Diet reconstruction and niche of Lake Ontario top predators and corresponding prey species

James Adam Mumby

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Diet reconstruction and niche of Lake Ontario top predators and corresponding prey species

By

James A. Mumby

A Thesis
Submitted to the Faculty of Graduate Studies
through the Great Lakes Institute for Environmental Research
in Partial Fulfillment of the Requirements for
the Degree of Master of Science
at the University of Windsor

Windsor, Ontario, Canada

2015

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by

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DECLARATION OF ORIGINALITY

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ABSTRACT

Lake Ontario supports a diverse offshore fish community consisting of salmonids and forage fish with little known about the resource partitioning and habitat use of these species. To assess this, I used stable isotopes to determine the isotopic trends (forage fishes only), niche structure and overlap of both salmonids and forage fishes. I also estimated the salmonid trophic position (TP) and diet using stable isotopes. Forage fishes had high resource partitioning but was low between *Myoxocephalus thompsonii* and *Cottus cognatus*. Regional and temporal discrete subpopulations driven largely by nitrogen were only present in *Alosa pseudoharengus*, *Osmerus mordax* and *Neogobius melanostomus*. Salmonids had low resource partitioning, particularly *Oncorhynchus tshawytscha* and inhabit the offshore. *A. pseudoharengus* comprised a major proportion of the salmonid diet, followed by *N. melanostomus* while *Salvelinus namaycush* had the highest TP. *Salmo salar* restoration may prove difficult to due to high isotopic and diet overlap with other salmonids.
DEDICATION

This thesis is dedicated to my parents, Irene C. and James A. Mumby Sr.
ACKNOWLEDGEMENTS

Thank you first and foremost to my supervisor, Dr. Aaron T. Fisk (GLIER), as well as to my co-supervisor, Dr. Timothy B. Johnson (OMNRF) for this exciting, challenging and unique opportunity. Thank you to the Glenora Fisheries Station (OMNRF), Lake Ontario Biological Station (USGS), and Canadian Centre for Inland Waters (DFO) scientific and laboratory staff for the collection of prey and salmonid samples. In addition, thank you to J. Brown, J. Ives, B. Metcalfe, K. Passow, and M. Yuille (all OMNRF) and C. Karboski (USGS) for sample preparation. Also, thank you to Sonya McMillan and Amy McPherson (both OMNRF) for analysing gut contents of all salmonids. Many thanks also given to A. Weidl, B. Charron, S. Isaac, K. Johnson and especially A. Hussey for stable isotope analysis in the Chemical Tracers Laboratory at GLIER. The support and never ending encouragement of my parents J. and I. Mumby, sister J. Mumby, and friends will be remembered. This project was funded by the Natural Science and Engineering Research Council Discovery Grant, Canada-Ontario Agreement Respecting the Great Lakes Basin Ecosystem funds, Ontario Ministry of Natural Resources and Forestry-ARMS base funds, and the University of Windsor.
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<td>analysis of variance</td>
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<td>CO₂</td>
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<td>DTDF</td>
<td>diet tissue discrimination factor, $\delta^{15}N$</td>
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<td><em>exempli gratia</em>, ‘for example…’</td>
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<td><em>et al.</em></td>
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<td>general linear model</td>
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<tr>
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<td>n</td>
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<td>PDB</td>
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$R_{\text{sample}}$
ratio of ‘heavy’ to ‘light’ isotope within a raw sample........................................7

$R_{\text{standard}}$
ratio of ‘heavy’ to ‘light’ isotope in an internationally accepted standard from the National Bureau of Standards .................................................................7

$\text{SEA}_C$
standard (40%) ellipse area..................................................................................38

$\text{SIAR}$
Stable Isotope Analysis in R ...............................................................................38

$\text{SIBER}$
Stable Isotope Bayesian Ellipses in R.................................................................38

$spp.$
species .................................................................................................................14

$\text{TL}$
trophic level ........................................................................................................4

$\text{TP}$
trophic position ...................................................................................................9

$\%$ parts per ten thousand, ‘per mille’ .................................................................7

$\%o^2$
isotopic niche width, ‘per mille squared’..........................................................39

$\delta X$
change in ratio of $X$ as compared to a standard, $X = \text{either}^{15}\text{N} (^{15}\text{N}:^{14}\text{N}), \text{or}^{13}\text{C} (^{13}\text{C}:^{12}\text{C})$ .........................................................................................................................6

$\delta, \Delta$
delta, ‘change in…’ ................................................................................................1

$\delta^{15}\text{N} \text{or} \delta^{13}\text{C}$
change in ratio of $^{15}\text{N}:^{14}\text{N}$ or $^{13}\text{C}:^{12}\text{C}$ as compared to a standard........................................1
\[ \Delta^{15}N \]

difference in $\delta^{15}N$ between consumer and prey source(s) ............................................9
CHAPTER 1

GENERAL INTRODUCTION

Ecology is a multidisciplinary science examining the aspects of Earth’s functionalities, which includes conducting studies from the biosphere level to the individual organism level (Molles & Cahill, 2008). At the organism level, ecology is the study of the interactions between organisms and their environment (Haeckel, 1866). Feeding interactions, often referred to as food web ecology, within and amongst species are a basic fundamental to understanding the associations between organisms. Lindeman (1942) was the first to describe feeding interactions as food web ecology, as organisms within an ecosystem could be assembled hierarchically into a series of feeding levels or “discrete trophic levels”. Feeding interactions have been used in many studies to determine and quantify anthropogenic effects on food webs (Pauly et al., 1998), population dynamics (Polis et al., 1997), top-down and/or bottom-up forces (Power, 1992), and many other aspects of ecosystem function and structure.

As food web ecology studies have become increasingly complex, and with the advancement of scientific technologies, new methods have been developed to describe trophic relationships that provide greater scope than traditional techniques, mainly gut contents. The use of stable isotopes as chemical tracers of diet in ecology began in the late 1970’s with studies exploring the distribution of carbon stable isotopes ($\delta^{13}$C) within mice, insects, and gastropods (Deniro & Epstein, 1978). Since this pioneering study, the use of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) stable isotopes have grown exponentially in ecology and had a major influence on how researchers quantify food web dynamics and interactions (Hobson et al., 1994; Cabana & Rasmussen, 1994). Stable isotopes have
considerable potential in large lake systems, including the Great Lakes, to determine spatial and temporal patterns between predator and prey that are more difficult to quantify using traditional methods such as gut contents.

Lake Ontario is a good model system to use stable isotopes to explore food webs because there are a number of top predators (e.g., salmonids) of both native and non-native origins. As well, the Lake Ontario salmonids support a valuable recreational fishery and there are large ongoing restoration efforts for the native species, Lake Trout (Salvelinus namaycush) and Atlantic Salmon (Salmo salar). Salmonids are also thought to play an important role for controlling important invasive fish species [Rainbow Smelt (Osmerus mordax), Alewife (Alosa pseudoharengus), and recently Round Goby (Neogobius melanostomus)] in Lake Ontario and other Great Lakes. There has not been a published comprehensive assessment of the diet on Lake Ontario salmonids [Brown Trout (Salmo trutta), Chinook Salmon (Oncorhynchus tshawytscha), Coho Salmon (Oncorhynchus kisutch), Lake Trout, and Rainbow Trout (Oncorhynchus mykiss)] within a single article since the mid 1980’s and early 1990’s (i.e., Brandt 1986a, Jones et al., 1993) and no diet study on Atlantic Salmon in Lake Ontario. Since Brandt (1986a) and Jones et al. (1993) much ecological change has occurred in Lake Ontario particularly with the arrival of invasive species. The use of stable isotopes as a tool to develop the dietary niche space and diet of the Lake Ontario salmonids will give insight to lake managers about annual salmonid stocking rates through salmonid isotopic overlap (e.g., resource partitioning).

This thesis examines the relative trophic positions, isotopic niche width, and dietary origin, using $\delta^{13}$C and $\delta^{15}$N, of the top predators, i.e., salmonids, and their corresponding prey/ forage fishes in offshore Lake Ontario. There is evidence of sensitive
predator-prey balance occurring in the Lake Ontario offshore food web (Jones et al., 1993; Halfon et al., 1996; Stewart & Sprules, 2011), where top predator abundance has relied on fish stocking to maintain numbers and restore native populations, but also to control invasive prey populations (Brandt, 1986a; Stapanian, 2007; Dettmers et al., 2012). To address this data and information gap, I will first quantify in chapter 2, the spatial and temporal trends of stable isotopes (\(^{13}\)C and \(^{15}\)N) in the abundant Lake Ontario salmon and trout (salmonid) forage fishes [Alewife, Round Goby, Rainbow Smelt, Deepwater Sculpin (\textit{Myoxocephalus thompsonii}) and Slimy Sculpin (\textit{Cottus cognatus})] to determine whether discrete populations exist on a temporal and spatial scale(s) within each species and quantify isotopic niche width and overlap to assess competition and habitat partitioning over space and time. In chapter 3, I will assess the trophic relationships and habitat partitioning of the dominant Lake Ontario salmonid species (Atlantic Salmon, Brown Trout, Chinook Salmon, Coho Salmon, Lake Trout, and Rainbow Trout) using \(\delta^{13}\)C and \(\delta^{15}\)N and stomach contents.

1.1 Food web ecology

Food webs have been used to interpret ecosystem and community function and biodiversity patterns and energy flow (Hall et al., 2000; Thompson et al., 2012). The first food web diagram to be constructed used the boll weevil (\textit{Anthonomus grandis}) and its’ predators (Pierce et al., 1912). Pierce et al. (1912) described the web as a complex, and this was the first food web study featuring an invasive species, the boll weevil. In 1913, Shelford (1913) outlined ecological groups and characterized the fish communities of Lake Michigan and stated that food chains were dependent upon a primary food source. Elton (1927) referred to “food-chains” as chains of animals that are linked together by
prey sources with a base that begins with plants and the addition of all food chains within a community were referred to as a “food-cycle”. Elton (1927) also stated that within a community of organisms, there are herbivores, carnivores, and scavengers. The introduction of “The Pyramid of Numbers” by Elton (1927) further quantitatively advanced the food web concept, which established the theory that organism diversity and biomass would be greatest at the lowest trophic level and decrease with each higher trophic level. The work by Pierce et al. (1912), Shelford (1913), and Elton (1927) provided valuable insight on trophic levels and biomass but did not involve a strategy to evaluate the physiological (e.g., energy flows), behavioural, predator-prey, and ecological interactions occurring within the food web.

Lindeman (1942) first defined ‘trophic dynamics’ in which organisms are grouped into a series of trophic levels (TL) by which each succeeding level is dependent on the preceding level as a source of energy. As well, higher trophic level consumers have a higher percentage loss of energy due to increased respiration but were suggested to be more efficient in the management of their food stocks (Lindeman, 1942). Cohen & Briand (1984) examined the movement of energy within ‘trophic links’, which represent a trophic relationship between two species, and stated that the mean number of links corresponds highly to the number of species within a given food web. Similar to Cohen & Briand (1984), Cousins (1987) found that the number of trophic levels within a food web is correlated to the ratio of predator size to prey size. In 1993, the food web concept was further developed to analyze differences in the trophic transfer efficiencies (percentage of energy transferred to a corresponding organism within a food web) within the trophic links (Hairston & Hairston, 1993). They discovered that ecosystems (e.g., littoral, pelagic, etc.) have different trophic transfer efficiencies between adjacent levels. As well, trophic
transfer efficiencies and the rate of energy fixation were found to be influenced by trophic structure. Trophic structure refers to the multiple feeding relationships within an ecosystem(s), which determine cyclic chemical patterns and the route of energy flows (Campbell & Reece, 2005).

The use of fixed trophic levels to describe food webs disregarded that ecosystems are highly complex and omnivory is common (Polis & Strong, 1996; Vander Zanden & Rasmussen, 1996; Persson, 1999). Omnivory is when a species or individual feeds on prey that are situated at different trophic positions (i.e., Lake Trout feeding on both zooplankton and prey fishes) (Vander Zanden et al., 1999a). The use of stable isotopes, mainly $^{15}N$, to construct food webs demonstrated that most animals do not fall on a discrete trophic level but usually fall between them, and has led to concept of trophic position (Vander Zanden et al., 1999a; 1999b). Trophic position is not limited to a discrete level but rather is a continuous variable that defines the position of an organism within a food web and recognizes that animals can be omnivores (Vander Zanden et al., 1999a; 1999b).

Classical food web studies were able to observe the complexity of trophic interactions but were limited in function and resolution and took long periods to construct (Paine, 1998). Classical food web studies were also based on observation and did not examine the functional or energetic importance of feeding linkages between organisms which hindered early food webs to trace mass energy flows through ecosystems (Polis, 1991; Hairston & Hairston, 1993; Polis & Strong, 1996; Vander Zanden & Rasmussen, 1996; Persson, 1999). As well, dietary data was not collected for all organisms in early food web studies and disregarded the use of trophic position to quantitatively to represent trophic structure (Vander Zanden & Rasmussen, 1996).
1.2 Stable isotopes in food web ecology

The use of stable isotopes, mainly nitrogen and carbon to trace and determine food web dynamics and structure, has become common in food web ecology including niche and diet (Fry, 1991; Vander Zanden et al., 1999a; Post, 2002). Niche is a set of habitats in which an individual or species inhibits; its interactions with other organisms; its effect on the environment; and the resources used or the diet of a species or individual (Lawrence, 2005). Gut contents or gut content analysis, the classic and most commonly used method, only provides a “snapshot view”, hours to a day, of the organism’s diet (Hyslop, 1980; Pinnegar & Polunin, 1999; Buchheister & Latour, 2011) and can be confounded by empty stomachs, unidentified materials and requirements for large sample sizes but may provide greater insight and quantity for specific diet items (Madenjian et al., 1998) which stable isotopes cannot fulfil. Stable isotopes have the ability to trace variables such as omnivory, food chain length, trophic position and energy flow through time (Tieszen et al., 1983; Estep & Vigg, 1985; Vander Zanden & Rasmussen, 2001). Many elements have different atomic forms called isotopes, which contain the identical quantity of protons and electrons but differ in the number of neutrons contained in the nucleus (Hoefs, 2009).

