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Spatial and trophic niches through ontogeny and the influence on native species restoration: Using Lake Ontario Atlantic salmon (Salmo salar) as a model species

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SPATIAL AND TROPHIC NICHES THROUGH ONTOGENY AND THE INFLUENCE ON NATIVE SPECIES RESTORATION: USING LAKE ONTARIO ATLANTIC SALMON (*SALMO SALAR*) AS A MODEL SPECIES

By

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SPATIAL AND TROPHIC NICHES THROUGH ONTOGENY AND THE INFLUENCE ON NATIVE SPECIES RESTORATION: USING LAKE ONTARIO ATLANTIC SALMON (*SALMO SALAR*) AS A MODEL SPECIES

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I hereby declare that this thesis incorporates material that is result of joint research, as follows:

In all cases, the key ideas, primary contributions, experimental designs, data analysis, interpretation, and writing were performed by the author under the supervision of Aaron Fisk and Tim Johnson. Colin Lake co-authored Chapter 5 and assisted with data acquisition, interpretation and writing of the manuscript.

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Chapter 2	Larocque, SM, Johnson, TB, Fisk, AT. Trophic niche overlap and abundance reveal potential impact of interspecific interactions on a reintroduced fish. Can. J. Fish. Aquat. Sci.	Accepted
Chapter 3	Larocque, SM, Johnson, TB, Fisk AT. 2020. Survival and migration patterns of naturally and hatchery-reared Atlantic salmon (*Salmo salar*) smolts in a Lake Ontario tributary using acoustic telemetry. Freshw. Biol. 65:835-848.	Published
Chapter 4	Larocque, SM, Fisk, AT, Johnson, TB. Improving trophic niche and diet resolution of the salmonid community of Lake Ontario using three stable isotopes and multiple tissues. Fish. Res.	Submitted

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ABSTRACT

Species reintroductions are an important aspect of conservation biology to prevent biodiversity loss, and post-release monitoring can help in understanding and improving restoration success. Generally, population sizes are monitored to determine if reintroductions are successful, however, it does not reveal why it is a success or failure. This thesis proposes that by understanding a species ecological niche within the introduced abiotic and biotic habitat throughout its life history, the mechanisms behind restoration success or failure can be better determined, as well as assist management with improving the potential for species restoration. Once extirpated, Atlantic salmon (*Salmo salar*) have been reintroduced into Lake Ontario, however, numbers of returning adults remain low. Thus, focusing on Lake Ontario Atlantic salmon provided an opportunity to assess restoration potential and improve restoration success.

The spatial and trophic niches of Lake Ontario Atlantic salmon were assessed at various life stages. This thesis begins with understanding the seasonal trophic niche of juvenile Atlantic salmon stocked into streams with different fish communities, and specifically to determine if trophic interactions and other species abundances limit restoration success. Stream resident fish communities appeared to partition resources across seasons such that abundant species had low trophic niche overlap with young-of-year Atlantic salmon minimizing overall competition given available resources. The next chapter followed the migration success of Atlantic salmon smolts coming from different rearing environments. Acoustic telemetry revealed that there was similar migratory performance and no impacts from weirs, yet survival was greater in naturally-reared smolts than hatchery-reared smolts. Survival was lowest at the release site indicating pre-

migration mortality, and specifically high stocking-related mortality of hatchery-reared smolts. Overall, when either stocked as parrs or smolts there was low mortality during the actual migration. Lastly, this thesis investigated the trophic and spatial niches of adult Atlantic salmon within the lake environment and compared them to the salmonid community. All salmonids primarily consumed alewife and exhibited some overlap in trophic niche due to this prey commonality and similarity in stable isotope values. Spatially, Atlantic salmon are using slightly different habitats than the other salmonids, regardless of consuming similar prey, thus limiting the spatial niche overlap within Lake Ontario.

This thesis has increased our understanding of Lake Ontario Atlantic salmon. There were no major ecological niche overlaps with other salmonids, limiting resources, or reduced survival of Atlantic salmon, from juveniles and smolts in the river to adults in the lake. However, this research revealed a few indirect aspects that could affect success and potentially limit restoration (e.g., stocking related survival, thiamine deficiency, spawning success) which could be further researched. Understanding ecological niches can be useful beyond Atlantic salmon restoration in Lake Ontario such as with other reintroduction projects, stocking programs and fisheries management. Researching different aspects of a species ecological niche, like its trophic and spatial niches at various life stages, provides management with information to increase the potential for reintroduction success, such that ultimately, reintroductions may be a more effective tool towards species conservation and increasing biodiversity.

DEDICATION

To my parents for fostering my love of nature and supporting all my outlandish decisions like to pursue a career in fish biology

more (include the Peel Region Police dive team!). At some point, during my graduate studies, these connections and the assistance provided helped with my thesis research and for that I am thankful.

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I have met some awesome and amazing humans both before and throughout my PhD, that really helped me out when the going got tough, but would also brighten my day, helped take the edge off and have fun, and created a memorable experience during my PhD: Abby, Ali, Amy, Ashley, beer, Bryan, Christine, Clare, Dana, Don, gin, Jerry (and my NY family), Jill, Jordan, Julia, Justine, Karista, Katelynn, Leia the furball, Marlena, Meghan, Natalie, Rob, Ryland, Scott, Sharon, Steve (RIP), and Tanya. There are so many to name but I am so grateful for all the help in some shape or form that got me to where I am today ♥

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CHAPTER 1 – GENERAL INTRODUCTION

1.1 Reintroduction biology

As the world witnesses increasing extinction rates and continued loss of biodiversity, there is a pressing need to increase conservation efforts and maintain ecosystem functions (Ricciardi and Rasmussen 1999; Cardinale et al. 2006; Ceballos et al. 2015). Habitat loss, followed by invasive species, are the main proponents for species declines and extinctions (Tilman et al. 1994; Pimm and Raven 2000; Lawler et al. 2006; Bellard et al. 2016), and habitat restoration is therefore an obvious approach to restore native species populations and biodiversity (Dobson et al. 1997; Lawler et al. 2006; Seddon et al. 2007). However, when native species population levels become too low and species are beyond the aid of habitat restoration or other factors causing species decline, additional restoration efforts must be considered, including: reinforcement or reintroduction (Seddon et al. 2014). Reinforcement involves releasing organisms into already existing populations to increase the abundance and population viability to prevent extirpation (Seddon et al. 2014). Reintroduction similarly involves releasing organisms but occurs after a species extirpation in an area to re-create a sustainable population (Seddon et al. 2014). Increasingly, species reintroduction projects are being employed as a conservation tool to reduce defaunation as the risk of species extinctions rise (Seddon et al. 2007, 2014).

Many reintroduction projects have a history of poor success rates in terms of re-establishing a self-sustaining population (Seddon et al. 2007, 2014; Sutherland et al. 2010; Jachowski et al. 2016). Beyond ensuring suitable habitat and eliminating the factors causing species decline, reintroduction efforts frequently fail through poor planning, lack of resources, and use of inappropriate and/or low numbers of founder

animals (Kleiman 1989; Fischer and Lindenmayer 2000; Colautti 2005; Seddon et al. 2007). Further, the lack of post-release monitoring prevents identifying the timing and cause of poor survival and population re-establishment (Seddon et al. 2007; Armstrong and Seddon 2008; Muths and Dreitz 2008; Jachowski et al. 2016). The importance of post-release monitoring has since been recognized in reintroduction guidelines (IUCN/SSC 2013), and consequently, monitoring has increased over time with some indication of increasing success of reintroductions (Ewen and Armstrong 2007; Armstrong and Seddon 2008; Lee and Hughes 2008). Monitoring vital rates of survival and recruitment, as well as population size and distribution are key factors that determine the potential for a species to re-establish (Lee and Hughes 2008; Cochran-biederman et al. 2014; Jachowski et al. 2016). However, solely monitoring population processes may not elucidate factors affecting demographic success or failure, which is particularly important when reintroductions fail. As habitat quality (including both abiotic and biotic components) is related to reintroduction success (Griffith et al. 1989; Ewen and Armstrong 2007), understanding a reintroduced species' movement, habitat and food resource selection, as well as interspecific interactions through predation and competition, can help determine limitations to reintroduction success (Ewen and Armstrong 2007; Jachowski et al. 2016). By better understanding a reintroduced species' ecological niche within the introduced habitat, and mechanisms behind reintroduction success or failure, the potential for species restoration can be determined.

1.2 Ecological niches

In its simplest form, a species' niche is the ecological space occupied by a species. The term niche was originally defined by Grinnell (1917) with a spatial habitat

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focus, while Elton (1927) placed a stronger emphasis on the functional role of the species in a community, particularly trophic relationships. However, Hutchinson (1957) popularized and combined both the habitat and functional roles of the previous definitions in re-defining a niche as a multi-dimensional space of both environmental conditions (abiotic) and resources (biotic) within which a species can maintain a viable population (Krebs 1972; Colwell and Rangel 2009; Holt 2009). Thus, an ecological niche incorporates a species' interactions with abiotic and biotic factors in its environment and it is the relationships among these that facilitates the co-existence of organisms within a community.

The niche concept has been partitioned into the "fundamental niche" which occurs in the absence of biotic interactions and the "realized niche" when biotic forces such as competition and predation restrict an organism in its physical environment through resource partitioning (Hutchinson 1957; Pianka 1974; Holt 2009). The degree of interspecific competition depends on the overall niche overlap of each species and resource availability, when taking into consideration all environmental variables. Thus, niche overlap is indicative of a lack of resource partitioning between species, and if severe enough one species could competitively exclude the other within the community during periods of low resource availability (Gause 1934; Hardin 1960; Krebs 1972; Pianka 1974). Typically, niche overlap only occurs partially and some amount of resource partitioning or niche segregation occurs among co-existing species. Studying the habitat, food resource utilization, and potential niche overlap of species can provide insight into competition and other biotic interactions impacting a species ability to persist

in a community (Zaret and Rand 1971; Schoener 1983; Ross 1986; du Preez et al. 2017; Matley et al. 2017).

Ecological niches can be segregated into specific parts to help understand a species ecological niche as a whole. Most commonly, niches and resource partitioning are studied from the habitat/spatial and food/trophic aspect, as well as time (Schoener 1974, 1983; Ross 1986). Spatial niches look at the abiotic and biotic habitat utilized by a species while trophic niches look at the food web structure (biotic) of a species. With technological advances, we are now able to study spatial and trophic niches in novel ways revealing new trends. For instance, species' habitat and spatial use can be determined at a greater resolution with the aid of telemetry or remote sensing of species (e.g., Morbey et al. 2006; Guzzo et al. 2016; Rous et al. 2017). Trophic niches can be better elucidated with the aid of stable isotopes as opposed to diet/stomach content studies alone which provide only a snapshot of an organisms' diet (Peterson and Fry 1987; Layman et al. 2007; Jackson et al. 2011). Combining information of both spatial and trophic niches, with the use of these new technologies, can provide an overview of a species' niche and may reveal previously unknown information on a species ecology, resource partitioning and interspecific competition (e.g., Speed et al. 2012; Matich and Heithaus 2014; Guzzo et al. 2016; Matley et al. 2017).

Passive acoustic telemetry offers a way to determine the presence and movement patterns of fish as tagged individuals are detected when within range of multiple data-logging receivers (Heupel and Webber 2012). Acoustic telemetry can monitor various aspects of spatial habitat use such as migration patterns, home range and activity space, habitat preferences, as well as the use of environmental factors (Heupel and Webber

2012). As individual fish are monitored, aside from spatial habitat use, ecological factors such as survival and migration success can be estimated with more precision using telemetry (Thorstad et al. 2007; Dudgeon et al. 2015). Both the survival and spatial habitat use determined from acoustic telemetry can provide insight into the spatial niche of a species.

Stable isotope analysis provides a way to study trophic ecology through measuring elemental isotopes (e.g., carbon, nitrogen, and sulfur) combined with the adage of "you are what you eat". For instance, ratios of nitrogen (δ^{15}N) incrementally increase with trophic levels and can estimate an organisms' trophic position in the food web while ratios of carbon (δ^{13}C) vary with primary producers and very little with trophic transfers and can estimate an organisms' source of dietary carbon (Layman et al. 2007; Boecklen et al. 2011). A third stable isotope ratio of sulfur (δ^{34}S) has been used to distinguish between feeding in marine vs freshwater environments (Peterson and Fry 1987; Doucett et al. 1999), and more recently within freshwater systems to differentiate benthic vs pelagic dietary sources (Croisetière et al. 2009; Colborne et al. 2016). Together, different stable isotopes (typically δ^{13}C and δ^{15}N) have been used to reconstruct diets, characterize trophic relationships, and construct food webs (see review by Boecklen et al. 2011). Further, with sophisticated analyses, such as using Bayesian statistics, stable isotope analysis can better elucidate trophic structure, by quantifying trophic niches and overlap (Bearhop et al. 2004; Jackson et al. 2011; Swanson et al. 2015) and diet estimates (using isotope mixing models; (Stock et al. 2018; Swan et al. 2020)).

Another important concept is ontogenetic niche shifts whereby a species' niche changes during their lifetime. For instance, juveniles of a given species may eat different prey items than adults, or live in completely different habitats, and will thus have different temporal niche boundaries based on life-stage (Werner and Gilliam 1984; Huntingford 1993). Evaluating ontogenetic spatial and trophic niches can potentially reveal the life stages that a species' niche overlaps with that of co-occurring species, and therefore inform the causal factors contributing to the success or failure of re-introduced species.

1.3 Changes in the Great Lakes

The Laurentian Great Lakes has experienced major ecological changes since European exploration and settlement began in the 1600s. With increasing human settlement, the Great Lakes ecosystems have experienced habitat degradation and loss, declines in water quality, and overfishing which led to declines in native fish populations including the extirpation of Atlantic salmon (*Salmo salar*) in Lake Ontario in the 1890s (Christie 1974; Smith 1995; Bogue 2000; Crawford 2001; Allen et al. 2013). Furthermore, non-native species introductions, eutrophication, and climate change have further altered fish community compositions (Christie 1974; Smith 1995; Bogue 2000; Crawford 2001; Allen et al. 2013). With the declines of native species populations, increase of invasive species, and the introduction and intensive stocking of Pacific salmon since 1968, the Laurentian Great Lakes, in particular the highly populated Lake Ontario, have a very different offshore fish community than pre-settlement days (Christie 1974; Crawford 2001; Mills et al. 2003; Owens et al. 2003). Recently, there have been efforts to restore native fish assemblages to the Great Lakes. In Lake Ontario, lake trout

(*Salvelinus namaycush*), coregonids (e.g., deepwater ciscoes such as bloater (*Coregonus hoyi*)), and Atlantic salmon are a large focus for species restoration (Ontario Ministry of Natural Resources and Forestry (OMNRF) 2019). However, beyond monitoring the number of fish returns and captures by management authorities, very little work has occurred to understand how these native fish, like Atlantic salmon, are integrating into the current fish community, habitat, and food web, and whether they have a realized niche that does not completely overlap with others.

Lake Ontario has undergone intense fish community changes since pre-colonization. Prior to European colonization, the common offshore fish community in Lake Ontario consisted of Atlantic salmon, lake trout, and burbot (*Lota lota*) as top predators, and planktivorous deepwater ciscoes (*Coregonus* spp.), deepwater sculpin (*Myoxocephalus thompsonii*) and slimy sculpin (*Cottus cognatus*) as prey fish (Christie 1974; Mills et al. 2003; Owens et al. 2003). Today, the offshore community consists of a different assemblage of fishes. There has been the addition of numerous non-native species, such as Chinook salmon (*Oncorhynchus tshawytscha*), Coho salmon (*Oncorhynchus kisutch*), rainbow trout (*Oncorhynchus mykiss*), and brown trout (*Salmo trutta*) as top predators, and alewife (*Alosa pseudoharengus*), round goby (*Neogobius melanostomus*) and rainbow smelt (*Osmerus mordax*) as forage fish (Crawford 2001; Mills et al. 2003; Mumby et al. 2018; OMNRF 2019). Some native species are still present but in lower abundance, such as lake trout, burbot, deepwater sculpin, and slimy sculpin, while the planktivorous deepwater ciscoes and Atlantic salmon were extirpated (although bloater and Atlantic salmon are currently undergoing re-introduction; Christie 1974; Mills et al. 2003; Owens et al. 2003; OMNRF 2019). The nearshore community

was and still is much more diverse in comparison but has also undergone changes in composition and abundance since European colonization. Thus, there is the possibility that spatial and trophic niches for fish have changed over time with the change in species assemblages in Lake Ontario. Historical prey resources and habitats that were critical for supporting native species may no longer be available or have been filled by another species, which can have implications for the restoration potential for native aquatic communities (Vander Zanden et al. 2003).

1.4 Restoration of native species assemblages

With the drastic change in the fish community and the decline of native species populations, there have been initiatives to restore native species in Lake Ontario via reintroductions. This is the case for Atlantic salmon in Lake Ontario where they were once extirpated and strains from different locations are being stocked into the lake in hopes to establish a sustainable population (OMNRF 2007, 2019; Glass 2010). Atlantic salmon have had a troubled history in Lake Ontario with sporadic attempts to be re-established. In the mid-1980s, New York State Department of Environment Conservation (NYSDEC) and OMNRF began Atlantic salmon stocking in Lake Ontario tributaries to assess the feasibility of Atlantic salmon restoration (Daniels 2003; Kerr 2006; Glass 2010). Although from these initial stocking efforts there were few adult returns, a long-term stocking program was renewed by OMNRF in 1995 and by 2006 the Lake Ontario Atlantic Salmon Restoration Project (ASRP) commenced with the goal to have a self-sustaining population of Atlantic salmon in Lake Ontario and its tributaries in 10-15 years (Daniels 2003; Glass 2010).

Unlike most reintroduction projects, there has been a high degree of effort to plan and manage the ASRP using results from scientific research. To date, the majority of research on Lake Ontario Atlantic salmon is from the juvenile life stage and has been focused on the survival/condition and interspecific competition with different genetic strains being stocked in laboratory settings (Van Zwol et al. 2012a, 2012b; He et al. 2015; Houde et al. 2015a, 2015b, 2017; Murphy et al. 2017; Smith et al. 2017), and habitat preferences and interspecific competition in the field (Stanfield and Jones 2003; Johnson 2008, 2013). This work is beneficial to understand how initially stocked fish may fare in the river systems of Lake Ontario and which genetic strain is the best suited for the current environment. Some research has occurred on adult Atlantic salmon in Lake Ontario, focusing on spawning habitat suitability and spawner interactions with other salmonids (J. Fitzsimons, unpubl. data *in* Daniels 2003; Scott et al. 2003, 2005) and recently, food-web structure within the lake itself (Mumby et al. 2018). There is also monitoring of juvenile, smolt, and adult catch rates on select tributaries by OMNRF (e.g., OMNRF 2019). Overall, very little is known about the ecology of the introduced Atlantic salmon beyond the laboratory and whether they are fitting into the current fish community. The returning numbers of adult Atlantic salmon are low, relative to the ASRP goals (OMNRF 2019), and yet there is little monitoring beyond juvenile and adult returns to understand when and where re-establishment is failing. Thus, Lake Ontario Atlantic salmon is a model species to investigate the ecological niche through spatial and trophic niches at different life stages among the abiotic and biotic environment, and whether it overlaps with that of co-occurring salmonid species, to better understand the

potential for restoration success and improve reintroductions through adaptive

management.

1.5 Study species

Although information on the current and historic Lake Ontario Atlantic salmon is

limited, inferences can be made from the Atlantic Ocean counterparts to understand the

general ecology and life history of Lake Ontario Atlantic salmon. Atlantic salmon are

mostly known as an anadromous species associated with the Atlantic Ocean, however in

Lake Ontario, Atlantic salmon were historically potamodromous, migrating to the lake as

an adult and returning to spawn in rivers (Guiry et al. 2016, 2020). Atlantic salmon are

fall spawners however, unlike Pacific salmon, there is the potential for repeat spawning

(i.e., iteropary) in Atlantic salmon. The rate of repeat spawning is roughly 10% but can

be quite variable with a few percent to over half the spawning population, spawning up to

4-5 times in anadromous populations, and females surviving more than males (Saunders

and Schom 1985; Fleming and Reynolds 2004; Halttunen 2011; Nyqvist et al. 2016). The

eggs in the gravel redd overwinter and hatch in the spring, with the fry emerging in May

or June (Scott and Crossman 1998). Anadromous juveniles may spend 1-5 years in the

stream, depending on the region and latitude, and reach a minimum size of 120 – 220 mm

before they smolt (Scott and Crossman 1998; Jonsson and Jonsson 2011). Lake Ontario

Atlantic salmon smolt at approximately similar sizes (average 150 mm), however, it is

unclear if it occurs in 1-3 years (M. Desjardins, pers. comm.). Once in the lake, Atlantic

salmon remain in shallow upper layers until the thermocline develops where they retreat

to cooler, deeper waters (Scott and Crossman 1998). They remain in the lake until

temperatures cool, and the adults proceed to migrate back to the rivers to spawn and repeat the cycle.

Compared to the pre-colonization fish community that Lake Ontario Atlantic salmon used to thrive in, the current environment and fish communities are much different. The historic niche that was occupied by Atlantic salmon may no longer exist and it is unknown if there is a realized niche available for Atlantic salmon today. The ecological niches may overlap too much in a top-predator heavy system and limit reintroduction success. Other salmonids may already occupy the same habitat and feed on the same resources as the reintroduced Atlantic salmon and compete and overlap in respective niches as a result, on top of which the other salmonids may have a competitive advantage of occupying the area first. Atlantic salmon can be outcompeted by other species such as brown trout and rainbow trout in certain habitats (Armstrong et al. 2003; Houde et al. 2015b), and this may limit food intake and habitat occupied by Atlantic salmon which would impact growth, survival, and future reproduction. Furthermore, with the limited monitoring of reintroduced Atlantic salmon in Lake Ontario, it is unknown whether their ecological niches may be overlapping with other salmonids at different life stages and environments. Similarly, Atlantic salmon stocked at early life stages, being more naturally-reared (e.g., as juveniles), than those stocked at later life stages (e.g., smolts or adults) may have different behaviours and survival (Thériault et al. 2010; Milot et al. 2013; Birnie-gauvin et al. 2018), adding a further layer of niche differentiation within a species to consider in species reintroductions. Therefore, studying the spatial and trophic niches of Atlantic salmon and other salmonids at different life stages/environments may reveal the mechanisms behind reintroduction failures or

successes and the influence on the restoration potential of Atlantic salmon in Lake Ontario.

1.6 Thesis overview

This dissertation focuses on Atlantic salmon in Lake Ontario from the perspective of improving native species restoration. The central objective was to show how examining species niches and overlaps can provide insight into potential limitations to restoration and more specifically, understand the ecological niche (via spatial and trophic niches) of Atlantic salmon, which was compared to other salmonids (potential competitors) to discern restoration potential in Lake Ontario. This research develops an understanding of the spatial habitat use and trophic resource use of Atlantic salmon, relative to the salmonids in Lake Ontario at key life stages in both streams and the lake.

Chapter 2 quantifies the trophic niche of juvenile Atlantic salmon stocked in stream environments over time and whether there are any strong, interspecific interactions with other species. Assessing both trophic niche overlap and species abundance can describe the strength and number of interspecific trophic interactions to determine the potential competitive impact on reintroduction success. For example, juvenile salmonids like brown trout, will likely have a large trophic niche overlap with juvenile Atlantic salmon (Stanfield and Jones 2003), however, if brown trout are lower in relative abundance there will be infrequent interspecific interactions, minimizing the potential competitive impact on Atlantic salmon. Using seasonal stable isotopes and abundance estimates for invertivorous fishes in three Lake Ontario tributaries, community isotopic structure, trophic niche overlap, and the impact of the niche overlap on juvenile Atlantic salmon (by incorporating relative abundance) was determined.

Seasonal patterns or differences among fish communities (varying numbers of potential competitors) were assessed to determine whether juvenile Atlantic salmon have trophic competitors to contend with in the stream environment.

Chapter 3 of this thesis assessed the movement patterns of the smolt life stage of Atlantic salmon as they migrate from the stream to Lake Ontario. This chapter looks at the differences between naturally-reared smolts (stocked as juveniles into streams) and hatchery-reared smolts in the migration patterns and survival to Lake Ontario. Although fish stocked later as smolts have increased survival while in the hatchery environment, they can avoid natural selection processes and later have reduced fitness relative to similarly aged fish that were stocked at earlier life stages (Milot et al. 2013; Birnie-Gauvin et al. 2018). Instead of comparing the spatial movements of Atlantic salmon smolts to other salmonid species, comparisons between naturally- and hatchery-reared smolts were made to determine if survival and spatial patterns vary due to rearing environment. Differences due to rearing environments would determine potential restoration limitations via reduced migration success. To better understand Atlantic salmon smolt migration in rivers, the correlation of migration timing to environmental variables, and whether man-made barriers like weirs may affect migration speed and survival were also investigated.

Chapter 4 quantifies the trophic niches and dietary overlaps of adult salmonids in Lake Ontario. The trophic niches of adult salmonids in Lake Ontario had been previously assessed in 2013 by Mumby et al. (2018), however, declines in alewife, a key prey species, may cause salmonids to shift their diets to other available prey. Improving our understanding of salmonid trophic niches and diets and how these change over time

provides insight on the available prey community and whether the trophic niche of Atlantic salmon strongly overlaps with other salmonids. Using stable isotopes (δ^{13}C, δ^{15}N and δ^{34}S), the trophic niche and estimated diets for six salmonid species from Lake Ontario in 2018 were determined. To improve our understanding of adult salmonid trophic niches and diets, both fin and muscle tissue was used to quantify temporal variability in diet, and spatial differences were investigated.

Chapter 5 of this thesis determines patterns in spatial use of adult Atlantic salmon in Lake Ontario. Discerning whether there is a spatial overlap between Atlantic salmon and other salmonids can determine if they occupy similar niches and potentially affect Atlantic salmon restoration success. However, in Lake Ontario, the movement ecology and habitat use of adult land-locked Atlantic salmon is unknown, particularly in relation to other salmonids as potential competitors. In this chapter, using a combination of acoustic telemetry and external anchor (i.e., Floy) tagged and recaptured fish, movement patterns and seasonal home ranges of adult Atlantic salmon were assessed. The spatial use of Atlantic salmon was then compared to the current knowledge of movements of other Lake Ontario salmonids to determine whether there is a high degree of spatial niche overlap.

Collectively, this thesis disentangles at which life stage Lake Ontario Atlantic salmon may be limited for resources (food and habitat) with the greatest niche overlap amongst the other salmonids in Lake Ontario, and what may be influencing Atlantic salmon survival. For example, if resources are limited and there is a strong niche overlap with Atlantic salmon with another species at any specific life stage, then it may result in potential competition or reduced survival and impede restoration potential. Strong niche

overlaps would identify the life stage and potential area that is limiting restoration

potential and influence management decisions to address such issues. Alternatively, if a

lack of niche overlap is observed than there may be other factors not assessed here that

can be attributed towards the low adult returns of Atlantic salmon and allude towards

other areas of research to improve restoration success. From an applied perspective, the

results of this research have direct management implications as they will provide

ecological information on Atlantic salmon and other salmonids in Lake Ontario, a

location that has a paucity of information due to its large scale, to aid in fisheries

management. This information can also be of value towards the management of other

Great Lakes salmonid fisheries and other locales where there are efforts to rehabilitate

Atlantic salmon. From a theoretical standpoint, this research provides a better

understanding of the interactions that occur in a top-predator heavy system as well as

how understanding spatial and trophic niches can determine limitations in restoration

potential.

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CHAPTER 2 – TROPHIC NICHE OVERLAP AND ABUNDANCE REVEAL

POTENTIAL IMPACT OF INTERSPECIFIC INTERACTIONS ON A

REINTRODUCED FISH

2.1 Introduction

In aquatic systems, stocking fish for reintroductions, supplementing wild populations, and enhancing fisheries occurs globally, and it is important to determine any limitations to stocking success (Minckley 1995; Brown and Day 2002; Molony et al. 2003). Removal of threats and having suitable habitat and food requirements are key factors to successful reintroductions (Harig et al. 2000; Cochran-Biederman et al. 2015). However, understanding a reintroduced species' interspecific interactions through potential competition can help determine biotic limitations to reintroduction success (Ewen and Armstrong 2007; Jachowski et al. 2016). The composition of the resident fish community may also influence the success of salmonid reintroductions (Harig et al. 2000; Scott et al. 2003; Cochran-Biederman et al. 2015). Not only can non-native species have negative influences on reintroduced species (Levin et al. 2002; Scott et al. 2003; Coghlan et al. 2007a) but so too can native species (Ward et al. 2008; Robinson and Ward 2011). Thus, existing resident species may be strong competitors or predators with stocked species for food resources and/or habitat (Griffith et al. 1989; Schooley and Marsh 2007; Ward et al. 2008) and influence the outcome of the stocking.

The extent to which species overlap in trophic niches can indicate the degree of sharing of resources and potential interspecific competition (Hutchinson 1957), yet the intensity or impact of resource sharing and competition may in part be related to the abundance of the species involved, particularly in resource limited situations. Niche complementarity suggests that species co-exist by utilizing different resources (MacArthur and Levins 1967; Schoener 1974). However, few studies have assessed both niche partitioning and abundances simultaneously (e.g., Sugihara et al. 2003; Mason et al.

2008). When combining niche complementarity with abundance, there is evidence that abundant species would have low trophic niche overlap with each other, thereby minimizing competition for resources and enhancing ecosystem function (Sugihara et al. 2003; Mason et al. 2008). However, it is unknown whether this holds true during ecosystem disruptions such as the addition of new species and estimating the potential competitive impact on a species may be important for ecosystem management and understanding community structure.

I provide a conceptual framework to estimate the potential competitive impact on a species of interest by combining the strength of interaction based on the degree of trophic niche overlap with the number of interactions from the other species' abundances (Figure 2.1). In this conceptual framework, both trophic niche overlap and relative abundances (proportion of abundance relative to the total abundance of the community) are on a continuous scale from low to high, however, the relative abundance of species in a community is considered to be high if it is greater than the relative abundance of the species of interest. If trophic niche overlap among species is low, then the strength of the interspecific interactions is weak (Figure 2.1, bottom quadrants) and although the potential number of interactions with a relatively abundant species can be high or frequent, it would be an example of niche complementarity and the resident species would have low impact on the introduced species (Figure 2.1 – bottom, right quadrant). The lower the relative abundance of the resident species with low trophic niche overlap, the lower the impact on the introduced species (Figure 2.1 – bottom, left quadrant), while less relatively abundant species with high trophic overlap would have a low impact due to the limited, but strong interactions with the introduced species (Figure 2.1 – top, left

quadrant). However, if an introduced species has a high trophic niche overlap with a relatively abundant species (Figure 2.1 – top, right quadrant), then it implies strong, frequent interactions with a species, and therefore potential competition for resources and a strong impact which could be a limitation on the success of introduction. Incorporating the abundance of the species present in the system can influence interpretations of the importance of a high trophic niche overlap.

Trophic niche overlap is frequently assessed using stable isotopes as they provide better estimates of trophic niches than stomach contents in describing longer term community or population structure (Peterson and Fry 1987; Layman et al. 2007; Jackson et al. 2011). Isotopic or trophic niche overlap has been previously used to assess diet partitioning between species and as a potential indicator of competition (Wang et al. 2018; Ogloff et al. 2019). Similarly, metrics have been used to describe the isotopic structure of the community (e.g., Layman metrics) and whether it varies among communities with different interspecific diet partitioning and trophic diversity (Layman et al. 2007; Sagouis et al. 2015). However, species abundance has yet to be incorporated into conventional trophic niche evaluations which leaves a gap in understanding the overall impact that the lack of diet partitioning may have on a species. The conceptual framework (Figure 2.1) provides a way in which the number of interactions based on other species' abundances can be used in combination with the strength of isotopic trophic overlap to determine the resulting impact to a species of interest. This framework can be applied to various scenarios in which changes in an ecosystem may warrant a better understanding of the trophic interactions and resulting potential competitive impacts to a species by including abundance, such as ecosystem disturbances or the

addition of a species (e.g., native or invasive). Here, I use an example with a reintroduced species to assess conventional isotopic analyses with niche overlap and isotopic structure with resident species. I also incorporate species abundance with niche overlap to better understand the overall impact of the community on the reintroduced species.

A species that may be negatively influenced through trophic interactions with resident taxa is Atlantic salmon (*Salmo salar*) in Lake Ontario. Since Atlantic salmon extirpation in the 1890s, Pacific salmonids (*Oncorhynchus* spp.), among other species, have been introduced into Lake Ontario and elsewhere in the Laurentian Great Lakes, and different fish communities exist in the streams where Atlantic salmon young-of-year (YOY) are currently being reintroduced (Christie 1974; Crawford 2001). Studies have shown that non-native juvenile brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*; Stanfield and Jones 2003; Coghlan et al. 2007b) and native sculpin spp. (Cottidae; Gabler and Amundsen 2006) reduced growth and/or survival of Atlantic salmon YOY and can therefore be considered competitors with Atlantic salmon YOY and were a priori hypothesized to be potential competitors in Lake Ontario tributaries. Streams selected for Atlantic salmon reintroduction in the Lake Ontario watershed were chosen based on quality of suitable habitat (Stanfield and Jones 2003), but few studies have assessed the impacts of the local fish communities for potential competition for food resources (Johnson and McKenna 2015; Houde et al. 2016). Interspecific trophic competition may influence the growth, survival, and ultimately success of Atlantic salmon reintroductions in Lake Ontario. Thus, the stocking of Atlantic salmon YOY in Lake Ontario tributaries makes for an ideal system to assess trophic interactions of a reintroduced species and the influence of the resident community.

Atlantic salmon YOY primarily consume aquatic macroinvertebrates (Keeley and Grant 1997; Coghlan et al. 2007a; Johnson 2013a, 2013b). By using stable isotopes to describe Atlantic salmon YOY diets, fish can be repeatedly sampled with non-lethal fin tissue (Sanderson et al. 2009; Hette-Tronquart et al. 2012) and determine how the trophic niche overlaps with the existing fish community of the same trophic guild. Dietary overlap with other salmonid and sculpin species may generate potential competition with Atlantic salmon YOY, and thus the degree of trophic niche overlap or trophic structure of different fish communities may influence Atlantic salmon reintroduction success. Diets within the fish community may also change seasonally depending on food availability. Convergences in diet may occur during times in which food resources are more limited, such as overwinter, as seen with YOY rainbow trout, brown trout, and Atlantic salmon (Johnson et al. 2017). Yet fish can also converge in diets during times with greater prey abundances and resource subsidies, such as terrestrial arthropods falling into streams in the summer (Nakano et al. 1999; Kawaguchi et al. 2001). Thus, seasonal variation in isotopic niche overlap may further influence the competitive impacts on Atlantic salmon.

In this study, it was examined whether the potential success of a reintroduced fish species in streams may be limited by a strong overlap in food resources with other species (interspecific competition), in particular abundant species. The objective of this study was to determine the degree of food resource overlap and potential competition within three different invertivore fish communities seasonally by assessing species abundance, the communities' isotopic trophic structure, and trophic niche overlap with Atlantic salmon YOY stocked into Lake Ontario tributaries. It was hypothesized that: 1) streams with more potential competitors (e.g., YOY brown trout, rainbow trout, and adult

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sculpin spp.) would have greater niche overlap with Atlantic salmon YOY and a smaller, condensed isotopic trophic structure, and 2) the greatest overlaps/smaller, condensed isotopic trophic structure would occur overwinter due to limited food resources and in summer due to abundance of terrestrial inputs. Lastly, it was determined whether Atlantic salmon were impacted (by having high niche overlap with abundant species) by resident fish species, in particular by potential competitors. These results will help determine the trophic interactions and relative impact with a reintroduced species over time and whether they may pose limitations to the successful reintroductions of Atlantic salmon in Lake Ontario.

2.2 Methods

Study area

The trophic niches of the invertivore fish community were assessed in three tributaries of Lake Ontario after being stocked with Atlantic salmon YOY by the Ontario Ministry of Natural Resources and Forestry (OMNRF). The study sites - Cobourg Brook (44.0315° N, 78.1453° W), Credit River (43.8024° N, 79.9959° W), and Duffins Creek (43.9483° N, 79.0802° W) – have similar cobble, gravel, and boulder dominated sediments and forested riparian vegetation, yet different flows, stream widths, as well as variation in fish communities at each site (Appendix 1). The OMNRF has stocked these sites in previous years and some Atlantic salmon that did not smolt in the spring may still be present as yearlings. All three sites have salmonids present, however, in terms of the presence of literature-based potential competitors (i.e., YOY brown trout, YOY rainbow trout, and adult sculpin spp.), Cobourg Brook had the most with brown trout YOY, rainbow trout YOY and adult slimy sculpin (*Cottus cognatus*), Credit River was

intermediate with brown trout YOY and adult mottled sculpin (*Cottus bairdii*), and

Duffins Creek had no potential competitors present.

Field Sampling

Between May 3 - 16 of 2017 Atlantic salmon YOY were stocked by OMNRF

Normandale Fish Culture Station (Turkey Point, ON Canada) throughout the mid to top

end of the three sites, such that the lower section of the site accounted for downstream

dispersal. Similar biomass was added to each stream although stocking numbers

themselves varied due to site length and size of fish. Cobourg Brook, Credit River, and

Duffins Creek stocked 2,500, 12,500, and 5,000 Atlantic salmon YOY with a biomass of

approximately 8.77, 8.49 and 8.57 g/m^2, respectively. Ten Atlantic salmon YOY from

Normandale Fish Culture Station were euthanized and frozen for later stable isotope

analyses to establish hatchery stable isotope values. Following stocking, at each field site,

sampling occurred four times: 3 weeks post-stocking (spring – May/June 2017), summer

(July/August 2017), fall (October 2017), and early spring the following year (overwinter

– March 2018). Stream width (m) and water velocity (m/s) were measured at a

representative location for each sampling event. Sampling consisted of using a 3-pass

electrofishing removal method to estimate fish community abundances throughout the

entire site. Using a backpack electrofisher (settings: 40 Hz, 250-450 V; make: Halltech

Aquatic Research, Guelph, ON, Canada) and two netters, each pass started at the

downstream end and worked upstream in a zigzag pattern, sampling all habitat types. All

captured individuals were processed and held in aerated coolers with stream water until

all three passes were complete prior to release. Fish processing involved identifying and

counting all fish for each pass, and a subset of fish per species (n < 20) were measured

for fork length (± 1 mm) and mass (± 0.1 g) and a small fin clip was taken from the upper

caudal fin and stored frozen for later stable isotope analyses. Fin was used as a non-lethal

alternative tissue to muscle for stable isotope analyses to minimize impacting abundances

through lethal sampling on small fishes over the seasons (Sanderson et al. 2009; Hette-

Tronquart et al. 2012). Small freshwater fishes tend to have a strong linear relationship

between fin and muscle, however, variation can exist across species (Sanderson et al.

2009; Hette-Tronquart et al. 2012; Hayden et al. 2017). Only potential invertivorous

species with >5 individuals within a stream and occurring in at least two seasons were

further analyzed (with one exception, brook trout (*Salvelinus fontinalis*) YOY in Duffins

Creek that was only sampled in the fall). Species deemed to be primarily piscivores or

herbivores as determined in the literature (Scott and Crossman 1998) were not included

for further analyses.

Stable Isotopes Analyses

All fin clips were freeze-dried at -48°C for 48 h and cut to the appropriate size for

weighing (600 – 800 μg) into tin capsules. Stable isotope analyses were completed using

a Delta Plus isotope-ratio mass spectrometer (Thermo Finnigan, San Jose, CA, U.S.A.)

coupled with an elemental analyzer (Costech, Valencia, CA, U.S.A.). Standard delta

notation (δ) was used to express stable carbon ($δ^{13}C$) and nitrogen ($δ^{15}N$) isotope ratios in

parts per thousand (‰) differences from a standard reference material as the following

equation: $δ^{13}C$ or $δ^{15}N = [(R_{sample}/R_{standard} − 1)] × 1000$ where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$,

respectively. Atmospheric nitrogen and Vienna Pee Dee Belemnite carbonate were the

standard reference materials for ${}^{15}N$ and ${}^{13}C$, respectively. Precision was assessed by the

standard deviation of replicate analyses of four standards (NIST1577c, internal lab

standard (tilapia muscle), USGS 40 and Urea (n=125 for all)), which measured $\leq 0.22‰$ for $\delta^{15}N$ and $\leq 0.22‰$ for $\delta^{13}C$ for all the standards. Accuracy was based on the certified values of USGS 40 (n=125 for $\delta^{13}C$ and $\delta^{15}N$) analyzed throughout runs and not used to normalize samples, which showed a difference of -0.01‰ for $\delta^{15}N$ and -0.02‰ for $\delta^{13}C$ from the certified value. All stable isotope analyses were completed by the Chemical Tracers Laboratory at the University of Windsor's Great Lakes Institute for Environmental Research, ON, Canada.

