and snag drifting materials (Minakawa and Gara, 2005). Canopy cover can mediate the responses to nutrient addition by shading streams (Ambrose et al., 2004).

Interaction between the environmental factors of the recipient ecosystem and animal vector characteristics from the donor ecosystem determine the quantity, quality, timing, and duration of a subsidy (Flecker et al., 2010; Subalusky and Post, 2019). Though not examined as part of this study, the differences in the magnitude of subsidies are likely also related to differences in the number and biomass of migrating lake fish. A small migration yields a minimal $\delta^{13}C$ difference, regardless of the stream characteristics, meaning it is difficult to determine which external factors are influencing the magnitude of the enrichment and could potentially result in an otherwise favourable characteristic appearing unfavourable. Conversely, a large migration could produce enough of a $\delta^{13}C$ difference for unfavourable factors to appear beneficial.

Differences in $\delta^{13}C$ values above and below barriers showed that below-barrier stream fish are consuming nutrients derived from fish that grew in the lakes rather than in the rivers. While much of the consumption was likely in the form of feeding directly on migrant tissue or eggs, it likely also involved nutrients entering the food web via primary producers incorporating the dissolved nutrients (Jones and Mackereth, 2016). This inference was supported by the negative association between rivers with large $\delta^{13}C$ differences and high proportions of agricultural land-use, as in these rivers nutrients likely are not the limiting factor and so are not being absorbed (Childress et al., 2014; Flecker et al., 2010; Robertson and Saad, 2011). Canopy cover, however, was not associated with $\delta^{13}C$ differences and so did not support the argument that subsidies were entering the food web via primary producers. Diet mixing models also indicated that resource subsidies encompass significant proportions of the diet of stream fish following the spawning migration in some systems.

Contrary to the hypothesis that fully impassable barriers would have greater $\delta^{13}C$ differences, barrier type was found to not influence the magnitude of the subsidy. Both complete and partial barriers had similar $\delta^{13}C$ differences across them, however, several partial barriers (e.g., Manitou River) had elevated $\delta^{13}C$ values both above and below barriers. This suggests there is a lack of true controls (i.e., an upstream section above a barrier with no subsidy) on some rivers examined. Neighbouring rivers with known complete barriers may provide appropriate controls in future research. The classification of barriers (i.e., complete or partial) was based on site visits and local knowledge, and as such, could also lead to errors, in addition to some complete barriers becoming partial barriers during especially high flows. In fact, stable isotope analyses could be used to classify the permeability of barriers based on the above-below barrier isotopic differences rather than how we perceive permeability.

The results of this study highlight the importance of resource subsidies in the Great Lakes basin. The nutrients in these subsidies have the potential to greatly benefit recipient stream ecosystems and are an important influence on trophic structure, such as increasing primary productivity (Childress and McIntyre, 2016; Subalusky and Post, 2019), benthic biomass (Larson et al., 2020), and juvenile salmonid growth (Flecker et al., 2010). In turn, the subsidies may influence both the recipient stream’s response to further inputs and in turn influence the donor ecosystem with reciprocal flows of energy and nutrients (e.g., Lake Superior) (Wipfli et al., 1998). Fragmentation of Great Lakes tributaries blocks the movement of spawning adults and prevents this nutrient feedback loop from benefiting headwater ecosystems and ultimately the populations of migrant lake fish. This study also demonstrates the usefulness of stable isotope analysis to understanding food chains and animal migrations in freshwater ecosystems (Jones and Mackereth, 2016; Schuldt and Hershey, 1995; Stockwell et al., 2014). Stable isotopes, analyzed across such biogeographic scales, can lead to better understand how migratory fishes, and their subsidies, are translated by recipient ecosystem characteristics.

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APPENDIX

Table 4.1. Total number of fish collected by species.

Species	Latin name	Total fish kept
Longnose dace	*Rhinichthys cataractae*	657
Sculpins	*Cottidae*	555
Round goby	*Neogobius melanostomus*	32
Western blacknose dace	*Rhinichthys obtusus*	60
White suckers	*Catostomus commersonii*	48
Horny head chubs	*Nocomis biguttatus*	12
Rainbow darters	*Etheostoma caeruleum*	36
Creek chubs	*Semotilus atromaculatus*	12

Table 4. 2. P-values and Cohen's d values following t- and Mann-Whitney tests comparing $\delta^{13}C$ values above and below each barrier. There is no barrier on Wilmot Creek, so the comparison occurred between the uppermost and lowest sites. Larger d-values imply a larger effect size.