Two categories of isotopes exist: radioactive (~1,200 isotopes) which are unstable and undergo decay (i.e., extra neutrons leave the atom) to increase nucleus stability (Davis & Foster, 1958; Möller et al., 1997); and stable isotopes (~300), that have an extra neutron which is stable and does not leave the nucleus and have the capability to measure environmental changes on long time scales (Dansgaard et al., 1993). Isotopes of an element are classified as either ‘light’ (e.g., $^{12}$C, $^{14}$N) or ‘heavy’ (e.g., $^{13}$C, $^{15}$N) depending on atomic mass (neutrons + protons) with ‘light’ isotopes being predominant in the
environment and ‘heavy’ isotopes occurring in only trace amounts (Hoefs, 2009). The occurrence of ‘heavy’ isotopes in the environment and their different chemical characteristics compared to the light isotope of the element, allows isotopes to have distinctive tracer capabilities which fluctuate in particular ecosystem surroundings (e.g., lake, atmosphere, ocean) (Peterson & Fry, 1987). The relative stable isotope abundance can change via biological interactions due the variable kinetics within an organism which result in ‘fractionation’ (Rounick & Winterbourn, 1986). Stable isotopes are written in δ-notation to express the mass-dependence between the stable isotopes of a particular element; which is the percentage between ‘heavy’ to ‘light’ isotope relative to a reference standard, calculated as:

\[ \delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 1000 \]

where \( X \) is the ‘heavy’ isotope (e.g., \( ^{13}\text{C}, ^{15}\text{N} \)), \( R_{\text{sample}} \) is the ratio of ‘heavy’ to ‘light’ within a raw sample and \( R_{\text{standard}} \) is the ratio of ‘heavy’ to ‘light’ isotope in an internationally accepted standard from the National Bureau of Standards (NBS) (Fry, 1991). These NBS standards for carbon and nitrogen are atmospheric nitrogen (\( \text{N}_2 \)) for \( R_{\text{nitrogen}} \) and PeeDee Belemnite (PDB) limestone for \( R_{\text{carbon}} \) (Estep & Vigg, 1985). The stable isotope fractionation variability between \( R_{\text{sample}} \) and \( R_{\text{standard}} \) occurs at very low concentrations and therefore \( \delta X \) is expressed in ‘per mille’ (‰) because the multiplication of 1000 causes the variation between \( R_{\text{sample}} \) and \( R_{\text{standard}} \) to be further evident (Peterson & Fry, 1987).

The use of the stable isotope approach by food web ecologists is founded on the proposition that the stable isotope ratios or values within the consumer tissue have the capability to predict the complementary diet of the consumer (DeNiro & Epstein, 1978;
The consumption of a primary producer by primary consumers and higher consumers in the food web commonly exhibit <1‰ in the relative values of δ\textsuperscript{13}C per trophic level (Hobson & Welch, 1992). This result allows for the estimation of the relative contributions of δ\textsuperscript{13}C from sources of primary productivity in systems where two or more isotopically distinct sources exist in the environment (i.e., nearshore vs. offshore; benthic vs. pelagic) (Hobson & Welch, 1995). Isotopic differences in primary productivity were first examined with C\textsubscript{3} (e.g., algae) and C\textsubscript{4} (e.g., drought tolerant) plants; in that C\textsubscript{4} plants are isotopically distinct and enriched in \textsuperscript{13}C, i.e., higher δ\textsuperscript{13}C values, opposed to C\textsubscript{3} plants (Bender, 1968; 1971). C\textsubscript{4} plants are enriched in \textsuperscript{13}C as they do not lose CO\textsubscript{2} during photosynthesis as opposed to C\textsubscript{3} plants which lose CO\textsubscript{2} during photosynthesis (Forsberg et al., 1993). This is due to different rates of carboxylation and diffusion of CO\textsubscript{2} into the cell as \textsuperscript{12}C-CO\textsubscript{2} is easier to disassemble during photosynthesis than \textsuperscript{13}C-CO\textsubscript{2} since \textsuperscript{13}C-CO\textsubscript{2} contains an additional neutron (O’Leary, 1988).

Carboxylation is Isotopic differences also exist between terrestrial and aquatic plants because during photosynthesis, the diffusional resistance to CO\textsubscript{2} is four times greater in water as opposed to air (Keeley & Sandquist, 1992). This rate of diffusional resistance establishes a stagnant boundary layer around benthic algae and macrophytes which decreases the diffusion rate of CO\textsubscript{2} compared to pelagic algae resulting in changes in the incorporation of \textsuperscript{12}C and \textsuperscript{13}C between pelagic and inshore carbon sources (Smith & Walker, 1980). Respectively, pelagic/planktonic algae use carbon-12 CO\textsubscript{2} more readily and are not restricted to CO\textsubscript{2} diffusion, while macrophytes and benthic algae are regularly forced to consume all available CO\textsubscript{2} during diffusion, resulting in insufficient change in δ\textsuperscript{13}C (Peterson & Fry, 1987; France, 1995). As a result, benthic algae are enriched in \textsuperscript{13}C,
higher $\delta^{13}$C, compared to pelagic algae and in turn affect the isotopic values of consumers (e.g., invertebrates, fishes) above them in the food web (France, 1995).

Nitrogen stable isotopes ($\delta^{15}$N) assist in the measurement of trophic position as consumers are typically enriched in $^{15}$N relative to their prey, particularly in aquatic food webs (DeNiro & Epstein, 1981; Hobson & Welch, 1995; Vander Zanden & Rasmussen, 2001). Consumers are enriched in $^{15}$N relative to their prey sources because consumers retain $^{15}$N during the catabolization of amino acids and excrete $^{14}$N in their excreta as $^{14}$N amino acids are easier to catabolize (Minagawa & Wada, 1984). The difference in $\delta^{15}$N between consumer and prey source(s) ($\Delta^{15}$N = $\delta^{15}$Nconsumer - $\delta^{15}$Nprey) is most often called the diet tissue discrimination factor (DTDF, $\Delta^{15}$N) and typically ranges from 3-4‰ (average = 3.4‰) in aquatic systems (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Cabana & Rasmussen, 1994; 1996; Vander Zanden & Rasmussen, 2001; Post, 2002). The trophic position (TP) of a consumer ($TP_{\text{consumer}}$) can be estimated using the following equation:

$$TP_{\text{consumer}} = \left[ \left( \delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}} \right)/3.4 \right] + TP_{\text{baseline}},$$

where $\delta^{15}$Nconsumer represents the $\delta^{15}$N value of a consumer, $\delta^{15}$Nbaseline represents the $\delta^{15}$N value of a species of known trophic position (e.g., algae, particulate organic matter, etc.), 3.4 is the theorized per trophic level increase, and $TP_{\text{baseline}}$ is the trophic position of an identified baseline organism (Vander Zanden et al., 1999a).

Consumers (e.g., salmonids) have the ability to acquire nitrogen from multiple spatial habitat sources (i.e., pelagic and/ or littoral food webs) via primary producers or detritus therefore increasing spatial heterogeneity (Post, 2002). Post (2002) developed a two- source food web equation for estimating trophic position to capture additional
heterogeneity:

$$TP = \lambda + (\delta^{15}N_{\text{secondary consumer}} - [\delta^{15}N_{\text{base1}} \times \alpha + \delta^{15}N_{\text{base2}} \times (1 - \alpha)]) / \Delta_{\text{nitrogen}},$$

where $\lambda$ represents the trophic position of an organism used to measure $\delta^{15}N_{\text{base}}$ (i.e., primary producers are 1), $\delta^{15}N_{\text{secondary consumer}}$ is the $\delta^{15}N$ value of a consumer, $\delta^{15}N_{\text{base1}}$ and $\delta^{15}N_{\text{base2}}$ is the isotopic variation among ecosystems at the base of the food web, $\alpha$ is the proportion of nitrogen in the consumer which is acquired from the base of the food web, and $\Delta_{\text{nitrogen}}$ is the trophic fractionation of nitrogen.

Diet tissue discrimination factors (DTDFs) can be highly influenced by species, environment, tissue type, and tissue lipid percentage (Lavoie et al., 2012). As well, DTDFs have been observed to decrease with increasing stable isotope value in the prey and can have a profound influence on trophic position and food chain length calculations (Overmyer et al., 2008; Caut et al., 2009; Dennis et al., 2010; Hussey et al., 2014). DTDFs are very important parameters in stable isotope mixing models to quantify diet, and are the key metric for assessing isotopes in food web studies (Bond & Diamond, 2011). Stable isotope values within organisms can vary temporally and spatially in aquatic ecosystems which can confound their use in quantifying food web characteristics (Vander Zanden et al., 1999a; Syväranta et al., 2006; Zambrano et al., 2010). Many previous stable isotope studies have analyzed the role of top predators and their prey sources on small aquatic spatial scales using stable isotopes (e.g., Estep & Vigg, 1985; Hobson & Welch, 1995; Vander Zanden et al., 1999b), but much less has been done on spatial and temporal patterns of top predators (e.g., salmonids) and corresponding forage fishes in large aquatic systems, such as the Laurentian Great Lakes. In conclusion, the use of stable isotopes as tools has the potential to determine habitat use on a spatial and
temporal scale for both salmonid and forage fishes. When paired with gut contents for ground-truthing, stable isotopes have the ability to reconstruct the diet of salmonid species in Lake Ontario. Ultimately, conclusions from this thesis will help elucidate whether these species exhibit high niche overlap and whether there is overlap for similar prey items. In addition, this research will explore whether discrete populations of salmonid prey species exist which could influence salmonid niche space and width depending where an individual salmonid lives within Lake Ontario at a given time and location.

1.3 Study system

The research for my M.Sc. was completed on Lake Ontario (Figure 1.1) featuring joint prey and top predator sampling in both Canadian and US waters. Lake Ontario is the 14th largest freshwater lake in the world, but among the Laurentian Great Lakes has the smallest surface area (18,960 km²) but the second largest mean depth (86.25 m) (Grady, 2007; Flint, 1986). The lake can be separated into three major regions: i) the large and deep main basin spanning from west to east; ii) the shallow Eastern/ Kingston Basin in the northeast section of the lake, which empties into the St. Lawrence River; and iii) the Bay of Quinte (Mills et al., 2005). The bathymetric profile of the lake has allowed for unique ecosystems (i.e., nearshore warm water communities and offshore cold water communities) to become established with an offshore area, dominated by native and introduced (stocked) non-native salmon and trout (salmonids) that feed on pelagic and benthic forage fishes (Brandt, 1986a; Dietrich et al., 2006; Murry et al., 2010), and a nearshore area (Eastern Basin & Bay of Quinte) dominated by warmwater fishes (percids, esocids, & centrarchids) (Christie, 1974; Hurley & Christie, 1977). Historically Lake
Ontario generated a large amount of fish biomass that supported one of the largest freshwater fisheries in the world (Atlantic Salmon) until approximately 1900 (Crawford, 2001).

1.4 Great Lakes Salmonid and Forage Fish Diets and Habitats

There are eight species of salmonids (Family – Salmonidae) currently found in the province of Ontario and are important in both the sport and commercial fisheries (Holm et al., 2010). Salmonids prefer cold to cool water lakes and streams and some salmonids are anadromous (Page & Burr, 2011). To better understand the importance of the salmonids to the Lake Ontario ecosystem and economy, we need to improve our understanding of the trophic niche and diet composition of these species and their prey base (only fishes). With this improved understanding, we can assess whether invasive species can have an effect on the structuring of the salmonid niche and diet, whether salmonid diet and niche vary over season and location, whether there are ontogenetic changes in diet and niche during the salmonid piscivory stage, and whether forage fishes can affect the assimilation of the stable isotope signature within salmonid tissue. As well, increased knowledge of the salmonid prey base will assist in an improved understanding of prey population dynamics, trophic structure, niche width, and whether total length (mm) is influenced by region and season. In order to answer the above questions, first the life history and diet of the salmonids and their corresponding forage fish base must be understood.

Adult Lake Ontario Chinook Salmon and Rainbow Trout occupy nearshore (∼20 m bathymetric depth) areas in early spring and move further offshore to deeper bathymetric depths (35-65 m) during the late spring and reside there over the summer
months (Stewart & Bowlby, 2009). This seasonal movement pattern is also observed in Coho Salmon and Atlantic Salmon (Scott & Crossman, 1973; Haynes & Keleher, 1986). These salmonids undertake this movement because as the nearshore warms, the salmonid migrate in search for preferred cooler waters that occur in the deeper offshore (Scott & Crossman, 1973; Haynes et al., 1986; Stewart & Bowlby, 2009). There is evidence that Rainbow Trout migrate with the thermal front as it progresses to the offshore (Haynes et al., 1986). This behaviour is probably also occurring for the other open-lake salmonid species (Atlantic Salmon, Chinook Salmon, and Coho Salmon). During the early fall, Chinook, Coho, and Atlantic Salmon migrate back to nearshore waters in preparation for spawning (Scott & Crossman, 1973; Hickey, 2002; Stewart & Bowlby, 2009; Johnson, 2014). Salmonids have the ability to move large distances. Lake Ontario Coho and Chinook Salmon have been reported to travel 500 km in four months (average 4 km/ day) during the spring and summer (MacKay, 1969; Scott & Crossman, 1973; Haynes & Keleher, 1986). Rainbow Trout remain in the offshore longer during the fall as individuals do not migrate up rivers until late fall or spring and usually spawn from late December to late April (Dodge & MacCrimmon, 1970; Stewart & Bowlby, 2009). River spawning occurs for Chinook and Coho Salmon from late September and early October and Atlantic Salmon can spawn as late as November (Scott & Crossman, 1973). Rainbow Trout and Atlantic Salmon are iteroparous (spawn more than once), while Coho and Chinook Salmon are semelparous (spawn only once and die after) (Scott & Crossman, 1973).