Data were corrected for lipids since the elemental carbon-nitrogen (C:N) ratios in this study were above ≥ 3.4 for 94% of samples and ≥ 4 for 5% of samples. All samples with a C:N ratio >3.4 were lipid corrected using the Kiljunen et al. (2006) non-linear mathematical lipid normalization model with the Post et al. (2007) percent lipid calculation as recommended by Skinner et al. (2016).

Data Analyses

Age classes (YOY, yearling, adult) were assigned to salmon and trout based on length distribution curves in which distinct length-age classes were seen (generally YOY were <125 mm, yearlings were >150 mm and <250 mm, and adults were >250 mm but this changed throughout the seasons). Brook trout was the only species with adults included in the analysis, as diet can include macroinvertebrates while other adult salmonids either had too few samples to be included (e.g., rainbow trout) or were considered primarily piscivorous which was confirmed with elevated $\delta^{15}N$ (e.g., brown trout). Each life stage for salmonid species were kept separate for analyses as YOY and yearlings can potentially be feeding on different items based on ontogenetic diet shifts (Keeley and Grant 1997; Mittelbach and Persson 1998).

To compare isotopic niche breadth between potential competitors (consumers of aquatic macroinvertebrates) and Atlantic salmon, the standard ellipse area was calculated for each species-life stage in each stream and season using the SIBER (Stable Isotope Bayesian Ellipses in R) package in R (Jackson et al. 2011). The corrected version of the standard ellipse area (SEA_C) was used, which contains ~40% of the isotopic data, thereby representing the core isotopic niche of each group while correcting for variable sample sizes (Jackson et al. 2011).

The maxLikOverlap function in SIBER was used to estimate the maximum likelihood proportional isotopic niche overlap of Atlantic salmon YOY on species-life stages (and species-life stages niche overlap on Atlantic salmon YOY) within the same stream and season using species-life stage-specific SEA_C. This provides two estimates of overlap depending on who is overlapping whom. For example, Atlantic salmon YOY could have 100% or 1 overlap with blacknose dace (*Rhinichthys atratulus*) adults whereas blacknose dace adults may only have 22% or 0.22 overlap with Atlantic salmon YOY depending on the position and size of each species-life stage SEA_C, in which niche overlap can range from a complete overlap of 1 to no overlap of 0. Both overlap estimates were included to assess for trends. Spring was excluded from the seasons when comparing overlaps with Atlantic salmon YOY as the isotopic signature had not equilibrated to the stream diet at this time (i.e., isotopes reflected hatchery feed; Appendix 2). This was to be expected as the isotopic value of fin can take approximately 2-3 months to equilibrate to their diet (or 4-5 tissue turnover half-lives) for rapidly growing, juvenile fishes (McIntyre and Flecker 2006; Heady and Moore, 2013). The log(x+1)-transformed proportion Atlantic salmon YOY overlaps onto species-life stages

(and vice versa) were compared among streams and season (excluding spring) with a two-way ANOVA without an interaction term as there was only interest in the main effects.

For each stream by season, the relative abundance of each species-life stage was calculated by the catch per unit effort (CPUE; number captured per electrofishing seconds) divided by the total fish CPUE over the sampling event. To assess for any trends in the catches, both the total fish CPUE and the relative abundance of Atlantic salmon YOY were compared across streams and seasons using a two-way ANOVA (without an interaction). The relative abundance of each species-life stage was then plotted by the trophic niche overlaps with Atlantic salmon YOY and each species-life stage. Proportional trophic niche overlaps greater than 0.5 were considered high. To be conservative, any species-life stage relative abundances that were greater than the minimum relative abundance of Atlantic salmon YOY from all sampling events (0.12) was considered high. The relative competitive impact of each species-life stage on Atlantic salmon YOY was estimated depending on where the species-life stage falls relative to the conceptualized framework quadrants.

Using the species-life stages mean $\delta^{13}C$ and $\delta^{15}N$ values, community-level niche space metrics (also known as Layman's metrics) were calculated for each stream by season following Layman et al. (2007) and adopting a Bayesian approach implemented by Jackson et al. (2011) using the laymanMetrics function in SIBER. The community (stream by season) was considered significantly different for a metric when the 95% Bayesian credible intervals did not overlap another stream by season. The following metrics were used: the total area of the convex hull, the mean distance to the centroid, the

range of carbon and nitrogen (δ^{13}C range and δ^{15}N range, respectively), the mean nearest neighbour distance, and the standard deviation (SD) of the nearest neighbour distance. An in-depth description for each metric can be found in Layman et al. (2007). These metrics were used to indicate the total extent of carbon and nitrogen resources exploited by the community and the distribution of species-life stages within the isotopic space.

All analyses were conducted in R version 3.6.1 (R Core Development Team, 2019) and significance was assessed at $\alpha = 0.05$ or whether 95% credible intervals did not overlap. Values are reported in mean $\pm$ SD. Assumptions of normality and homoscedasticity were visually assessed using qqplot and fitted versus residual plots.

2.3 Results

A total of 688 samples were analyzed for stable isotopes from the three tributaries collected between May 2017 to March 2018 over four sampling events. Atlantic salmon YOY sizes ranged from a minimum mean fork length of 55 ± 5 mm (Duffins Creek, May 2017) to a maximum mean fork length 117 ± 10 mm (Credit River, March 2018; Appendix 3). Atlantic salmon YOY were generally the most abundant fish in each stream for every season, followed by either slimy sculpin (Cobourg Brook), mottled sculpin (Credit River), or longnose dace (*Rhinichthys cataractae*; Duffins Creek; Appendix 3). The total CPUE did not vary by stream ($F_{2,6} = 5.139$, P = 0.050) but differed across seasons ($F_{3,6} = 19.133$, P = 0.002) in which total CPUE was lower overwinter (P <0.01) than any other season (P >0.05; Figure 2.2; Appendix 3). Further, the relative abundance of Atlantic salmon YOY did not vary by stream or season ($F_{2,6} = 3.595$, P = 0.0941; $F_{3,6} = 3.856$, P = 0.0751, respectively; Figure 2.2). The standard ellipse areas (SEAc) for each species-life stage by stream and season showed a distinct separation of the initial spring

Atlantic salmon YOY from all other fish from the same stream community and was fairly similar to hatchery conspecifics (Figure 2.3). However, by summer (or fall for Cobourg Brook), Atlantic salmon YOY ellipses had isotopic signatures that were more similar to the stream community (Figure 2.3). Otherwise, no distinct patterns were evident (Figure 2.3).

The proportion of Atlantic salmon YOY isotopic niche overlapping with other species-life stages niches within the same stream and season (excluding spring) ranged from 0 to 1 (Appendix 3). However, Atlantic salmon YOY overlaps with species-life stages were not significantly different among streams ($F_{2,40} = 0.891$, $P = 0.418$) or seasons ($F_{2,40} = 0.724$, $P = 0.491$; Figure 2.4). The isotopic niche overlap of other species-life stages onto Atlantic salmon YOY also ranged from 0 to 1 (Appendix 3). Similarly, species-life stages overlapping with Atlantic salmon were not significantly different among streams ($F_{2,40} = 0.730$, $P = 0.488$) or seasons ($F_{2,40} = 0.721$, $P = 0.492$; Figure 2.4). Across all co-occurrences with Atlantic salmon YOY (with either Atlantic salmon YOY overlapping species-life stages or vice versa), 28% (n = 13 of 45) had a high niche overlap (proportion > 0.5) with Atlantic salmon YOY, which primarily occurred in Credit River (n = 5) and Cobourg Brook (n = 5; Table 2.1). Atlantic salmon yearlings, blacknose dace, brown trout YOY and yearlings, rainbow trout YOY, and rainbow darter (*Etheostoma caeruleum*) all had a high niche overlap with Atlantic salmon YOY in at least one co-occurrence, and brown trout YOY had the greatest proportion of occurrences with a high niche overlap with Atlantic salmon YOY (Table 2.1). Brook trout adults and YOY, longnose dace, mottled and slimy sculpin, and white sucker (*Catostomus*

commersonii) had low or no niche overlap with Atlantic salmon YOY (Table 2.1; Appendix 3).

When comparing the proportion of trophic niche overlap (Atlantic salmon YOY overlapping species-life stages, and vice versa) to relative abundance of the species-life stages, there was an absence of species-life stages that had a high overlap with Atlantic salmon and high relative abundance (proportion > 0.12), aside from rainbow darter from Duffins Creek in which the relative abundance of Atlantic salmon YOY in the same season (fall) was 0.4 (Figure 2.2; Figure 2.5). The majority of species-life stages had low niche overlap with and low relative abundance to Atlantic salmon YOY with a few instances with high niche overlap and low relative abundance or low niche overlap and high relative abundance (Figure 2.5).

When assessing the Bayesian Layman metrics among streams and seasons, there was a relatively consistent pattern difference in which spring for all three streams had higher δ^{13}C range and mean distance to centroid than the other seasons within the same stream. The mean nearest neighbour distance and SD of the nearest neighbour distance also showed the similar pattern with higher values in spring than the other seasons but it was not significantly different for Duffins Creek (Figure 2.6). The total convex hull area had high values in spring but it was not significantly different from at least one other season within the same stream. The δ^{15}N range did not show any apparent distinction between seasons or streams (Figure 2.6). There were no significant differences between stream communities for any of the Layman metrics.

2.4 Discussion

Trophic niches of stocked Atlantic salmon YOY was assessed in multiple streams over seasons to determine whether potential competition with resident fishes may be occurring in Lake Ontario tributaries. Streams with greater or fewer a priori hypothesized potential competitors such as brown trout, overall did not appear to influence the isotopic niche space of Atlantic salmon YOY in any season. Using conventional stable isotope analyses, brown trout YOY strongly overlapped with Atlantic salmon YOY, however, with the inclusion of their low abundance it would not be perceived to have a large impact on Atlantic salmon YOY population growth or survival, as observed in the conceptual model. Combining abundance with stable isotope analyses revealed the impact of trophic interactions on a reintroduced species and provided insights on potential competition. Stream fish communities partitioned available resources such that trophic interactions were reduced with the stocked Atlantic salmon YOY, as evidenced by the low isotopic niche overlap with abundant species. The low abundance of species-life stages with a high niche overlap with Atlantic salmon YOY also indicates that there would be a low competitive impact to Atlantic salmon YOY populations. Further, there were no seasonal patterns (from summer to overwinter) in the relative overlap or niche size that would influence trophic interactions nor any changes in the relative abundance of Atlantic salmon YOY within the community. However, overwinter had the lowest total CPUE across streams due to low temperatures/conductivity which made electrofishing less effective. Across streams, the spring season had increased trophic niche breadth in the isotopic structure via Layman metrics, however, that was related to the isotope signatures of the stocked Atlantic salmon YOY not yet reaching dietary equilibrium with

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the stream from previous hatchery food. This study suggests potential dietary competition

from the invertivorous fish communities should not impact juvenile Atlantic salmon

populations in these streams, particularly if juvenile Atlantic salmon are stocked in high

abundances.

Isotopic niche overlap was not greater and isotopic structure was not

smaller/condensed overwinter or summer relative to other seasons as hypothesized.

Temporal reductions in food availability, like in winter, can increase niche overlap

between species of the same trophic guild (Shustov et al. 2014; Sánchez-Hernández et al.

2016). Similarly, periods of high food availability, like in summer, can also increase

trophic niche overlap when species feed opportunistically on similar abundant resources

(Kawaguchi et al. 2001; Chen et al. 2011). With the abundant stocking of Atlantic salmon

YOY in streams, resources were likely limited during all seasons as abundant species-life

stages had distinct trophic niches and partitioned resources. Resource limitation in all

seasons may explain the lack of seasonal differences in niche overlaps and isotopic

structure. Macroinvertebrate communities also change seasonally (Giller and Twomey

1993; Fierro et al. 2015), which will influence prey availability if fish species have

certain prey preferences, and therefore degree of overlap with other fish may also be

seasonally variable. As isotopes reflect a longer-term diet relative to stomach contents, as

was seen during the post-stocking spring when Atlantic salmon YOY isotopes had yet to

reflect stream isotopes, this method may not have been the most effective to capture

shorter-term within season changes in diet. Instead investigating the stomach contents of

invertivorous fish with the abundance and seasonality of macroinvertebrate can confirm

resource limitation and further understand the seasonality of trophic niche overlaps with Atlantic salmon YOY.

Of the few species with high overlap with Atlantic salmon YOY, brown trout YOY had a high niche overlap with Atlantic salmon (and vice versa) for most of their co-occurrences. There may be competition for food resources with Atlantic salmon and brown trout YOY in Lake Ontario tributaries, however, it did not always occur in all seasons for some streams (e.g., Credit River – fall). Brown trout had more co-occurrences of high overlap with Atlantic salmon YOY than rainbow trout, potentially indicating that rainbow trout is not as frequent a competitor with Atlantic salmon YOY. Neither sculpin species had a high overlap with Atlantic salmon YOY suggesting they are not trophic competitors, as has been seen in other systems (e.g., Gabler and Amundsen 2006). Across multiple studies, when co-occurring, brown trout consistently reduced Atlantic salmon growth in artificial streams, while rainbow trout had variable results (Van Zwol et al. 2012; Houde et al. 2015a, b, 2017). Brown trout YOY have been shown to strongly compete with Atlantic salmon YOY for habitat resources (Armstrong et al. 2003) and feed on similar aquatic invertebrates (Dineen et al. 2007; Johnson and McKenna 2015). However, brown trout may feed more heavily on terrestrial invertebrates in Lake Ontario tributaries (Johnson and McKenna 2015) and feeding on different seasonal prey may explain the one instance in which brown trout YOY did not highly overlap with Atlantic salmon. This study indicates that competitive interactions between Atlantic salmon and brown trout likely exist, yet unlike other studies with equal abundances of both species (e.g., Van Zwol et al. 2012; Houde et al. 2015a, b, 2017), the systems studied here had low relative abundance of brown trout YOY and high relative abundance of Atlantic

salmon YOY such that the overall impact of any potential competition with Atlantic salmon YOY would be low.

Together, trophic niche overlap and abundance can reveal instances where resource sharing could infer competition and the resulting level of impact on a species. The example with Atlantic salmon YOY was used to show how combining trophic niche overlap and abundance indicated that there was no impediment towards reintroduction success. Abundance has not been utilized in conjunction with stable isotopes, however, by doing so one can infer the potential level of impact through competition for food resources that conventional analyses may not reveal. In all three streams, abundant species did not have a strong niche overlap with the abundant Atlantic salmon YOY, similar to the niche complementarity hypothesis, where abundant species have different niches (Mason et al. 2008). In this study, most species had relatively low abundance and low niche overlap or few, weak interactions, thereby partitioning resources and having little impact on Atlantic salmon (Figure 2.1 – bottom, left quadrant). Having a highly diverse prey community may result in such low levels of competition among species-life stages (Sánchez-Hernández et al. 2017). A few species-life stages, like brown trout YOY, had high trophic niche overlap yet low relative abundance and thus strong but limited interactions, and thereby minimal impact to Atlantic salmon (Figure 2.1 – top, left quadrant). Isotopic niche partitioning has been seen in other systems between fish from the same trophic guild (Dromard et al. 2015; Britton et al. 2018), however, inclusion of relative abundance may show that niche separation is greater between abundant species, as suggested with niche complementarity (Mason et al. 2008). The methods and conceptual model for combining abundance and trophic niches can be applied in various

circumstances in which an ecosystem exhibits a disturbance or addition of a new species (reintroduced or invasive) and could be applied towards other conservation related issues. More studies should incorporate abundance estimates into trophic studies to better understand the impact of interspecific relationships, as was showed here.

All three stream communities had similar community isotopic structure and species-life stage niche overlaps with Atlantic salmon YOY, regardless of having greater or fewer potential competitors. Although there were more instances of co-occurring species-life stages having high niche overlap with Atlantic salmon YOY in the streams with moderate and high potential competition (Credit River and Cobourg Brook, respectively) than the stream with no potential competitors (Duffins Creek), the overall mean niche overlap of the streams were similar across streams and seasons. From a fish community perspective, the isotopic structure was quite similar across all streams and seasons (excluding post-stocking spring). Thus, there was consistent partitioning of resources among invertivorous fish in the community across seasons and streams, even though the fish communities were different. Similar species occurring across streams (e.g., blacknose dace), may have different trophic niche overlaps with Atlantic salmon YOY, yet species partitioned food resources to minimize competition by having either low abundance and high niche overlap (Figure 2.1 – top, left quadrant) or high abundance and low niche overlap (Figure 2.1 – bottom, right quadrant). From a community perspective, each stream showed niche complementarity and responded similarly to the addition of Atlantic salmon YOY, regardless of the individual species present. Determining trophic niches and abundance relationships among species may help determine how species organize themselves within communities regarding resource

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partitioning of the more abundant species and changes in niche space, as well as ecosystem functions and resilience to change.

There were some limitations to this study largely related to sampling logistics. With assessments restricted to the post-stocking period, albeit repeatedly over the year, the community may have already shifted to reach a new equilibrium with the reintroduced species, and any response to strong competition (e.g., species with both high overlap and high abundance) had already dissipated. Future research should include a pre- and post-stocking assessment to better quantify how community structure changes or reorganizes following species introduction. Further, due to previous stocking in the streams, the fish community may have already shifted to a new equilibrium prior to this study. Assessing the competitive impact on streams which are stocked with Atlantic salmon YOY for the first time may provide insight on how communities shift with novel disturbances and the duration it may take to reach a new steady state. Using stomach content analyses could also determine immediate community changes with species disruptions, and whether there are stronger competitive impacts upon the disturbance, however, lethal sampling would not permit the assessment of dietary changes over time. Improving upon the methodology of this study will further inform us on the ecological structure and resilience of communities with species reintroductions, among other ecological perturbations.

By sampling more streams, a more continuous gradient of community compositions could have been assessed including an unstocked stream without Atlantic salmon. Although streams with different resident fish communities were assessed across seasons, some could argue only three sites to be a limitation. All three streams had

similar species-life stage niche overlaps with Atlantic salmon YOY and community isotopic structure, which indicates consistency across streams in response to a reintroduction. These streams also have similar habitat characteristics typical of those stocked with Atlantic salmon YOY (e.g., cold-water streams with gravel, cobble-boulder streambeds) across Lake Ontario (McKenna and Johnson 2005; Coghlan et al. 2007; Johnson 2013b). Thus, the streams assessed represented conditions Atlantic salmon YOY encounter across Lake Ontario. Future studies could try to incorporate more streams to determine if there are any community composition or habitat-related trends related to niche overlaps with Atlantic salmon and competitive impacts, as well as increase statistical power for different analyses. More importantly, this methodology of determining competitive impact was successfully applied to three different streams and will be beneficial towards assessing community changes with a new species or other disturbances.

In conclusion, Lake Ontario Atlantic salmon was used as an example to show how the inclusion of abundance estimates with trophic niche interactions can be used to assess the competitive impact of the resident community on a reintroduced species. Conventional stable isotope analyses alone would have concluded that brown trout YOY have a high impact on Atlantic salmon YOY, however, the impact was low when abundance was considered. As fish stocking will remain an important management tool, understanding the community impact on the reintroduced species is essential for managing reintroduction success. The analysis suggests current practices of stocking Atlantic salmon YOY at higher density than resident salmonids is minimizing potential competitive impact and thus not limiting the reintroduction of the species. Incorporating

abundance improves our understanding of trophic interactions and potentially ecosystem functioning within the community. The stream fish communities assessed supported niche complementarity with low niche overlap among abundant species and Atlantic salmon YOY. Thus, the framework provided here could be applied to other circumstances beyond species reintroductions such as to better understand potential competitive impacts on other species of interest and determine whether these impacts influence community structure. It is important to understand species' interspecific interactions through potential competition to determine any biotic limitations that could affect community structure and resource partitioning, particularly with ecological disturbances and species additions.

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Table 2.1 The number of times a species-life stage was captured simultaneously (or co-occurring) with Atlantic salmon young-of-year (YOY) across seasons (excluding spring) and the number and proportion of the 40% isotopic niche overlaps that were greater than 0.5, grouped by location and species-life stages. Trophic niche overlaps refers to either Atlantic salmon YOY overlapping a species-life stage or vice versa and was counted once per co-occurrence (e.g., if both methods of overlap were > 0.5 it was only counted once).

Location	Co-occurrences	Overlaps > 0.5	Proportion of overlaps > 0.5
Cobourg Brook	16	5	0.31
Credit River	16	5	0.31
Duffins Creek	13	2	0.15

Species-life stages	Co-occurrences	Overlaps > 0.5	Proportion of overlaps > 0.5
Atlantic Salmon – Yearling	8	2	0.25
Brook Trout – YOY	1	0	0.00
Brook Trout – Adult	1	0	0.00
Brown Trout – YOY	4	3	0.75
Brown Trout – Yearling	2	1	0.50
Rainbow Trout – YOY	3	1	0.33
Rainbow Trout – Yearling	3	0	0.00
Blacknose Dace – Adult	6	3	0.50
Longnose Dace – Adult	5	0	0.00
Rainbow Darter – Adult	5	2	0.40
Mottled Sculpin – Adult	3	0	0.00
Slimy Sculpin – Adult	3	0	0.00
White Sucker – Adult	1	0	0.00
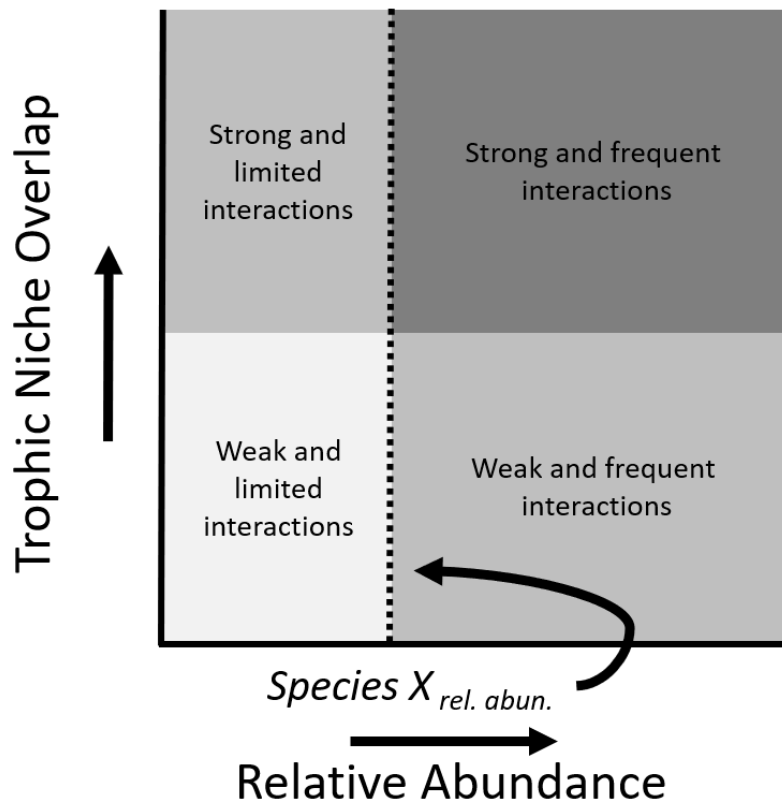
Figure 2.1 Conceptual interspecific interaction-abundance impact model based on trophic niche overlap between species X (e.g., species of interest) and other species in the community, and the relative abundance of other species in the community. Grey scale indicates potential level of impact to species X based on interaction strength of the niche overlap and number of potential interactions from other species' relative abundance if greater or lesser than relative abundance of species X, where light grey indicates negligible impact, grey is low to moderate impact, and dark grey is high impact. Note: species' relative abundance is the proportion of abundance relative to the total abundance of the community.
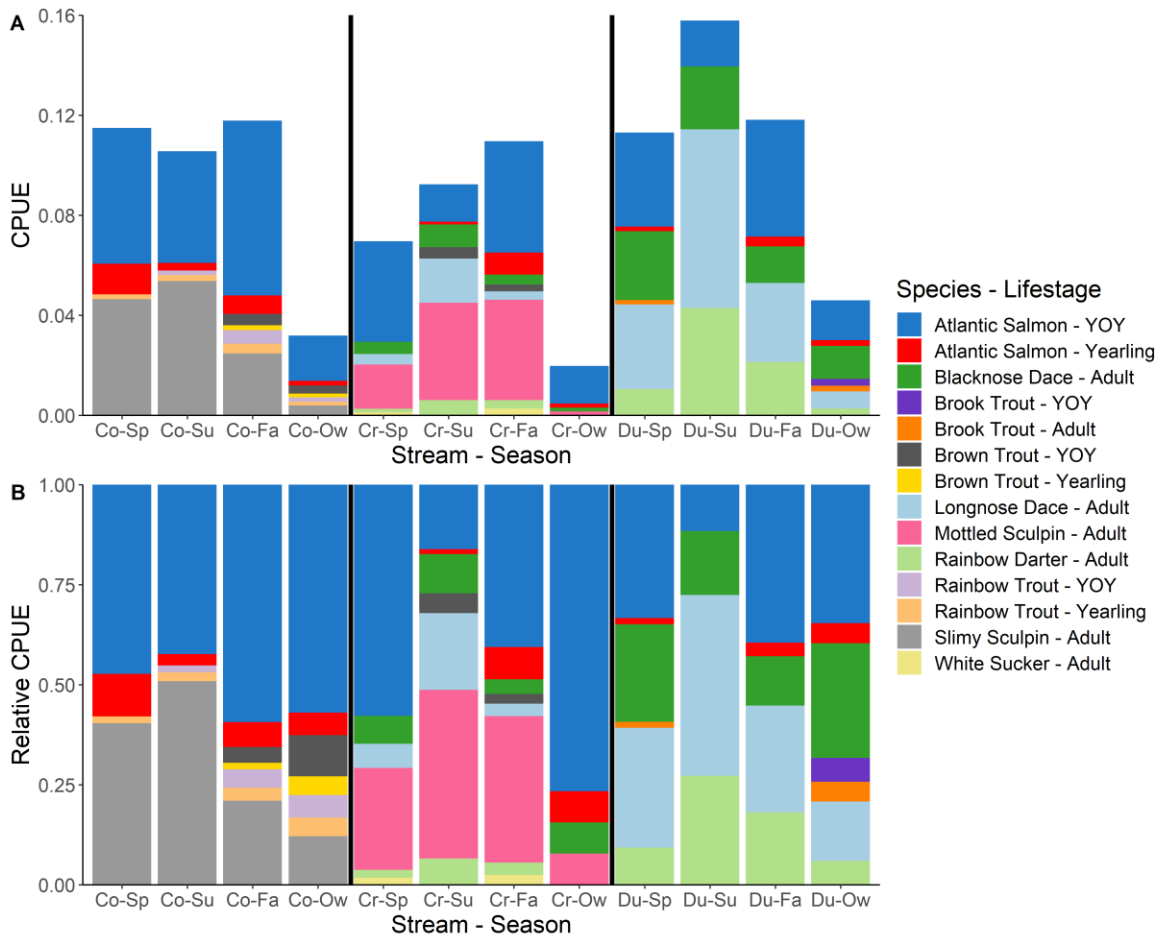
Figure 2.2 The A) total and species-life stage catch-per-unit-effort (CPUE; number captured per electrofishing seconds) and B) relative abundance of species-life stage in each stream (Co = Cobourg Brook; Cr = Credit River; Du = Duffins Creek) and season (Sp = spring; Su = summer; Fa = fall; Ow = overwinter). Stream barplots are segregated by black lines.
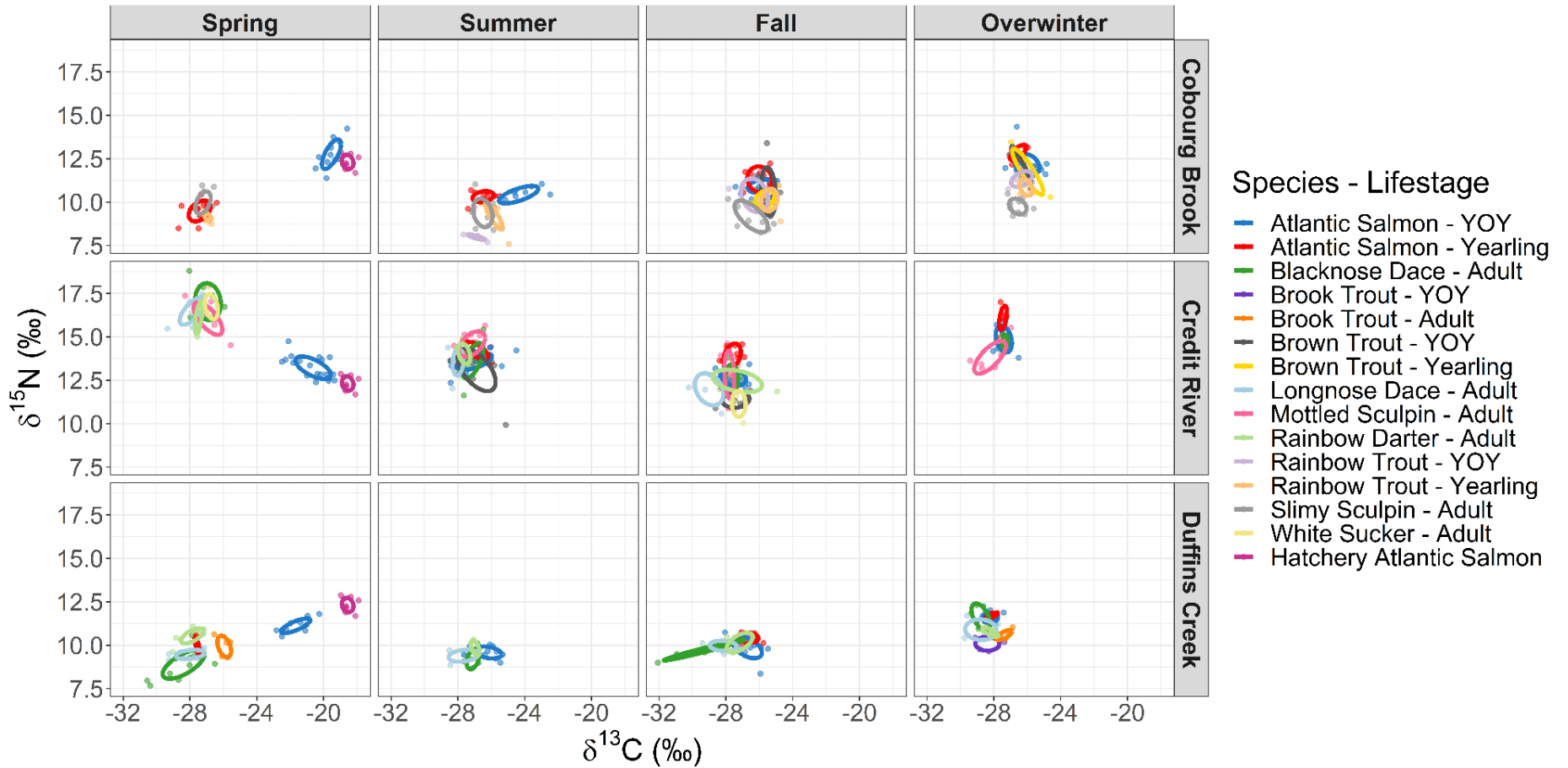
Figure 2.3 Stable isotope bi-plot of the isotopic niches of species-life stages of invertivores in the fish community by season and location. Thick circles enclose standard (40%) ellipse areas for each species-life stages. Hatchery Atlantic Salmon signatures are portrayed in spring for each location for reference.
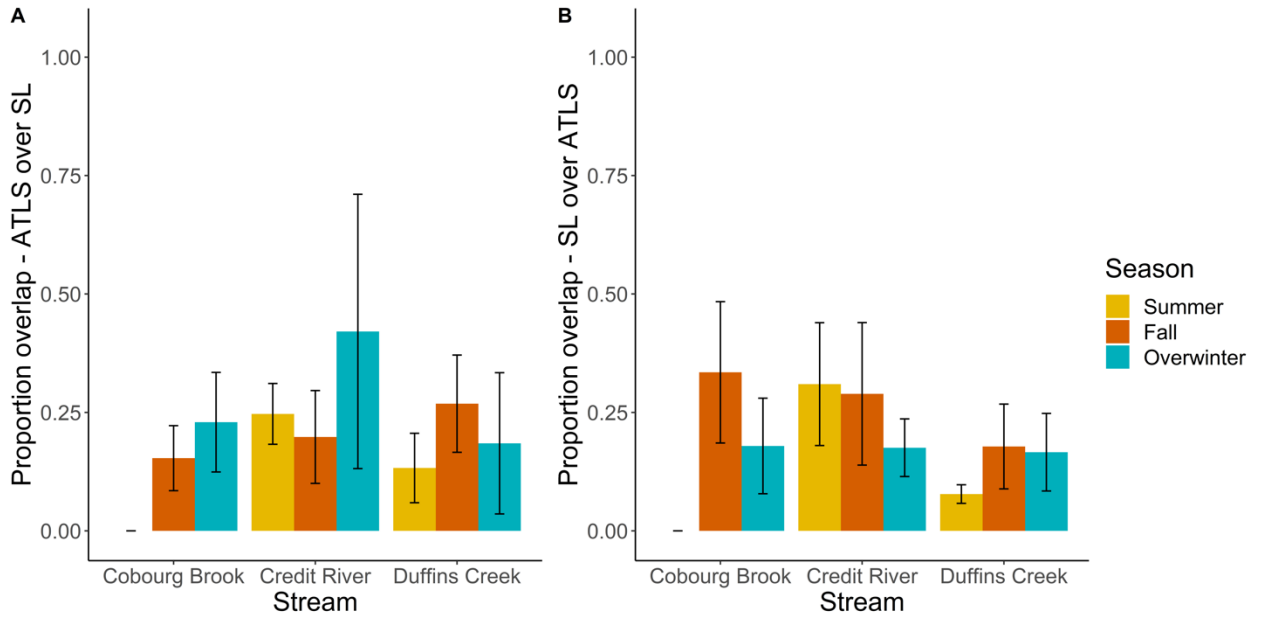
Figure 2.4 Mean ± SE of the proportion overlap of the standard ellipse area with A) Atlantic salmon young-of-year (ATLS) overlapping species-life stages (SL) and B) SL overlapping ATLS, by stream and season.
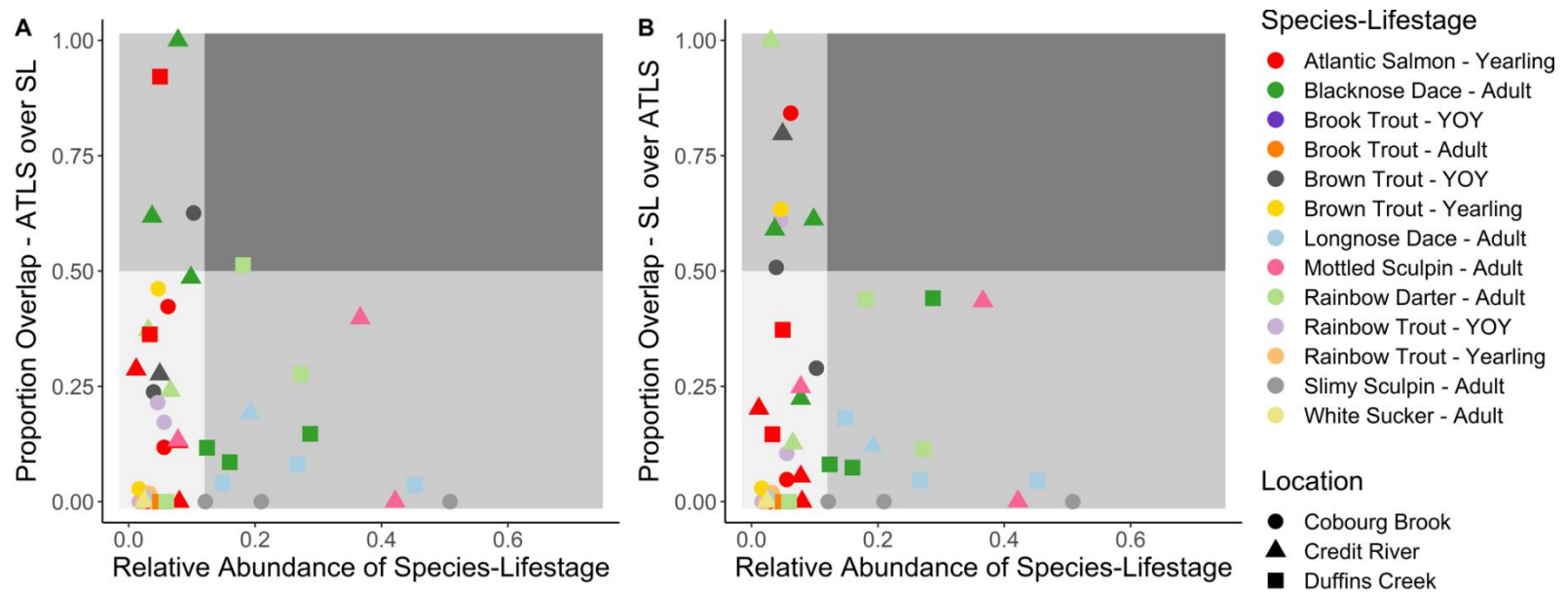
Figure 2.5 The proportion overlap of the standard ellipse area with A) Atlantic salmon young-of-year (ATLS) overlapping species-life stages (SL) and B) SL overlapping ATLS by the relative abundance of SL. Grey scale indicates the potential level of impact to ATLS based on interaction strength of the niche overlap as depicted in Figure 1. High niche overlap is considered > 0.5, and the lowest relative abundance of ATLS across sampling events was 0.12
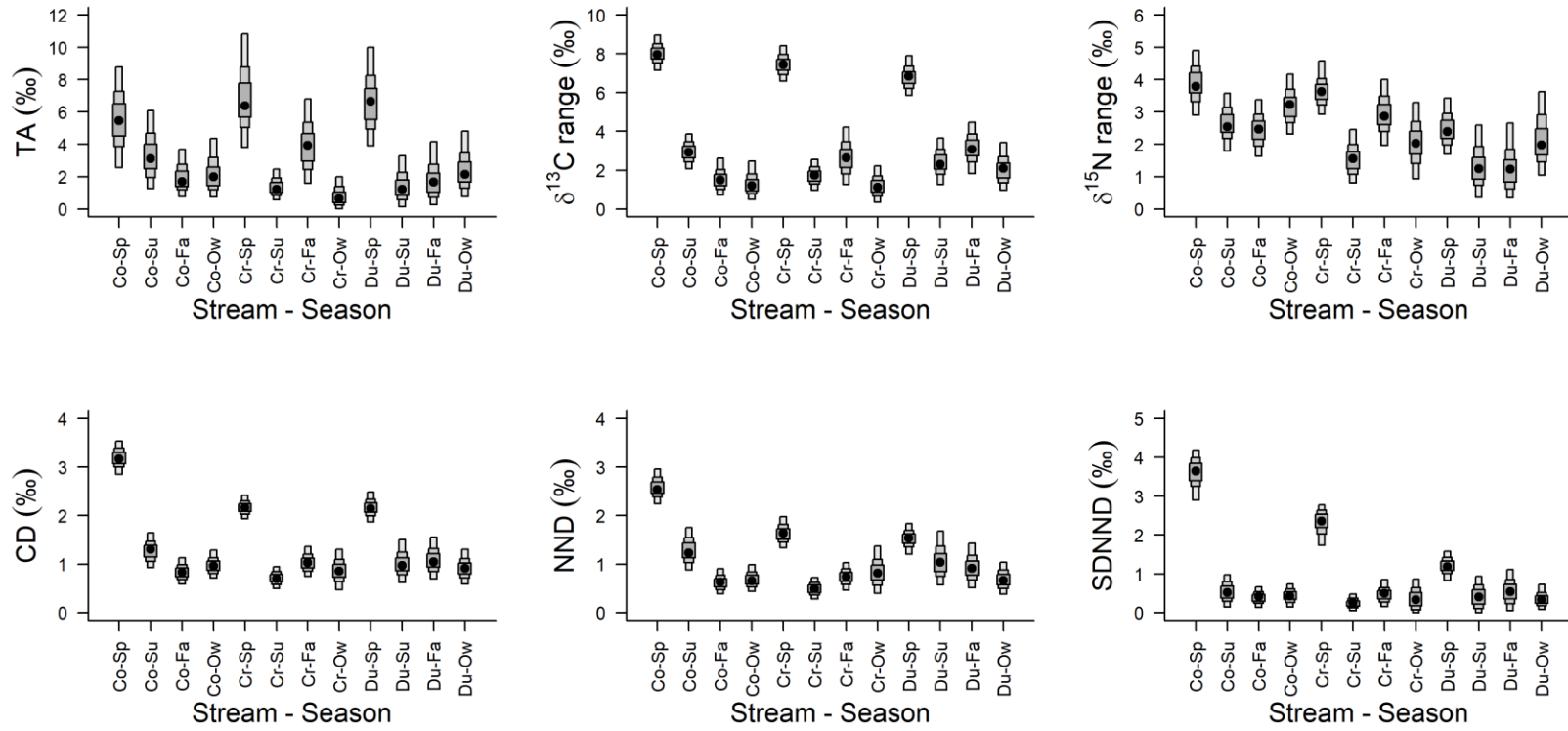
Figure 2.6 Density plots showing the isotopic structure or Bayesian Layman's metrics (TA = total convex hull area; CD = mean distance from the centroid; NND = mean nearest neighbour distance, SDNND = standard deviation of the nearest neighbour distance) for the fish community in each stream (Co = Cobourg Brook, Cr = Credit River, Du = Duffins Creek) and season (Sp = spring, Su = summer, Fa = fall, Ow = overwinter). The black dots represent the mode and boxed areas reflect the 95, 75 and 50% credible intervals.