Lake	River	Barrier #	Species	p-value	Cohen's D
Ontario	Cobourg	1	Longnose Dace	<0.001	3.55
Ontario	Cobourg	2	Longnose Dace	0.425	-0.41
Ontario	Cobourg	1	Sculpin	0.002	1.96
Ontario	Cobourg	2	Sculpin	0.570	-0.30
Ontario	Cobourg	3	Sculpin	0.006	-1.72
Ontario	Wilmot	0	Sculpin	<0.001	2.08
Ontario	Duffins	1	Longnose Dace	0.012	1.11
Ontario	Duffins	2	Longnose Dace	0.713	0.16
Ontario	Credit	1	Longnose Dace	<0.001	2.55
Ontario	Credit	2	Longnose Dace	<0.001	4.00
Ontario	Credit	3	Longnose Dace	0.005	-1.70
Ontario	Bronte	1	Longnose Dace	0.002	1.93
Ontario	Bronte	2	Longnose Dace	0.104	0.88
Ontario	Spencer	1	Longnose Dace	<0.001	2.75
Ontario	Four Mile	1	Goby	0.203	-4.41
Erie	Dedrick	1	Blacknose Dace	0.730	0.18
Erie	Dedrick	1	White Sucker	0.007	2.14
Erie	Big Cr	1	Sculpin	0.002	-2.07
Erie	Big Cr	2	Sculpin	<0.001	-3.20
Erie	Venison	1	Sculpin	<0.001	-3.93
Erie	Venison	2	Sculpin	0.012	1.44
Erie	Big Otter	1	Longnose Dace	0.038	1.15
Erie	Beaver Cr	1	White Sucker	0.002	1.97

Lake	River	Barrier #	Species	p-value	Cohen's D
Huron	Nine Mile	1	Longnose Dace	0.028	1.37
Huron	Sauble	1	Rainbow Darter	0.058	1.05
Huron	Pottawatomi	1	Blacknose Dace	<0.001	2.46
Huron	Sydenham	1	Longnose Dace	<0.001	2.31
Huron	Sydenham	1	Sculpin	<0.001	4.42
Huron	Beaver R	1	Sculpin	<0.001	2.45
Huron	Beaver R	2	Sculpin	0.009	1.51
Huron	Sturgeon	1	Sculpin	0.753	0.16
Huron	Manitou	1	Longnose Dace	0.002	1.98
Huron	Manitou	1	Sculpin	0.083	1.10
Huron	Little Thessalon	1	Longnose Dace	<0.001	7.91
Huron	Little Thessalon	1	Sculpin	<0.001	-4.02
Superior	Stokely	1	Sculpin	0.047	1.12
Superior	Stokely	2	Sculpin	<0.001	2.09
Superior	Chippewa	1	Longnose Dace	<0.001	6.13
Superior	Batchawana	1	Longnose Dace	<0.001	4.87
Superior	Batchawana	1	Sculpin	0.208	0.54
Superior	Speckled Trout	1	Sculpin	0.002	2.38
Superior	Coldwater	1	Longnose Dace	<0.001	5.79
Superior	Coldwater	1	Sculpin	<0.001	7.19
Superior	Baldhead	1	Longnose Dace	<0.001	4.82
Superior	Baldhead	1	Sculpin	<0.001	4.81
Superior	Gargantua	1	Longnose Dace	<0.001	1.75
Superior	Cypress	1	Longnose Dace	<0.001	2.35
Superior	Cypress	1	Sculpin	<0.001	2.96
Superior	Wolf	1	Longnose Dace	<0.001	12.03
Superior	Wolf	2	Longnose Dace	0.006	-1.69
Superior	Wolf	1	Sculpin	<0.001	5.79
Superior	Wolf	2	Sculpin	0.011	-1.55
Superior	Current	1	Longnose Dace	0.125	-0.82
Superior	Pine	1	Longnose Dace	0.008	1.82

Table 4. 3. Stream characteristics and Universal Transverse Mercator (UTM) coordinates of each river's lowest site. Watershed Area, Distance to Mouth, Slope, and Percent Farmland were collected using the Ontario Stream Assessment Tool. Canopy cover and Substrate were collected in the field.