The diet of Great Lakes adult Chinook and Coho Salmon consists mainly of Alewife and Rainbow Smelt (Brandt, 1986a; Stewart & Ibarra, 1991; Rand & Stewart, 1998; Jacobs et al., 2013). In addition, Coho Salmon in Lake Ontario also forged upon

Brown Trout and Lake Trout exhibit similar life history strategies to their open-lake, epilimnetic dwelling counterparts. Brown Trout inhabiting the Lake Ontario watershed commonly occur in both tributary and open lake habitats and within-basin movement of Brown Trout has been observed (Haynes & Nettles, 1983; Cunjak & Power, 1986; Zimmer & Power, 2006). In the province of Ontario, Brown Trout spawn from early October to late November in shallow, gravel lined riparian headwaters and are iteroparous (Mansell, 1966; Scott & Crossman, 1973; Zimmer & Power, 2006). In Lake Ontario, Brown Trout consume mainly Alewife (Brandt, 1986a; Rand & Stewart, 1998), Rainbow Smelt (Brandt, 1986a; Rand & Stewart, 1998), but also consume sculpin (species not identified) (Brandt, 1986a), Yellow Perch (Brandt, 1986a), and insects (Brandt, 1986a). The Great Lakes are southern range for Lake Trout and are well adapted to cold, deep oligotrophic lakes (Shuter et al., 1998; Page & Blur, 2011). During the summer, Lake Trout occupy the coldest waters but become well distributed during the fall (Mackenzie-Grieve & Post, 2006). The Lake Trout life history is described by late maturity, low reproductive potential, slow growth, and a slow replacement rate (Shuter et al., 1998). Post-spawned Lake Trout tend to move large distances away from spawning reefs in large lake systems and return the following October to spawn (Rahrer, 1965; Scott & Crossman, 1973). Great Lakes Lake Trout populations generally inhabit bathymetric depths shallower than 73 m (Dryer, 1966; Hansen et al., 1995). Great Lakes
Lake Trout prey upon Alewife (Madenjian et al., 1998, Madenjian et al. 2006, Jacobs et al., 2010), and Round Goby (Dietrich et al. 2006, Jacobs et al., 2010; Rush et al., 2012), Cottus spp. (freshwater sculpins) (Dryer et al., 1965, Madenjian et al., 1998, Madenjian et al. 2006, Jacobs et al., 2010), Rainbow Smelt (Dryer et al., 1965, Madenjian et al., 1998, Madenjian et al. 2006, Jacobs et al., 2010), Coregonus spp. (whitefishes) (Dryer et al., 1965, Madenjian et al., 1998, Madenjian et al. 2006), and invertebrates (Madenjian et al., 1998, Madenjian et al. 2006).

Historically, Slimy and Deepwater Sculpin are benthivorous fishes that forage on Mysis relicta and to a greater extent, Diporeia hoyi for Deepwater Sculpin (Brandt, 1986b; Madenjian et al., 2005). Slimy Sculpin are generally abundant between the lower metalimnion to 70 m bathymetric depth while, Deepwater Sculpin are abundant at bathymetric depths greater than 90 m, with both species overlapping between 70 to 90 m (Wells, 1968; Kraft & Kitchell, 1986). Planktivorous Rainbow Smelt and Alewife, both spawn in nearshore (bathymetric depths between 30 m and 5 m) and near-nearshore areas (bathymetric depths less than 5 m) during the spring (Rupp, 1959; Street et al., 1975; Walsh et al., 2005; O’Brien et al., 2012). During periods of high water stratification (e.g., well established thermoclines), Alewife and Rainbow Smelt have little niche overlap in the pelagic zone with age-1+ Rainbow Smelt inhibiting in the hypolimnion during the day and undergo diel vertical migration in the night into metalimnion and lower epilimnion zones to feed (Ferguson, 1965; Evans & Loftus, 1987). As well, during non-stratification cycles, Rainbow Smelt forage throughout the water column (Nellbring, 1989). During high stratification cycles, adult Alewives are dispersed in the metalimnion and epilimnion zones and in the absence of stratification, Alewives are most present along the profundal zone in depths less than 100 m (Olson et al., 1988; Johannsson & O’Gorman, 1991;
Walsh et al., 2008). Lake Ontario Alewives have been observed to undergo seasonal migrations to avoid cooler surface water temperatures during the winter (Bergstedt & O’Gorman, 1989). The Round Goby habitat spans from nearshore areas (river mouths, harbours) to offshore areas and prefer cobble and rocky substrates (Janssen & Jude, 2001). Round Gobies undergo offshore winter migration (late fall to early spring) likely due to the freezing of interstitial spaces (Kovtun, 1980; Miller, 1986; Lynch & Mensinger, 2012) and possibly to behaviourally thermoregulate. Much of the Round Goby diet is composed of Dreissenidae mussels although other invertebrates are consumed as well and is correlated with Round Goby length (Kuhns & Berg, 1999; Barton et al., 2005, Brush et al., 2012)

1.5 Rationale

The bathymetry (Flint, 1986), water temperature (Pickett & Richards, 1975), water currents (Simons & Schertzer, 1987), water volume (Grady, 2007), and diverse prey base (Christie, 1974) of Lake Ontario has allowed for cold water non-native and native Salmonidae species (Atlantic Salmon, Brown Trout, Chinook Salmon, Coho Salmon, Lake Trout, and Rainbow Trout) and their common corresponding forage fishes (Alewife, Round Goby, Rainbow Smelt, Deepwater Sculpin and Slimy Sculpin) to develop a coexisting food web structure. Lake Ontario supports a large Pacific salmonid (Chinook Salmon, Coho Salmon, & Rainbow Trout) recreational fishery, which has high economic value, and also helps control invasive forage fish abundance (Alewife & Rainbow Smelt) (Crawford, 2001; Madenjian et al., 2002).

The most recent published studies that examined diets composition of each
salmonid simultaneously (excluding Atlantic Salmon) were Brandt (1986a) and Jones et al. (1993). Much change has been observed in Lake Ontario, specifically the introduction of invasive species (Dreissenid mussels, predatory cladocerans, and Round Goby) since the late 1980’s/ early 1990’s. Brandt (1986a) examined the Lake Ontario salmonid diets (Atlantic Salmon was not examined) in an era before zebra mussels (Dreissena polymorpha) and Round Goby and concluded that salmonids fed almost exclusively on Alewife and Rainbow Smelt with significant diet overlap. Jones et al. (1993) examined the salmonid diet (excluding Atlantic Salmon) using predator-prey models during the early invasion stages of the zebra mussel. Jones et al. (1993) concluded that Chinook Salmon had the greatest allocated predation demand on large Alewives (66.4%), followed by Brown Trout (12.6%), Lake Trout (11.7%), Rainbow Trout (7.2%), and Coho Salmon (2.2%). Also, this is the first study also to examine the diet and niche structure of Lake Ontario Atlantic Salmon using stable isotopes. Atlantic Salmon were once abundant in Lake Ontario and were extirpated by the 1890’s due to anthropogenic practices (overfishing, wetland drainage, forest clearing near critical habitat, pollution, & dam/barrier construction) and the occurrence of thiamine deficiency through consumption of Alewives (Smith, 1892; Webster, 1982; Smith, 1995; Ketola et al., 2000). Since 2009, there has been a large increase in Atlantic Salmon stocking into Lake Ontario supported by the Ontario Federation of Anglers and Hunters and the Ontario Ministry of Natural Resources (FWS/GLFC, 2010; OFAH, 2013).

Recently, Rainbow Smelt populations have been highly reduced in both the nearshore and offshore areas of Lake Ontario compared to the Alewife population (OMNR, 2013). In addition, the Lake Ontario Rainbow Smelt population in 2012 was estimated at 63 million yearling and older fish, a historic low (ONMR, 2013). The recent
proliferation of the invasive Round Goby throughout the nearshore and offshore habitats of the Great Lakes has caused changes to the food web, including potential changes to the salmonid diet and niche structure (Kuhns & Berg, 1999; Janssen & Jude, 2001; Lauer et al., 2004; Barton et al., 2005; Rush et al., 2012). Round Goby have replaced Rainbow Smelt as the second most important Lake Trout diet item (Rush et al., 2012). Round Goby may serve as a functional analogue for sculpin as these species inhabit the benthic. The establishment of Dreissenidae mussels (*Dreissena polymorpha* & *Dreissena bugensis*) in Lake Ontario, has caused a rapid change in the carbon flow and biomass acquired by the top predators (salmonids) because of highly regulated bottom-up controls (Stewart & Sprules, 2011; Rush et al., 2012). Dreissenid mussels potentially caused Alewife and Rainbow Smelt to reside in deeper waters during April to June, as the dreissenid mussels caused changes in the flux of certain nutrients, with most nutrients now retained in the nearshore benthos (O’Gorman et al., 2000; Hecky et al., 2004). The retention of nutrients in the nearshore most likely coincided with a decline in plankton, benthos and bacteria biomass (O’Gorman et al., 2000; Stewart & Sprules, 2011). This change in primary productivity reduced predation by age-1 and older Rainbow Smelt on age-0 Rainbow Smelt and was observed to reduce predation by Alewife on juvenile Lake Trout emerging from nearshore spawning grounds (O’Gorman et al., 2000). In the past decade, there has been resurgence in the Deepwater Sculpin population in Lake Ontario (Lantry et al., 2007). This is likely due to Alewife population decline as Alewife most likely interfere with Deepwater Sculpin reproduction (consume Deepwater Sculpin juveniles) (Madenjian et al., 2005).
1.6 Objectives and Hypotheses

This thesis examines the trophic positions, habitat use and isotopic niche widths and overlap using δ¹⁵N and δ¹³C of the important forage fish (Chapter 2) and salmonids (Chapter 3) of Lake Ontario.

Chapter Two (Spatial and seasonal patterns of stable isotopes and isotopic niche width in Lake Ontario forage fish)

Using a large number of samples (n= 2037) collected in Lake Ontario in 2013, the objective of this chapter is to quantify trophic position, habitat use and isotopic niche widths of the five major forage fish species (related to salmonid diet) using δ¹⁵N and δ¹³C. Based on previous studies on the Great Lakes and other freshwater ecosystems, I hypothesize:

1) Round Goby and Rainbow Smelt will have the largest isotopic niche widths of the five forage species.

2) Isotopic niche overlap will only occur between Alewife and Rainbow Smelt, pelagic species, and between the other three benthic fishes.

3) Discrete subpopulations, based on stable isotopes, will be more evident in benthic fishes due to reduced spatial movement across the lake benthos than the more pelagic species.

Chapter Three (Niche space, overlap, and diet reconstruction of Lake Ontario salmonid species using stable isotopes and gut contents)

This chapter will examine the trophic positions, habitat use and isotopic niches of the five major Lake Ontario salmonids using δ¹⁵N and δ¹³C from samples collected in 2013. Based on previous studies on the Great Lakes and other freshwater ecosystems, I
hypothesize:

1) Lake Trout will have the most diverse diet and largest isotopic niches.

2) Chinook and Coho Salmon will have specialised diets and small isotopic niches.

3) Niche overlap should be highest among Pacific salmon species, and lowest between those species and Lake Trout.

4) Brown and Rainbow Trout will have diverse diets but Brown Trout will feed across habitats while Rainbow Trout will feed across trophic positions.

5) Stable isotope values of Atlantic Salmon should reflect an offshore value but the diet should be composed mostly of Alewife and Rainbow Smelt.
1.7 References


Hobson, K.A. & H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using \( \delta^{13}\)C and \( \delta^{15}\)N analysis. Marine Ecology Progress Series 84: 9-18.


Figure 1.1. Lake Ontario sampling sites completed using twelve different transects (six in the USA and six in Canada) and seven salmonid creel survey locations (all in Canada) in 2013. Transect length and direction represented by arrow length and position. Circles represent were transects were undertaken and stars present were salmonid creel surveys were administered.
CHAPTER 2
SPATIAL AND SEASONAL PATTERNS OF STABLE ISOTOPES AND ISOTOPIC NICHE WIDTH IN LAKE ONTARIO FORAGE FISH

2.1 Introduction

The Lake Ontario forage fish community is currently dominated by Alewife \((Alosa pseudoharengus)\); an invasive pelagic fish that is key in supporting the salmonid recreational fishery (Detmers et al., 2012). Rainbow Smelt \((Osmerus mordax)\), another invasive species, have undergone a large population reduction in recent years (Holden & Connerton, 2015), most likely due to foraging pressure from the large salmonid population. The most recent invading forage fish, the Round Goby \((Neogobius melanostomus)\), first sighted in western Lake Ontario in 1998, have become highly abundant in benthic habitats of the littoral and offshore regions of Lake Ontario (Owens et al., 2003; Pennuto et al., 2012). The only native offshore forage fish species are the Deepwater \((Myoxocephalus thompsonii)\) and Slimy \((Cottus cognatus)\) Sculpin. These populations appear to be small (Walsh et al., 2014), although there are some indicators (e.g., catch per trawl) that suggest a resurgence in Deepwater Sculpin (Lantry et al., 2007; OMNR, 2013). A number of other previously abundant native forage fish species, such as the Bloater \((Coregonus hoyi)\), are considered extirpated. Despite their importance to the Lake Ontario ecosystem and the other Laurentian Great Lakes, there is little current information on the ecology of the forage fish community, particularly habitat use and resource partitioning between species and how this varies across space and season.

Interactions among invasive forage fish species and salmonids are important to the functioning of the Lake Ontario ecosystem and influence the provision of ecological services. The annual stocking of salmonids into Lake Ontario began in the late 1960’s to
create a recreational fishery and regulate large populations of Alewife and Rainbow Smelt, which had become a nuisance and were negatively impacting ecosystem function and services (Christie, 1974). Currently, these invasive species, mainly the Alewife, continue to support valuable recreational salmonid fisheries in Lake Ontario and the other Great Lakes (Tody & Tanner, 1966; Dettmers et al., 2012; Jacobs et al., 2013). When Alewife populations declined (e.g., Lake Huron in the past ten years), highly sought-after Chinook Salmon (Oncorhynchus tshawytscha) populations also declined (Johnson et al., 2010; Bunnell et al., 2014). Complicating this situation is the bi-national (Canada and US) objective to restore self-sustaining populations of native salmonids, Lake Trout (Salvelinus namaycush) (Elrod et al., 1995; Krueger et al., 1995) and Atlantic Salmon (Salmo salar) (Ketola et al., 2000; Stewart et al., 2014), in the Great Lakes. A diet high in Alewife, can result in thiamine deficiency in native salmonids suppressing their natural reproduction (Krueger et al., 1995; Ketola et al., 2000). The dilemma for fish managers is how to balance the potentially conflicting objectives of maintaining recreational fisheries, largely based on non-native salmonids feeding on an abundance of Alewife, while sufficiently suppressing Alewife populations to allow for self-sustaining level of native salmonid reproduction (Stewart et al., 1991; Dettmers et al., 2012). The ecological influence of the recently invaded and abundant Round Goby in Lake Ontario also needs to be better understood, particularly considering their prevalence in the diet of Lake Trout (Rush et al., 2012, Colborne et al., 2015) and potentially other species (e.g., Brown Trout Salmo trutta).

Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) are a commonly used and powerful tool to assess trophic relationships, habitat use and overall food web structure (Cabana & Rasmussen, 1994; Post, 2002; Fry, 2006). Carbon isotopes show limited
change with each trophic level step (~1‰) in aquatic food webs but provide quantitative information on carbon sources and habitat use (Hobson & Welch, 1992); in lakes, δ¹³C is generally lower in pelagic zones and higher in benthic/littoral zones (France, 1995).

Values of δ¹⁵N increase ~3-4‰ between prey source and consumer (DeNiro & Epstein, 1981; Minagawa & Wada, 1984; Vander Zanden & Rasmussen, 2001), providing quantitative information on trophic position. Nitrogen isotopes can also vary between habitats, and taken with δ¹³C can provide key information on food web structure and species/population interactions. For example, isotopic niche width can be calculated based on the distribution of δ¹³C and δ¹⁵N data and can be compared between species or populations in an ecosystem, providing insights on potential competition and niche overlap (Jackson et al., 2011).

The objective of this study was to quantify the seasonal and regional trends in δ¹³C and δ¹⁵N to assess niche overlap and resource partitioning in these important species. This was accomplished through a large, seasonally and spatially comprehensive collection and analysis of samples (n= 2037) from 2013. Based on varying life histories amongst these species (e.g., pelagic [Alewife and Rainbow Smelt] vs benthic [Round Goby, Deepwater and Slimy Sculpin], Ferguson, 1965; Brandt, 1986; Evans & Loftus, 1987; Nellbring, 1989; Janssen & Jude, 2001; Madenjian et al., 2005), and past studies on isotopes in forage species (Rush et al., 2012) we expected significant differences in isotopic niches between them. An important goal is to understand if there are discrete subpopulations, potentially via spatial differences, of these species based on stable isotopes. For example, the Niagara River plume along the south shore (Takanori et al., 1999), nutrient upwelling along the northwestern shores (Simons & Schertzer, 1987; Mills et al., 2003), abyssal depths and downwelling in the southeast (Simons & Schertzer,
1987), and islands and embayments, and outflow in the northeast (Mills et al., 2003) should result in regional differences in isotope values at the base of these food webs. We hypothesize that: i) Round Goby and Rainbow Smelt should have the largest niche widths based on previously reported diet data (Evans & Loftus, 1987; Brush et al., 2012); ii) isotopic niche overlap should only occur between Alewife and Rainbow Smelt and between the three benthic fishes based on habitat preferences; and iii) discrete subpopulations, based on stable isotopes, will be more evident in benthic fishes due to reduced spatial movement compared with the more pelagic species (Rainbow Smelt and Alewife).

2.2 Methods

Fish Collection

Coordinated binational sampling occurred on Lake Ontario in 2013 which involved many different Canadian and American provincial/state and federal agencies organized under the Cooperative Science Monitoring Initiative (CSMI) program. Fishes were collected with a combination of vertical gillnets, horizontal gillnets, seine nets and trawl nets, which were set at depths of one to 175 m from April to October 2013 (Figure 2.1). In American waters, the transects completed were Nine Mile Point (depths from 15 to 175 m), Olcott (depths from 15 to 110 m), Oswego (depths from 4 to 50 m), Rochester (depths from 8 to 170 m), Smoky Point (depths from 18 to 78 m) and Thirty Mile Point (depths from 15 to 175 m). In Canadian waters, the transects completed were Cobourg (depths from 1 to 60 m), Flatt Point/Eastern Basin (depths from 5 to 35 m), Rocky Point (depths from 1 to 100 m), Port Credit (depths from 45 to 100 m) Niagara (depths of 18 to
80 m) and a transect across the Western Basin from Port Dalhousie to Humber Bay (from depths of 15 m in Port Dalhousie to approximately 120 m at the maximum to depths of 12 m in Humber Bay).

A variety of techniques were used to collect the forage fish. Seine nets were used to sample near-nearshore (0-5 metres depth) locations and vertical and horizontal gillnets were used to collect samples from the nearshore (5-30 metres depth) to offshore pelagic areas (>30 metres deep) deployed on the order of hours. Vertical gillnets were used to sample the upper 30 metres of the water column. Benthic areas of the nearshore and offshore (offshore benthic areas, >30 metres deep) were sampled using trawl nets for up to a period of 24 minutes depending on site depth and government agency.

During fish collection, fish were identified to species and then stored on ice to be sampled later in the laboratory. Before dissection, fish were weighed (g) and total length (mm) was recorded for all species with only fork length (mm) recorded for Alewife and Rainbow Smelt. Dorsal muscle was removed above the lateral line and posterior to the head, placed in a 2 ml cryovial, frozen and freeze dried for 48 hours at -20°C for stable isotope analysis. Table 2.1 provides the distribution of species sample sizes by quadrat, season and bathymetric depth.

Stable Isotope Analysis

Approximately two grams of freeze dried fish muscle tissue was homogenized to a fine powder using either surgical scissors or mortar and pestle depending on muscle size and density. Bulk (non-lipid extracted) powdered muscle samples were weighed into 5 × 9 mm tin capsules on a microbalance with weights between 400 to 600 µg. An elemental analyzer (Costech, Valencia, CA, USA) was used to combust the muscle sample into CO₂
and \( \text{N}_2 \) gases and the relative abundances of carbon \( (^{13}\text{C}/^{12}\text{C}) \) and nitrogen \( (^{15}\text{N}/^{14}\text{N}) \) were then determined using a Thermo Finnigan Delta V mass spectrometer (Thermo Finnigan, San Jose, CA, USA). The carbon to nitrogen ratio (C:N) was measured simultaneously during stable isotope analysis to determine if lipid contents were high in the muscle, C:N ratios \(<3.4\) were considered to have low lipid (Post, 2002). Few samples had C:N \(>3.4\) and therefore no lipid extraction was done on any samples. Standard delta notation (\( \delta \)) was used to express \( \delta^{15}\text{N} \) and \( \delta^{13}\text{C} \) in parts per thousand (‰) differences from a standard material as followed:

\[
\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000,
\]

where \( R = ^{13}\text{C}/^{12}\text{C} \) or \( ^{15}\text{N}/^{14}\text{N} \) (Hobson & Clark 1992, Fry, 1991). Standard reference materials included Pee Dee Belemnite for carbon and atmospheric nitrogen. During the analysis, National Institute of Standards and Technology (NIST) standards were used to calculate the precision and accuracy of analysis. NIST standards used for \( \delta^{15}\text{N} \) were NIST 8573 (L-glutamic acid), 8548 & 8547 (both ammonium sulphate) and for \( \delta^{13}\text{C} \) were NIST 8573 (L-glutamic acid) & 8542 (sucrose) \((n = 96 \text{ for each})\) and deviations of our analyses of standards using the NIST values were \( \leq0.0\%\) for both \( \delta^{15}\text{N} \) and \( \delta^{13}\text{C} \) from the certified values. The analytical precision based on NIST 1577c (bovine liver) and the internal lab standard Tilapia \((n = 318)\) had a standard deviation of \( <0.2\%\) for \( \delta^{15}\text{N} \) and \( <0.1\%\) for \( \delta^{13}\text{C} \).

**Statistical Analysis**

General linear models (GLMs) were used to investigate the impact of four explanatory variables on the values of \( \delta^{15}\text{N} \) and \( \delta^{13}\text{C} \) in Lake Ontario forage fish, including: (1) total length, (2) quadrat (a factor centered on differences in lake physiochemical properties; northwest, northeast, southwest, and southeast), (3) season (spring –
March 31 to June 30, summer – July 1 to September 30, fall – October 1 to December 31) and, (4) bathymetric depth (nearshore (<30 m) and offshore (>30 m). Nearshore and offshore waters were defined as where the thermocline intersected with the lake bed, which is approximately 30 m deep for Lake Ontario in late summer or early fall in the Great Lakes (Edsall & Charlton, 1997). The general linear models used a Gaussian or Gamma error distribution with either log, identity, or inverse link function as warranted by the data. A small number of extreme outliers exhibiting high leverage (i.e., high influence on the model) were removed from the analysis. Both a deletion test approach and an information-theoretic approach were used to identify the ‘best’ model (Crawley, 2005). For the deletion test approach, a maximal model was fit for each isotope-species combination that included all explanatory variables. After a series of deletion tests (Chi-square and F-tests), a minimal adequate model was determined when all terms remaining were significant. The minimal adequate model was also determined using the information-theoretic approach based on the model with the lowest Akaike Information Criterion from a complied pool of candidate models (Burnham & Anderson, 2004). The GLM goodness-of-fit was assessed using an approximate likelihood ratio test.

Stable Isotope Bayesian Ellipses in R (SIBER) in the package Stable Isotope Analysis in R (SIAR) v.4.2 (Parnell & Jackson, 2013) in R v.3.0.2 (R Development Core Team, 2013) was used to analyze isotopic niche space of the forage fish species in Lake Ontario. Developed by Jackson et al. (2011), SIBER uses a multivariate ellipse-based approach to compare groups of differing sample sizes. Standard (40%) ellipse areas (SEA_C) represented the core (40%) isotopic niche area and allowed for a strong comparison for varying sample sizes between species. Calculated using SEA_C, fraction
overlap (%) of the forage fish species isotopic niche was used to determine differences and similarities in niche space utilization.

2.3 Results

Fish size and stable isotope data

Round Goby had the smallest and Alewife the largest mean body lengths (mm) of the forage fish species collected from Lake Ontario, consistent with the known sizes of adults (Table 2.2). Alewife size (mm) did not vary by quadrat (p=0.57; ANOVA) or bathymetric depth (p=0.50), but got larger with season (p<0.01). Rainbow Smelt size (mm) did not vary by quadrat (p=0.16) or season (p=0.10) but increased with bathymetric depth of collection (p<0.01; <30 m = 99.9 ± 3.5 mm (mean ± SE); >30 mm = 113.7 ± 1.6 mm). Round Goby size (mm) varied by quadrat (p=0.01; largest in the southeast: 98.0 ± 4.1 mm; smallest in the northeast: 85.7 ± 2.3 mm) but did not vary by season (p=0.92) or bathymetric depth (p=0.14). Deepwater and Slimy Sculpin size (mm) varied by quadrat and got larger with season (both p<0.01); bathymetric depth was not assessed as neither sculpin species were collected in depths <30 metres. Values of $\delta^{13}$C ranged from -21.8 ± 0.1 (mean ± SE) in Round Goby to -24.7 ± 0.1 in Deepwater Sculpin, and $\delta^{15}$N ranged from 12.6 ± 0.04 in Alewife to 16.9 ± 0.04 in Deepwater Sculpin (Table 2.2).

Isotopic niche area and overlap

Across all seasons, quadrats and bathymetric depths, Round Goby had the largest isotopic niche area ($6.1^{\%}^2$, SEA$_C$), followed by Alewife ($3.4^{\%}^2$) while Rainbow Smelt, Slimy Sculpin and Deepwater Sculpin had the smallest and similar areas ($1.7-1.8^{\%}^2$; Table 2.3; Figure 2.2). This relative ranking of forage fish species by SEA$_C$ remained
even when data was analyzed by season, bathymetric depth or by quadrat (Table 2.3).
With the exception of Alewife, there was a general trend towards smaller \( \text{SEA}_C \) as season progressed from spring to fall with no obvious trends with quadrat or bathymetric depth. Only the Slimy and Deepwater Sculpin showed large isotopic niche overlap (63 to 69% between sculpin species) (Table 2.3). Round Goby isotopic niche overlapped 15% with Rainbow Smelt, which accounted for 4% of Round Goby’s isotopic niche width. No other species showed any isotopic niche overlap (Table 2.3).

**General Linear Model Regressions**

The minimal adequate models revealed significant habitat-related and spatial structuring of \( \delta^{13}C \) and \( \delta^{15}N \) of all five forage fish species (Table 2.4). Identification of the minimal adequate models was not affected by model selection as both the information-theoretic and deletion test approaches generated identical models. For all species, models explained more variation (51.8 to 63.0%) in \( \delta^{15}N \) than \( \delta^{13}C \) (4.5 to 42.2%) (Table 2.4).

Minimal adequate models explained more of the variation in Alewife \( \delta^{15}N \) (60.9%) than \( \delta^{13}C \) (18.5%), and indicated that quadrat, season and total length, and most of the corresponding interactions, were significant, but bathymetric depth was not for either isotopes (Table 2.4). The direction and strength of the total body length-\( \delta^{15}N \) relationship in Alewife varied significantly by season and quadrat: \( \delta^{15}N \) decreased with size in the spring for all regions (quadrat) (all quadrats during spring: \( p<0.001 \)) but increased during the summer months (all quadrats during summer: \( p<0.001 \)) except in the northeast (\( p=0.305 \)); only in the southeast was the total body length-\( \delta^{15}N \) relationship significant during the fall (\( p<0.001 \)). Fewer total body length-\( \delta^{13}C \) relationships were significant for Alewife, as \( \delta^{13}C \) increased with size across all quadrats during the spring.
except in the northwest (data not shown). Changes in $\delta^{13}$C increased and decreased with size depending on quadrat in the summer but only in the northwest were the relationship significant during the fall (data not shown).