CHAPTER 3 – SURVIVAL AND MIGRATION PATTERNS OF NATURALLY- AND

HATCHERY-REARED ATLANTIC SALMON (*SALMO SALAR*) SMOLTS IN A

LAKE ONTARIO TRIBUTARY USING ACOUSTIC TELEMETRY

3.1 Introduction

It has become a common practice to stock hatchery-reared fish to supplement wild populations and enhance fisheries (Minckley 1995; Brown and Day 2002; Molony et al. 2003). For instance, Atlantic salmon (*Salmo salar*) are commonly stocked as fry, parr, smolt and adult life stages in rivers to compensate for declining populations and supplement natural reproduction throughout the species' distribution range (Parrish et al. 1998; Saltveit 2006; Thorstad et al. 2012a). However, hatchery-reared fish have lower fitness compared to their wild conspecifics (Einum and Fleming 2001; Brown and Day 2002; Araki et al. 2007; Araki et al. 2008; Araki and Schmid 2010). Studies are relatively limited examining fitness differences among hatchery fish stocked at differing life stages, and thus different rearing duration in the natural environment. Although fish stocked at later life stages (e.g., smolts) have increased survival while in the hatchery environment, they can avoid natural selection processes and later on have reduced fitness relative to similarly aged fish that were stocked at earlier life stages (e.g., fry or parr; Thériault et al. 2010; Milot et al. 2013; Birnie-Gauvin et al. 2018). For example, coho salmon (*Oncorhynchus kisutch*) released as fry have been shown to exhibit more similar behaviour to wild fish than those released later as smolts (Theriault et al., 2010). Stocking fish earlier and being naturally-reared may have increased fitness and better represent wild fish than if stocked later.

Smolting, the transition from rivers to oceans (or lakes), can be a period of high natural mortality in Atlantic salmon (Klemetsen et al. 2003; Thorstad et al. 2011a). Studies indicate that hatchery-reared salmonid smolts have poorer survival once in the marine environment relative to wild smolts (Jonsson et al. 1991; Saloniemi et al. 2004;

Beamish et al. 2012) or to naturally-reared smolts (i.e., released earlier as parr and reared in rivers; Jokikokko et al. 2005). Similarly, hatchery Atlantic salmon released as parr have greater smolt migration survival than when released as either fry or smolts (Birnie-Gauvin et al. 2018). However, few studies have assessed riverine migratory performance differences in hatchery-reared and wild smolts (Thorstad et al. 2012a; Urke et al. 2013) and none to my knowledge have assessed these differences with hatchery- and naturally-reared smolts. There is some indication that hatchery-reared Atlantic salmon smolts have similar migratory performance (e.g., speed, times of day, effects of environmental parameters on migration initiation) yet lower overall survival than wild smolts (Thorstad et al. 2012a; Urke et al. 2013). Thus, presumably naturally-reared smolts would have migratory performances similar to wild and hatchery-reared smolts.

Migratory performance and survival of smolts may potentially be reduced in rivers with migratory barriers such as dams (Saltveit 2006; Holbrook et al. 2011; Stich et al. 2015; Huusko et al. 2018). Hydroelectric and water regulatory dams with turbines and/or augmented flow rates can cause immediate mortality, injury, migratory delays and/or impassable barriers which further reduce overall smolt survival and migratory success (Aarestrup and Koed 2003; Holbrook et al. 2011). Even weirs (e.g., mill dams or fish farming weirs) can reduce flows or increase presence of fish predators that can reduce survival of downstream migrating smolts (Aarestrup and Koed 2003). Thus, hatchery-reared Atlantic salmon smolts may have reduced survival relative to naturally-reared smolts which may be further compounded with the presence of weirs.

The Ontario Ministry of Natural Resources and Forestry (OMNRF) has been reintroducing Atlantic salmon to Lake Ontario since the 1990s by stocking different life

stages of hatchery-reared fish in select tributaries in which there is no known natural reproduction (OMNRF, 2017). Fish stocked as parr (<1 year old) reside in the river approximately one to two years until the appropriate size to smolt (e.g., naturally-reared smolts), while fish stocked as smolts will leave the river the same season upon stocking (e.g., hatchery-reared smolts). Using a rotary screw trap, OMNRF has observed both naturally- and hatchery-reared smolts moving through the Credit River system, a key tributary for Atlantic salmon stocking (OMNRF, 2016; 2017). However, the overall survival and movement strategies (e.g., speed, times of day, effects of environmental parameters on migration) for naturally- and hatchery-reared smolts to complete the migration to Lake Ontario are unknown. Furthermore, the presence of two weirs on the Credit River, which are common in the tributaries of Lake Ontario, may further reduce survival of smolts.

The use of acoustic telemetry and availability of smaller transmitters (herein called tags) allows for remote detection to determine an animals' movement and behaviour and better evaluate survival, timing (in association with environmental parameters), and performance of Atlantic salmon smolts during the river migration (Halfyard et al. 2013; Holbrook et al. 2011; Urke et al. 2013). Therefore, using acoustic telemetry, the aim of this chapter was to determine naturally- and hatchery-reared Atlantic salmon smolt survival and migration patterns in a tributary with weirs in order to improve the understanding of the smolt migration of a landlocked population and contribute to stocking strategies and reintroduction success. With no known natural reproduction in the system, naturally-reared smolts were the closest thing to truly "wild" smolts, yet whether they have increased survival relative to hatchery-reared smolts is

unknown. Therefore, the objectives were to determine whether hatchery-reared Atlantic salmon smolts released in the Credit River have lower survival yet similar movement strategies as naturally-reared smolts when migrating to Lake Ontario. Also, to determine if migration initiation was correlated with environmental variables to inform stocking timing, and whether weirs reduce survival and migration speed of smolts.

3.2 Methods

Study area and acoustic array

The study area was located on the Credit River, Ontario, Canada, starting in the upper reach of the Credit River down to Lake Ontario, a distance of approximately 75 river kilometers (rkms; Figure 3.1). The Credit River drains an area of approx. 850 km^2 and is characterized by a network of glacial spillways containing deposits of gravel with substantial groundwater inputs (Cunjak and Power 1986). The river is approximately 10 m wide at the release point and widens to approximately 30 m at the river mouth. Historic weirs (specifically mill dams with a 2-3 m vertical drop) with associated fishways are located 35 (Norval) and 60 (Streetsville) rkms downstream from the release point (see Appendix 4 for spacing).

Hatchery-reared smolts were released, and naturally-reared smolts were tagged, at locations previously stocked by OMNRF in the upper reach of the Credit River. In 2017, the release site and naturally-reared fish tagging location was on the West Credit branch of the Credit River (43.7958°, -80.0090°; Figure 3.1). In 2018, the release site and naturally-reared fish tagging location was moved 1.5 km downstream to the upper Credit River to obtain larger sample sizes of naturally-reared fish (n = 8 in 2017 vs n = 30 in 2018; 43.8021°, -79.9964°; Figure 3.1). Although release sites were different, for

analyses both release sites were set to 0 rkms for simplicity and given the proximity of the release sites for the two years.

An array of VR2W 180 kHz receivers (Vemco Ltd., Halifax, NS) were deployed throughout the Credit River over 75 river kms (n = 27 total sites; n = 23 deployed per year), however, for analyses, 12 sites were used based on grouping sets of receivers and removing those that had low detection probability (described later; Figure 3.1). Spacing of receivers and weirs are described in Appendix 4. Four receivers were located close to the release site (West Credit in 2017 and upper Credit in 2018) to indicate the start time and direction of movement as fish left the area. The release site receivers were grouped from both years and the first downstream site (n = 9 receivers total) into a single "start" location for analyses (Appendix 4). Receiver moorings were deployed in 0.5 – 2 m depths and cabled to shore with 4.76 mm diameter stainless steel cable. Receiver moorings (~ 25 kg) were constructed with a PVC pipe fitted into the open space of a cinderblock, with the remaining openings filled half-way with cement and a u-shaped rebar inserted into the cement to act as a handle/attachment point. Receiver moorings were monitored every month to ensure that they remained in proper positioning in the river, as high flows or people could move the moorings out of the water. Three receivers were deployed at the mouth of the Credit River in Lake Ontario and for analyses were grouped with two receivers at the end of the river into a single "end" location (Figure 3.1; Appendix 4). Additionally, six receivers were deployed along the nearshore and fourteen deployed in the offshore of the western basin of Lake Ontario to determine general lake movements of successful smolts (Figure 3.1). The river mouth and nearshore receiver moorings were connected to a ~25 – 40 kg anchor mooring by a weighted rope to be retrieved via

grappling by boat. Offshore receivers were attached to an acoustic release receiver associated with other telemetry projects. River mouth receivers were deployed during both years of the study, however, nearshore and offshore receivers were only deployed during 2018, of which the fourteen offshore receivers and one nearshore receiver (Burlington: 43.33060, -79.75633) were deployed prior to the smolt migration (April 14 - 25, 2018). The remaining five nearshore receivers were deployed after the migration by June 15, 2018 and were not useful for this study (Figure 3.1).

Range test tags were used in the array to determine the tag detection efficiency within the river and at the river mouth, and whether there was full detection coverage or if analyses had to be modified based on poor coverage (e.g., keeping sites for analyses, determining site specific probabilities). Two V9 range test tags (Vemco V9-2H 180 kHz; length: 26 mm; mass in air: 3.7 g; nominal delay: 15 or 30 min), with the same power output yet longer battery life as the V5 and predation tags used and thus representative of tagged fish (Vemco 2018), were placed at rkm 46.5 (representative of the river) and 74.5 (representative of the river mouth) at approximately 35 and 90 m away from the nearest receiver, respectively, and farther away than the width of the river. Tag detection efficiency was determined around the migration period for both 2017 and 2018. Due to the loss of range test tags, full coverage over the migration period was not always possible. Tag detection efficiency within the river was less than 60% at 35 m (56% in 2017 and 39% in 2018) at the location selected, and thus indicated that fish may migrate undetected at a particular receiver in the river. Tag detection efficiency at the river mouth was greater than 80% at 90 m (85% in 2017 and 82% in 2018). With the high detection efficiency from a longer distance from the range test tag and the general coverage of five

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receivers (grouped as the "end" point) as fish enter Lake Ontario, it was presumed that there was full detection of fish as they enter the river mouth and Lake Ontario, providing confidence in which fish successfully migrated. Due to the poor within river range testing and variable habitat within the river, receiver specific detection probabilities were determined from the probability of fish that migrated successfully to Lake Ontario being detected at each receiver location, as not all successful fish were detected at all river receivers. These detection probabilities were later used for within river survival analyses. Receiver locations were removed from analyses if detection probability was unreliable with values <50% at a site (n = 3 sites, where shallow water or tampering reduced detection ability; Appendix 4). Unfortunately, the locations with poor detection happened to be at sites closest to the weirs.

Source of fish

Hatchery-reared fish used for tagging (LaHave strain) were sourced from the OMNRF Normandale Fish Culture Station (Turkey Point, ON). Mean (± SD) fork length and mass of hatchery-reared fish in 2017 (n = 32) were 198 ± 12 mm and 93 ± 18 g, and in 2018 (n = 30) were 186 ± 21 mm and 76 ± 22 g. In the Credit River, naturally-reared Atlantic salmon were originally stocked as parr the previous spring which survived and grew to smolt size. Naturally-reared fish were captured using a backpack electrofisher (settings: 250-350 V, 40 Hz, make: Halltech Aquatic Research, Guelph, ON) within a 300 m stretch of the stocking sites in both years. Captured fish were tagged only if fork length was > 125 mm to ensure fish would smolt based on the literature and local information (Elson 1957; Scott and Crossman 1998; M. Desjardins, OMNRF, pers. comm.). Mean (± SD) fork length and mass of naturally-reared fish was 140 ± 8 mm and

31 ± 6 g in 2017 (n = 8), and 143 ± 13 mm and 32 ± 9 g in 2018 (n = 30). Fish were held in an aerated cooler filled with ambient river water prior to and post tagging. Overall, hatchery-reared fish (192 ± 18 mm) were significantly larger than naturally-reared fish (143 ± 12 mm; Mann Whitney U test: W = 2292.5; P < 001), however, they were representative of the size of fish that OMNRF typically stocks in streams and were thus comparable to naturally-reared fish.

Tagging

Two types of tags were used throughout the study: V5s (Vemco V5-2H 180 kHz; length: 13 mm; mass in air: 0.65 g; estimated battery life: 128 - 140 days; nominal delay: 40 – 80 s) and predation tags (Vemco V5D-1H 180 kHz; length: 13 mm; mass in air: 0.68 g; estimated battery life: 108 days; nominal delay: 40 – 80 s) which trigger a new identification code upon being consumed (Halfyard et al. 2017). In 2017, all tagged fish had V5 tags (n = 40), while in 2018 fish were tagged with either a V5 or predation tag (n = 15 for each tag type, for both hatchery- and naturally-reared fish). Due to hatchery protocols and logistics, individuals were anaesthetized using clove oil (50 mg/L) for hatchery-reared fish and MS-222 (100 mg/L) for naturally-reared fish. Individuals were weighed (round mass; ± 1 g) and measured (fork length; ± 1 mm). Tags were inserted through a ~ 1.5 cm incision on the ventral side of the fish off the midline using surgical tools sterilized in a 10% betadine solution. The incision was closed with 2 simple interrupted sutures (5-0 coated Vicryl Plus undyed braided suture; Ethicon, Inc.). Post-surgery, fish were placed in an aerated cooler and observed (< 15 min) for recovery from anaesthesia. Hatchery-reared fish were then transferred back to a holding tank until stocking (3 – 14 days post-surgery) where no mortality occurred during this time.

Naturally-reared fish were released after electrofishing was completed for the day to prevent additional stress of being recaptured (April 12-13, 2017 and April 6-7, 2018). Hatchery-reared fish were transported to the Credit River in a large, aerated holding tank (1 m x 2 m x 1.5 m) and stocked on April 21, 2017 and April 12, 2018. Tagging and release of fish occurred during similar times as OMNRF spring smolt stocking and prior to anticipated migration timing of May – June.

Environmental monitoring

Environmental variables were monitored from March to July in 2017 and 2018 to determine if there was any correlation with timing of migration of naturally- and hatchery-reared Atlantic salmon. Water temperature (°C) and flow ($m^3 \cdot s^{-1}$) were logged every 15 minutes at water quality monitoring stations maintained by the Credit Valley Conservation Authority (CVCA) within 5 km of release sites in which mean daily temperature and flow were calculated. Accumulated thermal units (ATU), the sum of daily mean temperatures, were calculated from March 1 onwards (for each year, respectively) when daily mean temperatures started to rise from 1°C. For hatchery-reared fish, ATUs were calculated from March 1 onwards using daily hatchery water temperatures (8 °C) until the stocking dates, after which ATUs were calculated as described above.

Data analyses

Survival analyses

To determine if successful migration varied by fish rearing, a logistic regression was used with rearing (naturally- or hatchery-reared) and year (2017 and 2018) as categorical variables on the success of migrating to Lake Ontario. An interaction term

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was not included as it was not significant (P > 0.05) but also when included in the model, it created an issue with perfect separation (in which there was only one outcome with naturally-reared smolts in 2017).

To determine whether survival varied within the river either at weirs or between receiver locations, a Cormack–Jolly–Seber (CJS) model for live recaptures was used (Cormack 1964; Jolly 1965; Seber 1965) within the program MARK (White and Burnham 1999) using the RMark package (Laake 2013) in R (version 3.4.2; R Core Team 2017). The CJS model calculates a maximum-likelihood estimate (± standard error) for survival (Φ or Phi) and probability of recapture (p). As salmon smolts have a unidirectional migration from the river to the lake, the CJS model can be used such that recaptures (i.e., tagged fish detected acoustically downstream from release) occur along a migratory corridor as opposed to distinct capture time periods (Halfyard et al. 2013; Michel et al. 2015). The distance between two receivers was considered the sampling interval for which survival was estimated. Thus, models estimated survival for each passive receiver interval along the progression of smolt migration. Survival estimates were standardized by the length of the receiver interval (i.e., survival per km). This was done by setting the time intervals (in reality, space intervals for this application – Appendix 4) in the process.data() function of RMark package to a vector of reach lengths (in units of km).

As fish migrate through the system, presence/absence (1,0) was determined at each receiver location for each fish to create a capture history (e.g., 111010100001). The presence of weirs was indicated for the receivers immediately downstream of the Norval and Streetsville weirs (35 and 60 kms from release), to determine if weirs explained a

reduction in survival (and no effect of p) during the migration. Presence of weirs and receiver location were not used together as model factors to assess whether weirs or location (i.e., spatial heterogeneity) better explained survival.

Factors that may affect Φ and p were assessed [fish rearing (Φ only), year, receiver location, presence of weirs (Φ only), and receiver specific detection probability (described previously; p only)] using all biologically plausible combinations/interactions, along with a "null model" in which the parameters for Φ and/or p are constant. Each factor-specific CJS model was compared with one another and the "null" model using Akaike's information criterion corrected for small sample sizes (AICc). Optimal models were identified as the model with the lowest AICc value and the highest model weights. Candidate models with ΔAICc values < 2 have similar explanatory power (Burnham and Anderson 2002). Prior to model selection, the global CJS model [Φ(Year*Weir*Rearing*Location) p(Year*Location*Detection)] was tested for goodness-of-fit (i.e., overdispersion) by calculating an overdispersion parameter ($\hat{c}$) from simulating model deviance using a bootstrapping method with n = 1000 simulations. The $\hat{c}$ was estimated by dividing the deviance estimate from the original global model by the mean of simulated deviances. A $\hat{c}$ of 0.943 was obtained, indicating no overdispersion, and thus AIC values were not adjusted (Burnham and Anderson 2002). Only the top 10 models are presented for efficiency.

Movement analyses

For all movement analyses, data associated with the last time a fish was detected at a site to indicate leaving (e.g., migrating) and first time a fish was detected at sites to indicate arriving was used. Migration initiation time was determined as fish left the

"start" site. It was not always possible to determine when unsuccessful fish began migration as some were not seen downstream nor upstream of the release/tagging site, and due to this discrepancy, unsuccessful fish were not considered in the analyses of migration initiation. Due to small sample sizes when split by year and fish rearing, day number, mean daily water temperature, ATUs and mean daily flow in which fish initiated migration is described. Successful hatchery-reared fish in 2018 migrated the day they were released, skewing potential migration initiation trends and were removed from analyses, creating an unbalanced design. Year and fish rearing were combined to have 3 groups (2017 - Hatchery; 2017 - Natural; 2018 - Natural) within a single environmental variable and conducted a Kruskal-Wallis test, followed by a pairwise Wilcoxon rank sum comparison with a Bonferroni correction.

Overall migration speed (km·hr^{-1}) was determined from successfully migrating fish only. Speed was calculated based on the total river distance of 75 km divided by the time taken from leaving the "start" site until arriving at the "end" site. A Kruskal-Wallis test with four groups (combination of year and fish rearing) was run to determine if there were differences in migration speed between naturally- and hatchery-reared smolts and years. To determine if migration speed varied throughout the river, the distance between successive sites was divided by the duration of time taken for an individual fish to leave the previous site and arrive at the next site. This removes any holding time at any one specific receiver and speeds may appear faster than overall migration. All fish (successful or not) were included. A linear mixed model was used to test for significant differences in migration speed between fish rearing, year and receiver location and all two-way interactions, with individual fish as a random factor followed by a post-hoc Tukey

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pairwise comparison of the least squares means to determine differences in migration speed by receiver location.

To determine whether fish migrate at different times of day, all fish leaving sites other than the "start" site were assessed to ensure detections were during migration only. Daily hours were broken up into four 6-hour intervals (00-06, 06-12, 12-18, 18-24). These times roughly distinguish between day and night, as dawn and dusk were at 06:00 and 20:00 approximately during the study period. Thus, 00-06 and 18-24 were considered night, while 06-12 and 12-18 intervals were considered day. For each 6-hour interval there were counts of detection events of an individual fish passing. To test for significant differences in detection events per fish during migration between fish rearing and time of day (four 6-hour intervals), a generalized linear mixed model (glmm) was performed with individual fish as a random effect using a Poisson distribution. A type II analyses of deviance was used to determine significant differences between variables followed by a post-hoc Tukey pairwise comparisons of the least squares means to determine differences in counts of detection events during the four periods of day.

The subset of fish tagged with predation tags were assessed for predation events (change of identification code) throughout the migration as well as within the lake. Lake Ontario movements were determined using detections from the acoustic telemetry array (described earlier) deployed within the western basin of Lake Ontario (Figure 3.1). General post-migration lake movements and predation events are described.

All analyses were conducted in R and significance was assessed at $\alpha = 0.05$ or the lack of overlap in 95% confidence intervals (CI). Unless stated otherwise, values are

reported in mean ± SD. Assumptions of normality and homoscedasity were visually

assessed using qqplot and fitted vs residual plots.

3.3 Results

Naturally-reared fish were 13.9 times more likely to successfully migrate to the

lake than hatchery fish when controlling for year ($Z = 4.315$, $P < 0.001$). Fish migrating

in 2017 were 5.5 times more likely to be successful than migrating in 2018, when

controlling for rearing group ($Z = 2.826$, $P = 0.004$; Table 3.1).

The best supported CJS model estimated survival per km using fish rearing*year

and location, and estimated probability of recapture using the calculated receiver specific

detection probability (Table 3.2). All top ten models had fish rearing and location

estimating survival, and nine of the top ten models had year estimating survival, while all

top ten models had detection efficiency estimating probability of recapture (Table 3.2).

The lack of weirs as a factor indicates that there were differences in survival by location

that were not attributed to weirs (Figure 3.2). Based on lack of overlapping 95% CI of

survival·km^{-1} estimates (Φ), the release point (0 km) had significantly lower survival

rates than all other locations, except at river km 4.5 which had large variability in

survival (large CIs; Figure 3.2). Naturally-reared smolts generally had greater survival

than hatchery-reared smolts in both years, yet naturally-reared smolts had a greater

reduction in survival in 2018 than 2017 (which was 100%) compared to hatchery-reared

smolts as indicated in the top model with the interaction between fish rearing and year.

These results corroborate with the logistic regression estimates of differences in overall

survival.

Successful, hatchery-reared smolts left on the same day they were stocked in 2018 (April 11; n = 4) and were not included for further analyses. Of the successful migrants, date of migration initiation varied between groups (X^2_2=7.390, P = 0.025), and naturally-reared fish migrated later in 2018 (May 11 ± 5 days, n = 18) than 2017 (May 4 ± 6 days, n = 8; P = 0.012; Figure 3.3 and 3.4A). While migration date of hatchery-reared fish in 2017 (May 10 ± 10 days, n = 12) was not significantly different from naturally-reared fish in either 2017 or 2018 (P = 0.120 and P = 0.882, respectively). Water temperatures when fish started migrating were different between groups (X^2_2=15.538, P < 0.001). Water temperatures were similar between naturally- (9.7 ± 2.2 °C) and hatchery-reared fish (11.2 ± 2.8 °C) in 2017 (P= 0.371) yet was significantly warmer for naturally-reared fish in 2018 (13.7 ± 1.1 °C; P= 0.002 and P = 0.005, respectively; Figure 3.4B). The ATUs when fish began migration varied between groups (X^2_2= 23.704, P < 0.001). ATUs did not differ between naturally-reared fish in 2017 (393 ± 56 °C) and 2018 (355 ± 60 °C; P= 0.209), however, hatchery-reared fish in 2017 migrated at significantly higher ATUs (626 ± 109 °C) than naturally-reared fish in 2017 (P < 0.001) and 2018 (P < 0.001; Figure 3.4C). Flow did not vary significantly for hatchery-reared fish in 2017, naturally-reared fish in 2017, and naturally-reared fish in 2018 (6.6 ± 3.4 m³·s⁻¹, 6.8 ± 2.9 m³·s⁻¹ and 4.8 ± 0.9 m³·s⁻¹, respectively; X^2_2= 3.928, P = 0.140; Figure 3.4D).

Although there were differences in survival of naturally- and hatchery-reared smolts, overall migration speed did not vary among fish rearing and years (X^2_3=6.562, P = 0.087). Mean migration speed for smolts was 0.70 ± 0.39 km·hr⁻¹. The migration speed throughout the river also did not vary by fish rearing (X^2_1=0.003, P=0.958), year (X^2_1=3.039, P=0.081), fish rearing and year (X^2_1=1.950, P=0.163), or interact with

receiver location (fish rearing * location: X^2_{10}=8.795, P=0.552; year * location: X^2_{10}=6.924, P=0.733). However, migration speed did vary by receiver location (X^2_{10}=97.743, P<0.001). Pairwise comparisons indicated that migration speed at the lower end of the river (except for the last site of entering Lake Ontario) was significantly faster (means ranged from 2.52 – 3.32 km·hr^{-1}) than the upper reaches (except for the first site; means ranged from 1.09 – 1.60 km·hr^{-1}; Figure 3.5). As fish reached Lake Ontario, mean migration speed slowed down to 0.92 ± 0.84 km·hr^{-1}.

When assessing if there were differences in the number of times fish were detected at receivers at different times of day while migrating, there was no significant difference between rearing groups on number of detection events (X^2_1=0.587, P=0.444), nor an interaction between fish rearing and time of day of detection (X^2_3 = 3.678, P = 0.298). There was a significant difference in the number of detections events at different times of day (X^2_3 = 70.216, P < 0.001). Fish were detected more frequently moving past receivers between the hours of 18-24, followed by 00-06, with the 6-hour intervals of 06-12 and 12-18 with the lowest detections of fish (Figure 3.6).

Smolts were detected in Lake Ontario after leaving the Credit River in 2018. Between the one nearshore and fourteen offshore receivers in Lake Ontario deployed at the time of migration, eight receivers detected 7 naturally-reared and 1 hatchery-reared smolts (Figure 3.7). Of the fish that out-migrated to Lake Ontario, 38% of naturally-reared and 25% of hatchery-reared smolts were later detected in the lake. Fish were generally detected within a few days to a week of leaving the Credit River, however two fish were detected later with one detected nearly a month after reaching Lake Ontario and nearing the end of the battery life of the tag. Fish were detected from a range of 15-40 km

from the Credit River. Two fish were detected on more than one receiver, in which each fish moved a cumulative 35 and 55kms (linear distance).

From the predation tagged fish, there was no detection of predation events during the smolt migration. Similarly, within Lake Ontario, two naturally-reared fish with predation tags were not predated at the time of detection.

3.4 Discussion

Overall, using acoustic telemetry provided a focused assessment of the migration of naturally- and hatchery-reared land-locked Atlantic salmon smolts in a Lake Ontario tributary. Naturally-reared Atlantic salmon smolts consistently had higher survival and successful migration to Lake Ontario than hatchery-reared smolts and 2017 yielded more successful smolts than 2018. Throughout the river migration, survival was lowest at the release/tagging point and was nearly 100% thereafter, while there did not appear to be any impact with downstream passage over the weirs. Although the two years had different temperature and flow regimes, the general movement patterns (speed and time of day) between the two groups were consistent.

Migration initiation

There were not adequate sample sizes of successful smolts to determine whether environmental variables drive migration initiation, however some trends were noticed when comparing within groups. Successful hatchery-reared smolts began migration later in 2017 than 2018, yet 2018 smolts skewed any correlations with environmental variables by migrating on the day of release. Stich et al. (2015a) found that hatchery-reared Atlantic salmon smolts stocked earlier in the year initiated migration sooner than those released later in the year. Also, hatchery-reared Atlantic salmon smolts stocked later in

the year (yet still within the natural smolt timing) had increased survival relative to those stocked earlier (Karppinen et al. 2013). Although hatchery-reared smolts were stocked at the same time as the stocking programs (to relate results to management) it resulted in earlier stocking in 2018 at lower temperatures, with earlier migration and lower survival. The temperature differences at the time of stocking between years may also contribute to migration timing. The differences seen in the migration timing of hatchery-reared smolts between years, at least when leaving the day of release in 2018, is more likely attributed to when they were stocked than environmental variables.

Although naturally-reared smolts left later in 2018 than 2017, the ATUs were not significantly different between years while mean daily temperature was greater in 2018 than 2017. There is indication that timing of smolt descent is influenced by degree-days or ATUs as opposed to actual water temperature (McCormick et al. 1998), or a combination of actual temperature and temperature increase in the water during spring (Jonsson and Ruud-Hansen, 1985; Jonsson and Jonsson, 2009a). In this study, the similar ATUs between years may be a good proxy for the effect of spring temperature trends on migration initiation. Smolt migration initiation has been influenced more strongly by ATU than daily mean temperature in both Chinook salmon (*Oncorhynchus tshawytscha*) (Sykes et al. 2009) and Atlantic salmon (Zydlewski et al. 2005; Stich et al. 2015a). Brown trout (*Salmo trutta*) migrated later in seasons with cooler spring temperatures (Jonsson and Jonsson, 2009b) as was seen here in this study on Atlantic salmon. Although only inferences can be made as temporal trends of water temperature and flow were different between years, it appears that from consistency between years, the

initiation of the naturally-reared Atlantic salmon smolt migration in this study was also influenced by ATUs or spring temperature trends rather than daily mean temperatures.

Flow is another factor that can stimulate smolt migration (McCormick et al. 1998; Jonsson and Jonsson, 2009a). In this study, flow was not significantly different between years or naturally- or hatchery-reared smolts, yet smolts left at slightly higher mean flows in 2017 than 2018. The increased survival of naturally- and hatchery-reared smolts in 2017 may be attributed to higher mean flows or that peak flows occurred during the smolt migration in 2017, while in 2018 peak flows occurred prior to migration. From 2011 to 2016, OMNRF used rotary screw traps on the Credit River to enumerate smolts during out-migration (OMNRF, 2017). Data from the screw traps may be used to further elucidate the consistency of ATUs and flow with migration initiation in Lake Ontario smolts.

Weir effects on smolt survival and speed

The two weirs on the Credit River did not impact downstream movement of smolts in both survival and speed. Previous studies have shown reduced survival and movement rates of smolts at dammed sections in regulated rivers (Holbrook et al. 2011; Stich et al. 2015a; Huusko et al. 2017). However, in this study, the weirs on the Credit River are relatively small low-head barriers originally constructed for milling operations in the early 1800s. Thus, the mill pond upstream of the weir may not reduce flow or disorient the fish as much as in regulated rivers with hydroelectric dams, nor the vertical drop (maximum of 3 m on the Credit River weirs) going over the weir did not appear to cause mortality (e.g., reduced survival downstream) with the associated flows. With the high flow rates in 2017 and 2018 relative to the Aarestrup and Koed (2003) study, the

downstream migration of smolts do not appear to be impacted by weirs on the Credit River. Instead of being slowed down by weirs, migration speed increased in the lower reaches of the river. Unfortunately, receivers deployed immediately downstream of the weirs were tampered with and removed from analyses so obtaining fine details of weir passage was not possible. However, mean survival estimates when passing the weir were > 99% while the interval prior to passing the weirs was slightly lower, suggesting other sections of the river incurred more mortality than those associated with the weirs. Generally, the mean mortality rates (1 – mean survival rates) per km throughout the Credit River (ranges from 0% - 5.7% mortality·km^{-1}) were either lower or within previously observed mortality rates in free-flowing rivers (0.3% – 7.0% mortality·km^{-1}; review by Thorstad et al. 2012a; Huusko et al. 2017), further indicating no weir effects on smolt migration or survival.

Hatchery- vs naturally-reared smolt implications

Naturally-reared smolts survived better than hatchery-reared smolts yet both groups had high initial mortality. Few studies have assessed wild or naturally- vs hatchery-reared smolt migration survival in rivers specifically. Of those studies, wild and hatchery smolts migrating the dammed Penobscot River, USA showed no difference in survival (Holbrook et al. 2011; Stich et al. 2015b) while on a free-flowing river wild smolts had greater survival than hatchery smolts (Hyvärinen and Rodewald 2013; Urke et al. 2013). Melnychuk et al. (2014) showed similar trends to this study between wild and hatchery-reared steelhead (*Oncorhynchus mykiss*) and also saw the majority of mortality occurring at the start of migration in the river. In this study, the main difference in naturally- and hatchery-reared smolt survival was seen at the point of release. As

otherwise, throughout the migration, survival as well as migration speeds and preference for migrating at night (18:00 to 06:00) for both naturally- and hatchery-reared smolts were similar, as was seen in Urke et al. (2013). This suggests that migratory performance and survival between naturally- and hatchery-reared smolts were similar aside from the initial mortality prior to migration. Other tagging studies have also experienced high initial mortality of stocked smolts (Holbrook et al. 2011; Thorstad et al. 2011b; Thorstad et al. 2012b; Huusko et al. 2017). It is not believed that direct tagging mortality occurred as hatchery fish in 2017 were held for over two weeks without incurring any mortality or tag expulsion (and thus only held for 72 hours in 2018). The lack of mortality of naturally-reared fish in 2017 further indicates that the capture and tagging methods used here did not cause tagging effects. There is the possibility of potential indirect tagging effects (e.g., predation) reducing survival of all groups (hatchery-reared more so) and not being detected thereafter. The stocking location in 2018, although having more naturally-reared smolts to tag, also had residential adult brown trout (a potential predator) that may have increased mortality relative to 2017 smolts, however the predation tags in 2018 indicated that this was not the case for those fish that were detected. There was a quick drop in water temperature from 4 to 0 ℃ three days after stocking in 2018 which may have provoked additional stress on both hatchery-and naturally-reared smolts, relative to 2017. However, those temperatures were above the lower critical temperature of Atlantic salmon (Elliott, 1991; Jonnson and Jonnson, 2009a) and detections of naturally-reared but unsuccessful (i.e., not detected completing the migration) smolts a month after the incident make this seem an unlikely cause of mortality.

The greater initial mortality of the hatchery-reared smolts relative to the naturally-reared smolts may be related to hatchery operations. Being raised in a hatchery condition longer and stocked as smolts (hatchery-reared group), as opposed to being stocked as parr (naturally-reared group), may have incurred epigenetic effects that were maladaptive upon being released into the river as a smolt. Genetically, the two groups came from the same strain and would have the same degree of inbreeding depression and domestication selection. However, epigenetic differences have been seen between hatchery and wild coho salmon smolts and may explain the reduced fitness between the groups (Le Luyer et al. 2017). Also, Milot et al. (2013) found that hatchery fish released as smolts had lower fitness than those released earlier as fry. Naturally-reared fish being subject to predation and environmental stressors longer may have been more fit at the time of tagging relative to hatchery-reared fish which had not been exposed to such pressures. Melynchuk et al. (2014) also allude to hatchery rainbow trout being less fit, naïve to river environments, and more prone to predation at the start of migration. Predation of hatchery-reared fish may be occurring from avian and mammalian predators which can predate upon smolts and not be later detected as the tag is physically removed from the river.

Aside from possible epigenetic or fitness differences, additional stocking stress or the time of stocking may cause the increased mortality of the hatchery-reared group. Stocking strategies (e.g., transportation and release methods) or hatchery-rearing methods can increase stress and reduce survival of smolts (Iverson et al. 1998; Barton et al. 1980; Finstad et al. 2003; Hyvärinen and Rodewald 2013). Handling and transportation of fish increases cortisol levels and has been correlated with lower survival of coho salmon smolts (Specker and Schreck, 1980; Schreck et al., 1989). Thus, the initial lower survival

of hatchery smolts may be a factor of stocking stress as performance-wise they were similar to naturally-reared smolts. The timing of stocking may also play a role in the increased mortality. Hatchery-reared smolts released earlier in cold waters had lower survival than those released later, closer to the time of natural migration (Karppinen et al. 2013). Karppinen et al. (2013) found that the early release group moved briefly downstream but then ceased migration and had increased exposure to predators. This could explain why no predation was seen, via predation tags, of hatchery-reared smolts near the receivers at the release point yet many smolts were not detected at the next site, 3.5 km downstream. Although it cannot be discerned from the study, various factors such as epigenetics, predation risk, transportation stressors, and stocking timing may have contributed towards the lower initial survival of hatchery-reared smolts compared to naturally-reared smolts.

Differences in hatchery- and naturally-reared smolt survival may be more prominent as they leave the rivers as opposed to during river migration. Relative to wild, hatchery-reared Atlantic salmon post-smolts in the ocean have reduced survival and/or return to natal rivers (Jonsson et al., 1991; Jonsson et al., 2003; Kallio-Nyberg et al. 2004; Saloniemi et al. 2004; Jokikokko et al. 2006), and hatchery-reared salmonids generally have reduced fitness in the wild (Araki et al. 2007; Araki et al., 2008; Milot et al., 2013). Interestingly, naturally-reared smolts had greater fjord survival than wild and hatchery-reared smolts (Flávio et al. 2019). Whether poor ocean/fjord survival of hatchery-reared smolts similarly translates to poor survival in a large lake, like Lake Ontario is unknown. Unfortunately, there was a delay in deploying receivers and there was not full coverage of the movements of smolts when entering Lake Ontario. Of the

fish that survived to Lake Ontario, slightly more naturally-reared smolts were detected than hatchery-reared smolts and there appeared to be no piscivore predation via the two predation tags detected. However, the array in Lake Ontario was not conducive to providing much detail regarding movement patterns. With increasing coverage of Lake Ontario with acoustic receivers, particularly near sites of river research, future studies could better assess smolt movements and survival in Lake Ontario.

Smolt success and Lake Ontario Atlantic salmon restoration

With ongoing restoration efforts of Atlantic salmon in Lake Ontario, it was important to understand the smolt migration success of the stocked fish. The relative survival of both naturally- and hatchery-reared smolts can help inform management with regards to stocking strategies and improving Atlantic salmon returns. For instance, it can be determined whether it is more effective to stock at the parr or smolt life stage given respective survival rates at each stage and rearing costs, or whether adjusting the timing of stocking can improve survival of hatchery-reared smolts. Naturally-reared smolts had greater migration survival than hatchery-reared smolts, and weirs were not a factor in migration survival. However, a better understanding of what caused reduced survival at the start of the migration may help improve migration success but also in predicting smolt numbers – whether it be assessing stocking strategies or hatchery-rearing methods. As smolt survival was very high further downstream, previous OMNRF rotary screw trap data could be compared to stocking numbers to obtain population estimates with the aid of the survival estimates from this study. Overall, acoustic telemetry revealed naturally- and hatchery-reared Atlantic salmon smolt migration patterns and success in a Lake

Ontario tributary in an effort to reveal potential survival bottlenecks to the restoration of Lake Ontario Atlantic salmon.