Lake	River	UTM Zone	Easting	Northing	Watershed Area km^2	Distance to Mouth km	Slope °	Canopy Cover	% Rocky Substrate	% Farm Land
Ontario	Moira	18T	309510	4893784	2738.2	1.9	1.9	96.0	50	16.2
Ontario	Cobourg	17T	726117	4871143	123.2	0.9	2.7	93.5	100	51.6
Ontario	Wilmot	17T	692441	4864336	88.2	1.0	2.7	82.8	40	64.2
Ontario	Duffins	17T	656516	4856799	260.0	6.1	0.3	73.5	15	59.8
Ontario	Credit	17T	605281	4825511	766.8	18.2	3.2	96.0	90	50.9
Ontario	Bronte	17T	588592	4809629	197.9	31.3	3.3	35.8	100	48.8
Ontario	Spencer	17T	583356	4791250	158.2	5.9	6.4	51.0	85	57.5
Ontario	20 Mile	17T	632232	4777840	292.1	6.9	1.8	61.3	64	75.8
Ontario	4 Mile	17T	652475	4786837	18.3	9.6	1.3	6.8	75	59.3
Erie	Dedrick	17T	543467	4722344	35.7	13.4	0.8	17.8	5	38.8
Erie	Big Creek	17T	540741	4744825	305.6	78.5	0.5	18.8	70	78.7
Erie	Venison	17T	537024	4722424	95.8	0.7	1.7	76.0	20	66.0
Erie	Big Otter	17T	522823	4745195	354.1	74.9	0.4	40.5	55	80.0
Erie	Beaver C	17T	483152	4727374	21.6	2.4	3.5	1.8	30	69.3

Lake	River	UTM Zone	Easting	Northing	Watershed Area km^2	Distance to Mouth km	Slope °	Canopy Cover	% Rocky Substrate	% Farm Land
Huron	9 Mile	17T	442444	4858620	244.9	0.9	4.0	96.0	80	66.3
Huron	Saugeen	17T	473588	4928039	3971.4	5.0	1.2	96.0	100	65.7
Huron	Sauble	17T	485333	4942366	588.0	22.9	0.7	96.0	55	64.2
Huron	Indian	17T	504067	4940771	81.0	0.4	20.9	53.3	90	53.6
Huron	Pottawatomi	17T	501933	4934256	109.2	5.9	4.0	55.3	88	57.5
Huron	Sydenham	17T	505320	4931373	185.7	6.7	3.5	29.5	55	53.0
Huron	Beaver R	17T	543584	4934518	637.1	0.5	8.8	77.5	80	57.4
Huron	Sturgeon	17T	600614	4953755	94.1	1.1	3.8	48.0	80	35.0
Huron	Manitou	17T	414177	5050695	335.6	0.8	4.5	90.3	90	11.0
Huron	Little Thessalon	17T	303562	5130926	138.1	71.4	0.2	52.0	100	0.2

Lake	River	UTM Zone	Easting	Northing	Watershed Area km^2	Distance to Mouth km	Slope °	Canopy Cover	% Rocky Substrate	% Farm Land
Superior	Stokely	16T	697880	5187623	47.2	0.8	4.2	57.0	30	0.0
Superior	Harmony	16T	700798	5191733	47.7	1.0	13.4	96.0	95	0.0
Superior	Chippewa	16T	695931	5200390	812.2	2.3	4.4	96.0	65	0.0
Superior	Batchawana	16T	689370	5204312	1218.7	10.1	0.7	96.0	20	0.0
Superior	Speckled Trout	16T	681347	5242994	47.9	0.3	9.5	71.0	85	0.0
Superior	Barrett	16T	673632	5252720	22.6	0.7	24.4	77.0	85	0.0
Superior	Coldwater	16T	666676	5260009	74.5	0.2	21.1	85.3	100	0.0
Superior	Baldhead	16T	662894	5261658	223.2	0.1	25.2	87.0	100	0.0
Superior	Gargantua	16T	650200	5272762	65.9	1.2	4.5	85.5	95	0.0
Superior	Wolf	16 U	387479	5408722	725.4	5.3	1.4	96.0	75	0.0
Superior	Portage	16 U	378104	5377594	78.8	1.5	3.8	90.0	90	1.5
Superior	Current	16 U	338333	5369144	659.0	0.4	11.1	96.0	100	0.0
Superior	Pine	16 U	311431	5326369	392.6	3.7	5.9	96.0	90	0.2