Rainbow Smelt stable isotopes GLMs explained 54.8 and 31.9% of the variability in $\delta^{15}$N and $\delta^{13}$C, respectively, with all four explanatory variables and most of the corresponding interactions being significant (Table 2.2). The total body length-$\delta^{15}$N relationship decreased for Rainbow Smelt during the spring ($p<0.001$) but was not significant for summer ($p=0.111$) and fall ($p=0.968$) (Figure 2.4). Rainbow Smelt $\delta^{13}$C increased with increasing total length only in the northwest and northeast during the spring, with no significant $\delta^{13}$C trends observed in the southwest and southeast. Carbon ($\delta^{13}$C) increased with increasing total length in the northeast during the summer, as no other significant trends were detected in the other quadrats during the summer. No significant trends were observed in the fall in any of the quadrats (data not shown).

For Round Goby, minimal adequate models explained 63.0 and 42.2% of the variability in $\delta^{15}$N and $\delta^{13}$C respectively, with all four variables and most of the corresponding interactions significant (Table 2.4). Round Goby $\delta^{13}$C decreased with increasing total length only in the summer except in the southwest (no significant $\delta^{13}$C trend observed) and only in the southeast quadrat during the fall. No significant $\delta^{13}$C trends were observed in the other quadrats during the fall and no significant $\delta^{13}$C trends were present in the spring in any of the quadrats (data not shown). A positive total body length-$\delta^{15}$N relationship was significant for Round Goby in spring ($p=0.003$) and summer ($p=0.030$) but not the fall ($p=0.598$) (Figure 2.5). Values of $\delta^{15}$N also varied between the north and south quadrats (the respective east and west quadrats were merged since low sample number in the four quadrat system did not produce significant isotopic differences
between the nearshore and offshore (i.e., bathymetric depth) in each season (Figure 2.6). Round Goby $\delta^{15}$N was higher in the offshore in all seasons (Figure 2.7). Values of $\delta^{13}$C were also merged between the north and the south but did not yield significant results.

Stable isotopes in Deepwater and Slimy Sculpin were not influenced by most of the variables or interactions (Table 2.2). Models for $\delta^{13}$C explained a very small proportion of the variability in Deepwater Sculpin (4.5%) and Slimy Sculpin (6.8%) but models explained more variability for $\delta^{15}$N (51.8% for Deepwater Sculpin; 57.4% for Slimy Sculpin). For Deepwater Sculpin, $\delta^{15}$N increased significantly with total length in all seasons (spring: $p<0.001$; summer: $p=0.012$; fall: $p<0.001$) (Figure 2.8). For Slimy Sculpin $\delta^{15}$N were found to significantly decrease over season with the lowest values observed in the fall (16.3 ± 0.1‰, mean ± SE) compared to 16.8 ± 0.1‰ during the spring and summer (Figure 2.9).

2.4 Discussion

Lake Ontario forage fishes had unique isotopic niches, both in size and overlap, suggesting partitioning of and minimal competition for dietary resources. The exception was the closely related sculpin species, Deepwater and Slimy, which had similar isotopic niche width sizes and significant overlap (>63%). These relative relationships held when isotopic niches were calculated for different seasons, quadrats, and depth of collection in the lake, strongly suggesting that these are species characteristics not environmentally driven. Stable isotopes revealed discrete subpopulations by region (quadrat) for Alewife, Rainbow Smelt and Round Goby in Lake Ontario, which varied between seasons for particular species, but not the sculpin species.
Isotopic Niche Width & Overlap

Round Goby had the largest overall isotopic niche width (6.1‰²), almost twice as large as Alewife and over three times the area of the other forage fish species. Some of this larger niche size was explained by differences across season, depth of collection and quadrat, although even when these influences are considered the Round Goby still had the largest niche widths of the species examined. Round Goby have been observed in multiple habitats and have moderately high site affinity once a home range has been established (Charlebois et al., 1997; Ray & Corkum, 2001), and isotope values may be reflecting regional and even smaller scale variation in habitat which is likely accounting for some of the variation in δ¹³C values observed. Additional variation in isotope values may also be associated with ontogenetic changes in the diet of Round Goby, which has been observed in bays of Lake Ontario and other regions of the Great Lakes, even when small and larger Round Gobies co-inhabit an area (Barton et al., 2005; Brush et al., 2012).

There is large broad variation in the Round Goby δ¹⁵N values (9.9 to 18.6), indicating that Round Goby consume prey from various trophic positions. This is likely due to that this species inhabit both deep water and littoral zones, and appear to migrate between them seasonally (Bunnell et al., 2005; Walsh et al., 2007). Deep-water habitats tend to have higher δ¹⁵N relative to littoral regions (Mulholland et al., 2000), which could explain some of the variation in δ¹⁵N in the Round Goby. Regardless, the Round Goby population as a whole is integrating a large range of carbon and nitrogen sources and habitats, and given it’s increasing importance as prey to a number of top predators (Rush et al., 2012; Hebert et al., 2014), this species has become an important, and unique, link in the Lake Ontario salmonid food web.
The relatively large isotopic niche area, and separation from the benthic species, indicated that Alewife are planktivores, consistent with previous studies that demonstrated they consume largely zooplankton, have plastic diets and will consume plankton of invasive origin relatively quickly after invasion (Mills et al. 1992; Bushnoe et al., 2003; Walsh et al., 2008; Stewart et al., 2009). Some season and quadrat variation in isotopic niche also support the plasticity of the planktonic diet of the Alewife, as these changes likely reflect change in diet due to variation in zooplankton abundance and diversity over season and space in Lake Ontario (Stewart et al., 2009). The importance of plankton in the diet of Alewife resulted in low $\delta^{15}N$ values, suggesting this species feeds at a lower trophic position than other forage fishes. Some variation in Alewife isotopes may also reflect predation on fish fry at certain times of the year, although this occurs infrequently in Lake Ontario (Krueger et al., 1995).

The unique isotopic niche of the Alewife compared with the other forage fish and low $\delta^{13}C$ (-28.1 to -20.6) is consistent with their offshore pelagic habitat use (Wells, 1968) and location of main prey (Mills et al., 1992; Walsh et al., 2008). Rush et al. (2012) presented stable isotope data on Alewife at discrete points from 1995 to 2008, and those data, in combination with our own, show little variation in either $\delta^{13}C$ or $\delta^{15}N$ suggesting little change in Alewife diet or niche in the past 20 years. There is evidence of shift in Alewife habitat use and diet since the invasion of dreissenid mussels in the late 1980’s/early 1990’s to cooler water and deeper depths in the spring (O’Gorman et al., 2000).

Stable isotopes revealed that Rainbow Smelt consume prey from various trophic positions (i.e., plankton to fish) based on a broad $\delta^{15}N$ spread but consume prey within a particular habitat based on a narrow range of $\delta^{13}C$. This fits with previous studies in Lake Ontario, where Rainbow Smelt were found to consume prey that were mainly offshore
pelagic and benthic and vary in trophic position (Brandt & Madon, 1986), preying primarily on fish and large invertebrates (e.g., *Mysis relicta*) (Parker Stetter et al., 2005). This range of $\delta^{15}N$ in Rainbow Smelt could be driven by ontogeny, as age-1 and greater individuals start to incorporate fish, including cannibalism, into their diet (Evans & Loftus, 1987), although we found $\delta^{15}N$ decreased with length in the spring and was not significant in the summer or fall. Diets probably did not change with increasing length as both small and large individuals fed on similar prey. Similar $\delta^{15}N$ values were found in Rainbow Smelt sampled from Lake Ontario (1995-2008; 15.4‰) (Rush et al., 2012), suggesting no recent change in diet despite the large population decline in yearling-and-older individual fish (OMNR, 2013), that are primarily piscivores.

Isotopic niche overlap between Rainbow Smelt and Round Goby was <15%, suggesting potential to share some resources. The overlap may be due to both species consuming benthic invertebrates, such as from the Order Diptera (e.g., Chironomidae) was has been reported as a diet item for both species, although more water column situated species (e.g., Copepoda) have also been reported for both (Evans & Loftus, 1987; Brush et al., 2012). Whether this 15% overlap is significant to either population is difficult to assess with these data, but competition between Round Goby and Rainbow Smelt for common resources may be contributing among other factors to the decline of Rainbow Smelt in Lake Ontario.

The two sculpin species, Deepwater and Slimy, had the highest $\delta^{15}N$ and no isotopic niche overlap with the other species. These species reside in the deep zones (>30 m) of Lake Ontario, with little to no migration to the nearshore benthic, and are clearly utilizing a unique deepwater carbon. The high $\delta^{15}N$ is most likely due to different ratios and higher $\delta^{15}N$ in the environment of deep-water regions, caused by benthic nutrient
cycling in the offshore (Mulholland et al., 2000), rather than feeding at a higher trophic level than the other forage fish species. Benthic areas are usually higher in $^{15}$N because of the greater uptake of nitrogen based compounds needed for biological function (Mulholland et al., 2000). Indeed, invertebrates, historically Diporeia hoyi and M. relicta, were the major prey items of both Deepwater and Slimy Sculpins (Kraft, 1977; Wells, 1980). D. hoyi decreased in the 1990’s in Lake Ontario (Dermott, 2001; Lozano et al., 2001; Birkett et al. 2015) and Walsh et al. (2008) found that the more recent diet of Lake Ontario Slimy Sculpin diet consists mainly of M. relicta, although Slimy Sculpin continue to favour Diporeia spp. when common in particular areas. There was minimal change to the isotopic niche area in both species by quadrat and season, and stable isotope values were not influenced by region (quadrat) and season, which suggests little differences in the diet of the sculpin species compared to historical gut content data and likely very little spatial variation in the stable isotopes of the deep-water zone of Lake Ontario.

The highest isotopic niche overlap was found between the sculpin species (>63%) which is consistent with diet overlap indexes based on stomach contents in the Great Lakes basin (51%, Hondrop et al., 2005 and >60%, Martin 1984). The higher overlap observed in our study may reflect a decrease in D. hoyi and greater reliance on Mysis species; in other Great Lakes Mysis contribute to the majority of the Deepwater Sculpin diet (Mychek-Londer et al., 2013). The influence of this high overlap on the population status of these species is unknown.

**Trends in Stable Isotopes: Evidence for Discrete Subpopulations**

Rainbow Smelt and Alewife, pelagic species expected to have a homogenous population of individuals because of increased mobility across and through the water column. Instead these species were found to have discrete spatial subpopulations based on
variation in stable isotopes across quadrats. This variation in isotopes between regions (quadrats) is likely driven by nutrient and water sources (e.g., Niagara River or urban areas such as Hamilton Harbour), and demonstrates that these subpopulations are utilizing different dietary resources and/or the stable isotope values of the dietary resources are different between quadrats due to lake physio-chemical properties. But this does not provide information on whether these subpopulations may overlap spatially at specific times of the year (e.g., winter). Currently we do not have data to support whether these sub-populations are established every year based on stable isotope values. If there is some evidence to support the establishment of forage fish sub-populations, this may have implications for how these forage fish are managed and evaluated as additional stable isotope data needs to be collected in the future.

In addition to quadrat, Alewife $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were influenced by body length and season. For the larger Alewife (>150 mm), isotope values were consistent across season and the variation observed by season was driven by changes in the isotopes of the smaller alewife (<150 mm). Smaller sized Alewife were found to feed on a higher $\delta^{15}\text{N}$ diet, which was probably driven more by habitat differences than trophic level as smaller Alewife are likely further nearshore than larger individuals. The overwintering habit of Alewives in Lake Ontario suggested that yearlings are more nearshore than adults (Bergstedt & O’Gorman, 1989), and this habit is probably similar during the spring. During the spring, Stewart et al. (2009) found that sub-adult (<109 mm) and adult (>109 mm) had different diets between each size cohort as adults contained much more *Bythotrephes longimanus* in their diets. Compared to adults, the sub-adult diet contained much more cyclopoid copepods (Stewart et al., 2009). Smaller individuals collected in 2013 probably also contained a high proportion of cyclopoid copepods which could have
increased the overall $\delta^{15}N$ value. As the seasons progressed and the small Alewife continued to feed, their isotope values converged towards the adult values, suggesting consumption of similar prey during the spring to fall periods, likely pelagic, offshore zooplankton. Sub-adults have been recorded to feed on >90% zooplankton not including *Cercopagis pengoi* and *B. longimanus* (Stewart et al., 2009), although Mills et al. (1992) and Urban & Brandt (1993) observed that sub-adults did not consume *M. relicta*.

Carbon isotope values showed similar trends with size to $\delta^{15}N$ in Alewife, but explained a third of the variation in stable isotope values. During the spring, $\delta^{13}C$ decreased with increasing size during the spring, suggesting larger Alewife are further offshore than smaller individuals. O’Gorman et al. (2000) found that spanning over a 20 year period that adults were more abundant in deeper locations than yearlings during the spring. The overwintering habit of Alewives in Lake Ontario also suggests this similar pattern with pelagic yearlings and demersal adults (Bergstedt & O’Gorman, 1989).

Similar to Alewife, Rainbow Smelt $\delta^{15}N$ decreased with increasing total length during the spring. During non-stratified periods, Rainbow Smelt forage throughout the water column (Nellbring, 1989), perhaps causing small individuals to consume benthic species including Mysids and other invertebrates potentially high in $\delta^{15}N$. This time of year would also allow larger, piscivorous adults to consume other pelagic fishes (i.e., Alewife) which may not be available during high stratification periods (e.g., summer). No total body length-$\delta^{15}N$ relationship was detected during the summer or fall probably due to similar diets. Thermal stratification may isolate Rainbow Smelt within the hypolimnion. Evans & Loftus (1987) suggested during high water stratification, both young and adult Rainbow Smelt consume similar prey resources (Brandt & Madon, 1986), but separate themselves within the water column due to differences in diel
behaviours. This spatial structure would allow both young and adults to feed on Mysids, which would account for comparable $\delta^{15}N$ values. This foraging behaviour appears to be present during the early fall as the thermocline has not yet fully disintegrated. Also similar to Alewife, models explained less of the variability of $\delta^{13}C$ than $\delta^{15}N$ in Rainbow Smelt. In the northeast, $\delta^{13}C$ was increased with total length in both the spring and summer, suggesting adults are in the northeast are associated more with benthic habitat compared to fish sampled from the other quadrants.