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Table 3.1 The proportion and number of acoustically tagged Atlantic salmon (*Salmo salar*) smolts that successfully migrated from the Credit River to Lake Ontario by year and fish rearing group.

Year	Fish Rearing	Proportion Successful	Successful (n)	Total Tagged (n)
2017	Naturally-reared	1.00	8	8
	Hatchery-reared	0.38	12	32
2018	Naturally-reared	0.60	18	30
	Hatchery-reared	0.13	4	30

Table 3.2 Top 10 models of survival of Atlantic salmon (*Salmo salar*) smolts in the Credit River during the migration to Lake Ontario based on AICc.

Model	npar	AICc	ΔAICc	weight
Phi(~Year * Rearing + Location)p(~Detection)	17	908.28	0.00	0.29
Phi(~Year * Rearing + Location)p(~Detection * Year)	19	909.37	1.09	0.17
Phi(~Year * Rearing + Location)p(~Detection + Year)	18	910.14	1.86	0.12
Phi(~Year + Rearing + Location)p(~Detection)	16	910.74	2.46	0.09
Phi(~Year * Location + Rearing)p(~Detection)	27	911.13	2.85	0.07
Phi(~Year + Rearing + Location)p(~Detection * Year)	18	911.81	3.53	0.05
Phi(~Year * Location + Rearing)p(~Detection * Year)	29	912.51	4.23	0.04
Phi(~Year + Rearing + Location)p(~Detection + Year)	17	912.59	4.31	0.03
Phi(~Rearing + Location)p(~Detection)	15	912.62	4.34	0.03
Phi(~Year * Location + Rearing)p(~Detection + Year)	28	913.17	4.89	0.03
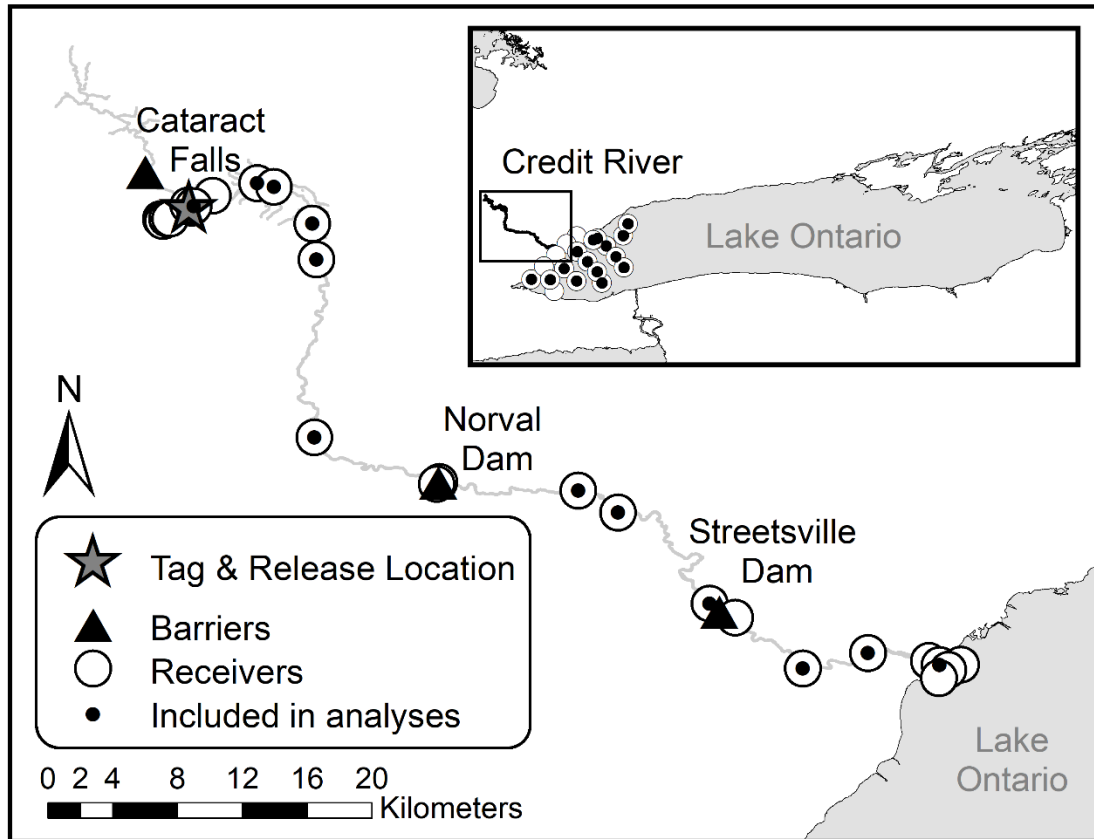
Figure 3.1 Location of acoustic telemetry receivers (and those included in analyses), barriers (labelled), and general tag and release site on the Credit River, Ontario, as well as receivers in the western basin of Lake Ontario (see inset). In 2017 Atlantic salmon (*Salmo salar*) smolts were tagged and released on the West Credit River, while in 2018 smolts were tagged and released on the Upper Credit River (approx. 1.5km downstream); both locations are depicted by a single symbol.
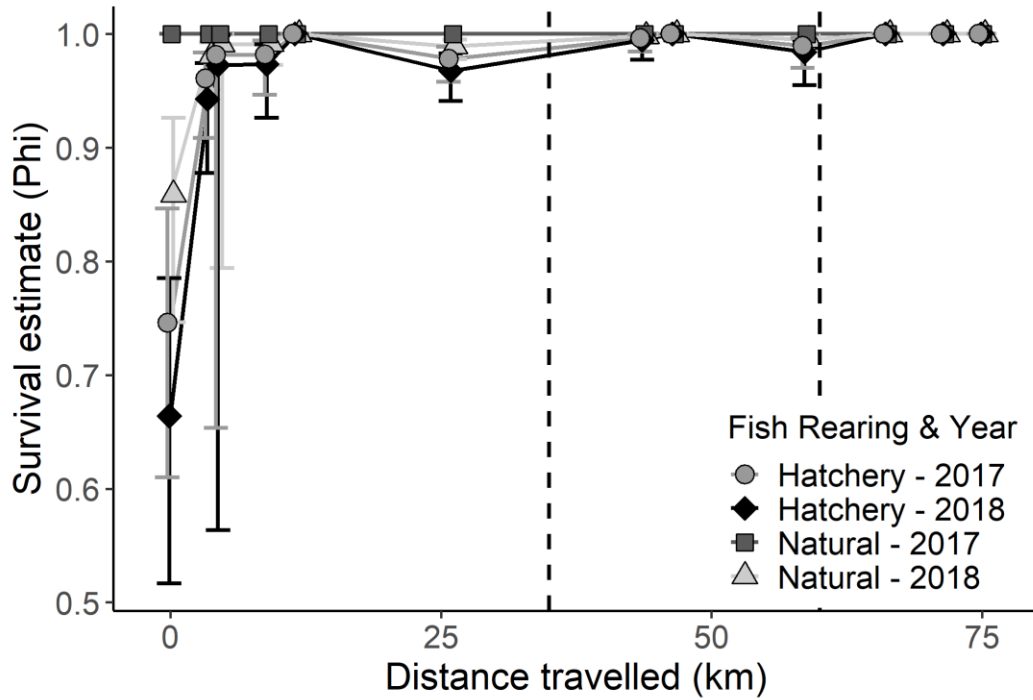
Figure 3.2 Non-cumulative mean (and 95% CI) estimated survival per km (Φ) to reach each receiver location of acoustically tagged hatchery- and naturally-reared Atlantic salmon (*Salmo salar*) smolts in 2017 and 2018 as they migrate from the release site in the Credit River (km 0) to Lake Ontario (km 75). Weirs are indicated by a dashed line.
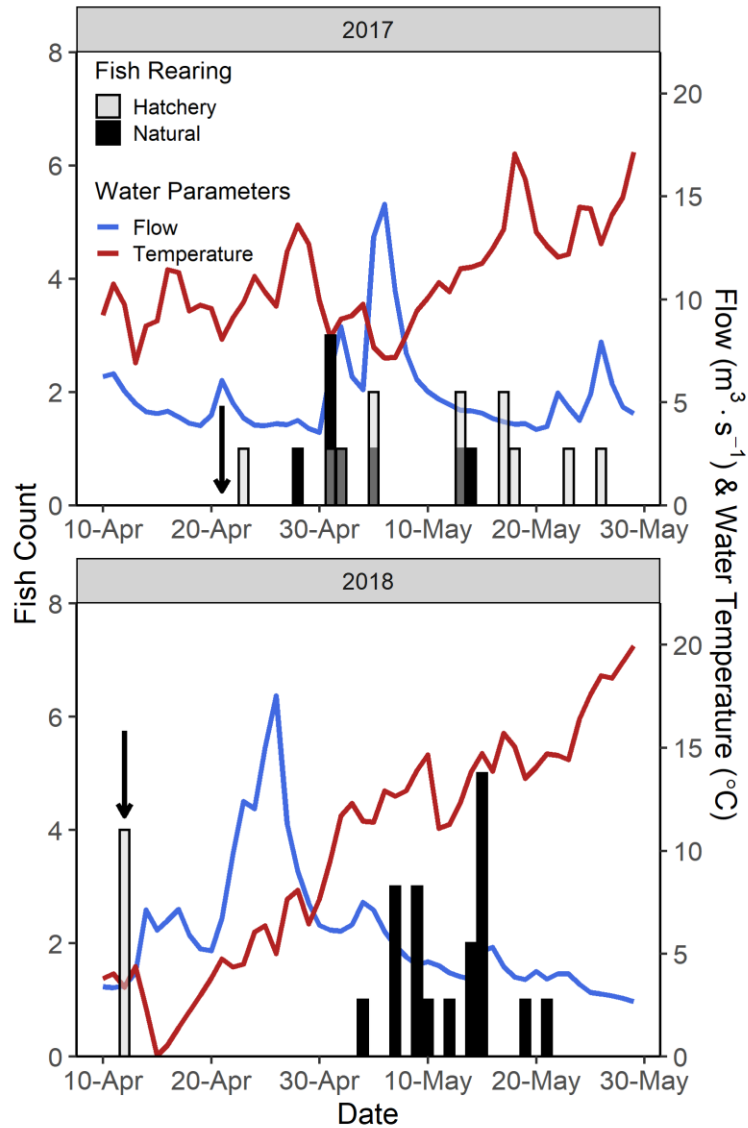
Figure 3.3 Temporal sequence for successful hatchery- (light gray bars) and naturally-reared (black bars) Atlantic salmon (*Salmo salar*) smolts initiating the migration in the Credit River to Lake Ontario over time relative to flow (blue line) and water temperatures (red line) in 2017 (upper panel) and 2018 (lower panel). Dark gray bars indicate an overlap of hatchery- and naturally-reared smolt counts, as bars are not stacked. Arrows represent the release date of hatchery-reared smolts.
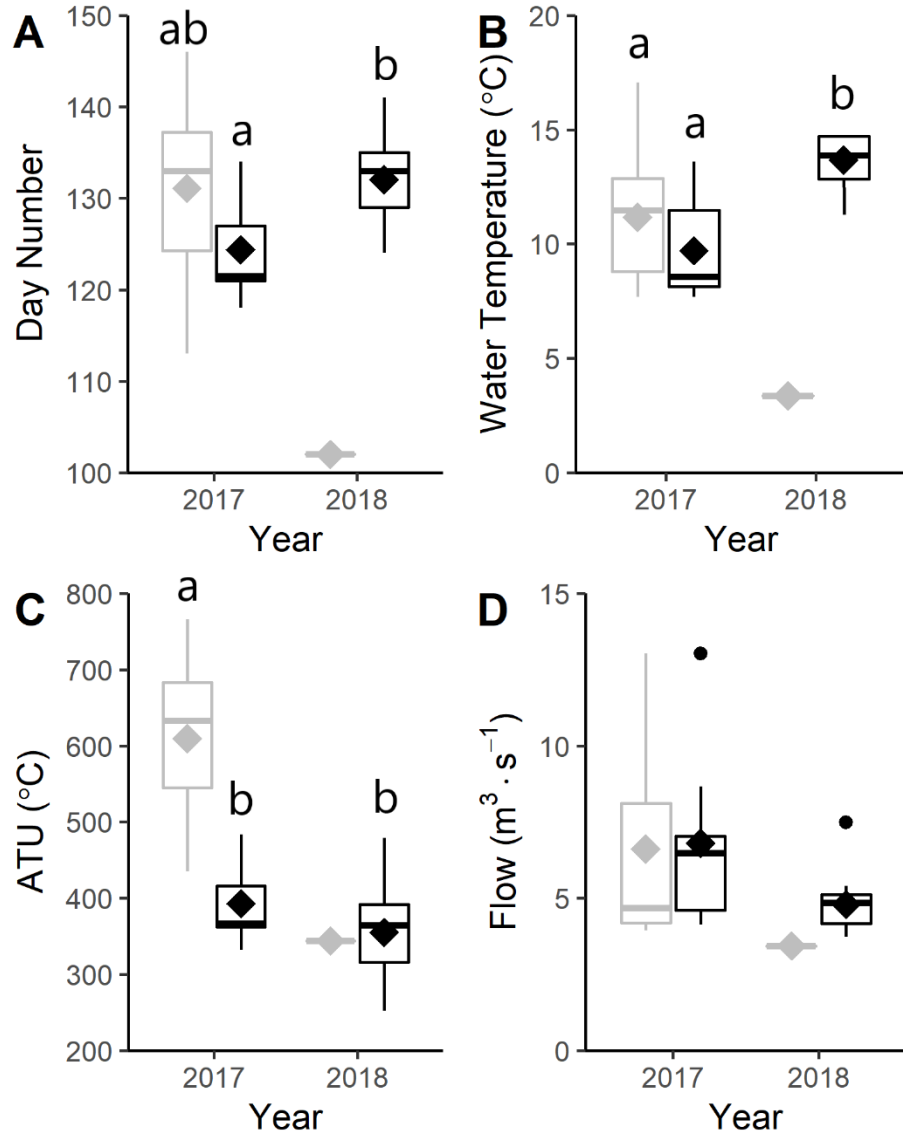
Figure 3.4 Box plots of environmental variables at initiation of migration of successful Atlantic salmon (*Salmo salar*) smolts migrating from Credit River to Lake Ontario in 2017 and 2018. Light gray boxes are hatchery-reared smolts, black boxes are naturally-reared smolts. Letters indicate significant differences based on Kruskal-Wallis analyses. Hatchery smolts in 2018 were not included in analyses. ATU = Accumulated Thermal Units.
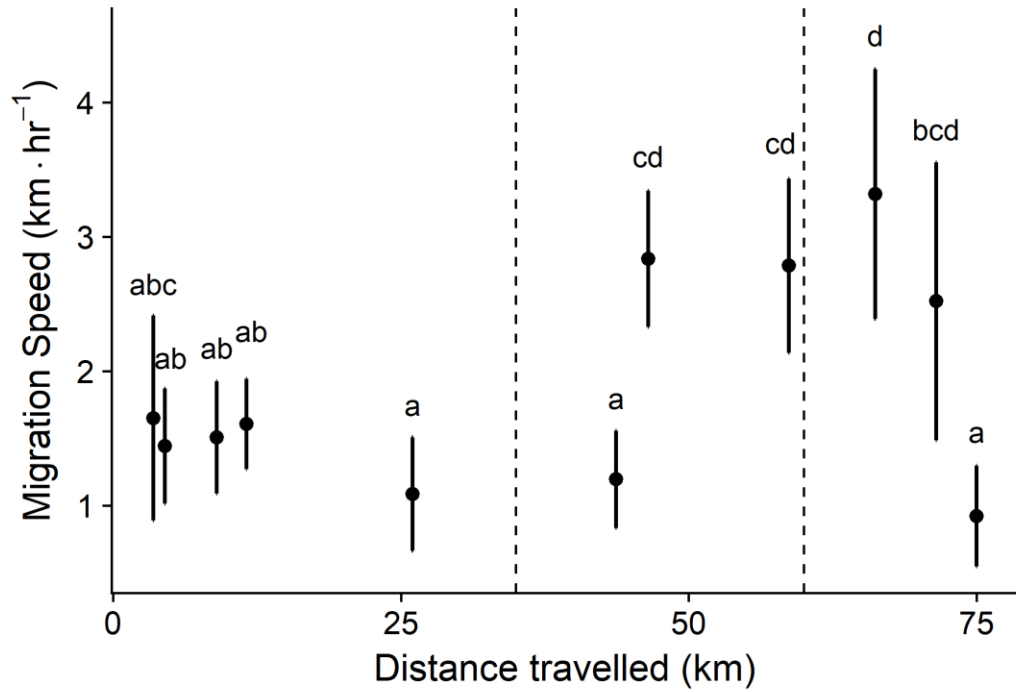
Figure 3.5 Mean (and 95% CI) migration speed of acoustically tagged Atlantic salmon (*Salmo salar*) smolts at different receiver locations as they move from the release site in the Credit River (0 km) to Lake Ontario (km 75). Weirs are indicated by a dashed line. Letters indicate differences based on Tukey's pairwise comparison.
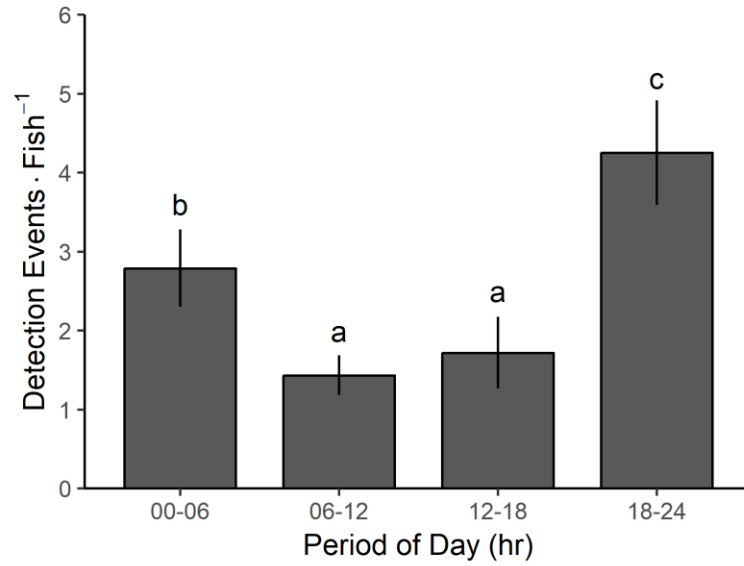
Figure 3.6 Mean (and 95% CI) number of detection events per individual acoustic tagged Atlantic salmon (*Salmo salar*) smolts for different times of day at receivers in the Credit River during migrations in 2017 and 2018.

Figure 3.7 Number of individual tagged Atlantic salmon (*Salmo salar*) smolts detected at receivers in western Lake Ontario in 2018. Note nearshore receivers not deployed during time of out-migration have been removed.

CHAPTER 4 – IMPROVING TROPHIC NICHE AND DIET RESOLUTION OF THE

SALMONID COMMUNITY OF LAKE ONTARIO USING THREE STABLE

ISOTOPES AND MULTIPLE TISSUES

4.1 Introduction

Salmonids are a culturally, economically and ecologically important species, by supporting numerous subsistence, commercial and recreational fisheries (Jacob et al. 2010; Criddle and Shimizu 2014; Lynch et al. 2016), by transferring nutrients between ecosystems during migrations (e.g., to and from rivers to spawn; Cederholm et al. 1999; Hilderbrand et al. 2004), and by serving as indicators of habitat quality and important links in food webs (Edwards et al. 1990). As a highly valued group, the sustainability of salmonid populations is important. For example, salmonids in the Laurentian Great Lakes, are considered the most socioeconomically valuable fishes in the basin, and they support a recreational fishery providing over $7.2 billion USD in annual economic benefit and nearly 50,000 jobs (Melstrom and Lupi 2013). However, there is a need to maintain a suitable predator-prey balance to support ecosystem health and sustainable, productive fisheries in the Great Lakes (Dettmers et al. 2012). To sustain the salmonid communities and fisheries, resource managers need to consider the stocking and harvest of salmonids, natural reproduction (Connerton et al. 2009), and prey supply (Jones et al. 1993; Murry et al. 2010). However, fisheries management also seeks to enhance and restore native salmonid populations in conjunction with supporting valuable salmonid fisheries. In Lake Ontario, there have been efforts to restore native lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*) populations (OMNRF 2019). With the stocking of top predators to a system, it is important to understand how different predator species interact and coexist in a system, and the additional pressures they may add to the prey base.

A potential for a shift in the predator-prey balance can lead to major trophic restructuring (Carpenter et al. 1985; Pauly et al. 1998). In the Great Lakes, non-native salmonids and lake trout were stocked in the 1960s to reduce abundant non-native alewife (*Alosa pseudoharengus*) populations (Crawford 2001). However, in Lake Huron, the Chinook salmon fisheries collapsed in the 2000s following declines in alewife abundance (Brenden et al. 2012). Yet not all salmonid populations collapsed, which may have been the result of species, like lake trout, shifting to different, more available prey (Diana 1990; Roseman et al. 2014). In Lake Ontario, changes in the prey fish community has occurred after the introduction of dreissenid mussels and round goby (*Neogobius melanostomus*) in the 1990s, followed by declines in slimy sculpin (*Cottus cognatus*), rainbow smelt (*Osmerus mordax*), and alewife populations (Mills et al. 2005; Lantry et al. 2014a, 2014b). However, the impacts to top predators from the change in prey is not fully understood, albeit alewife still appears to be a prominent prey item (Rush et al. 2012; Mumby et al. 2018b). In the past few years, further declines in alewife abundance (Weidel et al. 2019a) and a fluctuating but increasing amount of round goby in Lake Ontario (Gorman 2019) could impact salmonid species abundances and types of prey consumed. Understanding how salmonids adjust their diets given changes in the prey composition in Lake Ontario over time may assist with preventing fishery collapses and maintaining predator-prey balances.

Determining the trophic niches and diet estimates in Lake Ontario salmonids using stable isotopes has confirmed the consumption of primarily alewife and an overlap in diets among salmonids (Yuille et al. 2015; Mumby et al. 2018b), similar to stomach content studies (Brandt 1986; Rand and Stewart 1998; Nawrocki et al. 2020). However,

stable isotopes also show a species' diet variability as well as indicate consumption of other diet items that may not readily appear in stomach samples. For example, using stable isotopes Mumby et al. (2018b) found higher instances of brown trout consuming round goby than was found in stomachs. Further refining the diets of salmonids can occur as advances in stable isotope analyses, such as using Bayesian statistics, allow for more accurate trophic niche (Jackson et al. 2011; Swanson et al. 2015) and diet estimates (using isotope mixing models; (Stock et al. 2018; Swan et al. 2020)). The inclusion of sulfur (δ^{34}S) as a third isotope, can complement the typical carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes used in freshwater ecological studies to refine trophic niches and diet estimates (e.g., Colborne et al. 2016; Croisetière et al. 2009; Heuvel et al. 2019). In freshwater, δ^{34}S can distinguish whether fish obtain food from planktonic or benthic sources (Croisetière et al. 2009). Colborne et al. (2016) found that using 3 isotopes improved the resolution of lake trout diets in Lake Ontario, showing an increasing appearance of round goby in their diets. Using sulfur to determine diets and niches of all the Lake Ontario salmonids is likely to improve diet estimates as well as verify the high niche overlap of the species.

Stable isotopes are typically determined from muscle in fish, as the preferred tissue type (Pinnegar and Polunin 1999), however fin is an easily acquired alternative tissue that can be collected non-lethally. Non-lethal sampling of fish is of particular importance if sampling rare and endangered species, to reduce impacts to the population. Charest (2016) found age 2+ brook trout (*Salvelinus fontinalus*) fin to have a faster turnover rate than muscle. When compared to muscle, fin had increased variation in isotope signatures in adult salmonids which could be attributed to a faster tissue turnover

and changing diet compared to muscle or having different tissue compositions (e.g., the skeletal components in fin; Larocque et al., *in review*). With the rarity of encountering Atlantic salmon in Lake Ontario, non-lethal sampling of fin would limit population impacts from sampling and increase potential samples. The potential difference in tissue turnover rates of fin and muscle could also reveal time-scaled dietary differences, with fin potentially representing early spring/summer diets and muscle representing the previous year.

Potential spatial patterns may exist within Lake Ontario salmonid diets. Species that are more range restricted and localized may have populations that are segregated in the lake and have spatially distinct diets. Some species such as Chinook salmon are highly mobile (Adlerstein et al. 2007, 2008; Ivanova, unpublished data) and spatial patterns may not be as prevalent unless staging in certain areas for lengths of time. Other species, like brown trout and lake trout are thought to be more localized in their movements (Nettles et al. 1987; Binder et al. 2017; Raby et al. 2017) and may have distinct diets relative to the location of capture. Nawrocki et al. (2020) assessed the spatial diet of lake trout in Lake Ontario to find a high prevalence of alewife in diets with some spatial distinction in the stomach contents. Including spatial region where salmonids were captured in isotope mixing models can determine if there is spatial variation in salmonid diet estimates.

As stable isotope analyses advance, improvements can be made with understanding and comparing trophic niches and diets among six Lake Ontario salmonid species as the prey community changes. It can be determined whether there have been changes in the trophic niches and diets of salmonids within five years since the last

assessment by Mumby et al. (2018b). A significant effort was made to increase the sample sizes of Atlantic salmon within the same year to improve the accuracy of the species comparisons of niches to Atlantic salmon, albeit it was primarily with fin. The objectives of this study were to: 1) assess the trophic niches and overlaps of the salmonid community using both two (δ^{13}C and δ^{15}N) and three (δ^{13}C, δ^{15}N and δ^{34}S) isotopes using two tissues (fin and muscle); 2) estimate the diets of the salmonids with both two (δ^{13}C and δ^{15}N) and three (δ^{13}C, δ^{15}N and δ^{34}S) isotopes with fin and muscle; and 3) determine if there are any regional differences within salmonid diets. It was hypothesized that using three isotopes will reduce the niche overlap between salmonids, yet there will still be a high overlap with the reliance on alewife. It was also hypothesized that fin will show a more recent diet and have regional differences in species that are more localized (e.g., brown trout and lake trout), while muscle will reflect a longer-term diet that inherently would reduce regional differences, particularly with highly mobile species (e.g., Chinook salmon).

4.2 Methods

Sample collection

Adult salmonids (>300 total length (TL); Chinook salmon, coho salmon, brown trout, lake trout, and rainbow trout) were angled and captured from east, west, and central regions within Lake Ontario by local anglers at fishing derbies during June – July 2018 (Figure 4.1). Fish harvested by anglers were sampled after the derby had concluded each day. Salmonids were identified and measured for total length (mm). For each fish a skinless, boneless, muscle sample was taken from the left, dorsal side, posterior to the dorsal fin, as well as a fin clip taken from the tip of the upper caudal fin lobe. All

equipment was sterilized with 10% betadine solution and rinsed with distilled water between samples. All samples were rinsed with distilled water, placed in 2 ml cryovial tubes, and kept on ice until they could be later frozen. Atlantic salmon encounters are very rare and lethal sampling is best avoided, and as such were non-lethally sampled with the aid of charter captains as part of a citizen science project. On participating charters, any angled Atlantic salmon (and subsamples of other salmonids) were fin clipped and total length was approximated if possible (although did not always occur), prior to being released. Fin samples were collected from charter captains and kept frozen until subsequent processing, however if any mortalities occurred (via serious hook wounds) a muscle sample was taken and kept frozen. Fisheries and Oceans Canada also provided fin clips from any salmonids captured during local fish community electrofishing surveys near Toronto, ON. Prey fish species (alewife, deepwater sculpin (*Myoxocephalus thompsonii*), rainbow smelt, round goby, slimy sculpin) were obtained from government agency bottom and midwater trawl programs from April to October 2018. Prey fish were euthanized by percussive stunning, measured, and sampled for a muscle sample which was then frozen. Mysids (*Mysis diluviana*) were also collected during zooplankton tows over the same time period as the other prey species. Experimental protocol followed the Canadian Council on Animal Care guidelines (University of Windsor AUPP #16-08).

Stable Isotope Analyses

All samples were freeze dried at -48°C for 48 hours in preparation for SIA. Muscle tissue was crushed into a fine powder and fin tissue was cut into smaller pieces before weighing. Mysid samples included multiple individuals pooled together to achieve sufficient biomass to be analyzed. For SIA, $\delta^{13}C$ and $\delta^{15}N$ were analyzed separately to

δ^{34}S. Tissue samples were weighed out (0.4-0.8 mg for δ^{13}C and δ^{15}N, and 5.5-7.0 mg for δ^{34}S) and placed into a tin capsule for SIA. Isotope values were determined using a Delta V isotope ratio mass spectrometer (Thermo Finnigan, San Jose, CA, USA) equipped with an elemental analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). Isotopic ratios were reported as: $\delta X = [(R_{sample} / R_{standard}) - 1] \times 10^3$ where X is either ^{13}C, ^{15}N or ^{34}S, R is the ratio ^{13}C/^{12}C, ^{15}N/^{14}N or ^{34}S/^{32}S, and the standards used were C from Vienna Peedee Belemnite, N from atmospheric N, or S from the Canyon Diablo troilite.

Laboratory and National Institute of Standards and Technology (NIST; Gaithersburg, MD, USA) standards were analyzed every 12 samples. The analytical precision (standard deviation) for NIST standard 1577c (bovine liver), an internal laboratory standard (tilapia muscle), USGS 40 and Urea (n=86 for all) for δ^{13}C and δ^{15}N values was <0.20 and <0.19 ‰, respectively. Analytical precision for δ^{34}S from NIST 1577c, internal laboratory standard, USGS 42, NIST 8555 and NIST 8529 (n=118 for all) was <0.25 ‰. Accuracy was checked monthly using certified USGS 40 (n = 86) and was within 0.02 and 0.06 ‰ of the mean calculated values for δ^{13}C and δ^{15}N values. For δ^{34}S, accuracy using USGS 42 (n=118) was within 0.12 ‰ of the mean calculated values.

Due to high lipid content (C:N > 3.4) in the muscle tissues of salmonids (mean ± SD C:N = 4.78 ± 1.84) and prey (mean ± SD C:N = 4.60 ± 2.26), a lipid correction factor for δ^{13}C was applied using the Kiljunen et al. (2006) normalization model with the McConnaughey and McRoy (1979) lipid percent method (KMM). The KMM lipid normalization model was found to be the best fit lipid adjustment for muscle samples in adult salmonids (Skinner et al., 2016; Larocque et al. *in review*). Fin tissue had low lipid content (mean C:N ± SD = 3.31 ± 0.27) and did not require lipid extraction.

Statistical Analyses

The core trophic niche of salmonids was considered to be the isotopic space that contains 40% of the data (as opposed to the entire niche area by including 100% of the data; Jackson et al. 2011). With two isotopes, the core trophic niche was determined using the corrected version of the standard ellipse area (SEA$_C$) which corrects for variable sample sizes. The SEAc for each salmonid and the mean ± standard deviation (SD) for δ^{13}C, δ^{15}N, and δ^{34}S of each prey species were plotted in a stable isotope biplot (three combinations to represent the three isotopes) for visual inspection of the 2018 food web structure. The core trophic niche size or 40% standard ellipse volume (SEV) using the three isotopes (δ^{13}C, δ^{15}N and δ^{34}S) was determined for each species and tissue type in which the mean and uncertainty (95% credible intervals (CI)) were estimated using a Bayesian iterative approach as described (with code provided) in Rossman et al. (2016) using 5,000 iterations, a 1,000 burn in, and priors set as uninformed.

The trophic niche overlap using more than two isotopes can be calculated using the *nicheROVER* package (Lysy et al. 2014) in R which is an advanced ellipse-based model that can include more than two niche dimensions and present a probabilistic framework for calculating niche overlap (Swanson et al. 2015). The trophic niche overlap between salmonids and their SEAc was determined for both fin and muscle tissue, as well as with two isotopes (δ^{13}C and δ^{15}N) and three isotopes (δ^{13}C, δ^{15}N and δ^{34}S). The mean probability of overlap and 95% CI was calculated for each species combination and was used to express similarities and differences in isotopic niche space use and how it varies between tissues and number of isotopes used in the analyses. Spatial differences, based on region of capture, in trophic niche overlap between species was also determined using

two and three isotopes for both fin and muscle tissue. Within spatial regions, species with too few samples (<5) were excluded from analyses.

The relative likely contributions of prey species to the salmonid diets was determined using a Bayesian mixing model approach using *MixSIAR* package (Stock et al. 2018) in R. *MixSIAR* allows multiple isotopic tracers (e.g., $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) and uses a Markov Chain Monte Carlo simulation to model the probability of proportions of food sources in a consumer's diet based on the isotopic values of the food sources and the consumer. The mean and SD for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ of the five offshore prey fish species (alewife, deepwater sculpin, rainbow smelt, round goby, and slimy sculpin) and mysids were included in the model as sources (Table 4.1). Mumby et al. (2018b) used the same five prey fish sources for isotope mixing models, however, mysids were also included in the models here as they can also occur in salmonid diets although at low levels (Rush et al. 2012; Leonhardt et al. 2020). Trophic fractionation was estimated using the mean diet-tissue discrimination factor (DTDF) reported for temperate freshwater carnivorous fishes ($\Delta\delta^{13}C$: +0.91 ± 1.04 ‰; $\Delta\delta^{15}N$: +3.23 ± 0.41 ‰; Vander Zanden and Rasmussen, 2001). Few studies have assessed the DTDF in $\delta^{34}S$, however, Charest (2016) found that field experiments on brook trout had a $\Delta\delta^{34}S$ of -0.3 ± 1.2 ‰ for muscle and was lower compared to laboratory studies (e.g., Charest 2016; McCutchan et al. 2003). Given the differences between wild and laboratory results in the $\Delta\delta^{34}S$, the Charest (2016) field-based $\Delta\delta^{34}S$ was used for the DTDF in the models. The same trophic fractionation was used for fin and muscle tissues for each isotope. Models were run separately for each salmonid species. Eight configurations of the model were used to estimate salmonid species diets, which included all combinations of using either salmonid fin or muscle

tissue, two or three isotopes, and with or without spatial regions added as an additional variable. Models were run for 100,000 iterations, with a 50,000 burn in, thinned at every 50th value, and uninformed priors. The Gelman-Rubin convergence diagnostics was used to assess model fit. Model results of the proportion of diet that each prey species represents is reported in the mean and 95% CI.

All analyses were conducted in R v.4.0.2 (R Core Team 2020). Means $\pm$ SD are reported unless otherwise stated. Statistical significance was assessed at $\alpha = 0.05$ and the lack of overlap in 95% CI.

4.3 Results

Lake-wide

A total of 414 fin and 230 muscle samples were collected from six species of salmonids from Lake Ontario in 2018 and analyzed for stable isotopes. Mean ($\pm$ SD) length of salmonids ranged from 530 ± 61 (coho salmon) to 789 ± 118 mm (Chinook salmon; Table 4.1). From fin samples, mean $\delta^{13}C$ was lowest in Chinook salmon (-21.6 ± 0.8‰) and highest in brown trout (-20.5 ± 0.7‰), mean $\delta^{15}N$ spanned a wider range (15.4 ± 0.9‰ in rainbow trout to 17.7 ± 0.5 ‰ in lake trout), and mean $\delta^{34}S$ had a narrow range (4.8 ± 0.7‰ in rainbow trout to 5.2 ± 0.4‰ in coho salmon; Table 4.1; Figure 4.2 A,C,E). Salmonid muscle samples had slightly different values than fin. Muscle mean $\delta^{13}C$ was lowest in coho salmon (-21.9 ± 0.2‰) and highest in brown trout (-21.2 ± 0.5‰), with mean $\delta^{15}N$ spanning a wider range (15.1 ± 0.4‰ in Chinook salmon to 17.0 ± 0.4‰ in lake trout), and mean $\delta^{34}S$ a narrow range (5.0 ± 0.6‰ in rainbow trout to 5.3 ± 0.3‰ in Chinook salmon; Table 4.1; Figure 4.2 B,D,F).

The size of the trophic niche using all three isotopes, or standard ellipse volume, in fin was smallest in lake trout (0.18 ‰^{3}) and largest in rainbow trout (0.76 ‰^{3}), while in muscle, standard ellipse volume was smallest in Chinook salmon (0.09 ‰^{3}) and largest in Atlantic salmon (0.67 ‰^{3}; Table 4.1). Standard ellipse volume was significantly larger in fin than muscle for brown trout, Chinook salmon, and rainbow trout (Table 4.1; Figure 4.2). Trophic niche overlap varied between species, and the trends varied for a few species across tissue type and using two or three isotopes (Table 4.2). Using a third isotope did not significantly change the overlap within the same tissue, except for five instances that reduced overlap. Generally, across all methods lake trout had a negligible trophic niche overlap with all species (<7%). Using fin, Atlantic salmon, Chinook salmon, and coho salmon had low-moderate overlap with all species (13-41%) except lake trout. However with muscle, Atlantic salmon had moderate overlap with brown trout and rainbow trout (34-52%), Chinook salmon only had low-moderate overlap with coho salmon and rainbow trout (18-29%), and coho salmon only had low-moderate overlap with Chinook salmon and rainbow trout (12-45%; Table 4.2). Brown trout overlapped rainbow trout the most (21-47% across tissues and using 2 or 3 isotopes), with lower overlap (<23%) with the remaining salmonids. Across all methods, rainbow trout had low-moderate overlap with brown trout (16-31%), followed by Atlantic salmon (3-19%), and low overlap with Chinook salmon and coho salmon (<13%; Table 4.2).

The proportion of prey in the diet of salmonids based on isotope mixing models was primarily alewife across most species in both fin and muscle tissue and using 2 or 3 isotopes (Figure 4.3). Isotope mixing models indicated that when using fin, Atlantic salmon fed almost exclusively on alewife (88%), yet when using muscle still fed on

alewife at the highest rate (44%) but also fed on all other prey species (5-20% per item; deepwater sculpin the lowest and mysids the highest). With muscle, the small sample size (n = 6) may have influenced the ability of the model to find an accurate solution for Atlantic salmon as the diet item errors were large. Diet mixing models indicated brown trout feeding almost exclusively on alewife for both tissue types (>73%), however, with fin and three isotopes, there was indication that there could be some consumption of round goby (22%; Figure 4.3). Chinook salmon and coho salmon fed almost exclusively on alewife in models using fin (>75%), however, with muscle, they fed on both alewife (55-60%) and mysids (~35%; Figure 4.3). Lake trout was the only species where diet was not almost exclusively alewife in any tissue or number of isotopes in the model. Isotope mixing models indicated that when using fin, lake trout primarily fed on round goby and on some alewife (more with 3 isotopes), with a small contribution of the other prey species. When using muscle, models indicated that lake trout fed the most on alewife (~45%) but also fed on all other prey species (5-20% per item; deepwater sculpin the lowest and rainbow smelt the highest), similar to Atlantic salmon. Rainbow trout fed almost exclusively on alewife (88-94%) for both tissue types and number of isotopes used. However, a diet item may be missing in the models for brown trout and rainbow trout. Brown trout had higher δ^{13}C values in fin and muscle tissues than any prey species plus the DTDF, and rainbow trout had lower δ^{15}N values in both tissues and higher δ^{13}C values in fin than any prey species plus the DTDF which can influence model outcomes. Similarly, it should be noted that muscle isotope mixing models had a high negative correlation between alewife and *Mysis* spp. (particularly for Chinook salmon and coho salmon) indicating the model had a poor ability to distinguish between these two species

and may be overestimating the contribution of *Mysis* spp. in model outputs of Chinook

salmon and coho salmon (Appendix 5).

Regional variation

Isotope values of species varied among region and as a result some of the trophic

niches of the salmonid species shifted in isotope space across spatial regions for either fin

or muscle (Appendix 6; Appendix 7). The shift in trophic niches across regions was more

prominent in fin than muscle, as the trophic niche overlaps between some species was

significantly different across regions for fin (Appendix 8). Trophic overlap did not

change between species across regions for muscle (when using 2 or 3 isotopes; Appendix

9).

Using three isotopes, fin isotope mixing models resulted in the proportion of prey

in the diet of salmonids to vary regionally for some species (Figure 4.4). Atlantic salmon,

coho salmon, and rainbow trout had similar diets throughout all regions and matched the

lake-wide model (Figure 4.3; Figure 4.4). Brown trout had a higher proportion of round

goby in their diet in the west (80%), which decreased with an increasing proportion of

alewife in the diet from central to east (75 to 95%). Lake trout also had an increased

proportion of round goby in the diet in the west (48%) as opposed to the central and east

where alewife increased in the diet (33 – 51%) and round goby were reduced (28-31%).

Lake trout had the most varied diet within the central region. Chinook salmon primarily

had a diet of alewife (41-81%), however, in the central and east regions there was a small

increase in consumption of rainbow smelt (18-30%) and mysids (10-19%). Using two

isotopes with fin had slightly different isotope mixing model outcomes for rainbow trout

and Chinook salmon (Appendix 10); however, the three isotope mixing model estimates were reported as it increased diet resolution.

There were no major differences in muscle using two or three isotopes in the isotope mixing models and only the three isotope model is reported (Figure 4.4; Appendix 10). Using three isotopes and muscle, isotope mixing models showed most species primarily consumed alewife across regions, with little regional variation. Atlantic salmon, brown trout, rainbow trout and lake trout had similar diets throughout all regions and matched the lake-wide model (Figure 4.3; Figure 4.4). Chinook salmon and coho salmon had a slight increase in consumption of mysids in the central region (39 and 43%, respectively), which decreased with the increased consumption of alewife in the east region (70 and 76%, respectively; Figure 4.4). Again, muscle isotope mixing models had a high negative correlation between alewife and *Mysis* spp. (particularly for Chinook salmon and coho salmon), which would have influenced the regional differences seen.

4.4 Discussion

Lake-wide and regional trophic niches were assessed and diets were estimated for six salmonid species in Lake Ontario in 2018 using three isotopes ($\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$) from fin and muscle tissue. This assessment occurred 5 years since the previous stable isotope-based diet estimates in 2013 (Mumby et al. 2018b) and added more components to improve the understanding of salmonid diets at different spatial and temporal scales in Lake Ontario. Adding a third isotope ($\delta^{34}S$) to the analyses increased the resolution of the trophic niche overlaps and diet estimates, similar to work done in Lake Erie fish (Heuvel et al. 2019). However, muscle results were not as affected by the additional sulfur isotope compared to fin, as there were only minor differences between the two vs three isotope

diet estimates. Trophic niche overlap either did not change or was decreased by adding

δ^{34}S, supporting the hypotheses that adding another isotope would reduce the trophic

niche overlap among salmonids. Some of the prey sources for isotope mixing models had

variable δ^{34}S, which resolved some diet estimates when prey species had similar δ^{13}C and

δ^{15}N values (e.g., rainbow smelt and round goby), and was seen as more accurate

(Colborne et al. 2016), particularly for fin which had more variation than muscle between

two and three isotope isotope mixing models.

Generally, diet estimates for both fin and muscle tissue indicated that alewife is

the primary prey for salmonids in Lake Ontario. The dominance of alewife in the diet of

salmonids in Lake Ontario is not surprising given previous studies in Lake Ontario,

including those using stomach contents, fatty acids, and stable isotopes (Brandt 1986;

Rand and Stewart 1998; Yuille et al. 2015; Mumby et al. 2018b; Futia et al. 2019).

Although both tissue types estimated high proportion of alewife in salmonid diets, there

was some variation between tissues that could suggest fin shows a more recent diet than

muscle and has a faster tissue turnover, which is not necessarily due to differences in

tissue composition. Lake-wide, fin models with three isotopes indicated that lake trout

and brown trout also fed on round goby, and the prevalence of round goby in the diet was

reduced when muscle data was analyzed. Round goby occupies the nearshore during the

spring/summer and migrates deeper during winter in Lake Ontario (Walsh et al. 2007).

Brown trout generally stay nearshore (Nettles et al. 1987) and salmonids like lake trout

can inhabit the nearshore in the spring (Aultman and Haynes 1993) and thus could

consume round goby during the habitat overlap in the spring/summer which would be

reflected in fin isotopes. The greater consumption of round goby by brown trout and lake

trout, and minimal consumption by the other salmonids has also been observed in Lake

Michigan (Leonhardt et al. 2020). Although Chinook salmon and coho salmon were

estimated to consume more mysids based on muscle isotope mixing models compared to

fin, this was likely an overestimation due to the high negative correlation between alewife

and mysids and the lower muscle $\delta^{13}C$ values in the salmon. It is suspected that both

Chinook salmon and coho salmon consumed alewife in large proportions regardless of

tissue type, and do not show diet switching temporally.

Spatial variation in diets occurred for a few salmonid species with fin tissue. The

more localized species, lake trout and brown trout, showed the greatest regional

differences in diet as hypothesized. Both lake trout and brown trout had higher round

goby consumption in the west than the east, as indicated by fin isotope mixing models.

Although the abundance of round goby has not been reported regionally, stomach

contents of lake trout from 2018 also showed variable round goby consumption in

different regions, but with the greatest consumption occurring in the central region

(Nawrocki et al. 2020). Similar spatial distinctions have occurred in Lake Michigan in

which brown trout and lake trout fed on more round goby in the spring in the eastern

region (Happel et al. 2018; Leonhardt et al. 2020). Increased round goby consumption in

Lake Michigan occurred in habitats where round goby would more easily be acquired by

predators (e.g., sandy bottoms with reduced structure; Leonhardt et al. 2020), which may

potentially occur in Lake Ontario as well. Brown trout and lake trout diets did not vary

regionally with muscle isotope mixing models which could reflect that the prey they feed

on (as well as most other salmonids) over the longer term is consistently available

throughout the lake (e.g., alewife). An exception was Chinook salmon and coho salmon

which consumed slightly more mysids in the central region with fin tissue. These regional differences, albeit minor, were not anticipated with Chinook salmon being a highly mobile species and may be related to model error associated with strong, negative correlations between mysids and alewife in the model. Using other methods to analyze spatial variability in diet via stomach contents or fatty acid profiles can confirm regional variation of salmonid diets in Lake Ontario. Most salmonids did not display major spatial distinctions in their diets which suggests that the availability and consumption of prey is similar across Lake Ontario, except for the more localized species, brown trout and lake trout, that showed some regional variation in dietary consumption of round goby.

The trophic niches and diets of salmonids from Lake Ontario in 2018 are similar to those in 2013, suggesting limited diet changes. Based on δ^{13}C and δ^{15}N, mean values in muscle from 2018 have increased in δ^{13}C for Atlantic salmon, brown trout and rainbow trout by ~0.6‰, decreased in δ^{13}C for coho salmon by 0.5‰, and all species decreased in δ^{15}N by ~0.5‰ compared to 2013 (Mumby et al. 2018b). These differences could be related to larger sample sizes (and greater isotopic variation) in 2013, longer collection duration of salmonids occurring from April to December in 2013, as opposed to from June to July in 2018, as well as natural changes in baseline isotope values in the environment over time. When comparing muscle δ^{13}C and δ^{15}N values, the degree of niche overlap between salmonids was lower in 2018 than 2013, with some variation seen among species, yet the major trend of lake trout having very low overlap with any salmonid remained the same. However, more similar niche overlap trends were prevalent between the muscle isotopes from Mumby et al. (2018b) and fin isotopes of this study which could be an inherent factor that fin had larger samples than muscle in this study. In

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terms of estimated diets, both studies indicated the high prevalence of alewife in the diets of salmonids, however, fin showed a better direct comparison with the estimates of Mumby et al. (2018b), in particular with the consumption of round goby by brown trout and lake trout. The muscle isotope mixing model estimates indicated *Mysis* spp. contributed to Chinook salmon and coho salmon diets (although this may be due to model error), and Atlantic salmon and lake trout had a more variable diet with alewife as the main prey. The models in this study included *Mysis* spp., had higher δ^{13}C values in round goby, and used a lipid correction factor instead of lipid extracted samples which may contribute to these slightly different findings than Mumby et al. (2018b). From 2013 to 2018, with the establishment of round goby and declines in alewife populations (Gorman 2019; Weidel et al. 2019a) salmonids are still acquiring the majority of their energy from alewife.

The salmonid community exhibits some trophic overlap with the shared reliance on alewife, however other dietary, spatial, or habitat differences reduce that overlap. With fin, Atlantic salmon had greater overlap among all salmonids except lake trout, by consuming primarily alewife. Atlantic salmon in Lake Huron exhibited niche overlaps with Chinook salmon, coho salmon and lake trout similar to this study (Gerig et al. 2019), suggesting similar niches and diets in these salmonids across Great Lakes. Muscle isotope mixing models indicated Atlantic salmon to have a slightly more varied diet, similar to Atlantic salmon from Lake Huron (Roseman et al. 2014), however, the small sample size of muscle (n = 6) may have influenced model outcomes. Stomach samples of Atlantic salmon have contained primarily alewife, but round goby was also found (Larocque, unpublished data), suggesting Atlantic salmon does consume species other

than alewife in Lake Ontario. As a species that is being restored to Lake Ontario, it is difficult to acquire Atlantic salmon samples, and this study has the largest data set within the same year to better understand the diets of Atlantic salmon.

With the use of δ^{34}S, it was indicated that brown trout consume primarily alewife as well as round goby, which corresponds to brown trout diets in Lake Michigan (Leonhardt et al. 2020). Brown trout had higher δ^{13}C than the prey sources sampled plus the DTDF and a prey species (likely a nearshore fish species) may be missing in the diet estimates, however, there is confidence in the results that alewife and round goby are major components of their diets but with some regional differences. Similarly, rainbow trout had higher δ^{13}C and lower δ^{15}N relative to the prey sources sampled plus the DTDF suggesting that a lower trophic position and nearshore prey item is missing in the model. It is suspected that terrestrial insects form a proportion of the rainbow trout diet as has been seen in previous stomach content studies in other Great Lakes (Diana 1990; Roseman et al. 2014; Leonhardt et al. 2020).

Chinook salmon and coho salmon had similar diets with alewife as the dominant prey species but also included *Mysis* spp. estimated from muscle isotope mixing models. The consumption of mysids is likely an erroneous result of the model for a few reasons. Although the consumption of *Mysis* spp. by Chinook salmon and coho salmon has occurred in Lake Huron and Lake Michigan, it was at very low levels (<1% and <13%, respectively; Roseman et al. 2014; Leonhardt et al. 2020). The *Mysis* spp. estimates were driven by the lower δ^{13}C of the salmon muscle and the strong, negative correlation with alewife in the models due to similar δ^{15}N and δ^{34}S, such that the proportion within the muscle isotope mixing models is likely overestimated. Rush et al. (2012) included *Mysis*

spp. in their isotope mixing models to assess lake trout diets in Lake Ontario, which estimated low levels of mysids in the diet (<3%). However, the mean δ^{15}N of mysids was much lower (9.8 ‰) in Rush et al. (2012) compared to this study (12.6 ‰) which could be a difference between fall vs spring sampling of mysids, respectively, and thus be nearly two trophic levels away from salmon and unlikely to have high estimates. In Lake Ontario, *Mysis* spp. have seasonal variation in their diets (O'Malley et al. 2017) which is also reflected in isotopic values across seasons (Uzarski et al. *in prep*). Future studies should use the average isotope values across seasons for mysids, which may have a lower δ^{15}N and reduced the prevalence of mysids in the models with Chinook salmon and coho salmon in this study. Furthermore, there is variation in alewife δ^{13}C and δ^{15}N with size, season and spatially, in which Chinook salmon and coho salmon may be consuming smaller alewife (lower δ^{13}C signatures) and not necessarily *Mysis* spp. (Mumby et al. 2018a). A more comprehensive analyses including a size variation of alewife in the isotope mixing models would also verify the consumption of *Mysis* spp. or small alewife, and give insight on the age classes of alewife that salmon are consuming. It is likely that instead of mysids, there were regional and seasonal differences in the size of alewife that Chinook salmon and coho salmon were consuming. Although originally including *Mysis* spp. in the diet estimates was to improve results, the high negative correlation with alewife and lack of supporting evidence suggests that Chinook salmon and coho salmon were primarily consuming alewife and unlikely consuming *Mysis* spp. at such high levels.

Lake trout had very low trophic niche overlap with the other salmonids by having higher δ^{15}N, as was also seen in Mumby et al. (2018b), yet still shared alewife as a dominant prey species. The mismatch of the niche overlap and diet estimates could in

part be related to δ^{15}N increasing with depth and lake trout utilizing and feeding at deeper

depths than other salmonids (Sierszen et al. 2014; Raby et al. 2020). Also, lake trout can

be cannibalistic and feed on young salmonids which would elevate their ^{15}N (Dietrich et

al. 2006; Roseman et al. 2014). Thus, the estimates of having a varied diet with

increasing consumption of round goby (especially in the west), appears accurate but

likely overestimated. Nawrocki et al. (2020) found more alewife in stomach contents of

lake trout from Lake Ontario in 2018 (>75% average individual diet percentage) than

estimated by stable isotopes in this study. If deeper depths had inflated ^{15}N in lake trout,

it would have reduced alewife diet estimates as well as the appearance of a lack of trophic

niche overlap. Lake trout are likely predominantly feeding on alewife, but also

consuming more round goby in the west (and in general) with a more varied diet than

other salmonids.

Stable isotope analysis provided insight into the trophic niches and diets of

salmonids in Lake Ontario. Using different tissues, adding a third isotope (δ^{34}S), and

investigating spatial distinctions in trophic niches and diets, provided more details and

improve the resolution of salmonid diets. Fin and muscle tissue reflected different

temporal scales in the diet that provided some indication of when certain species may be

consuming non-alewife species in greater abundance, in particular, round goby

consumption in the shorter-term by brown trout and lake trout. Round goby consumption

varied spatially for brown trout and lake trout and may reflect areas of increased prey

abundance or habitat-related predation. There have been no major changes in the diets of

Lake Ontario salmon from 2013 to 2018, despite some changes in the abundances of the

prey base. It is important to monitor and increase our understanding of the Lake Ontario

food web, especially with respect to species restoration of Atlantic salmon and lake trout, but also for maintaining salmonid populations for recreational fishing. Including a spatial diet component indicated that some species like brown trout and lake trout may need to be monitored regionally, more so than other species which could be using the entire lake and have populations intermix. Overall, the salmonid community in Lake Ontario primarily consumes alewife and trophic niches overlap to some degree. Maintaining a predator-prey balance is important to preserve healthy and productive populations of salmonids in light of on-going ecological change.

4.5 References

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Table 4.1 Summary of the total length (mm), sample size (n), isotope values (mean ± SD ‰), and the standard ellipse volume (40% SEV; ‰^{3} with upper and lower credible intervals) of fin and lipid corrected muscle for six salmonid species, and prey species from Lake Ontario 2018. Sample sizes in brackets were samples measured for length.

Tissue	Species	n	Length	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	SEV
Fin	Atlantic Salmon	52 (32)	554 ± 72	-21.2 ± 0.7	15.7 ± 0.7	5.1 ± 0.3	0.29 (0.21 - 0.40)
	Brown Trout	79 (63)	543 ± 93	-20.5 ± 0.7	15.6 ± 0.8	4.9 ± 0.7	0.50 (0.38 - 0.65)
	Chinook Salmon	114 (104)	770 ± 123	-21.6 ± 0.8	16.0 ± 0.6	5.2 ± 0.2	0.21 (0.17 - 0.27)
	Coho Salmon	51 (38)	531 ± 70	-21.3 ± 0.4	16.3 ± 0.8	5.2 ± 0.4	0.27 (0.19 - 0.37)
	Lake Trout	50 (49)	704 ± 102	-21.1 ± 0.5	17.7 ± 0.5	5.0 ± 0.3	0.18 (0.13 - 0.25)
	Rainbow Trout	68 (53)	607 ± 99	-20.5 ± 0.8	15.4 ± 0.9	4.8 ± 0.7	0.76 (0.57 - 1.01)
Muscle	Atlantic Salmon	6 (6)	544 ± 86	-21.4 ± 0.5	15.6 ± 0.3	5.1 ± 0.2	0.67 (0.26 - 1.57)
	Brown Trout	49 (49)	549 ± 51	-21.2 ± 0.5	15.7 ± 0.4	5.3 ± 0.3	0.19 (0.13 - 0.26)
	Chinook Salmon	61 (60)	821 ± 103	-21.8 ± 0.3	15.1 ± 0.4	5.3 ± 0.2	0.09 (0.06 - 0.11)
	Coho Salmon	30 (29)	529 ± 48	-21.9 ± 0.2	15.2 ± 0.4	5.1 ± 0.2	0.13 (0.08 - 0.20)
	Lake Trout	48 (48)	709 ± 96	-21.8 ± 0.4	17.0 ± 0.4	5.0 ± 0.4	0.13 (0.09 - 0.18)
	Rainbow Trout	36 (35)	649 ± 52	-21.4 ± 0.3	15.3 ± 0.6	5.0 ± 0.6	0.28 (0.19 - 0.41)
Prey	Alewife	22 (9)	139 ± 30	-22.3 ± 0.5	12.8 ± 0.9	5.4 ± 0.3	0.44 (0.26 - 0.73)
	Deepwater Sculpin	10	-	-23.0 ± 0.4	16.9 ± 0.5	5.8 ± 0.2	0.42 (0.20 - 0.82)
	Mysis diluviana	10	-	-24.0 ± 0.6	12.6 ± 1.8	5.3 ± 0.3	1.18 (0.55 - 2.36)
	Rainbow Smelt	10 (2)	98 ± 1	-22.8 ± 0.4	14.6 ± 0.6	5.2 ± 1.0	0.89 (0.42 - 1.79)
	Round Goby	17 (6)	99 ± 27	-22.6 ± 1.3	14.9 ± 1.7	4.4 ± 0.9	1.85 (1.03 - 3.23)
	Slimy Sculpin	10 (5)	104 ± 3	-23.0 ± 0.4	16.2 ± 0.4	6.0 ± 0.2	0.40 (0.19 - 0.79)

Table 4.2 Mean (and 95% credible intervals) posterior probability distribution of trophic niche overlap (%) of salmonid species from Lake Ontario in 2018, determined for fin and muscle tissues, using two ($\delta^{13}C$ and $\delta^{15}N$) or three ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) stable isotopes using the 40% standard ellipse areas. ATLS = Atlantic salmon, BRTR = brown trout, CHIN = Chinook salmon, COHO = coho salmon, LKTR = lake trout, RBTR = rainbow trout.

	ATLS	BRTR	CHIN	COHO	LKTR	RBTR
Fin - 2 isotopes						
ATLS		27 (18-38)	31 (22-40)	22 (14-32)	0 (0-1)	34 (22-47)
BRTR	23 (15-33)		12 (7-18)	10 (6-17)	0 (0-1)	47 (36-58)
CHIN	32 (23-43)	17 (11-25)		25 (18-33)	0 (0-1)	19 (11-28)
COHO	34 (23-47)	13 (6-23)	36 (27-46)		6 (3-11)	15 (6-28)
LKTR	0 (0-1)	0 (0-1)	0 (0-1)	4 (1-11)		0 (0-1)
RBTR	19 (12-28)	31 (23-39)	10 (6-15)	8 (4-13)	0 (0-1)	
Fin - 3 isotopes						
ATLS		35 (24-47)	28 (20-37)	25 (16-36)	1 (0-2)	41 (28-56)
BRTR	12 (8-18)		6 (4-10)	7 (4-12)	0 (0-1)	44 (34-55)
CHIN	31 (21-42)	22 (14-31)		28 (20-37)	0 (0-1)	19 (11-30)
COHO	27 (17-38)	20 (10-34)	26 (19-35)		6 (3-11)	18 (8-32)
LKTR	0 (0-1)	0 (0-2)	0 (0-1)	6 (1-15)		0 (0-2)
RBTR	8 (5-12)	25 (18-32)	3 (1-5)	3 (2-6)	0 (0-1)	
Muscle - 2 isotopes						
ATLS		50 (22-79)	5 (0-17)	5 (0-16)	0 (0-0)	34 (13-60)
BRTR	16 (8-32)		5 (2-9)	4 (1-7)	0 (0-1)	21 (12-31)
CHIN	6 (1-21)	5 (1-13)		29 (20-41)	0 (0-0)	20 (9-34)
COHO	7 (0-25)	4 (0-14)	45 (31-59)		0 (0-0)	12 (3-28)
LKTR	0 (0-1)	0 (0-1)	0 (0-0)	0 (0-0)		0 (0-0)
RBTR	17 (8-33)	30 (18-44)	13 (6-21)	7 (3-14)	1 (0-2)	
Muscle - 3 isotopes						
ATLS		52 (24-80)	0 (0-2)	6 (0-19)	0 (0-1)	46 (21-73)
BRTR	5 (2-10)		4 (1-7)	2 (1-5)	0 (0-1)	23 (12-36)
CHIN	0 (0-2)	9 (2-21)		18 (9-31)	0 (0-0)	20 (8-37)
COHO	3 (0-9)	6 (1-17)	24 (13-36)		0 (0-0)	19 (6-39)
LKTR	0 (0-0)	0 (0-1)	0 (0-0)	0 (0-0)		0 (0-1)
RBTR	3 (1-7)	16 (9-25)	4 (2-7)	3 (1-7)	0 (0-1)	
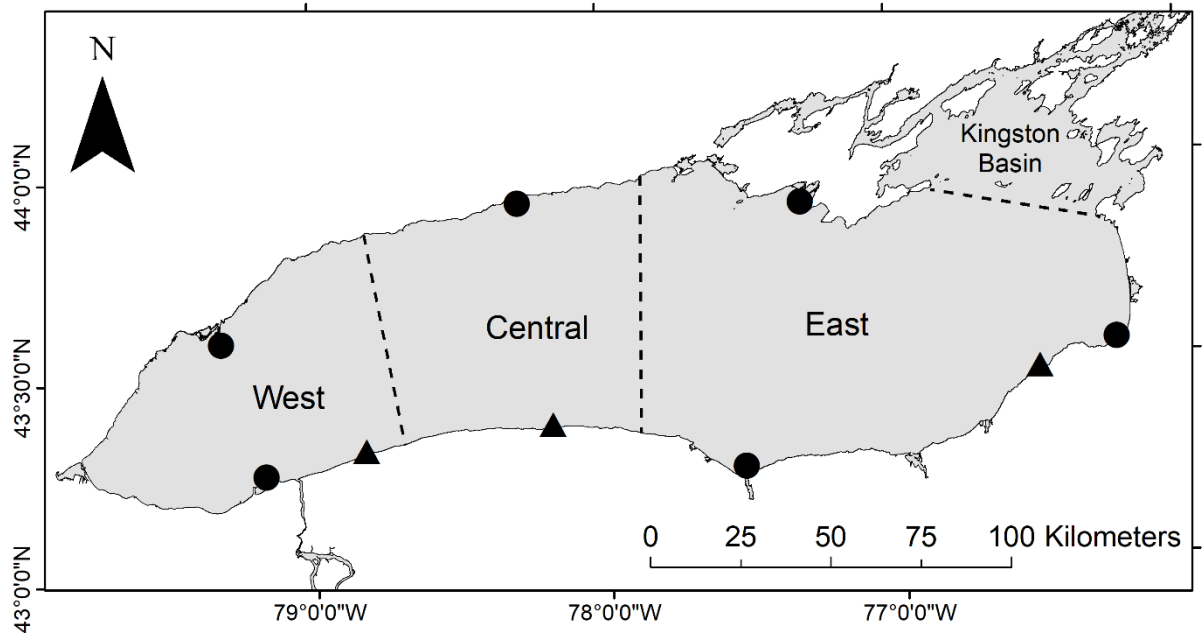
Figure 4.1 Salmonid sampling locations during fishing derbies (triangles) and participating anglers (circles) throughout the different spatial zones of Lake Ontario in 2018.
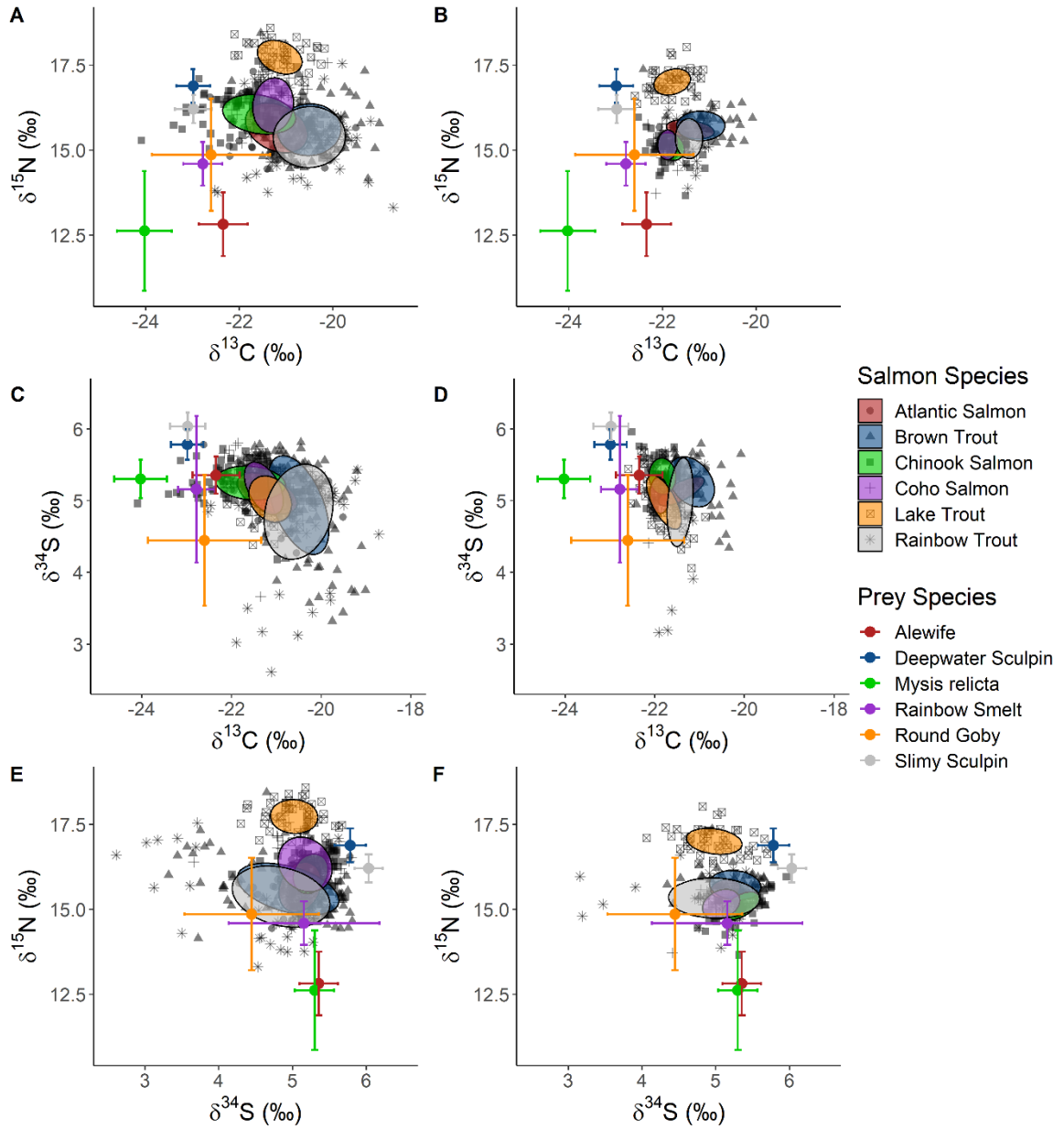
Figure 4.2 Combinations of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ stable isotope biplots of the isotopic niches of Lake Ontario salmonids using fin (left panels) and muscle (right panels) and mean ± standard deviation stable isotope ratios of prey collected in 2018. Coloured circles enclose the standard ellipse area (40%) of the two isotopes displayed for all salmonid species. Individual salmon data points are represented by shapes.
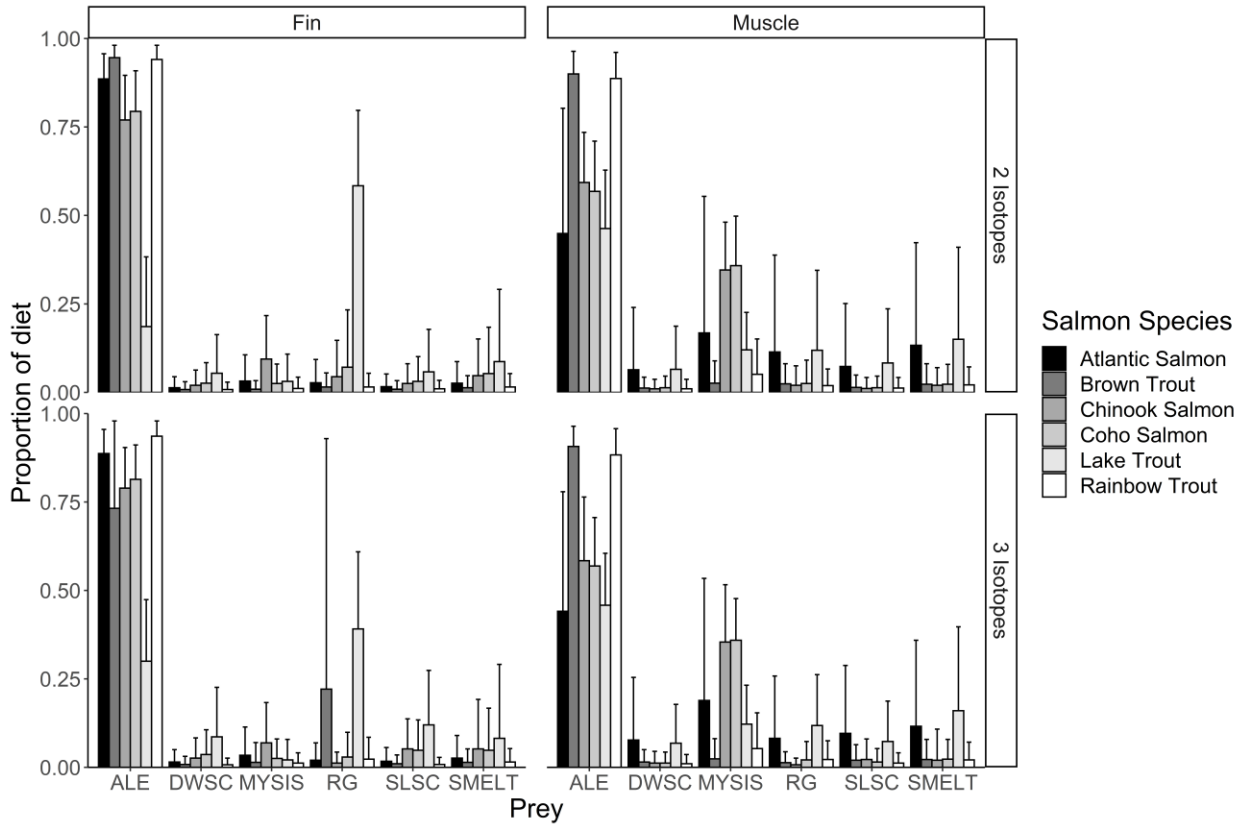
Figure 4.3 Mean (and 95% credible interval) estimated diet contributions of Lake Ontario salmonids in 2018 from isotope mixing models in MixSIAR, using salmonid fin (left panels) or muscle (right panels) that were estimated using 2 isotopes (δ^{13}C and δ^{15}N; top panels) and 3 isotopes (δ^{13}C, δ^{15}N and δ^{34}S; bottom panels). ALE = alewife; DWSC = deepwater sculpin; RG = round goby; MYSIS = Mysis spp.; SLSC = slimy sculpin; SMELT = rainbow smelt.
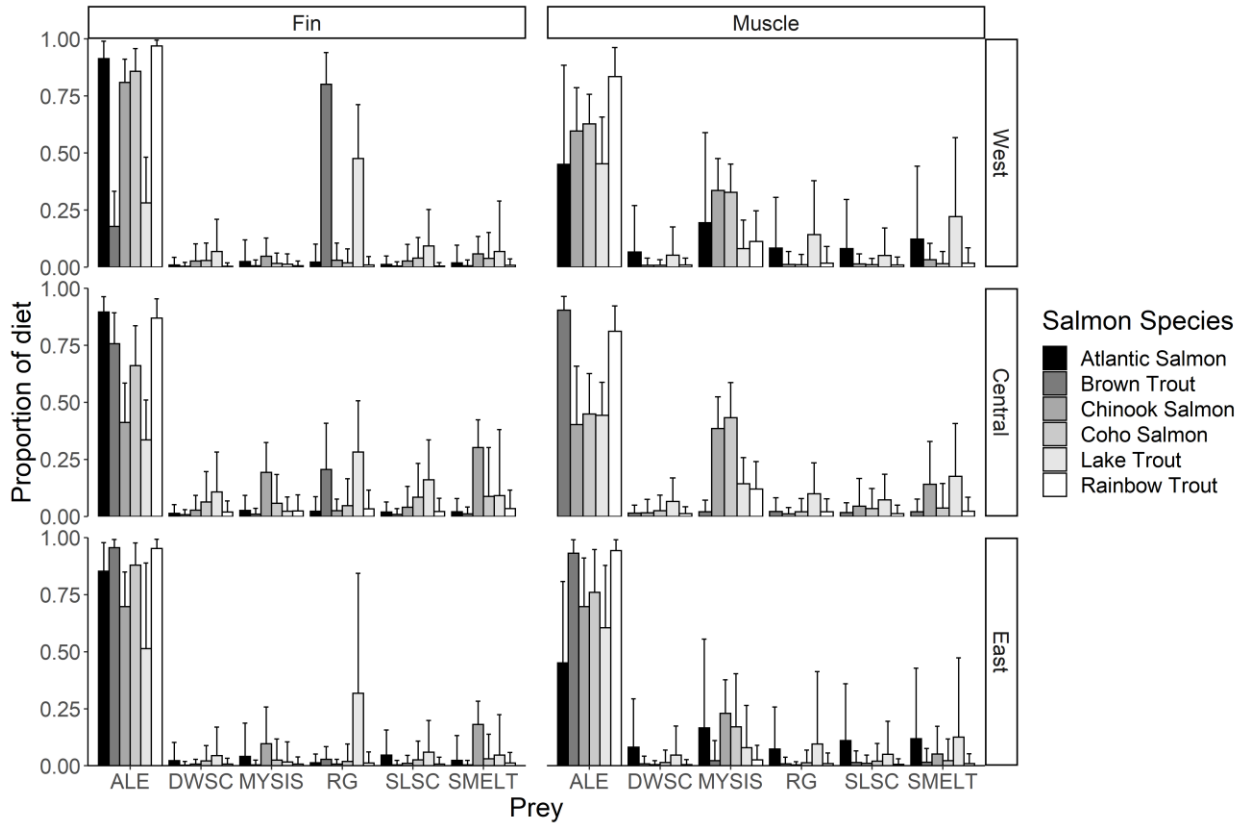
Figure 4.4 Mean (and 95% credible interval) estimated diet contributions of salmonids in different regions of Lake Ontario in 2018 from isotope mixing models in MixSIAR, using salmonid fin (left panels) and muscle (right panels) that were estimated using 3 isotopes (δ^{13}C, δ^{15}N and δ^{34}S). ALE = alewife; DWSC = deepwater sculpin; RG = round goby; MYSIS = Mysis spp.; SLSC = slimy sculpin; SMELT = rainbow smelt.

CHAPTER 5 – PATTERNS IN SPATIAL USE OF LAND-LOCKED ATLANTIC

SALMON (*SALMO SALAR*) IN A LARGE LAKE

5.1 Introduction

Knowledge of the movement ecology of fish populations to understand habitat use, migratory pathways, life history, and population dynamics is beneficial for fisheries management and restoration success (Berger-tal and Saltz 2014; Crossin et al. 2017). From a fisheries management perspective, knowledge of movement patterns and spatial ecology can assist in locations of management boundaries (Binder et al. 2017; Hayden et al. 2014; Hussey et al. 2017), spatial-temporal requirements for habitat protection (Rous et al. 2017; Simpfendorfer et al. 2010), and identifying potential sources of mortality (Cooke et al. 2011; Raby et al. 2015) and stock assessment parameters (e.g. spawning site fidelity, residential vs migratory populations; Espinoza et al. 2016; Zemeckis et al. 2014). Similarly for stocked fish, understanding the post-release spatial ecology and stocking success can assist with management decisions for reasons mentioned above but also in evaluating restoration success (Berger-tal and Saltz 2014; Klinard et al. 2020).

Understanding large-scale movements of salmonids in the Laurentian Great Lakes has aided in the management of these socially and economically important species (Crossin et al. 2017; Melstrom and Lupi 2013). Using mark-recapture techniques such as tagging fish with coded wire tags or external Floy tags that are later recaptured by anglers has revealed long distance movements of individual Chinook salmon (*Oncorhynchus tshawytscha*) in both lakes Huron and Michigan (Adlerstein et al. 2008, 2007). However, there can be biases with mark-recapture techniques if recaptures are reliant on where angler effort exists (e.g., nearshore and/or near ports). With advances in technology, the use of acoustic telemetry has improved our knowledge of the movement ecology of salmonids in the Great Lakes (Krueger et al. 2018). Acoustic telemetry is the remote

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detection of tagged fish when in range of acoustic receivers in the water. The use of acoustic telemetry provides information on the whereabouts and pathways of individual fish to determine movement patterns and home ranges that mark-recapture studies may not reveal. For example, acoustic telemetry revealed spawning locations as well as spatial movement distinctions in populations of lake trout (*Salvelinus namaycush*) in Lake Huron (Binder et al. 2017; Riley et al. 2014) and migration pathways of lake trout in Lake Ontario (Ivanova et al. 2020). Acoustic telemetry is a suitable technique for understanding the movement ecology of mobile salmonid species in the Great Lakes.

In Lake Ontario, Atlantic salmon (*Salmo salar*) has been the subject of restoration efforts since the 1990s (OMNRF 2017). Atlantic salmon were extirpated from Lake Ontario in the 1890s due to overharvesting, and habitat degradation and loss (Christie 1974; Crawford 2001). Since then, Lake Ontario has undergone extensive changes to the fish community with the invasion and proliferation of non-native alewife (*Alosa pseudoharengus*) which was followed by the stocking of non-native Pacific salmonids in the 1960s to reduce alewife populations (Crawford 2001; Dettmers et al. 2012), and the introduction of dreissenid mussels and round goby (*Neogobius melanostomus*) in the 1990s (Mills et al. 2003). Restoring native species to Lake Ontario, like Atlantic salmon, will involve co-existing with a different fish community and consuming different prey than historically. To restore self-sustaining populations, Atlantic salmon are regularly stocked at different life stages (fry or fingerling, parr, smolt) into tributaries and infrequently directly into Lake Ontario as adults (typically as excess broodstock) where they are considered land-locked. The movements of young stocked Atlantic salmon are relatively restricted within the tributaries, until smolts migrate to Lake Ontario. However,

in Lake Ontario, the movement ecology and habitat use of adult land-locked Atlantic salmon is unknown, particularly in relation to other salmonids as potential competitors.