Models were strongest for $\delta^{13}C$ in Round Goby than any of the other forage fish species in Lake Ontario, which makes sense given this species seasonal migration to nearshore waters during the spring and summer from deeper waters in the winter where Round Gobies overwinters. Carbon ($\delta^{13}C$) decreased with increasing total length in the southeast during the fall. Round Goby migrate to the nearshore during the spring and summer (Pennuto et al., 2010; Lynch & Mensinger, 2012), although lower $\delta^{13}C$ values suggest that larger (~150 mm) Round Gobies occupy deeper depths than smaller (<150 mm) individuals.

Models for $\delta^{15}N$ were also strongest for Round Goby than any other forage fish species, although the differences were not as pronounced as the increase in $\delta^{15}N$ with total length during the spring and summer was probably related to Round Goby migration as there is likely increased benthic nutrient cycling with increasing depth. The increase in $\delta^{15}N$ with increasing size indicted a difference in diet. Barton et al. (2005) found that the importance of quagga mussels ($Dreissena bugensis$) in the diet increased with increasing total length and individuals located in >5 m depths consumed more mussels and less amphipods. Larger individuals appear to have a narrow diet base, perhaps feeding exclusively on mussels. Smaller Round Gobies have been found to consume a wider
variety of diet while inhabiting the nearshore and tributaries (Barton et al., 2005; Pennuto et al., 2010), and are perhaps considered generalists over larger Round Goby. In the Kingston Basin, diet differences were observed between small and large individuals during the spring (Brush et al., 2012). Diets appear to become similar in the summer as larger individuals migrate into the nearshore. Round Gobies collected in the fall, especially small individuals might have a diverse diet as indicated by the observed large isotopic range. Brush et al. (2012) noted that during the fall in the Kingston Basin that all Round Gobies collected had a diverse range of prey. During this season, nearshore and offshore individuals had similar $\delta^{15}$N values. Round Gobies sampled from the south shore had higher $\delta^{15}$N values across all seasons than individuals from the north shore of Lake Ontario. The large inputs of nitrogen based products into Lake Ontario, via the Niagara River is likely the driver of higher $\delta^{15}$N values detected in south shore inhabiting Round Gobies.

Models explained very little of the $\delta^{13}$C variation in both sculpin species, which would suggest a homogenous population and the adequate minimal models are likely not ecological significant. However, as these species co-inhabit the deep water region of Lake Ontario (>30 m), as stable isotopes may not be able to detect regional differences due to a limited prey base and prey preference and as well as the homogenization of the offshore lake benthic (i.e., uniform stable isotope values across the benthic). Discrete subpopulations were postulated for the sculpin species because these species exhibit little migration between the nearshore and offshore and have limited movement across the offshore lake bottom/ inter-basin movement (Wells, 1968; Brandt, 1986), but our data does not support this contention.
Ontogenetic shifts in diet are present in Deepwater Sculpin (59 to 186 mm; total length) across all seasons based on $\delta^{15}$N length relationships. Prior to the decline of *D. hoyi*, Kraft & Kitchell (1986) found that larger Deepwater Sculpin did not consume larger prey items, but now with the near absence of *D. hoyi* in the Great Lakes, results suggested that increasing prey size with increasing Deepwater Sculpin size is probably positively correlated. *Senecella calanoides* was observed to occur at high frequencies in Lake Michigan Deepwater Sculpin diets (Mychek-Londer et al., 2013). Smaller Deepwater Sculpin (50-90 mm; from Brandt, 1986) may be consuming a higher proportion of *S. calanoides* relative to larger Deepwater Sculpin to compensate for the loss of *Diporeia* species as this size cohort may not have the gape size to ingest larger *M. relicta*. The consumption of *Senecella calanoides* would decrease the $\delta^{15}$N in smaller individuals. There was also a larger variation in $\delta^{15}$N values in smaller Deepwater Sculpin which suggested that these individuals consume a larger prey suite than larger Deepwater Sculpin.

**Summary**

Isotopic niche width was found to be unique among the Lake Ontario forage fishes with high resource partitioning, excluding the sculpin species. Diet likely has a strong role in the niche overlap of these species, as Alewife are planktivores; Rainbow Smelt are piscivores and invertivores; while Round Gobies and the sculpin species (Deepwater and Slimy) are strictly invertivores, but consume varying prey types due to differences in habitat preference. Discrete subpopulations were only detected for Alewife, Rainbow Smelt, and Round Goby in terms of isotopic trends. Smaller Alewife were discovered to have ontogenetic diet shifts during the spring and summer and reside more nearshore than adults. Water stratification perhaps influenced the $\delta^{15}$N differences in
Rainbow Smelt, as adults and yearlings were demonstrated to feed at different trophic positions during the spring across Lake Ontario. Round Goby migration to the nearshore was evident during the spring and summer while smaller individuals consume prey situated more nearshore and larger individuals consume prey further offshore. Even though discrete subpopulations were not detected in the sculpin species, an ontogenetic diet shift appeared to be significant in Deepwater Sculpin. The results gathered from this study potentially show that salmonids with diverse diets should have large isotopic niche width and isotopic values will likely change over season and with location along with bathymetric depth.
2.5 References


Hobson, K.A. & H.E. Welch. 1992. Determination of trophic relationships within a high Arctic marine food web using $\delta^{13}$C and $\delta^{15}$N analysis. Marine Ecology Progress Series 84: 9-18.


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Table 2.1. Number of samples by season (Spring, Summer, Fall), bathymetric depth (<30 m, >30 m), and quadrat (NW, NE, SW, SE) per forage fish species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Season</th>
<th>Bathymetric Depth</th>
<th>Quadrat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring</td>
<td>&lt;30 m</td>
<td>&gt;30 m</td>
</tr>
<tr>
<td>Alewife</td>
<td>327</td>
<td>223</td>
<td>579</td>
</tr>
<tr>
<td>Rainbow Smelt</td>
<td>177</td>
<td>85</td>
<td>270</td>
</tr>
<tr>
<td>Round Goby</td>
<td>130</td>
<td>260</td>
<td>188</td>
</tr>
<tr>
<td>Deepwater Sculpin</td>
<td>111</td>
<td>0</td>
<td>223</td>
</tr>
<tr>
<td>Slimy Sculpin</td>
<td>85</td>
<td>0</td>
<td>209</td>
</tr>
</tbody>
</table>
Table 2.2. Total length (mm), stable isotopes ratios and C/N ratio (mean ± 1 SE) of Alewife, Rainbow Smelt, Round Goby, Deepwater Sculpin and Slimy Sculpin collected from April to November 2013 across Lake Ontario.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Total Length (mm)</th>
<th>δ¹³C</th>
<th>δ¹⁵N</th>
<th>C/N ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alewife</td>
<td>802</td>
<td>140 ± 1.41</td>
<td>-24.1 ± 0.04</td>
<td>12.6 ± 0.04</td>
<td>4.0 ± 0.03</td>
</tr>
<tr>
<td>Rainbow Smelt</td>
<td>355</td>
<td>110 ± 1.48</td>
<td>-23.6 ± 0.02</td>
<td>15.0 ± 0.07</td>
<td>3.5 ± 0.01</td>
</tr>
<tr>
<td>Round Goby</td>
<td>448</td>
<td>90 ± 1.53</td>
<td>-21.8 ± 0.09</td>
<td>13.6 ± 0.06</td>
<td>3.4 ± 0.01</td>
</tr>
<tr>
<td>Deepwater Sculpin</td>
<td>223</td>
<td>126 ± 1.69</td>
<td>-24.7 ± 0.06</td>
<td>16.9 ± 0.04</td>
<td>4.1 ± 0.06</td>
</tr>
<tr>
<td>Slimy Sculpin</td>
<td>209</td>
<td>97 ± 1.34</td>
<td>-24.6 ± 0.05</td>
<td>16.6 ± 0.05</td>
<td>3.8 ± 0.04</td>
</tr>
</tbody>
</table>
Table 2.3. Isotopic niche width (SEA_{C}: ‰²) for all samples by season, bathymetric depth and quadrat, and overlap (% for all samples) of main forage fish species (ALE=Alewife, RBS=Rainbow Smelt, RDG=Round Goby, DWS=Deepwater Sculpin, SLS=Slimey Sculpin) collected from Lake Ontario in 2013. Standard ellipse area (SEA_{C}: ‰²) calculated for season (SPR=Spring, SUM=Summer, FAL=Fall), bathymetric depth (<30 m, >30 m), and quadrat (NW, NE, SW, SE) per forage fish species.

<table>
<thead>
<tr>
<th>Species</th>
<th>SEA_{C} (‰²)</th>
<th>Season (‰²)</th>
<th>Bathymetric Depth (‰²)</th>
<th>Quadrat (‰²)</th>
<th>Isotopic Overlap (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>SPR SUM FAL</td>
<td>&lt;30 m &gt;30 m NW NE SW SE</td>
<td>ALE RBS RDG DWS SLS</td>
<td></td>
</tr>
<tr>
<td>ALE</td>
<td>3.4</td>
<td>2.3 2.5 3.1</td>
<td>3.4 3.3</td>
<td>4.3 2.6 3.6 3.7</td>
<td>-- 0 0 0 0</td>
</tr>
<tr>
<td>RBS</td>
<td>1.8</td>
<td>1.8 1.4 0.9</td>
<td>2.1 1.7</td>
<td>1.5 1.6 1.2 2.3</td>
<td>0 --- 0 0 0</td>
</tr>
<tr>
<td>RDG</td>
<td>6.1</td>
<td>7.6 5.5 4.8</td>
<td>5.5 4.0</td>
<td>3.2 4.4 4.1 5.6</td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td>DWS</td>
<td>1.8</td>
<td>1.6 2.6 1.6</td>
<td>N/A 1.8</td>
<td>- 1.2 1.3 1.3</td>
<td>0 0 0 0 0</td>
</tr>
<tr>
<td>SLS</td>
<td>1.7</td>
<td>2.0 1.2 1.3</td>
<td>N/A 1.7</td>
<td>- 2.3 1.5 1.1</td>
<td>0 0 0 0 0</td>
</tr>
</tbody>
</table>

Note: No samples were collected <30 m for either sculpin spp. and <10 sculpin spp. samples total were collected in the northwest (NW) quadrat. For isotopic overlap, please read in the left to right direction, i.e., the SEA_{C} of Rainbow Smelt overlaps only 4% of the Round Goby SEA_{C}.  

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Table 2.4. Details and formulation of the minimal adequate models for each species – isotope combination. QUAD = quadrat, SEAS = season, D30 = nearshore/offshore break point and TL = total length (in mm).

<table>
<thead>
<tr>
<th>Species</th>
<th>Isotope</th>
<th>Minimal Adequate Model</th>
<th>Error</th>
<th>Link</th>
<th>Residual Deviance</th>
<th>Residual df</th>
<th>Null Deviance</th>
<th>Null df</th>
<th>Deviance Explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alewife</td>
<td>δ¹³C</td>
<td>~ QUAD + SEAS + TL + QUAD:SEAS + QUAD:TL + SEAS:TL + QUAD:SEAS:TL</td>
<td>Gaussian</td>
<td>Identity</td>
<td>662.4</td>
<td>776</td>
<td>812.3</td>
<td>799</td>
<td>18.5%</td>
</tr>
<tr>
<td></td>
<td>δ¹⁵N</td>
<td>~ QUAD + SEAS + TL + QUAD:SEAS + QUAD:TL + SEAS:TL + QUAD:SEAS:TL</td>
<td>Gaussian</td>
<td>Identity</td>
<td>375.7</td>
<td>776</td>
<td>961.0</td>
<td>799</td>
<td>60.9%</td>
</tr>
<tr>
<td>Rainbow Smelt</td>
<td>δ¹³C</td>
<td>~ QUAD + SEA + D30 + TL + QUAD:SEA + QUAD:D30 + QUAD:TL + SEA:D30 + SEA:TL + D30:TL + QUAD:SEA:D30 + SEA:D30:TL</td>
<td>Gaussian</td>
<td>Identity</td>
<td>52.9</td>
<td>336</td>
<td>77.7</td>
<td>354</td>
<td>31.9%</td>
</tr>
<tr>
<td></td>
<td>δ¹⁵N</td>
<td>~ SEA:D30 + SEA:TL + D30:TL + Q:SEA:D30 + SEA:D30 + SEA:TL</td>
<td>Gamma</td>
<td>Identity</td>
<td>1.1</td>
<td>339</td>
<td>2.3</td>
<td>354</td>
<td>54.8%</td>
</tr>
<tr>
<td>Round Goby</td>
<td>δ¹³C</td>
<td>~ QUAD + SEA + D30 + TL + QUAD:SEA + QUAD:D30 + QUAD:TL + SEA:D30 + SEA:TL + D30:TL + QUAD:SEA:D30 + SEA:D30:TL</td>
<td>Gaussian</td>
<td>Identity</td>
<td>847.2</td>
<td>431</td>
<td>1466.1</td>
<td>447</td>
<td>42.2%</td>
</tr>
<tr>
<td></td>
<td>δ¹⁵N</td>
<td>~ QUAD + SEA + D30 + TL + QUAD:SEA + QUAD:D30 + QUAD:TL + SEA:D30 + SEA:TL + D30:TL + QUAD:SEA:D30 + SEA:D30:TL</td>
<td>Gamma</td>
<td>Identity</td>
<td>1.6</td>
<td>429</td>
<td>4.3</td>
<td>447</td>
<td>63.0%</td>
</tr>
<tr>
<td>Deepwater Sculpin</td>
<td>δ¹³C</td>
<td>~ SEAS</td>
<td>Gamma</td>
<td>Identity</td>
<td>0.3</td>
<td>217</td>
<td>0.3</td>
<td>219</td>
<td>4.5%</td>
</tr>
<tr>
<td></td>
<td>δ¹⁵N</td>
<td>~ QUAD + SEA + TL + QUAD:SEA + SEA:TL</td>
<td>Gamma</td>
<td>Identity</td>
<td>0.2</td>
<td>215</td>
<td>0.3</td>
<td>222</td>
<td>51.8%</td>
</tr>
<tr>
<td>Slimy Sculpin</td>
<td>δ¹³C</td>
<td>~ QUAD + SEA + TL + QUAD:SEA</td>
<td>Gamma</td>
<td>Identity</td>
<td>0.2</td>
<td>202</td>
<td>0.2</td>
<td>208</td>
<td>6.8%</td>
</tr>
<tr>
<td></td>
<td>δ¹⁵N</td>
<td>~ SEAS</td>
<td>Gaussian</td>
<td>Identity</td>
<td>106.8</td>
<td>205</td>
<td>119.1</td>
<td>205</td>
<td>57.4%</td>
</tr>
</tbody>
</table>