In addition to Atlantic salmon, Lake Ontario contains five other salmonids all of which are stocked (Chinook salmon, coho salmon *O. kisutch*, rainbow trout *O. mykiss*, lake trout *Salvelinus namaycush*, and brown trout *Salmo trutta*) and all of which can potentially overlap in spatial and trophic ecology. The diets of all salmonids in Lake Ontario are dominated by alewife, including that of Atlantic salmon (Brandt 1986; Mumby et al. 2018; Rand and Stewart 1998; Larocque et al. *in review*). Round goby are also consumed by lake trout and brown trout in greater numbers than the other salmonids, while low proportions of rainbow smelt (*Osmerus mordax*) and sculpins (*Cottus cognatus* and *Myoxocephalus thompsonii*) are occasionally consumed by all salmonids (Mumby et al. 2018; Larocque et al. *in review*). Spatially there is potential for distinction between salmonids. In Lake Huron, Chinook salmon are highly mobile, while lake trout occupy smaller home ranges and move <100km (Adlerstein et al. 2007; Binder et al. 2017). In Lake Ontario, lake trout occupy deeper depths than Chinook salmon and brown trout (Olson et al. 1988; Raby et al. 2020), while brown trout stay closer to shore than lake trout and Chinook salmon (Nettles et al. 1987; Olson et al. 1988). Thus, there is some trophic overlap among all salmonids and discerning whether there is also a spatial overlap between Atlantic salmon and other species can determine if they occupy similar niches and potentially affect Atlantic salmon restoration success.

Understanding the movements and spatial ecology of Atlantic salmon in Lake Ontario will enable fisheries managers to determine habitat use and population boundaries in relation to other salmonids and evaluate restoration success while in the

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lake environment. In this study, a combination of acoustic telemetry and Floy marked and recaptured fish was used to assess movement patterns of adult Atlantic salmon in Lake Ontario. The specific objectives were to better understand land-locked Lake Ontario Atlantic salmon spatial use in which to: 1) determine seasonal home ranges, 2) determine patterns in horizontal and vertical space use, and 3) compare distances moved from acoustic telemetry to mark-recaptures of Floy tagged fish.

5.2 Methods

Study site and acoustic receiver array

Lake Ontario is one of the five Laurentian Great Lakes in North America, and has an average depth of 86 m, maximum depth of 245 m, and a surface area of ~19,000 km^2. Between the study period of November 2015 and June 2020, a range of 159 to 382 acoustic telemetry receivers (69-kHz VR2W, Innovasea, Bedford, Nova Scotia, Canada) were annually deployed within Lake Ontario, as part of ongoing acoustic telemetry projects through the Great Lakes Acoustic Telemetry Observation System (GLATOS) network (Figure 5.1; Krueger et al. 2018). Receiver groupings with available data covering the open waters of Lake Ontario are primarily located in the western (n = 12 in 2016; 49 in 2017; 51 in 2018; 57 in 2019) and eastern regions (n = 144 in 2016; 193 in 2017; 206 in 2018; 32 in 2019), with additional receivers in the Bay of Quinte, Toronto Harbour, Hamilton Harbour, and the Niagara River. In Lake Ontario, receiver spacing varied between 1 to 15 km apart, with grid patterns used in the western and eastern regions, and a bathymetry driven design around the St. Lawrence Channel. Due to logistics, there is currently a lack of receiver coverage in the central region of Lake Ontario which will influence results, and data interpretations consider this caveat.

Receiver moorings vary between telemetry projects but were generally composed of concrete blocks (~25 – 60 kg) as anchors connected to 28-cm diameter trawl floats by a 3 m length of polypropylene rope. Receivers were attached midway along the rope with the hydrophone pointing upwards and suspended ~2 m above the lake bottom. Some moorings included a ~ 30 m weighted rope running from the receiver mooring to a terminal anchor which served as a drag line for grappling when retrieving the receivers for download. Other receivers had acoustic releases (AR) situated between the anchor and receiver lughead with the float attached above the receiver on a separate 2-m rope. Receivers were typically downloaded annually, with the last full Lake Ontario receiver array downloaded in 2019, and a partial Lake Ontario download in 2020 with data available until 18 June, 2020. The partial download explains the poor receiver coverage of eastern Lake Ontario for 2019 (n = 32) as only receivers that there was data for were included, as more receivers were deployed but not downloaded at the time of this paper.

Atlantic salmon tagging and stocking

Broodstock Atlantic salmon (Sebago and LaHave strains) used for acoustic tagging and Floy tagging were sourced from either the OMNRF Normandale Fish Culture Station (Turkey Point, ON) or Harwood Fish Culture Station (Harwood, ON). A total of 47 Atlantic salmon were acoustically tagged across three periods: spring 2016 (n = 20), winter 2017 (n = 19), and spring 2019 (n = 8; Table 5.1). Fish were anaesthetized using a chemical solution of buffered tricaine methanesulfonate (MS-222; 200 mg/L; 2016 tagging) or electro-sedation using electric fish handling gloves (Smith-Root Inc., Vancouver, Washington, USA; 2017 and 2019 tagging) and placed in a surgery cradle where water was continuously flushed over the gills during the surgery. A ~20 mm

incision was made on the ventral side of the fish off the midline and a V13 69 kHz

transmitter (hereafter called tag; n = 22; 36 x 13 mm, 6.3 g weight in water, nominal

delay 180 s; Innovasea) or V13P 69 kHz tag (n = 25; 46 x 13 mm, 6.9 g weight in water,

nominal delay 180 s; Innovasea) equipped with pressure sensors was inserted into the

body cavity. The incision was closed with 3 simple interrupted sutures (2-0 coated Vicryl

Plus undyed braided suture; Ethicon, Inc.). Fish were also Floy tagged in the dorsal

musculature at the posterior margin of the dorsal fin to externally identify tagged fish and

fork length (FL) was measured to the nearest 1 mm. Surgeries took <3 min and fish were

transferred back to a holding tank post-surgery until stocked. In 2016, 10 fish had an

additional external pop-off data storage tag attached by a harness through the dorsal

musculature (for details see Raby et al. 2017). Fish were monitored daily and held for a

minimum of a week prior to stocking (Table 5.1). Tagged fish were hand-netted into a

stocking truck equipped with an aerated tank along with untagged excess broodstock for

transport to and release in Lake Ontario.

   Additional releases of surplus broodstock fish from 2018 to 2020 were Floy tagged

on-site and released in Lake Ontario for mark-recapture by anglers. Eleven Floy tagging

events occurred at six different release locations in which a total of 1915 fish were Floy

tagged and subsequently released (Table 5.2). Floy tags were colour specific to release

locations and contained a unique tag ID and a phone number for anglers to call in with

capture information.

Data preparation

   Detection data were available from March 2016 to June 2020. Detection data

were filtered to check for mortality or expelled tags and those individuals were

subsequently removed from analyses. Fish were inferred to be dead if they exhibited

uncharacteristic constant depth-use profiles from the depth sensor data and stayed within

the same area of the array. Individuals that had few detections over a short period of time

(<1 month) were also removed from analyses, although mortality cannot be confirmed.

Detection data was assessed for false detections, however, based on the sparseness of the

array, the criteria for filtering false detections would remove real data and was not done

(Pincock 2012). All analyses were completed in R version 4.0.2 (R Core Team 2020) and

data preparation was conducted with the assistance from the R package *glatos* (Holbrook

et al. 2020).

Each Atlantic salmon detection was assigned a location that was randomly

estimated within 700 m of the receiver which accounted for the uncertainty associated

with the actual location of tagged individuals due to the detection range of the receivers.

Using 700 m is a realistic distance for fish to be detected at, in which detection

probability is still high (~80%), and random distances were determined using a detection

probability curve developed from V13 range testing in Lake Ontario (Klinard et al.

2019). For each individual, location and depth estimates were calculated using a 30-min

weighted, arithmetic mean position algorithm to derive centers of activity (COAs)

following the methods described in (Simpfendorfer et al. 2002). A 30-min time interval

was chosen as Atlantic salmon are a mobile species and to maximize the number of

positions within a day. Using 30-min COAs reduces the occurrence of temporal

autocorrelation and helps standardize the number of detections between individuals (e.g.,

a sedentary fish near a receiver could have up to 60 detections in 30 min as opposed to a

mobile fish that swam by and was detected once). A subset of the detection data that was

only detected in Lake Ontario (excluded Bay of Quinte receivers) was used to calculate COAs to analyze lake movement and depth use (see below), as otherwise, detection data from the Bay of Quinte skewed spatial behaviour within the lake.

Seasonal designations were given to each COA, based on the detection time, and estimates of Lake Ontario's temperature dynamics and thermocline delineation from three temperature profiles collected using chains of temperature loggers deployed in eastern Lake Ontario (43.962° N, 76.586° W) from May 2017 to April 2018 (Ivanova et al. *submitted*). Season was defined by spring (warming isothermal – May to July), summer (established thermocline – July to November), fall (thermocline breaking down and cooling – November to January), and winter (temperature is no longer declining and isothermal – January to May).

Floy tag recapture information collected from anglers were verified and confirmed. There were a few instances (n = 8) where the tag ID was unknown, yet tag colour was reported, and so it was assumed the fish was from the most recent tagging event at that release location. Recapture data was included until October 2020.

Spatial analyses

Seasonal horizontal autocorrelated kernel density estimates (AKDE) representing the core activity space (50%) and activity space extent (95%) of individuals were calculated from the COAs of each Atlantic salmon using the akde function in the R package *ctmm* (Fleming and Calabrese 2020). Traditional kernel density estimation (KDE) assumes that location data are independent and identically distributed and with higher frequency sampling of locations such as can occur with acoustic telemetry, KDEs often underestimate home range areas (Fleming et al. 2015; Noonan et al. 2019). AKDE

uses continuous time movement modeling to account for autocorrelation in the data which reduces the bias in home range area estimates seen in traditional KDEs (Fleming and Calabrese 2020; Noonan et al. 2019). The AKDE was developed for and tested with terrestrial organisms in which positions are nearly continuous, while acoustic telemetry position estimates depend on the number and locations of receivers, potentially having temporal gaps in the dataset. However, AKDEs are still likely to be more accurate than KDEs based on acoustic telemetry simulation data (Larocque et al. *in prep*) and was subsequently used here to calculate seasonal home ranges. Seasonal AKDEs were grouped across years due to the low sample sizes of fish with few detections when split among years, and to reduce any influence of an expanding array over the years.

The area (km^2) of each individual's seasonal home range was calculated and differences in the size of the 95% and 50% AKDEs across seasons was assessed using an ANOVA with tag ID as a random effect, and differences were determined using posthoc Tukey's test. Individual seasonal 95% and 50% AKDEs were combined into a single raster layer to visualize the extent of overlap in activity space and core ranges amongst individuals within each season, similar to Brooks et al. (2019), using ArcGIS v.10.8.1 (ESRI, Redlands, California). Colour coding of individuals overlapping is held constant across seasons. The full extent of the seasonal 95% and 50% home range areas were calculated across seasons to determine how the home ranges varied spatially by season.

For Atlantic salmon with more than one season of data and more than 100 COA estimates per season for adequate seasonal representation, the degree of overlap in the AKDEs (which uses the entire probability distribution, not the 95% or 50% range as above) between seasons was estimated for each individual using a bias-corrected

Bhattacharyya Coefficient (BC) in the *ctmm* package (Winner et al. 2018). This estimator

gives a point estimate and a 95% confidence interval on the overlap statistic to account

for any uncertainty in the home range estimate. The BC indicates the similarity between

two AKDEs with values ranging from 0 (no overlap between probability distributions)

and 1 (identical probability distributions; Winner et al. 2018). Note that the AKDEs can

be larger than the Lake Ontario boundary and the BC overlap does not take that into

account and could potentially underestimate the true overlap within the lake only.

Movement and depth analyses

The maximum distance an acoustic tagged fish moved from the release location

was determined from the raw detection data, and spatial and temporal plots of detections

were assessed to determine whether fish crossed from the western to the eastern region,

or vice versa. Similarly, the distance and duration from the release location to the capture

location of Floy tagged fish were determined. There were no differences in distance or

duration before capture between tagging events (ANOVA – distance: $F_{8,79}=0.273$,

p=0.973; duration: $F_{8,79}=1.166$, p=0.330), and data from all tagging events were grouped

together and summarized.

It was also determined if there were any seasonal and/or diurnal patterns in

horizontal space use (bathymetric depth and distance from shore) and depth use with

acoustic tagged fish in the main lake area based on the 30-min COA positions which had

removed any Bay of Quinte detections. Bathymetric depth and nearest distance to shore

were determined for each COA position. COA positions were overlayed with the Lake

Ontario bathymetry raster collected by NOAA National Geophysical Data Center to

obtain bathymetric depth. The distance from the COA positions to the nearest mainland

shoreline was obtained using the Lake Ontario shoreline polygon modified from the

bathymetry raster in which islands had been removed. Distances could not be determined

when incorporating islands, which were primarily associated with the eastern region, and

was not perceived to greatly influence results. Some COA positions were not designated

a bathymetric depth (likely from being too close to shore) and were removed for that

particular analyses. Depth values were the mean 30-min depths from the COA

calculations determined from each Atlantic salmon tagged with depth sensors and

adequate data (n = 8).

Linear mixed models were used to assess seasonal and diel patterns in

bathymetric depth, distance to shore, and depth use with the *nlme* package in R (Pinheiro

et al. 2020). For each model, response variables were log transformed to meet the

assumptions of normality and heteroscedasticity. Fixed predictor variables for each

model were season, time of day, season x time of day, and year, and tag ID was included

as a random effect. Due to an imbalance in sample sizes, only spring and winter seasons

were assessed for depth use. Time of day was categorical with four 6-hr intervals: late

night 00–06 hr; morning 06–12 hr; midday 12–18 hr; early night 18–24 hr. These times

roughly distinguish between day and night, as dawn and dusk are approximately at 06:00

and 20:00. Thus, 00-06 and 18-24 were considered night, and 06-12 and 12-18 intervals

were considered day. Year was added as a categorical covariate to help control for the

changing array, in which receiver coverage expanded and covered deeper locations over

the years. Only 2018 and 2019 years of data were available for fish with depth sensors

and depth use estimates. A posthoc Tukey's test determined which season, time periods

and years differed when they were significantly influenced by bathymetric depth, distances from shore, or depth use.

All analyses were conducted in R and significance was assessed at α = 0.05. Unless stated otherwise, values are reported in mean ± standard error (SE). Assumptions of normality and heterogeneity were visually assessed using qqplot and fitted vs residual plots.

5.3 Results

Of the 47 acoustically tagged Atlantic salmon, 2 (4%) were captured, 8 (17%) were never detected, 16 (34%) were considered dead, 7 (15%) had less than one month of data, and 14 (30%) were alive with good quality data, 8 of which had depth sensors, and used in subsequent analyses. Seasonally, the 95% AKDE of activity space indicated that Atlantic salmon are generally using all areas of Lake Ontario in every season (Figure 5.2). Differences in the extent of overlap of individuals was related to the season of a stocking event and the number of individuals representing a season (fall had the fewest individuals (n = 3) contributing to the AKDE), otherwise there was no specific region that home ranges converged upon and AKDEs were widespread. The size of the 95% AKDEs ranged from 6.8 to 18851 km^2 and did not vary between seasons (χ^2_3=4.308, p = 0.230; Table 5.3). The 50% AKDE appeared to show seasonal variation; Atlantic salmon used all areas of Lake Ontario in spring and summer and had more restricted spatial use in fall and winter (Figure 5.3), however, there was no significant difference in the size of 50% AKDEs across seasons (χ^2_3=2.700, p = 0.440; Table 5.3). Individuals with data from multiple seasons, had intermediate to high overlap in the AKDE distributions between all seasons: spring and summer (BC > 0.9, n =2), spring and fall (BC = 0.74, n=1), spring

and winter (0.62 < BC < 1.00, n =6), summer and fall (BC = 0.93, n=1), summer and

winter (0.68< BC < 0.98, n=2), and fall and winter (BC = 0.82, n =1; Appendix 11).

The mean maximum distance that acoustic tagged Atlantic salmon moved from

their release location was 150.49 ± 25.41 km with a range of 13.26 to 253.16 km. More

than half of the salmon were detected on both the western and eastern regions of Lake

Ontario (64%, n = 9 of 14), and 43% (n = 6 of 14) moved back and forth between the

western and eastern region at least once, as is reflected in the AKDEs. Two fish that did

not cross the lake were tagged in 2019 and did not have a dataset with a full array

download to confirm if they too crossed the lake.

With the Floy tagging data, there were 88 recaptures from 11 tagging events for a

mean recapture rate of 4.47 ± 0.30 % (total recapture rate of 4.60%; Table 5.2). The mean

distance from the release location to the capture location of Floy tagged fish was 69.36 ±

8.89 km with a range of 0.1 to 296.4 km within Lake Ontario. One recapture occurred

along the St. Lawrence River at Lake St. Francis which was 475.4 km from release

location. Floy tagged fish spent on average 128 ± 12 days in the lake until capture (range:

2-557 days). Spatially, the capture locations occurred around the entire perimeter of Lake

Ontario, except northeast Lake Ontario and more captures occurred closer to the release

locations (Figure 5.4).

The distance from shore that Atlantic salmon were detected in ranged between 0.1

to 25.9 km and varied by season and time of day but did not interact (season:

χ^2_3=1122.089, p<0.001; time of day: χ^2_3=37.700, p<0.001; interaction: χ^2_9=15.757, p =

0.072). Atlantic salmon were closest to shore in the fall (0.32 ± 0.02 km), followed by

summer (0.82 ± 0.03 km), spring (3.03 ± 0.10 km), and winter (15.62 ± 0.55 km; Figure

5.5A). Atlantic salmon also moved slightly further from shore during the afternoon hours (12-18 hrs; 5.07 ± 0.30 km; Figure 5.5B). Distance from shore also varied by year (χ^2_3=562.709, p<0.001) in which 2019 COA positions (5.72 ± 0.28 km) were further from shore than other years (2016: 2.46 ± 0.09 km; 2017: 3.96 ± 0.23 km; 2018: 3.46 ± 0.20 km), matching the array expansion further from shore over the years.

The bathymetric depth that Atlantic salmon were detected at ranged between 0.3 to 153.8 m depth. Bathymetric depth interacted with season and time of day (season: χ^2_3=581.997, p<0.001; time of day: χ^2_3=5.510, p=0.138; interaction: χ^2_9=17.973, p=0.035) and had a year effect (χ^2_3=468.576, p<0.001). Similar to distance from shore, Atlantic salmon were at the shallowest depths during fall (15.5 ± 1.3 m), followed by spring and summer (24.3 ± 0.3 m and 29.6 ± 0.8 m, respectively), and winter (65.0 ± 1.5 m; Figure 5.6). The time of day did not vary within the spring, summer, and winter, however, in the fall, fish were detected at shallower bathymetric depths in the early night (18-24hrs: 7.7 ± 1.6 m; Figure 5.6). Bathymetric depth of COA positions were shallowest in 2016 (19.1 ± 0.2 m) and 2017 (26.0 ± 0.5 m), followed by 2018 (33.7 ± 0.5 m), and deepest in 2019 (40.7 ± 1.1 m), matching the array expansion into deeper waters over years and being able to better detect fish offshore.

Average depth use in Lake Ontario ranged between 0.02 and 28.5 m among the 8 individuals with depth sensor tags, in which the majority of depth detections were shallow (<4 m) across seasons, with occasional dives in the spring of up to 13 m and the deepest dives occurring during the winter (Figure 5.7A). Models indicated that depth use was best predicted by an interaction with season and time of day (time of day: χ^2_3=190.447, p<0.001; season: χ^2_1=20.793, p<0.001; interaction: χ^2_3=31.724, p <0.001)

and did not vary by year (χ^2_1=0.308, p=0.579). Atlantic salmon were deeper during

daytime hours (06-12hrs: 1.8 ± 0.6 m, and 12-18hrs: 1.8 ± 0.5 m) in the spring than

nighttime hours (Figure 5.7B). Winter showed a similar trend of being deeper during

daytime hours (06-12hrs: 5.9 ± 0.1 m, and 12-18hrs: 2.9 ± 0.0 m). Winter was deeper

than spring during the morning (06-12 hrs; Figure 5.7B).

5.4 Discussion

Understanding the movement and home ranges of Atlantic salmon in Lake

Ontario expands our limited knowledge of land-locked Atlantic salmon ecology while

providing information that can assist in the restoration efforts of this native species and

salmonid fisheries management. Using acoustic telemetry and Floy tag recaptures, land-

locked Atlantic salmon movements in a large lake could be monitored which has yet to

be described. Survival of stocked adult Atlantic salmon with quality data was low (30%).

Atlantic salmon were wide ranging and moved between the eastern and western regions

of Lake Ontario, using the majority of the lake for the 95% activity space which was

confirmed with Floy tag recaptures. There were no major seasonal differences in home

ranges, and those seen in the 50% core home ranges could be partially attributed to

release locations/timing and/or returning to rivers in the fall and reduced overwintering

movements. Within individuals, there were intermediate to high overlaps of the home

ranges between seasons further indicating no seasonal disparities in the overall wide

range movements of Atlantic salmon in Lake Ontario. Atlantic salmon primarily used the

nearshore (within 5km and 25m bathymetric depths) but moved further offshore in winter

(15km and 60m bathymetric depth). Small diel vertical movements occurred, moving 1-5

m deeper during the day but generally Atlantic salmon stayed in fairly shallow depths (<4 m) in the water column with occasional deeper dives (max of 28.5 m).

Adult Atlantic salmon had a relatively low post-stocking survival which may be influenced by additional stressors related to hatchery conditions and transportation (Brown and Day 2002; Cowx 1994). The continuous monitoring of acoustic telemetry and the added benefit of depth data could verify a stocking mortality of 34%, while 30% of fish survived and had good quality detection data. Atlantic salmon smolts from other acoustic telemetry tagging studies have incurred high mortality post-stocking, not related to the actual tagging event (Holbrook et al. 2011; Huusko et al. 2018; Larocque et al. 2020; Thorstad et al. 2012). Stocking of larger fish is correlated with decreased post-release mortality (Brown and Day 2002), however, Atlantic salmon may be a particularly sensitive species to additional stressors based on these high levels of mortality post-stocking, especially after spawning in the fall (e.g., winter 2017 acoustic tagging event). Tagging was not perceived to influence mortality in this study, as no mortalities occurred prior to the stocking event. It is likely that handling and transportation stressors may have induced the post-release mortality. Coho salmon (*Oncorhynchus kisutch*) have shown increased corticosteroids, a measure of stress, and mortality from transportation (Specker and Schreck 1980). Although hatcheries try to optimize conditions to reduce stress and mortality, revisiting and monitoring stress levels during the stocking process may lead to methods to improve post-release survival in sensitive species.

The combination of acoustic telemetry and Floy tag recaptures provides both fine- and large-scaled details of fish movements. Acoustic telemetry receivers collected data year-round, in areas further offshore than anglers occupy. With the expansion of the

acoustic receiver array in Lake Ontario over years, there was greater offshore depth coverage and resulting detections of Atlantic salmon at greater bathymetric depths. Although the year factor was accounted for in the analyses, increased receiver coverage throughout the entire lake would be optimal but extremely logistically challenging. Regardless, the year-round coverage from acoustic telemetry revealed seasonal movements and depth use that would otherwise not be observed, particularly overwinter in which deeper bathymetric depths further from shore occurred. Conversely, Floy tagging fish had a 40x larger sample size and showed a similar lake-wide movement trend to telemetry results based on angler recaptures. Floy tagging can be beneficial by obtaining large sample sizes for determining larger-scale movements as seen here and given enough recaptures could potentially determine the location and timing of river entry for spawning more easily than acoustic telemetry in such a large lake. However, the effectiveness of Floy tag recaptures depends on the angling effort which may be spatially and temporally biased. Interestingly, one Floy tagged fish was recaptured in the St. Lawrence River. Based on one Floy tag recapture and lack of acoustic tagged fish being detected entering the St. Lawrence River, the amount of straying towards the St. Lawrence River and potentially the ocean were extremely low, verifying that Lake Ontario Atlantic salmon are primarily land-locked, as historical populations appeared to be (Guiry et al. 2016, 2020). Using both methods together increased the confidence that Atlantic salmon have a large home range and individuals were quite variable in their movements.

The movement ecology of Atlantic salmon in land-locked lakes bears similarities to anadromous populations migrating in the ocean. Anadromous Atlantic salmon are

highly mobile performing large forays in the ocean before migrating back to the rivers to spawn (Jonsson and Jonsson 2011). Few studies have determined the ocean movements of Atlantic salmon using pop-off satellite archival tags and/or data storage tags (Reddon et al. 2011; Chittenden et al. 2013; Hedger et al. 2017; Lacroix 2013; Strøm et al. 2018, 2017). Salmon from both the Miramichi River and Bay of Fundy, Canada followed the coastline during the oceanic migration to feeding grounds towards the Labrador Sea (Lacroix 2013; Strøm et al. 2017). However, the movement patterns appear to be quite variable among individuals (Lacroix 2013; Strøm et al. 2018, 2017). In this study, Atlantic salmon were found to move long-distances and use the nearshore, although the exact pathway was unknown and whether for certain they followed the coastline as in the ocean. In the ocean, Atlantic salmon spend most of their time in the upper water column (<10 m) presumably feeding on fish, diving infrequently to deeper depths of up to 1000 m (Reddon et al. 2011; Hedger et al. 2013; Lacroix 2013; Strøm et al. 2018, 2017). Lake Ontario Atlantic salmon were also found to use primarily shallow depths (<10 m) which is likely attributed to feeding on pelagic alewife. Deeper dives in the ocean have been suggestive of benthic feeding, which may be occurring periodically in Lake Ontario as well since benthic round goby was found in a Lake Ontario Atlantic salmon stomach (Larocque, unpublished data) and was estimated to contribute ~10% of the diet using stable isotope analyses (Larocque et al. *in review*). Seasonal and diel differences in depth use have also occurred in the ocean, in which Atlantic salmon were deeper during the daytime, as seen in this study, and during late winter/early spring (Reddon et al. 2011; Hedger et al. 2017; Strøm et al. 2018, 2017). Seasonal depth use followed the mixed layer or stratification of the thermocline (Hedger et al. 2017; Strøm et al. 2018). Lake

Ontario Atlantic salmon could be using the same strategy, however, more depth data across all seasons would better discern this and with only spring and winter data available would be why major seasonal depth differences were not seen. The similarities in the roaming behaviour and depth use of Atlantic salmon in the ocean compared to large lakes could assist in determining foraging activities/methods among other aspects of movement ecology.

Atlantic salmon start moving into rivers to spawn between early summer and fall but is highly variable throughout its range (Hansen and Jonsson 1991; Scott and Crossman 1998). In Canada, Atlantic salmon spawn between October and November but varies by latitude (Scott and Crossman 1998). The movement of Atlantic salmon closer to shore and at shallower bathymetric depths in the fall may indicate movement into rivers for spawning, as has been seen with anadromous populations (Davidsen et al. 2013). Fall was also the season with the fewest individuals detected which could mean some individuals had already moved into the rivers by this time. Regardless, it is suggestive with the movements closer to shore from spring through fall that Atlantic salmon may be preparing to move into the rivers. Over the time of the study, there was not adequate receiver coverage at river mouths to determine if fish are homing to a river or when they enter, which could confirm whether the fall movements closer to shore are related to spawning. Since 2018, fish counters with cameras have been installed on two rivers (Credit River, ON and Ganaraska River, ON) to monitor Atlantic salmon returns to answer questions pertaining to migration timing and numbers (OMNRF 2019), however, there are many tributaries that are not monitored in Lake Ontario that Atlantic salmon historically used (Parsons 1973). For example, in 2018, fishway cameras indicated five

Atlantic salmon moving upstream in September and October on the Credit River but this may differ among years (OMNRF 2019). Floy tagging recaptures within rivers would also confirm river returns and spawning locations. An alternative hypothesis to the fish movements observed is that these stocked adult Atlantic salmon may not behave like those stocked as parr or smolts and not stage outside of rivers as they have no natal river to home in on. Thus, it is possible the movements closer to shore are merely anecdotal of returning to rivers until there is more information.

Spatial overlap could occur seasonally between some Lake Ontario salmonids and Atlantic salmon. In Lake Ontario, brown trout tend to stay nearshore (<2 km) year-round and spend the spring and summer near the thermocline (mean (± SD) depths of 14.6 ± 6.7 m) at warmer temperatures (13.4 ± 3.7 ℃; Nettles et al. 1987; Olson et al. 1988). Atlantic salmon may overlap in the nearshore area but at shallower depths with brown trout from spring to fall, however, brown trout populations were more localized moving <200 km (Nettles et al. 1987) unlike Atlantic salmon which may differentiate spatial use between the two species. Notably, most Atlantic salmon are incidentally angled when fishers are targeting brown trout in the spring, indicating spatial overlap during this season (E. Lantiegne, pers. comm.). Atlantic salmon may also have some spatial overlap with coho salmon and rainbow trout (*Oncorhynchus mykiss*). In the spring, coho salmon and rainbow trout were angled close to the surface in the nearshore of Lake Ontario (Aultman and Haynes 1993), using similar depths as Atlantic salmon in this study. However, coho salmon movements are unknown in lake environments and whether coho salmon and Atlantic salmon have distinct distributions to reduce overlap in other seasons is unknown. Rainbow trout seem to only spatially overlap with Atlantic salmon in the spring. In Lake

Ontario, rainbow trout move from the nearshore at shallow depths in the spring to further offshore (40 to 65 bathymetric m) and deeper (11-16 m) in the summer and fall (Stewart and Bowlby 2009) which does not overlap with the nearshore, shallow depth spatial use of Atlantic salmon in the summer and fall.

Spatial use of Atlantic salmon differed vertically from lake trout and Chinook salmon. Lake trout stay below the thermocline (25.4 ± 8.9 m) at cooler temperatures (10.1 ± 2.8 ℃; Olson et al. 1988) but can appear nearshore during the spring before moving to deeper waters as temperatures rise in the summer (Lane et al. 1996; Raby et al. 2020). Thus, lake trout occupy deeper waters than Atlantic salmon in Lake Ontario, and do not appear to spatially overlap. Lake trout also have localized movements (<100 km; Binder et al. 2017; Ivanova et al. *submitted*) that may further segregate spatial use of the two species. Chinook salmon appear to move nearshore in the spring and further from shore as waters warm up in the summer, while occupying depths near or above the thermocline (18.3 ± 7.3 m) at warmer temperatures (14.4 ± 2.9 ℃; Olson et al. 1988; Raby et al. 2020; Stewart and Bowlby 2009). During the fall, Chinook salmon can move closer to shore (25-35 bathymetric m) and occupy shallower depths (9-12 m) consistent with river mouth staging, and similar to Atlantic salmon (Stewart and Bowlby 2009). Chinook salmon are also wide ranging and move large distances (Adlerstein et al. 2007, 2008; Ivanova et al., *submitted*). Atlantic salmon may spatially overlap horizontally with Chinook salmon, particularly with the long-distance movements and distances from shore, however, there is segregation in depth use. Raby et al. (2020) found Chinook salmon with pop-off data storage tags occupied deeper depths in the summer (21.3 ± 1.7 m) than spring (14.4 ± 2.5 m) which is deeper than spring Atlantic salmon in this study,

but also Chinook salmon underwent extensive deep dives during the winter (>160 m) with a max depth of 218 m observed (Raby et al. 2017), while Atlantic salmon stayed relatively shallow (max depth of 28.5 m). Based on the data acquired from acoustic telemetry in Atlantic salmon there is minor spatial overlap with other salmonids in Lake Ontario, occurring primarily during the spring with some species. However, verifying the spatial use with acoustic telemetry across all species may provide details that previous studies were not able to capture. Also, increased receiver array coverage, Atlantic salmon sample sizes and detections across seasons (particularly for depth use) would further expand our understanding of Atlantic salmon spatial use and overlap among Lake Ontario salmonids.

Understanding the movement ecology of Atlantic salmon will influence management decisions and restoration efforts. The highly mobile, wide ranging movements of Atlantic salmon in binational (Canada/USA) waters reflects the importance of government agencies working together to ensure sustainable fisheries and species restoration. Monitoring the movements and survival of stocked adult Atlantic salmon indicated that stocking strategies could reduce stressors to improve survival, albeit few adults tend to be stocked relative to younger life stages. The diet similarities among Lake Ontario salmonids could potentially elicit competition between species if resources were low in abundance. However, there appears to be spatial segregation either horizontally or vertically among species such that they are feeding at different depths in the water column and/or bathymetric depths and distance from shore compared to Atlantic salmon. Salmonids are most likely to spatially overlap in nearshore waters during the spring, and monitoring of salmonids may be best focused in those areas at this

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time. Further studies to determine the timing and location of river entry for spawning will also aid fisheries management and monitoring restoration success of Atlantic salmon in Lake Ontario. Using a combination of acoustic telemetry and Floy tag recaptures, this is the first study on the detailed spatial use and movements of Lake Ontario Atlantic salmon providing insight on the movement ecology of land-locked populations.

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Table 5.1 Summary of Atlantic salmon (*Salmo salar*) acoustically tagged and released into Lake Ontario over three periods. Sample sizes (n) in brackets refer to fish that were tagged and analyzed (e.g., survived and had adequate data for analyses) with depth sensor tags. Fork length (mm) is mean ± standard deviation.

Release group	Tagging date	Tagging location	Release date	Release location	n tagged	Strain	Age	Fork length	n analysed
Spring 2016	2016-03-30	Harwood	2016-04-06	Glenora	20 (0)	LaHave	3.5	426 ± 25	5 (0)
Winter 2017	2017-12-14	Normandale	2017-12-22	Port Dalhousie	19 (17)	Sebago	2	325 ± 18	4 (3)
Spring 2019	2019-04-10	Harwood	2019-05-06	Port Credit	8 (8)	LaHave	4	459 ± 38	5 (5)

Table 5.2 Summary of Atlantic salmon (*Salmo salar*) floy tagging events and recaptures in Lake Ontario, 2018-2020.

Release location	Tagging date	Source	Strain	Age	Mean weight (g)	n tagged	n captured
Bronte Harbour	2018-11-28	Normandale	Sebago	3	2050	199	6
Cobourg Marina	2019-04-30	Harwood	LaHave	4	968	556	23
Grimsby	2019-11-21	Normandale	Sebago	3	1860	208	8
Grimsby	2019-11-27	Normandale	Sebago	3	1964	92	5
Port Dalhousie	2018-11-29	Normandale	Sebago	3	2050	96	5
Port Dalhousie	2019-12-11	Normandale	Sebago	4	3421	164	13
Port Dalhousie	2020-06-02	Normandale	Sebago	4.5	5710	43	4
Port Hope	2019-11-22	Harwood	Sebago	7	3500	43	0
Port Hope	2019-12-12	Harwood	LaHave	7	4050	50	0
Port Hope	2020-01-09	Harwood	LaHave	7	4150	215	10
Port of Newcastle	2019-04-30	Harwood	LaHave	4	968	249	14

Table 5.3 The mean ($\pm$ SD) size (km^2) of individual Atlantic salmon (*Salmo salar*) 50% and 95% autocorrelated kernel density estimates (AKDEs), and the total area (all individuals combined) of the 50% and 95% AKDE seasonal home ranges in Lake Ontario.

Season	n	Individual AKDE size 50%	95%	Total area of combined AKDE 50%	95%
Spring	12	4252 ± 1275	9215 ± 2240	18852	18852
Summer	6	6754 ± 2804	11038 ± 3567	17958	18852
Fall	3	2724 ± 2544	6742 ± 5993	7809	18697
Winter	9	2929 ± 1754	4884 ± 2528	14510	18852
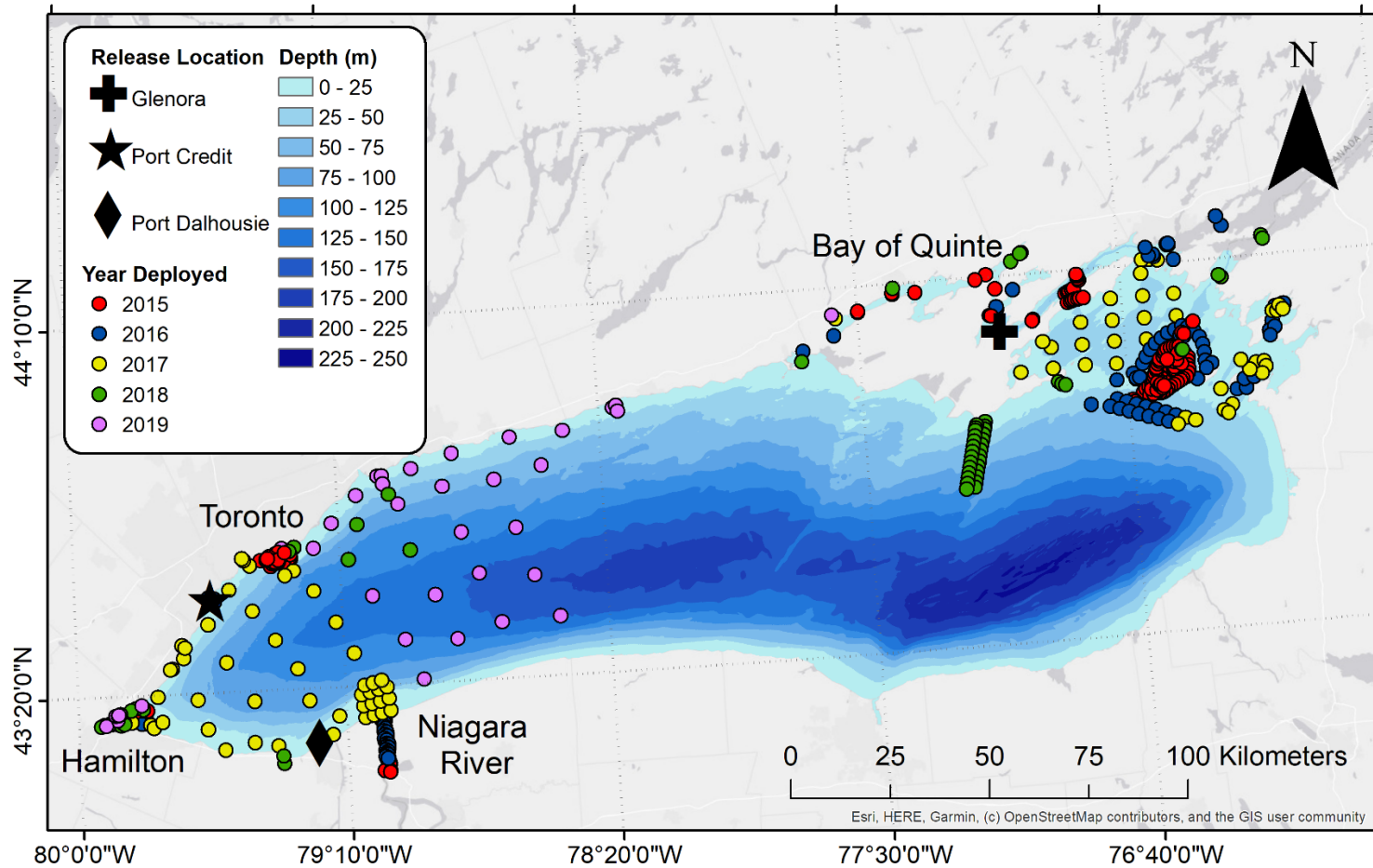
Figure 5.1 Acoustically tagged Atlantic salmon (*Salmo salar*) release locations (symbols), and acoustic telemetry receiver locations by initial year of deployment (coloured circles) in Lake Ontario. Note: receivers were deployed in subsequent years after initial deployment.
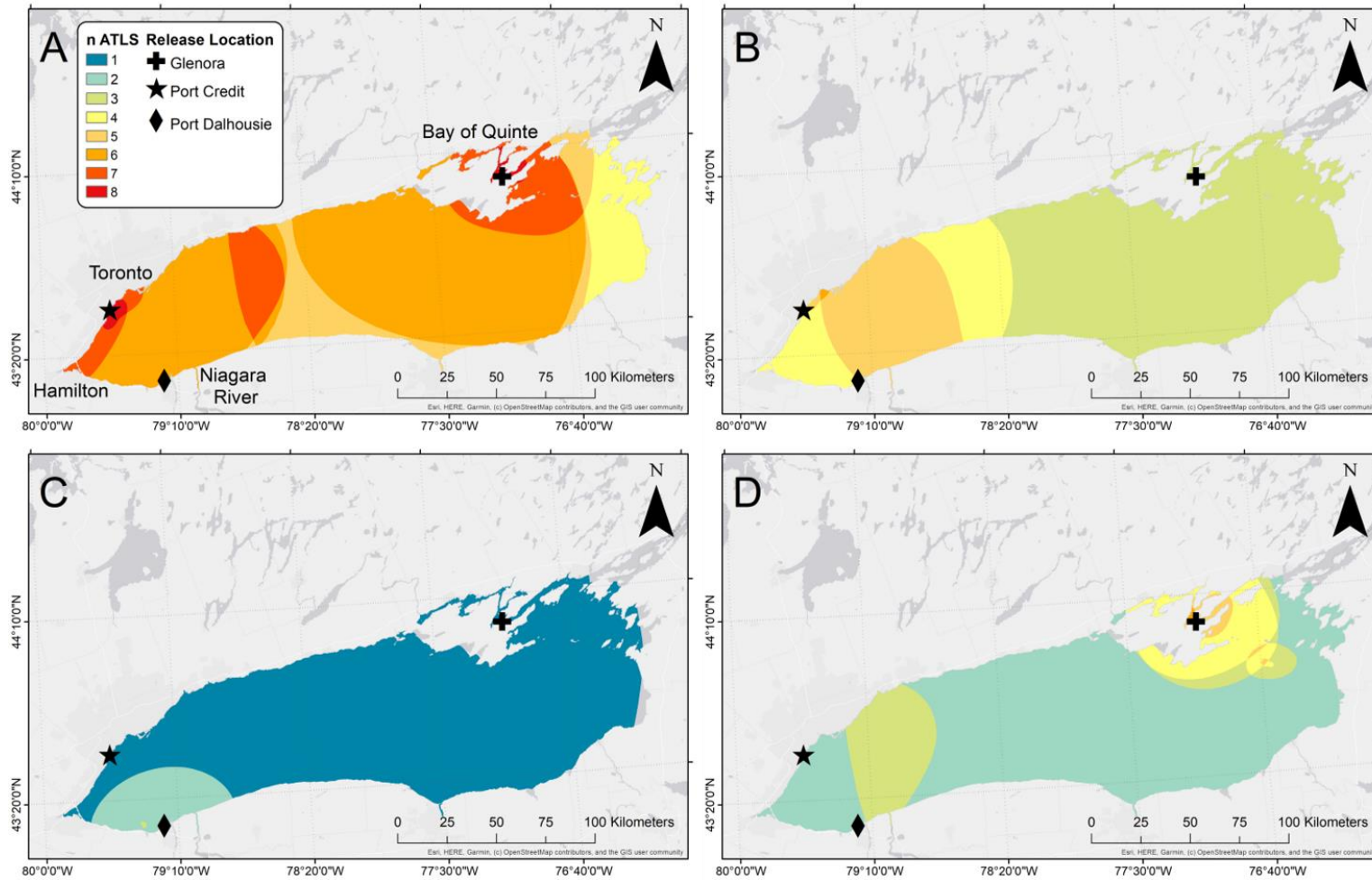
Figure 5.2 Estimated seasonal home ranges (95% autocorrelated kernel density estimation) for Atlantic salmon (ATLS; *Salmo salar*) in A) spring (n = 12), B) summer (n = 6), C) fall (n = 3), and D) winter (n = 9) in Lake Ontario. Warmer colours indicate areas of high use by individuals.
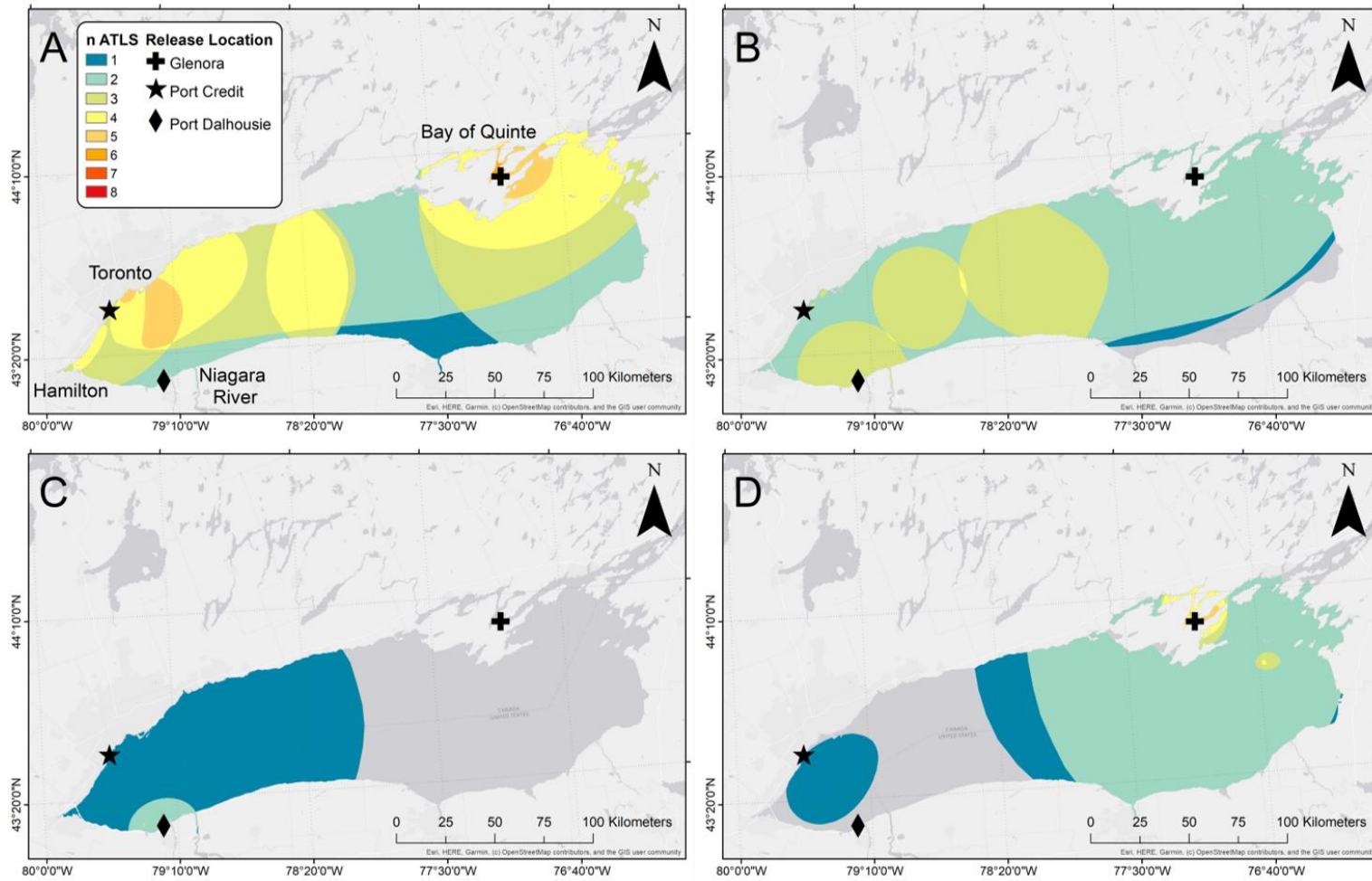
Figure 5.3 Estimated seasonal home ranges (50% autocorrelated kernel density estimation) for Atlantic salmon (ATLS; *Salmo salar*) in A) spring (n = 12), B) summer (n = 6), C) fall (n = 3), and D) winter (n = 9) in Lake Ontario. Warmer colours indicate areas of high use by individuals.
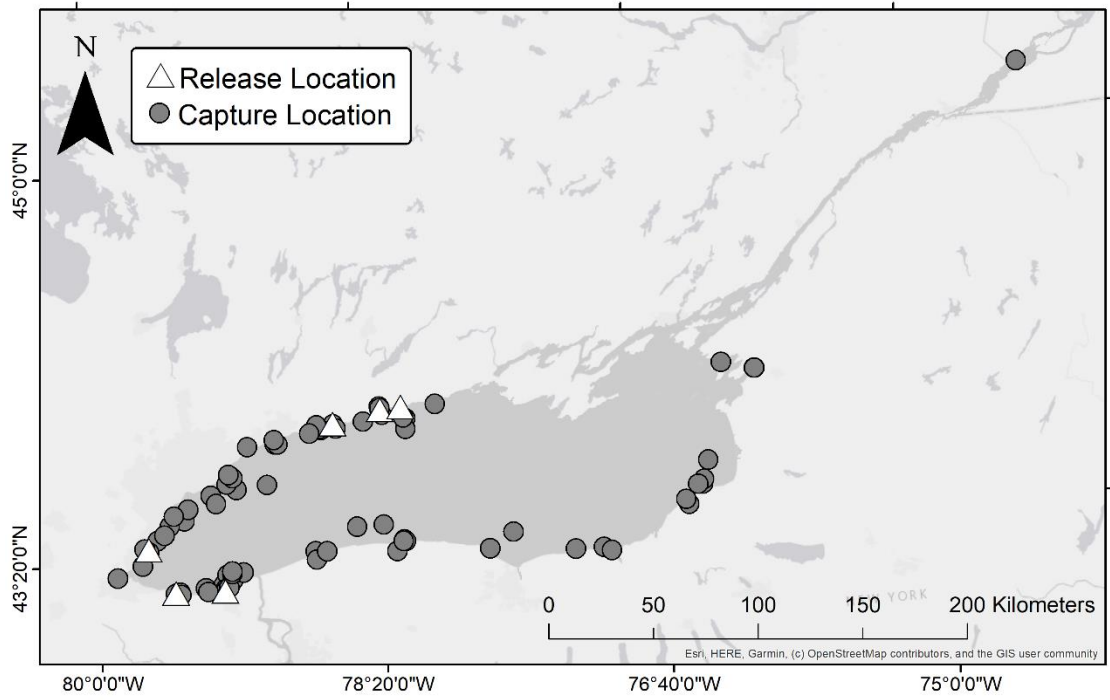
Figure 5.4 Release and capture locations of floy tagged Atlantic salmon (*Salmo salar*) in Lake Ontario, 2018-2020.
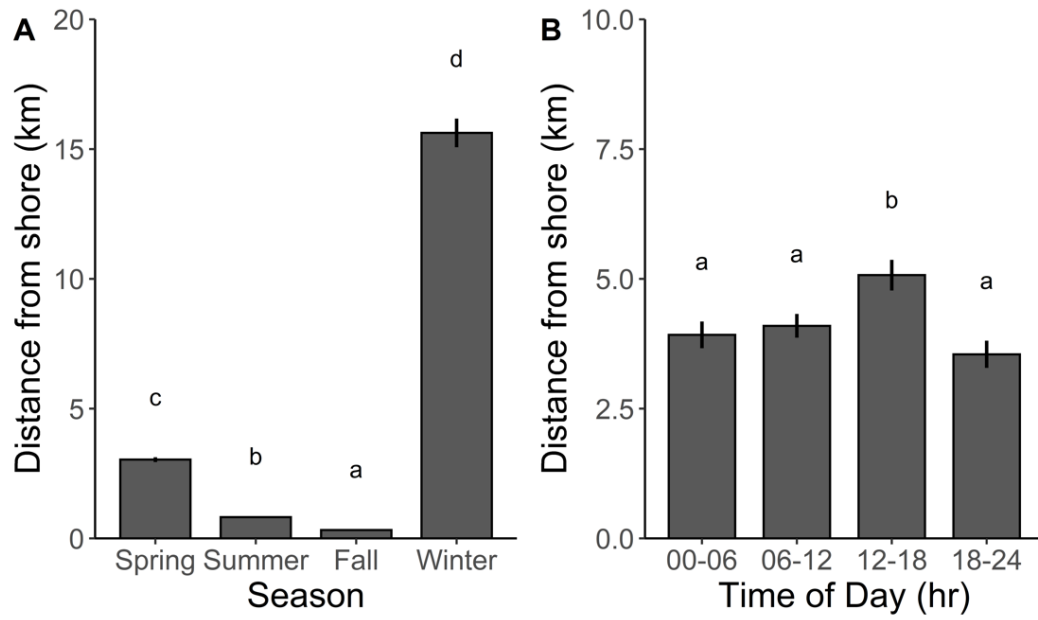
Figure 5.5 Mean (± SE) distance from shore (km) that acoustically tagged Atlantic salmon (*Salmo salar*) were detected across A) seasons and B) time of day in Lake Ontario, 2016-2019.
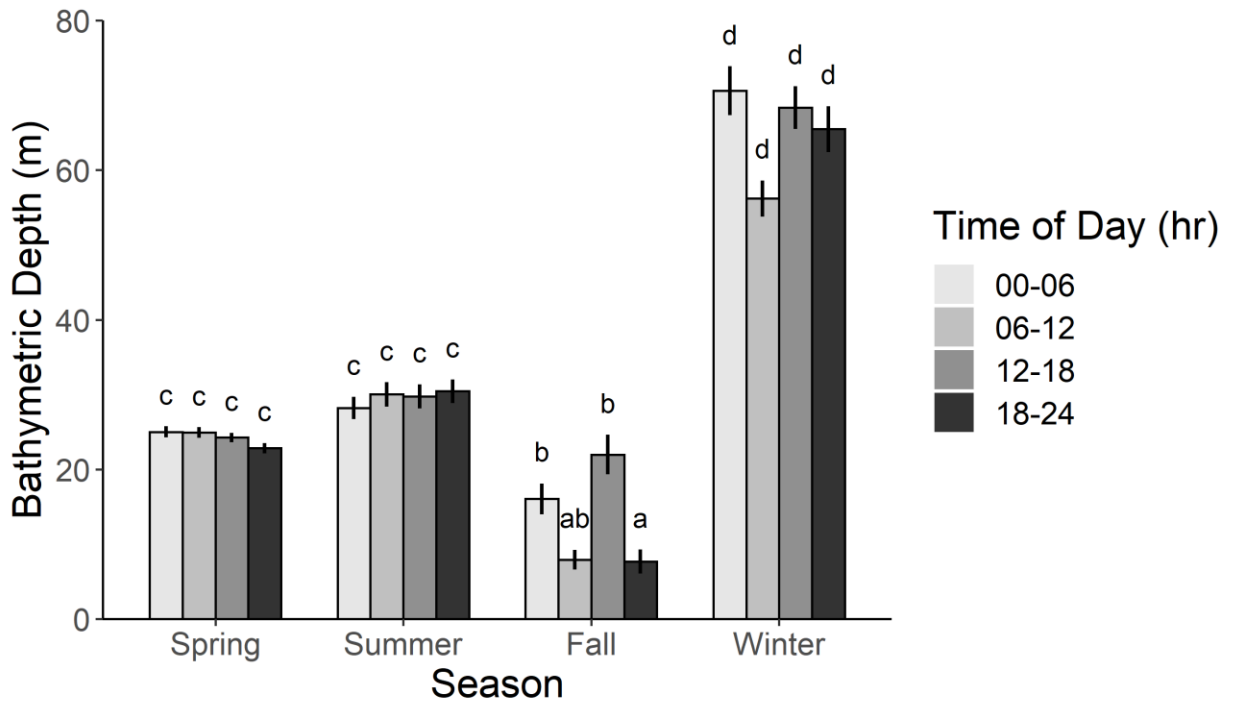
Figure 5.6 Mean (± SE) bathymetric depths (m) that acoustically tagged Atlantic salmon (*Salmo salar*) were detected at by season and time of day in Lake Ontario, 2016-2019.
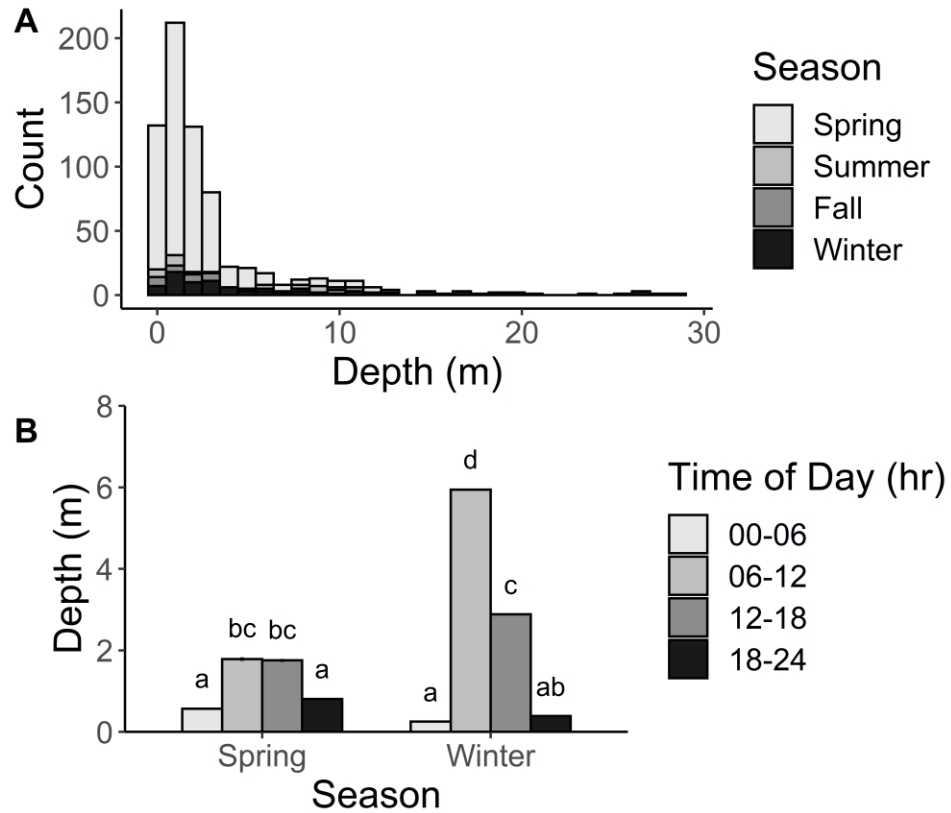
Figure 5.7 Depth use of acoustically tagged Atlantic salmon (*Salmo salar*) in Lake Ontario by A) histogram of depths by season and B) linear mixed model results of the mean ± standard error seasonal and time of day depth use trends. Note: summer and fall were not included in the model due to sample imbalances.

CHAPTER 6 – GENERAL DISCUSSION

6.1 Summary

Species reintroductions are an important aspect of conservation biology to prevent biodiversity loss (Seddon et al. 2007, 2014). Post-release monitoring of species is recognized as an important aspect of species reintroductions (IUCN/SSC 2013), which has resulted in an increasing number of successful reintroductions by monitoring population processes like survival and recruitment and using adaptive management (Ewen and Armstrong 2007; Armstrong and Seddon 2008; Lee and Hughes 2008; Cochran-Biederman et al. 2015). However, by understanding a species' ecological niche within the introduced abiotic and biotic habitat throughout its life history, the mechanisms behind reintroduction success or failure can be better determined, as well as determine where improvements are needed with adaptive management to increase the potential for species restoration.

The goal of this thesis was to evaluate the spatial and trophic niches through ontogeny to reveal the life stages that a species' niche overlaps with that of co-occurring species, have limited resources, or reduced survival, and therefore inform the causal factors contributing to the success or failure of reintroduced species. The reintroduction of Atlantic salmon (*Salmo salar*) in Lake Ontario, one of the Laurentian Great Lakes, was used as a model species to determine the ecological niche at different life stages in order to assess the restoration potential and improve the success of its stocking. The fish community is very different since Atlantic salmon extirpation and there are now many other top-predator salmonids in Lake Ontario, and a different prey base, dominated by alewife (*Alosa pseudoharengus*) which may create greater niche overlap with other species and a smaller realized niche available for Atlantic salmon, reducing the

restoration potential. As such, the various chapters of this thesis investigated the spatial

and trophic niches of Atlantic salmon at different life stages to better understand the

ecological niche of Atlantic salmon and whether it overlaps with the fish community, in

particular salmonids, to ultimately determine the restoration potential and improve

restoration success through adaptive management.

The spatial and trophic niches of Lake Ontario Atlantic salmon were assessed at

various life stages. Chapter 2 of this thesis begins with understanding the seasonal trophic

niche of juvenile Atlantic salmon stocked into streams with different fish communities,

and specifically to determine if trophic interactions and abundances limit restoration

success. Including abundance into quantifying trophic niches and the influence on a

species is novel and provided insight into how trophic niche overlaps may impact a

species. Young-of-year (YOY) brown trout (*Salmo trutta*) could be a strong competitor

by having a high trophic niche overlap with YOY Atlantic salmon but at low abundances

relative to the high stocking density of YOY Atlantic salmon minimizes the impact.

Stream resident fish communities appeared to partition resources across seasons such that

abundant species had low trophic niche overlap to minimize overall competition with

YOY Atlantic salmon given available resources, fitting the niche complementarity

hypothesis, where abundant species have different niches (Mason et al. 2008). A

limitation to the study was not assessing the trophic niches of the streams prior to the

stocking event, as well as using streams that have been previously stocked to show how a

fish community responds to new species as stream communities may already be in an

equilibrium and trophic niches have diverged with Atlantic salmon from previous

stocking activities. Also, monitoring prey availability could have deduced if food were

limiting in the system which would impact competition potential. Overall, this chapter does indicate that in areas currently stocked with YOY Atlantic salmon, the stream fish communities would not have strong, interspecific interactions with Atlantic salmon juveniles influencing survival, and therefore would not negatively affect restoration success.

Chapter 3 of this thesis followed the migration success of Atlantic salmon smolts coming from different rearing environments. Smolt migration is a period of high natural mortality (Klemetsen et al. 2003; Thorstad et al. 2011) and few studies have assessed riverine migratory performance and survival differences in hatchery- and naturally-reared smolts (hatchery fish released earlier as parr), particularly in rivers with weirs which may further reduce survival. Acoustic telemetry revealed that there was similar migratory performance and no impacts from weirs yet different relative survival of hatchery- and naturally-reared smolts. Survival was lowest at the release site indicating pre-migration mortality, and specifically high stocking-related mortality of hatchery-reared smolts. Stress from handling and stocking of fish can cause mortality in salmonids (Specker and Schreck 1980; Schreck et al. 1989) and in this case using acoustic telemetry allowed monitoring of immediate stocking survival. Overall, the actual smolt migration incurred little mortality when stocked either as parr or smolts and was not a limiting factor in Atlantic salmon survival and reintroduction success.

Chapters 4 and 5 of this thesis investigated the trophic and spatial niches of adult Atlantic salmon within the lake environment and compared the results to the salmonid community. All salmonids primarily consumed alewife and exhibited an overlap in trophic niche due to this prey commonality and similarity in stable isotope values and/or

diet estimates. Although there have been recent declines in alewife and greater prevalence of round goby (*Neogobius melanostomus*), the lack of major variation in trophic niches and diets over time compared to previous analyses by Mumby et al. (2018), suggests that alewife is not a limiting resource in Lake Ontario for the current salmonid populations. Some salmonids, including Atlantic salmon, had more variable diets in Lake Huron following alewife collapse (Roseman et al. 2014) and a similar increase in diet variability was not seen here. Thus, due to the abundance of alewife, the trophic niche overlap among salmonids would not necessarily infer strong competition with Atlantic salmon and impact Atlantic salmon restoration potential. However, thiamine-deficiency linked to the high consumption of alewife by Atlantic salmon could influence the restoration success (Ketola et al. 2000; Madenjian et al. 2008). Furthermore, it appears that Atlantic salmon may be foraging in and using slightly different habitats than the other salmonids, irrespective of consuming similar prey, thus limiting the spatial niche overlap within Lake Ontario. The nearshore, shallow depth use of Atlantic salmon may overlap with other salmonids during the spring, otherwise, all salmonids use slightly different depths and distances from shore from one another. Overall, by combining the trophic and spatial niches of adult Atlantic salmon in the lake there would be less overlap and competition with the other salmonids in Lake Ontario than by assessing individual niche axes separately, and therefore, not greatly influencing Atlantic salmon survival and restoration.

6.2 Implications and future research

Based on the collective research in this thesis, there were no major ecological niche overlaps with other salmonids, limited resources, or reduced survival throughout

the life history of Atlantic salmon, from juveniles and smolts in the river to adults in the lake. This thesis has increased our understanding of land-locked Atlantic salmon in Lake Ontario, and how they interact with the surrounding biotic community and environment. Although no clear patterns or limitations to Atlantic salmon restoration were found with regards to ecological niche overlap among the top-predator, salmonid species, there were a few implications revealed by this research that warrant further investigation and consideration by management. Also, other perspectives related to invasion ecology may provide insight into additional factors that may improve restoration potential of Atlantic salmon.

Stocking stresses potentially led to increased mortality of Atlantic salmon smolts and adults. In both smolts and adults, there was indication of stocking-related mortality by monitoring their movements with acoustic telemetry. Although, the mortality of excess broodstock adults is not of major management concern as it is a rarely stocked life stage, the mortality associated with smolt stocking could potentially be reduced to improve Atlantic salmon restoration. Salmonids have variable but high mortality rates associated with early life stages, in which hatcheries can improve that initial survival, bypassing natural mortality. There will still be some mortality upon stocking, although post-release mortality decreases with the stocking of later life stages and larger fish (Brown and Day 2002). For example, stocked Atlantic salmon embryos had as low as 0.01% survival, while fry ranged up to 8% with a mean of 2% survival, and parr had up to 66% survival in Lake Ontario tributaries (Coghlan and Ringler 2004; Coghlan et al. 2007). In Chapter 3, the hatchery-reared smolts had a mean survival of 26% from release through migration which appears uncharacteristically low as a later life stage. Atlantic

salmon smolts from other acoustic telemetry tagging studies have incurred high mortality post-stocking, not related to the actual tagging event (Holbrook et al. 2011; Thorstad et al. 2012; Huusko et al. 2018). Various reasons could be related to the increased mortality; however, stocking stresses appear at the forefront. Future studies should assess stress and mortality of Atlantic salmon related to transport and handling, including water quality, temperature and fish densities, which can all increase stress upon stocking (Portz et al. 2006).

The consumption of alewife as a dominant prey item for adult Atlantic salmon can result in a thiamine (vitamin B_1) deficiency and indirectly impact Atlantic salmon populations (Ketola et al. 2000; Madenjian et al. 2008). Thiamine levels are passed on from maternal tissues to embryonic tissues. Low thiamine levels in salmonid eggs can lead to early mortality syndrome (EMS), in which early life stages have reduced survival, and in some cases 100% mortality of Atlantic salmon fry (Fisher et al. 1996; Fitzsimons et al. 1999). Atlantic salmon appear to be more prone to reduced survival from EMS than other Great Lakes salmonids (Fisher et al. 1996; Fitzsimons et al. 1999; Ladago et al. 2020). Thus, Atlantic salmon population recruitment may potentially be reduced from consuming primarily alewife. Future research should investigate the thiamine levels in adult Atlantic salmon of Lake Ontario to determine if thiamine deficiency is a limiting factor in the restoration success of this species.

Accessibility to spawning grounds and successful spawning also influences recruitment in Atlantic salmon. Spawning was the one life stage that was not investigated in this thesis. Dams and other barriers have been constructed on Great Lakes tributaries since European settlement. With the salmonids in the Great Lakes, there are various

fishways to promote fish passage (Hatry et al. 2013). However, few fishways have been evaluated for fish passage (Hatry et al. 2013). Using telemetry (e.g., passive integrated transponder (PIT); acoustic) technology, fish passage can be evaluated and potentially modified and improved (e.g., Pratt et al. 2009). Also, other salmonids are migrating upstream in the fall with Atlantic salmon, as seen at fishway monitoring sites (OMNRF 2019). Differences in population sizes, body size, or aggression levels may prevent species that may be in lower abundance, smaller or less aggressive, like Atlantic salmon, to effectively pass. Future research should investigate fish passage efficiency amongst salmonids in key spawning tributaries of Lake Ontario. Furthermore, once successfully reaching spawning grounds, it is important to determine whether Atlantic salmon can successfully spawn with other salmonids around. In Lake Ontario tributaries, interspecific interactions with Atlantic salmon can reduce successful spawning, particularly in the presence of Chinook salmon (*Oncorhychus tshawytscha*; Scott et al. 2003, 2005). Future research determining Atlantic salmon spawning success through egg thiamine deficiency, fish passage, and interspecific interactions at the spawning grounds would fill in knowledge gaps for understanding Atlantic salmon restoration potential beyond aspects covered in specific chapters of this thesis.

Other perspectives and disciplines, such as with invasion ecology that focuses on preventing non-native species establishment, may alternatively be used to improve reintroduction success. For example, like non-native species establishments, species reintroductions may also be influenced by propagule pressure and priority effects. Propagule pressure is a concept related to the establishment success of non-native species being positively correlated to the density of individuals introduced, the number of

introduction events, and the frequency of introductions (Kolar and Lodge 2001). Specifically, non-native introduced salmonids that successfully established were stocked more often and in greater numbers than those that failed to establish (Colautti 2005). Thus, with Lake Ontario Atlantic salmon, the continued stocking and/or increased amount of stocking may, over time, translate into improved returns and establishment. Another aspect to consider is the priority effect in which the effect of species on one another depends on the order in which they arrive at a site (Alford and Wilbur 1985). For example, invasive plant species were more likely to competitively dominate an area and reduce biodiversity if planted before native species (Dickson et al. 2012). Similarly, survival of a coral reef fish was greater when arrival was before competitors, yet habitat complexity further increased survival, regardless of arrival time (Geange and Stier 2010). There may be merit in determining if Atlantic salmon juveniles benefit from being stocked in streams without other salmonid competitors, due to priority effects. However, in Lake Ontario other salmonids are already present, and it would be difficult to test if priority effects influenced survival of adult Atlantic salmon in the lake itself. Using ideas from invasive ecology provides some additional insights and reinforces that taking a multi-disciplinary approach, like assessing different axes of ecological niches as done in this thesis, can reveal patterns and potential aspects to consider with assessing restoration potential.

6.2 Conclusion

In this thesis, through the use of acoustic telemetry and stable isotopes, the ecology of Atlantic salmon in Lake Ontario and its tributaries was further understood, with a focus on determining the spatial and trophic niches amongst other top-predator,

salmonids. Observing juveniles and smolts in rivers and adults in lake environments, across these different life stages, it was determined that there were no major limitations to restoration success in the areas assessed. However, by assessing the ecological niche of a reintroduced species among potential competitors, it has aided in understanding restoration potential for a few reasons. This research has revealed aspects of land-locked Atlantic salmon ecology that were previously unknown which can assist in other Atlantic salmon stocking programs world-wide. Although no direct impediments to restoration success were revealed, this research has led to a few indirect aspects that could affect success and revealed potential restoration limitations (e.g., stocking related survival, thiamine deficiency, spawning success) for future research. Also, there is a greater understanding of the salmonid community, in both river and lake environments from this research which can aid in Great Lakes fisheries management of multiple species.

Using both acoustic telemetry and stable isotopes helped determine longer-term patterns within niche space. Acoustic telemetry can monitor the movements and survival of an individual, providing information on stocking survival, habitat use, migration timing, among other topics that can be of benefit for fisheries management (Thorstad et al. 2007; Binder et al. 2017; Crossin et al. 2017; Klinard et al. 2020). Determining fish movements and habitat use of a species in low abundance (e.g., a species at risk, reintroduced, or naturally rare) can be difficult using estimates from minimal captures whereas acoustic telemetry can track those few individuals and provide quality data. Acoustic telemetry also revealed fine-scale details on the movement patterns of Atlantic salmon in a large lake that has not been previously determined. Stable isotope analysis was a useful tool to understand the general diet and trophic niche space of a species,

relative to stomach contents (Peterson and Fry 1987; Vander Zanden et al. 2015). Using

fin tissue, allowed for non-lethal sampling, particularly of juveniles, which is important

in studies with repeated seasonal sampling but also for low abundance species to have

minimal impact on their populations (e.g., Hette-Tronquart et al. 2012; Graham et al.

2013). Together, acoustic telemetry and stable isotope analyses improved the

understanding of the spatial and trophic niches of land-locked Atlantic salmon and their

restoration potential in Lake Ontario.

Overall, this thesis supports the idea that by understanding the ecological niches

of reintroduced species within the abiotic and biotic habitat, in combination with

monitoring, can determine restoration limitations (or lack thereof), understand why

reintroductions may succeed or fail, and assist in species restoration through adaptive

management to increase restoration success. This approach can be useful beyond Atlantic

salmon restoration in Lake Ontario but with other reintroduction projects, particularly if

restoration success has been difficult to acquire, or there has been little post-release

monitoring. Researching different aspects of a species' ecological niche, like its trophic

and spatial niches at various life stages, provides management with information to

increase the potential for reintroduction success, such that ultimately, reintroductions may

be a more effective tool towards species conservation and increasing biodiversity.

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APPENDICES

Appendix 1 Site characteristics and electrofishing effort for each seasonal sampling event in the three study streams of Lake Ontario.

Location	Potential Competitors	Species-life stage Richness	Season	Water Temperature (°C)	Site Length (m)	Stream Width (m)	Stream Depth (m)	Water Velocity (m/s)	Total Electrofishing Seconds
Cobourg Brook	3	7	Spring	13.5	285	5	0.4	0.89	3665
			Summer	15.5	285	6	0.3	0.79	3335
			Fall	7.7	285	5.5	0.25	0.95	2588
			Overwinter	0.6	285	5.5	0.3	0.72	3352
Credit River	2	8	Spring	14.4	350	13	0.4	1.04	4973
			Summer	16.8	350	13	0.3	1.03	4625
			Fall	10.4	350	10	0.3	0.74	2966
			Overwinter	2.5	350	9	0.3	0.96	3903
Duffins Creek	0	7	Spring	14.8	175	6	0.4	0.85	2865
			Summer	17.2	175	5	0.3	0.77	1863
			Fall	10.3	175	4.5	0.2	0.78	1778
			Overwinter	1.2	175	5.5	0.25	0.72	2196

Appendix 2 Cluster analyses methods and results

To identify any spatial, seasonal, or species patterns in the isotopes, Ward's method of hierarchical clustering was used on the stable isotopes using Euclidean distances between samples (Ward, 1963). The optimal number of clusters was determined based on the majority of the results of 30 indices using NbClust (Charrad et al., 2014) package in R. This approach created clusters of samples with similar patterns of isotopic values which were plotted against season, stream and species to visualize any distinctive patterns.

Cluster analyses indicated that the optimal number of clusters with the isotope data was three (Figure S1a). When clusters were plotted against season, stream, and species-life stages, some patterns emerged (Figure S1b-d). Cluster 1 represented Atlantic salmon YOY in the spring in all streams including the hatchery, as was represented by the separated ellipses from the rest of the fish community in spring for all streams (Figure 2.3). Cluster 2 represented samples from the Credit River, in all seasons and all species (except spring Atlantic salmon YOY), while Cluster 3 represented Cobourg and Duffins in all seasons and for all species (except spring Atlantic salmon YOY). Samples from the Credit River generally had a higher δ^{15}N (Figure S1b; Appendix 3). Although Cobourg and Duffins were not split into separate clusters, the Duffins Creek community had slightly lower δ^{13}C values than Cobourg Brook (Figure S1b; Appendix 3).
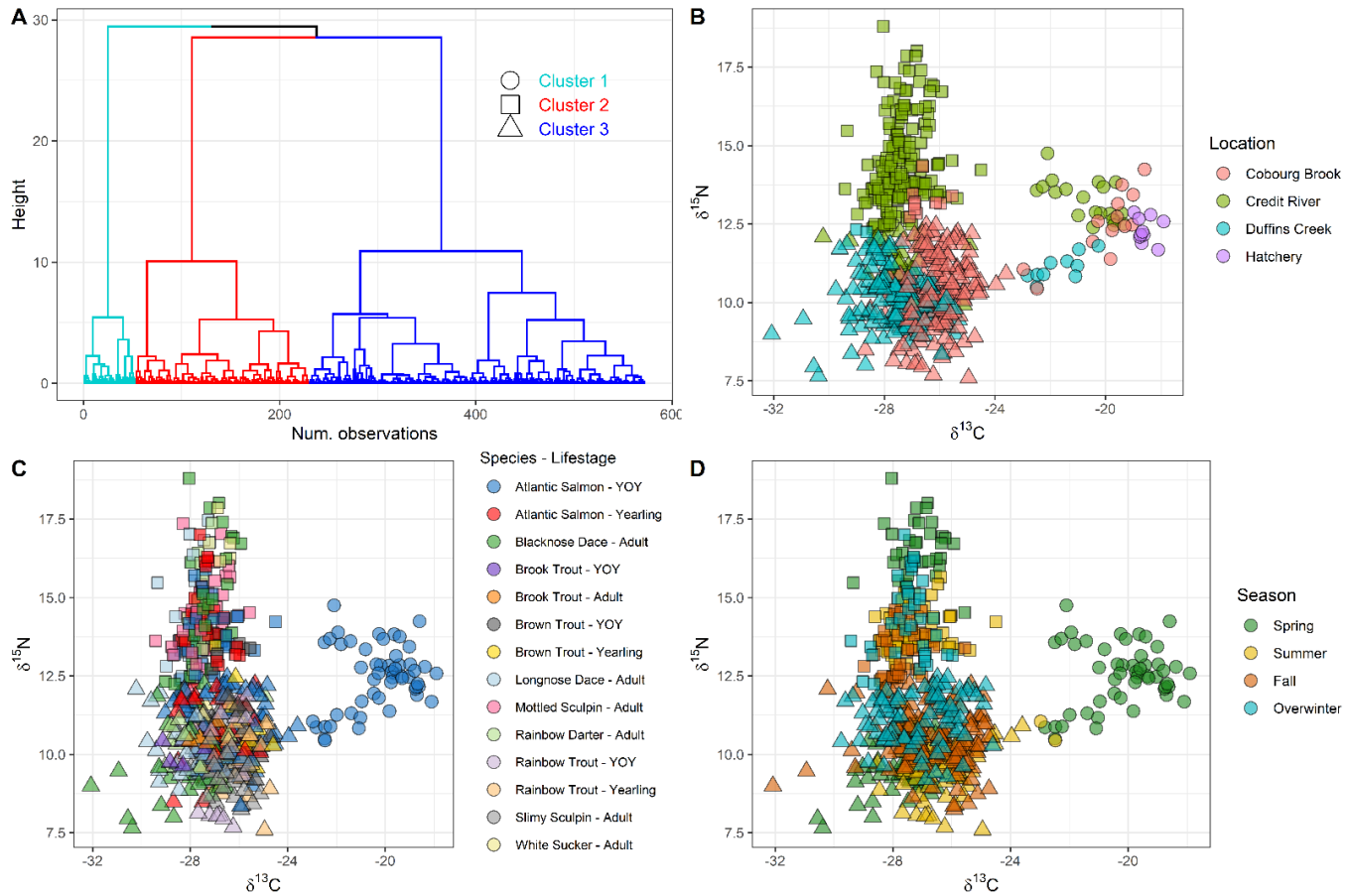
Figure S1 Hierarchical cluster analyses of all stable isotope samples with cluster dendrogram and resulting clusters (shapes) (A), plotted against sample location (B), species-life stage (C), and season (D).

Appendix 3 The number of stream fishes captured and sampled (n), mean (± SD) fork length (FL), stable isotope ratios, C:N ratio, standard ellipse area (SEAc), and proportion of Atlantic salmon young-of-year (YOY) (ATL) isotopic niche overlap on species-life stages (SL) within a location and season (and vice versa) for each species-life stage and overall totals (bolded) by location and season in Lake Ontario. Any overlaps that are ≥ 0.5 are italicized to emphasize as a strong interaction (see Figure 2.1). CB = Cobourg Brook, CR = Credit River, DC = Duffins Creek, ND = Normandale Fish Culture Station.