Note: Minimal adequate models with <50% deviance explained were not included as figures.
Figure 2.1. Lake Ontario forage fish sampling sites completed using twelve different transects (six in the USA and six in Canada) in 2013. Transect length and direction represented by arrow length and position.
Figure 2.2. Stable isotope bi-plot for Alewife, Rainbow Smelt, Round Goby, Deepwater Sculpin and Slimy Sculpin collected from Lake Ontario in 2013. Thick circles enclose standard (40%) ellipse areas (SEA_C) for all species with Alewife represented by a long dashed grey circle, Rainbow Smelt by a solid black circle, Round Goby by a dotted black circle, Deepwater Sculpin by a long dashed black circle, and Slimy Sculpin by a solid grey circle. Individual data points (light grey) are represented by crosses for Alewife, diamonds for Rainbow Smelt, triangles for Round Goby, circles for Deepwater Sculpin, and x’s for Slimy Sculpin.
Figure 2.3. The relationship between total length (mm) of Alewife and $\delta^{15}$N values for each quadrat (NW = northwest, NE = northeast, SW = southwest and SE = southeast) and season (Spring = black open circle, Summer = blue cross and Fall = red filled circle) collected in Lake Ontario in 2013. Numbers in parentheses indicate the sample sizes for the (top to bottom) Spring, Summer, and Fall seasons. Regression lines and 95% confidence intervals shown only for significant total body length-$\delta^{15}$N regressions.
Figure 2.4. The relationship between total length (mm) of Rainbow Smelt and $\delta^{15}N$ values by season (Spring, Summer and Fall) collected in Lake Ontario in 2013. Regression lines and 95% confidence intervals shown only for significant total length ~ $\delta^{15}N$ regressions.
Figure 2.5. The relationship between total body length (mm) of Round Goby and δ₁⁵N values for each season (Spring, Summer and Fall). Regression lines and 95% confidence intervals shown only for significant total body length-δ₁⁵N regressions.
Figure 2.6. Box plots of Round Goby $\delta^{15}$N values between north and south shore of Lake Ontario (north = northwest and northeast quadrats combined and south = southwest and southeast quadrats combined) and season (Spring, Summer and Fall). The boxplot indicates the following: median (thick line), 25\textsuperscript{th} and 75\textsuperscript{th} percentile of data (outer thinner lines), 5\% and 95\% confidence intervals (dashed lines) and outliers (open circles).
Figure 2.7. Box plots of Round Goby $\delta^{15}$N values between bathymetric depth (nearshore <30 m and offshore >30 m) and season (Spring, Summer and Fall). The boxplot indicates the following: median (thick line), 25$^{th}$ and 75$^{th}$ percentile of data (outer thinner lines), 5$^{th}$ and 95$^{th}$ confidence intervals (dashed lines) and outliers (open circles).
Figure 2.8. The relationship between total body length (mm) of Deepwater Sculpin and $\delta^{15}$N values for each season (Spring, Summer and Fall). Regression lines and 95% confidence intervals shown only for significant total body length-$\delta^{15}$N regressions.
Figure 2.9. Violin plots of Slimy Sculpin $\delta^{15}\text{N}$ values for each season (Spring, Summer and Fall). Sample size indicated in parentheses. Shape of the plots is from locally weighted density of the data estimated by kernel method. The boxplot within each violin plot indicates the following: median (open circle), 25th and 75th percentile of data (dark box) and 5% and 95% confidence intervals represent the ends of the plot.
CHAPTER 3
NICHE SPACE, OVERLAP, AND DIET RECONSTRUCTION OF LAKE ONTARIO
SALMONID SPECIES USING STABLE ISOTOPES AND GUT CONTENTS

3.1 Introduction

Lake Ontario supports a large and diverse salmonid community consisting of abundant, non-native Chinook Salmon (*Oncorhynchus tshawytscha*), Coho Salmon (*Oncorhynchus kisutch*), Rainbow Trout (*Oncorhynchus mykiss*) and Brown Trout (*Salmo trutta*) and less abundant native Lake Trout (*Salvelinus namaycush*) and Atlantic Salmon (*Salmo salar*). Collectively these fishes serve as the apex predators in the offshore, consuming large biomasses of forage fishes and exerting a cascading food web effect on lower trophic levels (Jones et al., 1993; Mills et al. 2003; Stewart et al., 2013).

Additionally, the salmonid recreational fishery generates an annual economic impact in excess of $100 million (Connelly and Brown, 2009; Anonymous, 2012). To sustain the salmonid community, Canadian and U.S. resource managers coordinate stocking of more than five million trout and salmon annually (NYSDEC, 2014; OMNRF, 2015). Decisions around stocking must account for anticipated survival of stocked fish (Coghlan et al., 2007; Lantry et al., 2011), natural reproduction (Connerton et al., 2009; Nack et al., 2011), and prey supply (Jones et al., 1993; Murry et al., 2010) in order to maintain a suitable predator-prey balance to support ecosystem health and productive fisheries (Dettmers et al., 2012; Stewart et al., 2013).

Ecological change (e.g., invasive species, climate change, etc.) is altering the structure and efficiency of the Great Lakes food webs (Mills et al., 2003; Bunnell et al., 2014), requiring a more holistic approach to resource management. Shifts in abundance of predator and prey may have important consequences for the dual objectives of fishery
promotion and species restoration (Jones et al., 1993; Stewart et al., 2013). Understanding the niche area (breadth) and overlap in dietary niche of the salmonid community will provide natural resource managers with critical information to optimise ecological and economic benefits associated with the Lake Ontario offshore fish community.

Stable isotope ratios of carbon (δ\textsuperscript{13}C) and nitrogen (δ\textsuperscript{15}N), are commonly used to describe trophic interactions, food web structure, and energy pathways in aquatic ecosystems (Peterson and Fry, 1987; Post, 2002). Unlike gut contents which provide only a snapshot of the most recent feeding event, stable isotopes reflect the time-integrated signature of energy sources assimilated into the predator tissue over a period of several months (Peterson and Fry, 1987; Pinnegar and Polunin, 1999). This longer term assimilation provides a more accurate reflection of the trophic interactions among predators and their prey than stomach/gut content analysis given the environmental heterogeneity experienced by most predators. Carbon isotopes reflect the ultimate source of carbon (primary production) for the predator because of minimal enrichment (~1‰ per trophic level) as they move through the food web (Post, 2002; Hecky & Hesslein, 1995). In freshwater ecosystems, nearshore/benthic primary producers tend to be enriched in \textsuperscript{13}C (more positive values of δ\textsuperscript{13}C) relative to pelagic (offshore) producers (France, 1995). In contrast, nitrogen isotope values tend to increase ~3.4‰ per trophic level (Post, 2002) and are therefore useful in estimating trophic position (Minagawa and Wada, 1984). The combination of δ\textsuperscript{13}C and δ\textsuperscript{15}N in food web studies objectively characterise the sources and relative position of producers and consumers at ecologically relevant scales.

While qualitative description of food webs is informative, ecologists continue to seek more quantitative ways to describe trophic properties. Layman et al. (2007) proposed six different community-wide metrics of trophic structure based on stable isotopes.
these, total convex hull area (TA), or the total area encompassed by all individuals of a species in $\delta^{13}$C - $\delta^{15}$N bi-plot space, was quickly adopted as a measure of total niche space occupied by the organism. Layman et al.’s (2007) TA metric is sensitive to small sample size, leading Jackson et al. (2011) to propose the use of standard ellipses (Batschelet, 1981), to describe and make inferences on isotopic niche space. In addition to describing size and overlap of individual species niches, ecologists have long depended on characterisation of diet to understand trophic interactions (Brandt, 1986; Stewart & Ibarra, 1991; Rand & Stewart, 1998). Isotope mixing models allow for the quantification of dietary proportions and are rapidly becoming a standard quantitative method for estimating diet (Post, 2002; Parnell et al., 2010). Combining the strengths of time-integrated assimilated isotope signatures with quantitative tools to describe and compare diet and trophic niche properties has provided ecologists with the tools needed to discern and describe key factors driving community structure.

Given the ecological and economic importance of salmonids in the offshore of Lake Ontario, surprisingly few studies have directly compared the diet and feeding relationships of these coexisting species. The offshore forage fish community of Lake Ontario is now relatively simple, consisting of Alewife, Rainbow Smelt, Round Goby Neogobius melanostomus, Slimy Sculpin Cottus cognatus and Deepwater Sculpin Myoxocephalus thompsonii. Coregonids and cyprinids, more abundant in the other Great Lakes, are poorly represented in Lake Ontario. As such, the potential for dietary overlap is high. All salmonid species in Lake Ontario favour the abundant Alewife to varying degrees (Brandt, 1986; Rand and Stewart, 1998). In Lake Ontario, as with many other locations in the Great Lakes, Pacific salmon tend to be dietary specialists (Stewart and Ibarra, 1991; Rand and Stewart, 1998; Jacobs et al., 2013; Roseman et al., 2014), while
Lake Trout are more generalists (Dietrich et al., 2006; Madenjian et al., 2006; Rush et al., 2012). Little is known about Atlantic Salmon given their extirpation from Lake Ontario over 100 years ago. Differences in thermal preference may allow some spatial segregation of species that otherwise consume similar prey (Stewart and Bowlby, 2009), although ecological change is driving large scale shifts in the distribution and behaviour of forage fish and salmonids (O’Gorman et al., 2000; Stewart et al., 2009; Rush et al., 2012) that will further refine niche boundaries.

Given the ecological and economic importance of salmonids in the offshore of Lake Ontario, and the present paucity of comparative and quantitative information on feeding ecology of these species, the objective of this study was to describe the diet and quantify the size and overlap of the trophic niche for abundant salmonids. On-going changes in the composition and abundance of the forage fish community (Lantry et al., 2007; Walsh et al., 2014), mounting evidence that naturalised populations may be reducing the ability to manage predators solely through stocking (Connerton et al., 2009; Nack et al., 2011), sustained interest in capitalising on the economic benefits of a fishery (Dettmers et al., 2012; Stewart et al., 2013), and on-going need to rehabilitate native species (Stewart et al., 2013; Lantry et al., 2014) combine to dictate a critical need to understand complementarity in niche of the Lake Ontario salmonids. We hypothesize that 1) Lake Trout will have the most diverse diet and largest isotopic niches, 2) Chinook and Coho Salmon will have specialised diets and small isotopic niches, and 3) niche overlap should be highest among Pacific salmon species, and lowest between those species and Lake Trout, 4) both Brown and Rainbow Trout will have diverse diets but Brown Trout will feed across habitats while Rainbow Trout will feed across trophic positions, and 5)
stable isotope values of Atlantic Salmon should reflect an offshore value but the diet should be composed mostly of Alewife and Rainbow Smelt.

3.2 Methods

Fish Collection

Adult salmonids (Atlantic Salmon, Chinook Salmon, Coho Salmon, Brown Trout, Lake Trout, and Rainbow Trout) and corresponding forage fishes (Alewife, Rainbow Smelt, Round Goby, Deepwater Sculpin, and Slimy Sculpin) were collected from Lake Ontario in 2013 as part of the Cooperative Science Monitoring Initiative (CSMI) program. Fishes were collected from April to December 2013, with additional Atlantic salmon samples incorporated from 2008-2011 owing to low sample sizes in 2013. All salmonids analysed for this study were “adults” >300mm. Salmonid samples were obtained primarily from creel surveys, with additional samples coming from agency index gillnet programs. Forage fishes were obtained from gillnets and bottom trawls. Gillnets were fished horizontally on the bottom (graded mesh, monofilament 19-mm to 152-mm) or vertically (surface to 30m depth, monofilament mesh ranging from 19-mm to 39-mm). Additional description of gear and programs can be found in NYSDEC (2014) and OMNRF (2015). Depths of collection of the fishes ranged from 1 to 175m with approximately half the effort in Canadian waters and half in the US (Figure 3.1).

During fish processing, both adult salmonids and salmonid forage fishes were identified to the species level, weighed (g) and both total length (mm) and fork length (mm) were measured. A skinless, boneless, dorsal muscle sample was removed from each fish for stable isotope analysis. For creel caught salmonids, the isotope sample was
obtained using an Unicore 3.5 mm biopsy punch (Ted Pella, Redding, CA, USA). All stable isotope samples were placed in 2 ml cryovials, frozen, and freeze dried at -20°C in preparation for stable isotope analysis. For all salmonids, the stomach was removed, placed in 85% ethanol and frozen until later analysis.

**Stable Isotope Analysis**

After freeze drying, muscle samples were pulverized into a fine powder using either mortar and pestle or surgical scissors depending on muscle density and size. Salmonid muscle samples were lipid extracted due to high C:N ratios (>3.4) while lipids were not removed from prey due to lower C:N ratios (≤3.4) (Post, 2002). Both lipid extracted and non-lipid extracted samples were weighed into 5 × 9 mm tin capsules on a microbalance containing 400 to 600 µg of sample. Combustion of the muscle sample into N₂ and CO₂ gases was executed using an elemental analyzer (Costech, Valencia, CA, USA) and a Thermo Finnigan Delta V mass spectrometer (Thermo Finnigan, San Jose, CA, USA), was used measure the relative abundances of carbon (¹³C/¹²C) and nitrogen (¹⁵N/¹⁴N) and within a particular sample. Standard delta notation (δ) was used to expressed stable carbon (δ¹³C) and nitrogen (δ¹⁵N) isotope ratios in parts per thousand (‰) differences from a standard reference material as the following equation: δ¹³C or δ¹⁵N = [(Rsample/Rstandard – 1)] × 1000 where R = ¹³C/¹²C or ¹⁵N/¹⁴N (Fry, 1991; Hobson & Clark, 1992). Standard reference materials were Pee Dee Belemnite for carbon and atmospheric nitrogen. National Institute of Standards and Technology (NIST) standards were used to calculate the accuracy of the analysis. NIST standards used for δ¹³C were sucrose (NIST 8542) and L-glutamic acid (NIST 8573), and for δ¹⁵N were ammonium sulphate (NIST 8548 and 8547) and L-glutamic acid (NIST 8573) (n= 96 for each). NIST standards deviated from the certified values by ≤0.1‰ for both δ¹³C and δ¹⁵N. Analytical
precision was based on the internal lab standard Tilapia and bovine liver (NIST 1577c) 
\((n=318)\) and had a standard deviation of <0.1‰ for \(\delta^{13}C\) and <0.2‰ for \(\delta^{15}N\).