Location	Season	Species	Life stage	Caught	n	FL (mm)	δ¹³C	δ¹⁵N	C:N	SEAc	ATL over SL	SL over ATL
CB	Spring	Atlantic Salmon	YOY	199	11	74 ± 6	-19.5 ± 0.6	12.8 ± 0.8	3.8 ± 0.2	1.17	-	-
		Atlantic Salmon	Yearling	45	12	106 ± 13	-27.4 ± 0.6	9.5 ± 0.6	3.6 ± 0.1	1.17	-	-
		Rainbow Trout	Yearling	7	7	100 ± 11	-27.0± 0.2	9.2 ± 0.3	3.6 ± 0.1	0.16	-	-
		Slimy Sculpin	Adult	170	10	68 ± 13	-27.2 ± 0.4	10.0 ± 0.6	3.7 ± 0.1	0.88	-	-
			Total	**421**	**40**	**-**	**-25.1 ± 3.5**	**10.5 ± 1.6**	**3.7 ± 0.1**	**0.84**	**-**	**-**
CB	Summer	Atlantic Salmon	YOY	149	10	96 ± 7	-24.4 ± 1.1	10.4 ± 0.5	3.5 ± 0.1	1.42	-	-
		Atlantic Salmon	Yearling	10	10	135 ± 11	-26.5 ± 0.6	10.3 ± 0.3	3.5 ± 0.0	0.63	0.00	0.00
		Rainbow Trout	YOY	6	6	61 ± 6	-26.9 ± 0.5	8.0 ± 0.2	3.6 ± 0.1	0.15	0.00	0.00
		Rainbow Trout	Yearling	8	8	126 ± 17	-25.8 ± 0.5	9.2 ± 0.7	3.5 ± 0.0	0.71	0.00	0.00
		Slimy Sculpin	Adult	179	10	74 ± 15	-26.5 ± 0.6	9.4 ± 0.8	3.6 ± 0.1	1.52	0.00	0.00
			Total	**352**	**44**	**-**	**-26.0 ± 1.2**	**9.6 ± 1.0**	**3.5 ± 0.1**	**0.89**	**0.00**	**0.00**
CB	Fall	Atlantic Salmon	YOY	181	14	107 ± 10	-25.9 ± 0.8	10.9 ± 0.4	3.5 ± 0.1	0.93	-	-
		Atlantic Salmon	Yearling	19	8	142 ± 9	-26.0 ± 0.7	11.3 ± 0.7	3.5 ± 0.1	1.85	0.42	*0.84*
		Brown Trout	YOY	12	8	88 ± 12	-25.5 ± 0.4	10.6 ± 1.3	3.6 ± 0.1	1.99	0.24	*0.51*
		Brown Trout	Yearling	5	5	163 ± 19	-25.7 ± 0.5	10.2 ± 0.5	3.5 ± 0.1	0.98	0.03	0.03
		Rainbow Trout	YOY	14	6	90 ± 8	-26.3 ± 0.8	10.4 ± 0.9	3.6 ± 0.0	2.64	0.21	*0.61*
		Rainbow Trout	Yearling	10	10	156 ± 9	-25.4 ± 0.5	10.1 ± 0.6	3.4 ± 0.1	1.01	0.02	0.02
		Slimy Sculpin	Adult	64	9	74 ± 15	-26.5 ± 1.0	9.2 ± 0.9	3.7 ± 0.1	2.29	0.00	0.00
			Total	**305**	**60**	**-**	**-25.9 ± 0.8**	**10.4 ± 1.0**	**3.5 ± 0.1**	**1.67**	**0.15**	**0.33**
CB	Winter	Atlantic Salmon	YOY	61	17	105 ± 12	-26.0 ± 0.7	12.2 ± 0.6	3.5 ± 0.1	1.46	-	-
		Atlantic Salmon	Yearling	6	5	139 ± 11	-26.6 ± 0.5	12.9 ± 0.4	3.5 ± 0.1	0.59	0.12	0.05
		Brown Trout	YOY	11	8	82 ± 11	-26.4 ± 0.6	12.0 ± 0.9	3.7 ± 0.1	0.67	*0.63*	0.29

Location	Season	Species	Life stage	Caught	n	FL (mm)	$\delta^{13}C$	$\delta^{15}N$	C:N	SEAc	ATL over SL	SL over ATL
CB	Winter	Brown Trout	Yearling	5	5	161 ± 24	-26.0 ± 0.9	11.8 ± 1.2	3.5 ± 0.1	2.00	0.46	*0.63*
		Rainbow Trout	YOY	6	6	111 ± 19	-26.3 ± 0.6	11.3 ± 0.4	3.6 ± 0.1	0.88	0.17	0.10
		Rainbow Trout	Yearling	5	5	158 ± 8	-26.1 ± 0.4	10.9 ± 0.5	3.5 ± 0.1	0.65	0.00	0.00
		Slimy Sculpin	Adult	13	9	83 ± 11	-26.6 ± 0.5	9.8 ± 0.4	3.7 ± 0.1	0.76	0.00	0.00
			Total	**107**	**55**	**-**	**-26.2 ± 0.6**	**11.6 ± 1.1**	**3.6 ± 0.1**	**1.00**	**0.23**	**0.18**
CR	Spring	Atlantic Salmon	YOY	200	20	67 ± 5	-20.6 ± 1.0	13.2 ± 0.6	3.7 ± 0.2	1.68	-	-
		Blacknose Dace	Adult	24	10	74 ± 14	-26.9 ± 0.7	17.0 ± 1.0	3.7 ± 0.1	2.65	-	-
		Longnose Dace	Adult	21	7	66 ± 22	-27.8 ± 0.7	16.5 ± 0.7	3.7 ± 0.1	1.49	-	-
		Mottled Sculpin	Adult	88	8	59 ± 15	-26.9 ± 0.8	16.1 ± 0.9	3.7 ± 0.2	1.95	-	-
		Rainbow Darter	Adult	7	5	63 ± 9	-27.5 ± 0.2	16.1 ± 0.9	3.7 ± 0.1	0.60	-	-
		White Sucker	Adult	6	5	62 ± 39	-26.7 ± 0.4	16.7 ± 0.7	3.7 ± 0.1	0.99	-	-
			Total	**346**	**55**	**-**	**-24.8 ± 3.3**	**15.3 ± 1.8**	**3.7 ± 0.2**	**1.56**	-	-
CR	Summer	Atlantic Salmon	YOY	69	20	88 ± 11	-27.0 ± 1.0	13.6 ± 0.5	3.6 ± 0.2	1.29	-	-
		Atlantic Salmon	Yearling	5	5	133 ± 11	-26.9 ± 0.6	14.2 ± 0.5	3.5 ± 0.1	0.91	0.29	0.20
		Blacknose Dace	Adult	42	10	71 ± 10	-27.1 ± 0.6	13.6 ± 1.0	3.8 ± 0.1	1.62	0.49	*0.61*
		Brown Trout	YOY	21	10	68 ± 5	-26.9 ± 1.1	13.1 ± 1.2	3.7 ± 0.1	3.71	0.28	*0.80*
		Longnose Dace	Adult	82	10	84 ± 14	-28.0 ± 0.3	13.5 ± 0.7	3.8 ± 0.1	0.81	0.19	0.12
		Mottled Sculpin	Adult	180	10	71 ± 4	-27.2 ± 0.7	14.6 ± 0.7	3.7 ± 0.1	1.65	0.00	0.00
		Rainbow Darter	Adult	28	9	54 ± 9	-27.6 ± 0.4	14.0 ± 0.6	3.7 ± 0.1	0.68	0.24	0.13
			Total	**427**	**74**	**-**	**-27.2 ± 0.9**	**13.7 ± 0.8**	**3.7 ± 0.2**	**1.52**	**0.25**	**0.31**
CR	Fall	Atlantic Salmon	YOY	132	10	107 ± 12	-27.6 ± 0.7	12.7 ± 0.5	3.5 ± 0.1	1.19	-	-
		Atlantic Salmon	Yearling	26	10	152 ± 8	-27.6 ± 0.5	13.9 ± 0.7	3.5 ± 0.1	1.13	0.00	0.00
		Blacknose Dace	Adult	12	5	78 ± 9	-27.7 ± 0.3	12.6 ± 0.8	4.2 ± 0.3	1.14	*0.62*	*0.59*
		Brown Trout	YOY	8	7	106 ± 12	-27.4 ± 0.8	11.4 ± 0.4	3.6 ± 0.1	1.27	0.00	0.00
		Longnose Dace	Adult	10	5	96 ± 17	-29.0 ± 0.8	12.0 ± 0.9	3.8 ± 0.0	2.73	0.00	0.00
		Mottled Sculpin	Adult	119	10	79 ± 10	-27.8 ± 0.3	12.8 ± 1.3	3.5 ± 0.1	1.31	0.40	0.43
		Rainbow Darter	Adult	10	5	61 ± 6	-27.3 ± 1.4	12.5 ± 0.6	4.3 ± 0.7	3.21	0.37	*1.00*
CR	Fall	White Sucker	Adult	8	5	151 ± 28	-27.2 ± 0.4	11.1 ± 0.7	3.7 ± 0.1	1.11	0.00	0.00

Location	Season	Species	Life stage	Caught	n	FL (mm)	δ¹³C	δ¹⁵N	C:N	SEAc	ATL over SL	SL over ATL
			Total	**325**	**57**	**-**	**-27.7 ± 0.8**	**12.5 ± 1.1**	**3.7 ± 0.4**	**1.64**	**0.20**	**0.29**
CR	Winter	Atlantic Salmon	YOY	59	9	117 ± 10	-27.4 ± 0.5	14.9 ± 0.7	3.5 ± 0.1	1.18	-	-
		Atlantic Salmon	Yearling	6	6	143 ± 15	-27.5 ± 0.2	16.1 ± 0.7	3.5 ± 0.1	0.50	0.13	0.05
		Blacknose Dace	Adult	6	5	72 ± 7	-27.3 ± 0.2	14.7 ± 0.4	4.0 ± 0.1	0.26	*1.00*	0.22
		Mottled Sculpin	Adult	6	6	76 ± 16	-28.2 ± 0.9	13.8 ± 0.9	3.1 ± 0.9	2.19	0.13	0.25
			Total	**77**	**26**	**-**	**-27.6 ± 0.6**	**14.9 ± 1.0**	**3.5 ± 0.5**	**1.03**	**0.42**	**0.18**
DC	Spring	Atlantic Salmon	YOY	108	10	56 ± 5	-21.7 ± 0.8	11.1 ± 0.4	3.9 ± 0.1	0.78	-	-
		Atlantic Salmon	Yearling	5	5	116 ± 10	-27.6 ± 0.1	10.0 ± 0.5	3.6 ± 0.0	0.16	-	-
		Blacknose Dace	Adult	79	12	59 ± 11	-28.4 ± 1.2	8.9 ± 0.8	5.0 ± 0.4	2.50	-	-
		Brook Trout	Adult	5	5	205 ± 20	-26.0 ± 0.4	9.9 ± 0.6	3.5 ± 0.0	0.84	-	-
		Longnose Dace	Adult	97	10	55 ± 17	-28.0 ± 0.8	9.5 ± 0.3	3.9 ± 0.1	0.72	-	-
		Rainbow Darter	Adult	30	11	53 ± 8	-27.9 ± 0.6	10.5 ± 0.4	3.5 ± 0.1	0.73	-	-
			Total	**324**	**53**	**-**	**-26.6 ± 2.6**	**10.0 ± 0.9**	**4.0 ± 0.6**	**0.96**	**-**	**-**
DC	Summer	Atlantic Salmon	YOY	34	10	73 ± 6	-26.2 ± 0.8	9.6 ± 0.3	3.6 ± 0.1	0.85	-	-
		Blacknose Dace	Adult	47	5	61 ± 11	-27.1 ± 0.3	9.2 ± 0.5	3.8 ± 0.1	0.73	0.09	0.07
		Longnose Dace	Adult	133	5	77 ± 16	-27.7 ± 0.8	9.4 ± 0.3	4.0 ± 0.2	1.08	0.04	0.05
		Rainbow Darter	Adult	80	5	55 ± 3	-27.0 ± 0.2	9.8 ± 0.4	3.6 ± 0.1	0.35	0.28	0.11
			Total	**294**	**25**	**-**	**-26.8 ± 0.8**	**9.5 ± 0.4**	**3.7 ± 0.2**	**0.75**	**0.13**	**0.08**
DC	Fall	Atlantic Salmon	YOY	83	11	96 ± 9	-26.7 ± 0.8	9.9 ± 0.6	3.6 ± 0.1	1.53	-	-
		Atlantic Salmon	Yearling	7	7	144 ± 8	-26.7 ± 0.6	10.4 ± 0.3	3.5 ± 0.1	0.62	0.36	0.15
		Blacknose Dace	Adult	26	5	70 ± 3	-29.3 ± 2.3	9.7 ± 0.6	3.7 ± 0.1	1.06	0.12	0.08
		Longnose Dace	Adult	56	5	65 ± 4	-28.2 ± 0.8	10.0 ± 0.3	3.7 ± 0.1	0.86	0.08	0.05
		Rainbow Darter	Adult	38	5	62 ± 6	-27.2 ± 0.7	10.2 ± 0.5	3.7 ± 0.1	1.31	*0.51*	0.44
			Total	**210**	**33**	**-**	**-27.4 ± 1.4**	**10.0 ± 0.5**	**3.6 ± 0.1**	**1.07**	**0.27**	**0.18**
DC	Winter	Atlantic Salmon	YOY	35	10	91 ± 6	-28.2 ± 0.4	11.6 ± 0.3	3.6 ± 0.1	0.44	-	-
		Atlantic Salmon	Yearling	5	5	142 ± 7	-28.2 ± 0.3	11.7 ± 0.2	3.6 ± 0.0	0.18	*0.92*	0.37
DC	Winter	Blacknose Dace	Adult	29	5	68 ± 6	-28.8 ± 0.5	11.6 ± 0.7	3.9 ± 0.1	1.33	0.15	0.44
		Brook Trout	YOY	6	6	105 ± 24	-29.8 ± 3.5	9.8 ± 0.7	3.7 ± 0.1	1.04	0.00	0.00

Location	Season	Species	Life stage	Caught	n	FL (mm)	δ^{13}C	δ^{15}N	C:N	SEAc	ATL over SL	SL over ATL
		Brook Trout	Adult	5	5	201 ± 23	-27.4 ± 0.4	10.6 ± 0.3	3.5 ± 0.1	0.35	0.00	0.00
		Longnose Dace	Adult	15	5	67 ± 5	-28.8 ± 0.9	10.9 ± 0.6	3.8 ± 0.1	2.01	0.04	0.18
		Rainbow Darter	Adult	6	5	55 ± 6	-28.2 ± 0.4	10.8 ± 0.2	3.8 ± 0.1	0.29	0.00	0.00
			Total	**101**	**41**	**-**	**-28.5 ± 1.5**	**11.0 ± 0.8**	**3.7 ± 0.1**	**0.81**	**0.18**	**0.17**
ND	Spring	Atlantic Salmon	YOY	-	10	67 ± 7	-18.6 ± 0.3	12.3 ± 0.4	3.7 ± 0.1	0.41	-	-

Appendix 4 The distance in river kilometers (rkm) from the release point (0 rkm) in the Credit River to Lake Ontario (75 rkm) of all receiver sites, weirs, and range test sites in the study from Chapter 3, the number of receivers per site, as well as any notes pertaining to inclusion of sites for analyses.

Rkm	# of receivers	Notes
0	9	Combined receivers for "start" site
3.5	1	
4.5	1	
9	1	
11.6	1	
26	1	
34.8	1	Poor detection; removed from analyses
35	0	Norval Weir
35.2	1	Tampered with and poor detection; removed from analyses
43.7	1	
46.5	1	
46.5	0	Range test location
58.7	1	
60	0	Streetsville Weir
60.4	1	Stolen 1 year, tampered with and poor detection; removed from analyses
66.2	1	
71.5	1	
74.5	0	Range test location
75	5	Combined receivers for "end" site; includes river mouth receivers in the lake

Appendix 5 An example matrix plot of estimates of each prey proportions calculated in the muscle three isotope mixing model for Chinook salmon from the MixSIAR package output, represented by simulated values of the dietary proportions in the histograms (proportion in both axes). Correlation values between sources are inside the boxes to the left of histograms, with font size increasing from weak to strong correlation. Sources close to each other resulted in strong, negative correlations (alewife vs. *Mysis diluviana*).
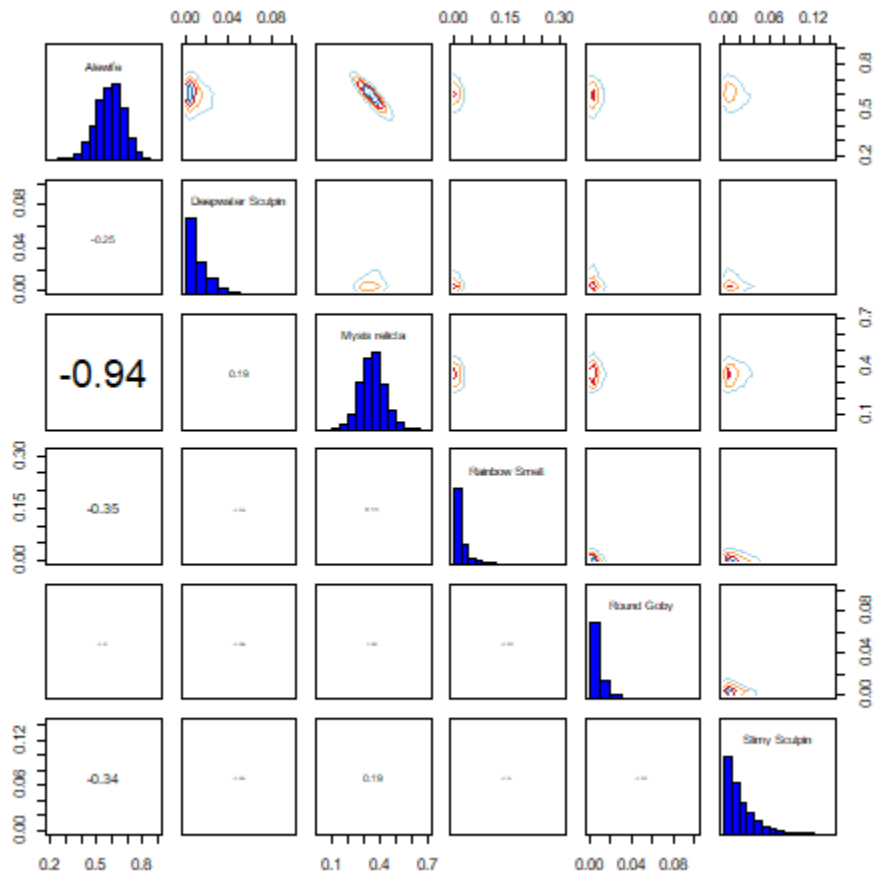
Appendix 6 Summary of the total length (mm), sample size (n), isotope values (mean ± SD ‰), and the standard ellipse volume (40% SEV; ‰^{3}) of fin and lipid corrected muscle across different spatial regions for six salmonid species from Lake Ontario 2018. Note: SEV calculations for species with low sample sizes did not always converge and is designated with NA.

Tissue	Species	Region	n	Length	δ^{13}C	δ^{15}N	δ^{34}S	SEV
Fin	Atlantic Salmon	West	26	596 ± 72	-21.1 ± 0.5	15.6 ± 0.7	5 ± 0.3	0.3 (0.19 - 0.47)
		Central	7	566 ± 29	-20.4 ± 0.6	15.3 ± 0.5	4.9 ± 0.3	0.73 (0.3 - 1.62)
		East	19	535 ± 76	-21.6 ± 0.6	15.9 ± 0.8	5.3 ± 0.2	0.4 (0.24 - 0.68)
	Brown Trout	West	29	526 ± 184	-20.3 ± 0.8	16 ± 0.9	4.2 ± 0.5	0.64 (0.41 - 0.99)
		Central	16	565 ± 64	-20.4 ± 0.6	15.6 ± 0.6	5 ± 0.4	0.49 (0.27 - 0.85)
		East	34	540 ± 41	-20.7 ± 0.5	15.3 ± 0.4	5.5 ± 0.2	0.18 (0.12 - 0.27)
	Chinook Salmon	West	72	717 ± 112	-21.5 ± 0.9	16.1 ± 0.6	5.2 ± 0.2	0.27 (0.21 - 0.36)
		Central	20	838 ± 103	-22 ± 0.5	16.3 ± 0.3	5.4 ± 0.2	0.2 (0.12 - 0.34)
		East	22	860 ± 85	-21.3 ± 0.4	15.7 ± 0.5	5.4 ± 0.2	0.2 (0.12 - 0.33)
	Coho Salmon	West	45	518 ± 58	-21.3 ± 0.4	16.3 ± 0.8	5.2 ± 0.4	0.28 (0.2 - 0.39)
		Central	4	548 ± 45	-21.6 ± 0.4	16.6 ± 0.5	5.2 ± 0.3	NA
		East	2	711 ± 1	-21 ± 0.2	15.1 ± 0.1	5.3 ± 0.1	NA
	Lake Trout	West	18	686 ± 116	-20.9 ± 0.4	17.8 ± 0.4	4.9 ± 0.3	0.26 (0.15 - 0.45)
		Central	30	719 ± 95	-21.3 ± 0.4	17.8 ± 0.4	5.1 ± 0.3	0.18 (0.12 - 0.28)
		East	2	643 ± 39	-20.9 ± 0.6	16.9 ± 1.4	5 ± 0.2	NA
	Rainbow Trout	West	41	556 ± 109	-20.7 ± 0.8	15.4 ± 1.1	4.7 ± 0.7	1.09 (0.75 - 1.57)
		Central	13	655 ± 44	-20.4 ± 0.6	15.5 ± 0.5	5.2 ± 0.2	0.38 (0.19 - 0.71)
		East	14	659 ± 62	-19.9 ± 0.4	15.3 ± 0.5	5.1 ± 0.5	0.39 (0.21 - 0.71)
Muscle	Atlantic Salmon	West	3	582 ± 105	-21.8 ± 0.2	15.6 ± 0.1	5 ± 0.1	1.39 (0.38 - 4.27)
		East	3	506 ± 56	-21 ± 0.2	15.6 ± 0.4	5.3 ± 0.2	NA
	Brown Trout	Central	16	565 ± 64	-21.1 ± 0.7	15.8 ± 0.6	5 ± 0.4	0.49 (0.27 - 0.87)
		East	33	541 ± 42	-21.2 ± 0.4	15.7 ± 0.4	5.4 ± 0.2	0.14 (0.09 - 0.21)

Tissue	Species	Region	n	Length	$\delta^{13}C$	$\delta^{15}N$	$\delta^{34}S$	SEV
Muscle	Chinook Salmon	West	21	774 ± 109	-21.9 ± 0.3	15 ± 0.4	5.1 ± 0.3	0.17 (0.1 - 0.28)
		Central	20	838 ± 103	-22 ± 0.3	15.3 ± 0.3	5.5 ± 0.2	0.14 (0.08 - 0.24)
		East	20	852 ± 82	-21.6 ± 0.2	15 ± 0.5	5.4 ± 0.1	0.17 (0.1 - 0.29)
	Coho Salmon	West	25	518 ± 30	-21.9 ± 0.2	15.1 ± 0.5	5 ± 0.2	0.14 (0.09 - 0.23)
		Central	4	548 ± 45	-22.1 ± 0.1	15.2 ± 0.4	5.3 ± 0.2	NA
		East	1	710	-21.5	15.1	5.6	NA
	Lake Trout	West	16	700 ± 103	-21.7 ± 0.4	17.1 ± 0.4	4.9 ± 0.4	0.3 (0.16 - 0.53)
		Central	30	719 ± 95	-21.9 ± 0.3	17 ± 0.4	5 ± 0.4	0.16 (0.1 - 0.24)
		East	2	643 ± 39	-21.4 ± 0.7	16.8 ± 0.7	5 ± 0.4	NA
	Rainbow Trout	West	10	634 ± 52	-21.6 ± 0.3	15.5 ± 0.6	4.6 ± 0.8	0.65 (0.31 - 1.3)
		Central	13	655 ± 44	-21.5 ± 0.2	15.2 ± 0.6	5.3 ± 0.1	0.3 (0.15 - 0.56)
		East	13	654 ± 61	-21.2 ± 0.2	15.4 ± 0.6	5 ± 0.6	0.5 (0.26 - 0.92)

Appendix 7 Combinations of δ¹³C, δ¹⁵N and δ³⁴S stable isotope biplots of the isotopic niches of salmonids using fin tissue (left panels) and muscle tissue (right panels) across spatial regions of Lake Ontario in 2018. Coloured circles enclose the standard ellipse area (40%) of the two isotopes displayed for all salmonid species.
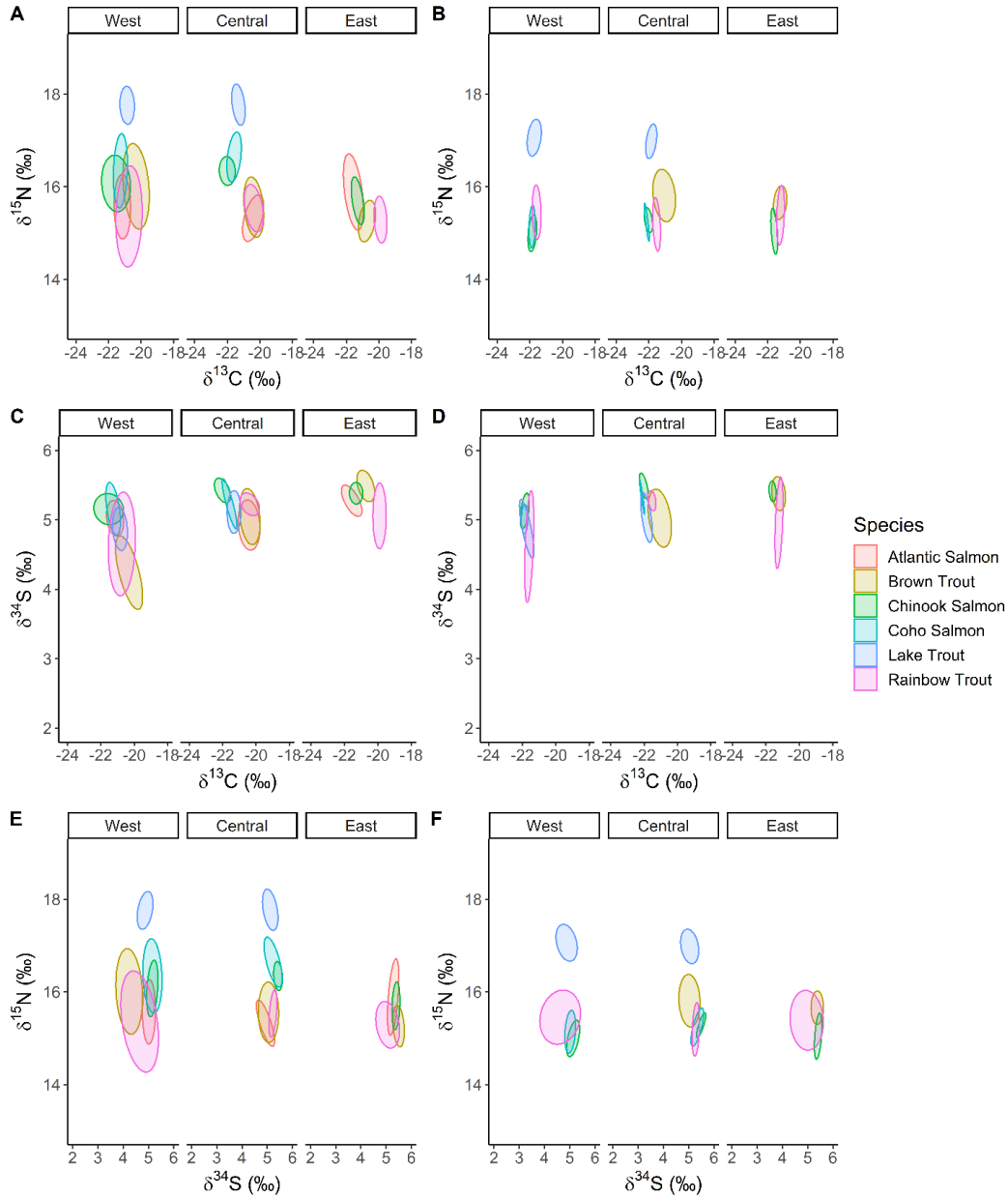
Appendix 8 Posterior probability distribution of trophic niche overlap (%) of salmonid species within different regions in Lake Ontario in 2018, determined for fin tissue, using two ($\delta^{13}C$ and $\delta^{15}N$) or three ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) stable isotopes and the 40% standard ellipse areas. Data displayed represents the mean isotopic overlap between each species combination with the 95% credible interval from 10,000 Monte-Carlo simulations. ATLS = Atlantic salmon, BRTR = brown trout, CHIN = Chinook salmon, COHO = Coho salmon, LKTR = lake trout, RAIN = rainbow trout.
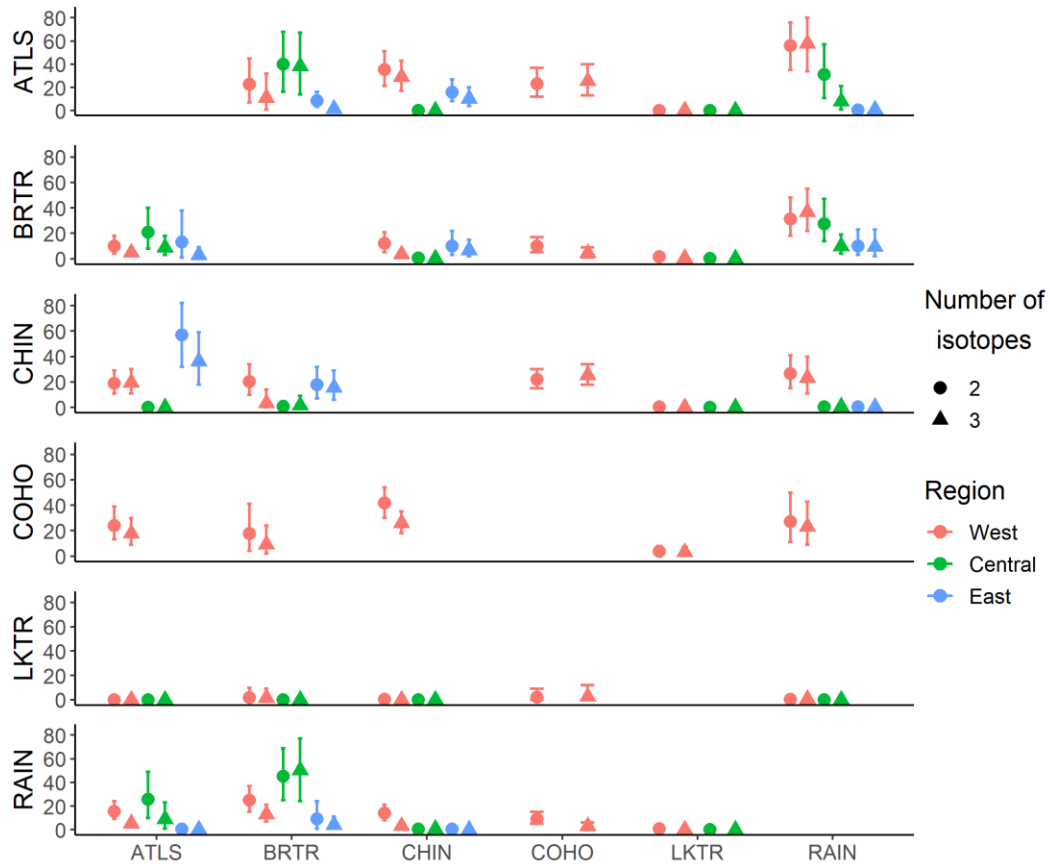
Appendix 9 Posterior probability distribution of trophic niche overlap (%) of salmonid species within different regions in Lake Ontario in 2018, determined for muscle tissue, using two (δ^{13}C and δ^{15}N) or three (δ^{13}C, δ^{15}N and δ^{34}S) stable isotopes and the 40% standard ellipse area. Data displayed represents the mean isotopic overlap between each species combination with the 95% credible interval from 10,000 Monte-Carlo simulations. BRTR = brown trout, CHIN = Chinook salmon, COHO = Coho salmon, LKTR = lake trout, RAIN = rainbow trout.
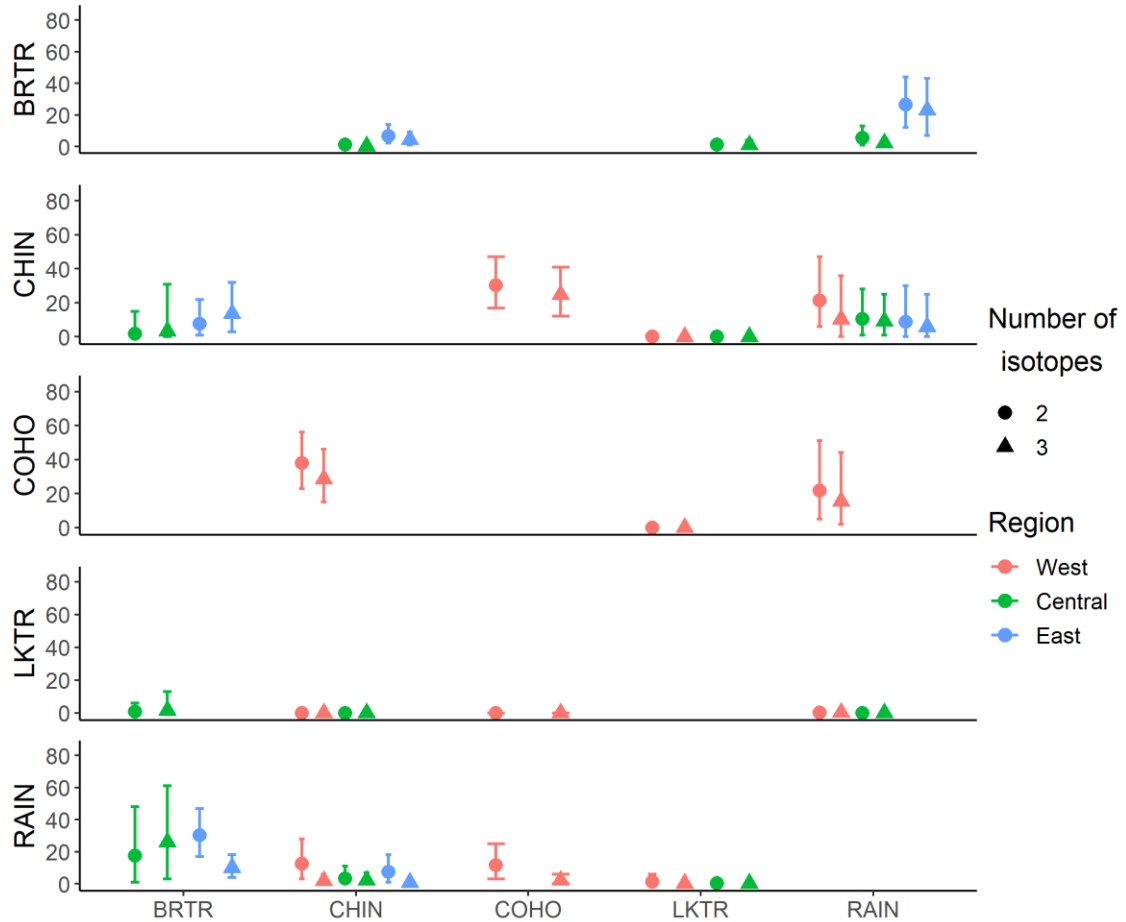
Appendix 10 Mean estimated prey item contributions (and 95% credible interval) of salmonids in different regions of Lake Ontario in 2018 from diet mixing models in MixSIAR, using salmonid fin (left panels) and muscle tissue (right panels) that were estimated using 2 stable isotopes (δ^{13}C and δ^{15}N). ALE = alewife; DWSC = deepwater sculpin; RG = round goby; MYSIS = *Mysis* spp.; SLSC = slimy sculpin; SMELT = rainbow smelt.
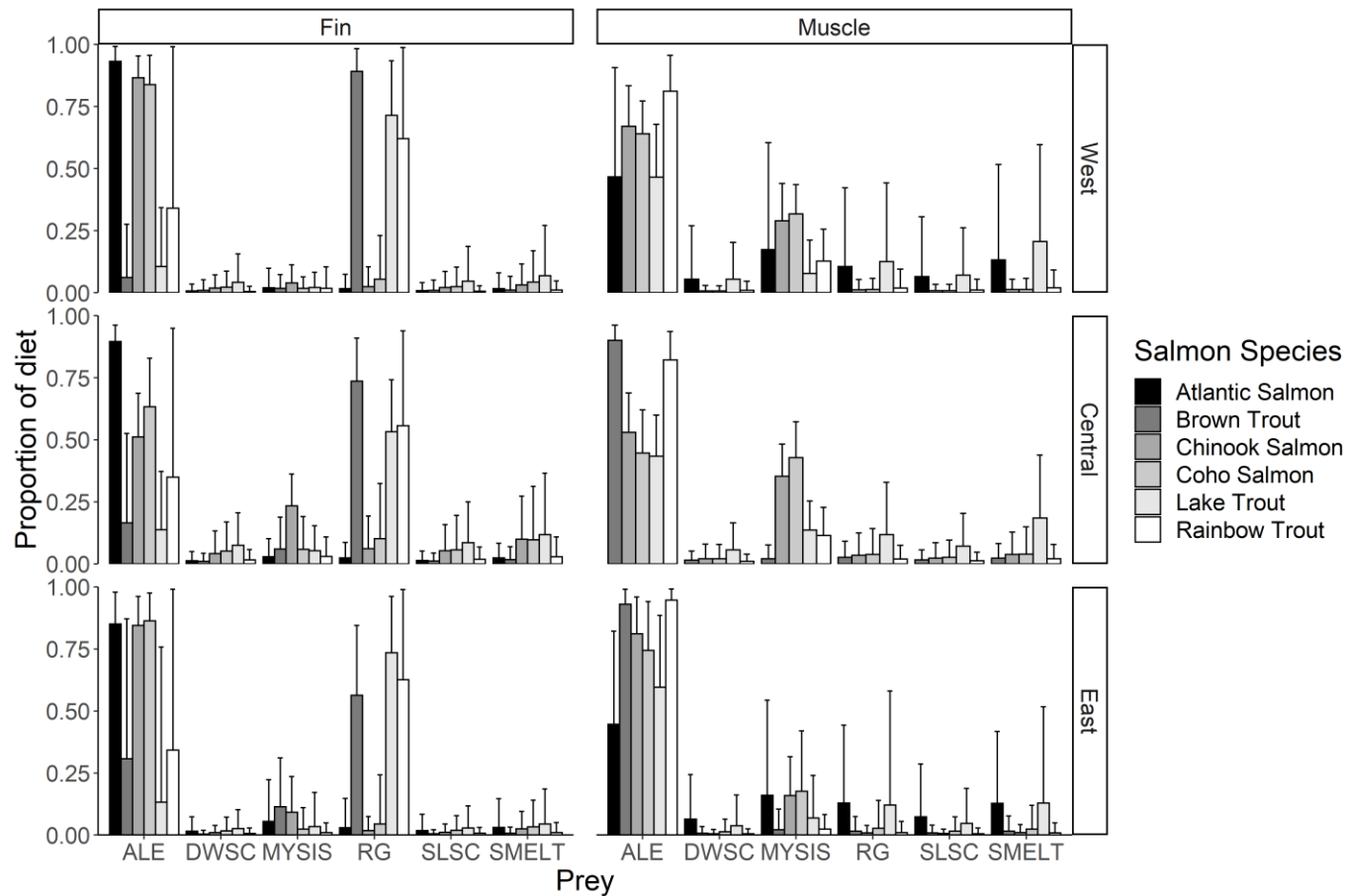
Appendix 11 Inter-season autocorrelated kernel density estimate (AKDE) overlap estimates, represented as the bias-corrected Bhattacharyya Coefficient and 95% confidence intervals (CI), for acoustically tagged Atlantic salmon (*Salmo salar*) in Lake Ontario, 2016-2020.

Fish ID	Seasons	Overlap Estimate	Lower 95% CI	Upper 95% CI
24469	Spring, Winter	0.788	0.287	1.000
24475	Spring, Winter	0.622	0.461	0.780
24476	Spring, Winter	0.998	0.930	1.000
24477	Spring, Summer	0.953	0.423	1.000
24477	Spring, Winter	0.764	0.328	0.997
24477	Summer, Winter	0.681	0.128	1.000
24478	Spring, Winter	0.910	0.405	1.000
AAS13	Spring, Summer	0.985	0.869	1.000
AAS13	Spring, Fall	0.745	0.305	0.996
AAS13	Spring, Winter	0.995	0.948	1.000
AAS13	Summer, Fall	0.937	0.460	1.000
AAS13	Summer, Winter	0.983	0.828	1.000
AAS13	Fall, Winter	0.818	0.325	1.000

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