**Salmonid Gut Content Analysis**

Gut contents were quantified by volume, by first determining the mass of the gut 
contents (by volume displacement, assuming a density of 1 g/ml) and then sorting the 
contents to the lowest taxonomic level, assigning proportions to those groupings, and 
where possible measuring the length of the prey item. Invertebrates (always <15% of the 
stomach volume) and unidentifiable prey items were excluded from the calculations of 
prey proportions. Empty stomachs were not included in the analysis.

**Statistical Analysis**

The isotopic niche of the salmonids was determined using Stable Isotope Bayesian 
Ellipses in R (SIBER) in the package SIAR v.4.2 (Parnell & Jackson, 2013) in R v.3.0.2 
(R Core Development Team, 2013). SIBER uses a multivariate ellipse-based approach to 
compare groups of differing sample sizes (Jackson et al., 2011). Core isotopic niche was 
represented using standard (40%) ellipse areas corrected for small sample size (SEA\(_C\)) 
which allowed for comparison of differing sample sizes between species. Fraction overlap 
(%) among the species’ SEA\(_C\) was used to express similarities and differences in niche 
space utilization. The relative likely contribution of forage fish to the salmonid diet were 
determined using a Bayesian mixing model approach in the package SIAR (Stable Isotope 
Analyses in R) v.4.2 (Parnell & Jackson, 2013) in R v.3.0.2 (R Core Development Team, 
2013). Any correlations between prey species were identified by diagnostic matrix plots 
where a decrease in the contribution to the salmonid diet of a prey species caused an 
increase in contribution of the other prey species due to the requirement of a sum to 1 
total dietary contribution.
Two separate diet tissue discrimination factors (DTDFs) were developed to infer dietary proportions. DTDFs are a key metric for assessing isotopes in food webs and are important in quantifying diet via stable isotope mixing models (Bond & Diamond, 2011). We estimated DTDF for all salmonids excluding Lake Trout using Chinook Salmon. We used Chinook Salmon because 1) the gut contents of Chinook Salmon >500 mm in Lake Ontario are exclusively Alewife, 2) Chinook Salmon were the most abundantly sampled predator, and 3) the $\delta^{15}N$ of Chinook Salmon was very similar to the other salmonids species. The lack of diet variation is key in developing a precise estimate of DTDF. To generate DTDF, we calculated the mean $\delta^{13}C$ and $\delta^{15}N$ for Chinook Salmon $\geq$500 mm fork length (mean= 796 mm, $n= 218$) and Alewife between 170 and 190 mm total length (mean=180 mm, $n= 181$). Fork length was used because it was recorded for each Chinook Salmon individual while total length was sparsely recorded for each individual. The mean $\delta^{13}C/ \delta^{15}N$ of Alewife ($\delta^{13}C= -23.95‰$, $\delta^{15}N= 12.67‰$) was then subtracted from the mean $\delta^{13}C/ \delta^{15}N$ of Chinook Salmon ($\delta^{13}C= -22.18‰$, $\delta^{15}N= 16.14‰$) to obtain the DTDF values. The DTDFs values calculated were 1.77‰ for $\Delta^{13}C$ and 3.46‰ for $\Delta^{15}N$.

A separate DTDF was calculated for Lake Trout because this species had a much higher mean $\delta^{15}N$ value compared to the other salmonid species. In 2013, Lake Ontario Lake Trout (mean total length 665 mm) consumed 72% Alewife (Table 3.1), which compared favourably with the 65% reported for similar sized Lake Michigan Lake Trout which were entirely piscivorous (Madenjian et al. 1998). As such, we used Alewife as the base prey to calculate the appropriate DTDF. Using Madenjian et al.’s (1998) relationship between Lake Trout total length and the size of Alewife consumed, we estimated Lake Trout $>600$ mm favour Alewife $\geq 128$ mm. The mean $\delta^{13}C/ \delta^{15}N$ of Alewife ($\delta^{13}C= -24.19‰$, $\delta^{15}N= 12.53‰$) was then subtracted from the mean $\delta^{13}C/ \delta^{15}N$ of Lake Trout
(\delta^{13}C = -21.88\%o, \delta^{15}N = 17.42\%o) to obtain the DTDF values. The DTDFs values calculated were 2.31\%o for \Delta^{13}C and 4.89\%o for \Delta^{15}N. The DTDF values were adjusted to 4.1\%o for \Delta^{15}N and 1.75\%o for \Delta^{13}C with the use of SIAR because these DTDF values represented the similar dietary proportions observed in the 2013 Lake Ontario diets.

Trophic position (TP) was calculated for each salmonid species using a one-source model (Vander Zanden et al., 1999).

\[ TP_{\text{consumer}} = (\frac{(\delta^{15}N_{\text{consumer}} - \delta^{15}N_{\text{baseline}})}{3.4}) + TP_{\text{baseline}} \]

The assumed trophic increase value of 3.4 in \delta^{15}N between prey and predator (i.e., DTDF) is a common generalisation (Minagawa & Wada, 1984; Post, 2002), but the calculated DTDF values for the Lake Ontario salmonids were used to obtain a better representation of the appropriate salmonid TP (Lake Trout \Delta^{15}N = 4.1, all other salmonids \Delta^{15}N = 3.46). Alewife was used as the baseline organism because Alewife comprise a large proportion of salmonid diets (Brandt, 1986; Rand & Stewart, 1998) and were used to calculate salmonid DTDF values. The Alewife were assigned TP=3 because they are secondary/ planktivorous consumers (Walsh et al., 2008; Stewart et al., 2009).

3.3 Results

*Salmonid size and stable isotope data*

A total of 672 predators and 2037 prey muscle samples were analysed for stable isotopes from Lake Ontario in 2013. Fork length was used for predators because total length was sparsely recorded, and all predator species have a similar tail morphology. Mean size of salmonid predators ranged from 517 ± 15.19 mm (mean ± SE) (Brown Trout) to 700 ± 11.78 mm (Chinook Salmon) (Table 3.2). Salmonid prey ranged in size
(total length) from 90 ± 1.53 mm (Round Goby) to 140 ± 1.41 mm (Alewife) (Table 3.2). Both prey and predators were sampled throughout Lake Ontario across bathymetric depths of 1 to 175 m and in all seasons excluding winter. Individual species differences in regards to number collected varied with bathymetric depth owing to species-specific thermal preference.

Values of $\delta^{15}$N were lowest in Rainbow Trout (15.6 ± 0.07, mean ± SE) and highest in Lake Trout (17.5 ± 0.05) (Table 3.2), and spanned a wider range than $\delta^{13}$C (-22.1‰ to -21.4‰) (Table 3.2). Carbon isotope ratios ($\delta^{13}$C) were significantly correlated with fork length for Chinook Salmon, Coho Salmon, Lake Trout and Rainbow Trout (Table 3.3). Nitrogen isotope ratios ($\delta^{15}$N) were significantly correlated with fork length for Brown Trout and Rainbow Trout (Table 3.3).

**SIBER niche metrics and trophic position**

Isotopic niche area ($\text{SEA}_C$) ranged from 0.6‰² for Chinook Salmon to 1.4‰² for Rainbow Trout (Table 3.4). The isotopic niche for Rainbow Trout was oriented vertically (wide range of $\delta^{15}$N) while the Brown Trout isotopic niche was oriented horizontally (wide range of $\delta^{13}$C) (Figure 3.2). Isotopic niche overlap was detected between all species except for Lake Trout (Table 3.4; Figure 3.2). The relatively large isotopic niche for Atlantic Salmon overlapped considerably with Chinook Salmon (96%) and Coho Salmon (75%), while Coho Salmon and Rainbow Trout had considerable overlap with Atlantic Salmon (65 and 67%, respectively) and Chinook Salmon (81 and 74%, respectively) (Table 3.4 row data, Figure 3.2). Meanwhile, the relatively small isotopic niche for Chinook Salmon meant it had little exclusivity in its niche (Table 3.4, column data), and collectively its entire niche overlapped with other species (Figure 3.2). Brown Trout had
low niche overlap (<50%) and a high degree of isotopic distinctness from all other salmonids (Table 3.4).

The trophic position of Lake Ontario salmonids were estimated to be at or approximately TP= 4 (Table 3.4). Even with much higher δ¹⁵N values and no overlapping niche area with the other salmonids, the trophic position of Lake Trout was only 0.2 higher than the average (4.0) (Table 3.4).

Salmonid diets based on stable isotopes and gut contents

Stable isotope mixing model analyses using SIAR estimated that adult Lake Ontario salmonids consumed prey items from pelagic, offshore origins with Alewife as the most common prey type with dietary proportions ranging from 0.56 to 0.86 (Table 3.1). Alewife was also the most common prey item, based on volume, within the gut contents (Table 3.1). Round Goby contributed between 0.12 (Rainbow Trout) to 0.29 (Brown Trout) of the diet based on mixing models (Table 3.1). Both stable isotopes and gut contents suggest that Rainbow Smelt are consumed by Lake Trout, Chinook Salmon and Coho Salmon (stable isotopes only), with both methods showing similar dietary proportions (albeit higher proportions for stable isotopes) for all species (Table 3.1).

Slimy and Deepwater Sculpin species are consumed in low proportion by Lake Trout (guts) although stable isotope mixing models suggest all other species may consume both sculpin species in very low proportions (Table 3.1).

3.4 Discussion

Lake Ontario salmonid species had similar trophic positions and isotopic niches with large overlap between species suggesting high potential for competition for dietary
resources. Lake Trout was an exception as its isotopic niche did not overlap with the other salmonids and it had a higher trophic position. Little is known about the ecology of Atlantic Salmon in Lake Ontario, but we found high isotopic niche overlap with other species, raising concerns about restoration potential for this species given the large population sizes of the other salmonid species. Lakewide diet estimates, based on stable isotopes and gut contents, revealed that Alewife was present in high proportions in all of the salmonids with lesser proportions of Round Goby and Rainbow Smelt. This suggests that Lake Ontario salmonids have adapted to incorporate Round Goby into their diets but Alewife consumption still remains high among the salmonids.

Atlantic Salmon isotopic values indicated an offshore signal with a diet dominated by Alewife, with a lesser contribution of Round Goby as opposed to Rainbow Smelt. Rainbow Smelt was the primary prey and Round Goby was the secondary fish prey in Lake Huron Atlantic salmon populations (Roseman et al., 2014). Even with Alewife comprising the large dietary proportion, the isotopic niche (1.0‰) of this species suggests that the diet consists of more prey items compared to the other species, consistent with other studies that have found them to have a large prey diet but diet varies by geographic location (Kirn & LaBar, 1996; Ketola et al., 2000; Roseman et al., 2014). Atlantic Salmon did not exhibit a body size relationship for either isotope, suggesting less individual variation in prey and/or habitat use. However, the combination of a smaller sample size and the fact that the majority (76%) of the Atlantic Salmon were of a relatively similar size (500-599 mm) may have resulted in insufficient statistical power to detect an allometric pattern.

Chinook Salmon had the smallest isotopic niche (0.6‰) of the six salmonid species studied and also had a specialized diet composed primarily of Alewife. Chinook
Salmon were also estimated to have the smallest isotopic niche in a previous Lake Ontario study in which Alewife was also suspected as the main prey source (Yuille et al., 2015). Alewife has been the main prey item of Chinook Salmon for many years and excessive predator demand on forage fishes remains as a management issue and that severe recruitment failure in Alewife could cause the high predator demand not to be met (Brandt, 1986; Stewart & Ibarra, 1991; Jones et al., 1993; Murry et al., 2010; Stewart & Sprules, 2011). As size increased δ^{13}C decreased suggesting that Chinook Salmon are distributed further offshore as they grow. In the nearshore, the diet of smaller Chinook Salmon is likely largely Round Goby and Alewife probably plays a much larger role in the diet of larger individuals in the offshore.

Coho Salmon were predicted to have the smallest isotopic niche matching that of Chinook Salmon but were found to have niche width equal to Lake Trout, which were regarded to have a diverse diet (Brandt, 1986). Contrasting to our study, Yuille et al. (2015), found that the niche of Coho Salmon was the smallest of all salmonids and yearly diet shifts have occurred in Lake Ontario Coho Salmon populations (Rand & Stewart, 1998). Even though the diet of Coho Salmon did not have similar dietary proportions to Lake Trout, the niche area was the same. Like Chinook Salmon, smaller Coho Salmon have may inhabit nearshore areas with higher δ^{13}C values. Smaller Coho Salmon may be feeding on Round Goby which are abundant in the nearshore (Pennuto et al., 2012). Larger adults appear to inhabit the offshore pelagic where this species probably consumed a high proportion of Alewife. Alewife accounted for 100% of the stomach contents collected from Coho Salmon in 2013, but all individuals from which stomachs were collected were greater than 475 mm fork length. Higher δ^{13}C values and a negative
correlation between the size of Coho Salmon and $\delta^{13}C$ values are consistent with nearshore Round Goby being important in the diet of small adult Coho Salmon.

Brown Trout have a narrow $\delta^{15}N$ range but broad $\delta^{13}C$ range suggesting feeding across habitats, both in the nearshore/ or benthic and offshore pelagic, consistent with our hypothesis. Complementary results on Brown Trout were found by Yuille et al. (2015). Stomach contents analysis indicated that Brown Trout prey largely on Alewife and Round Goby, but isotopic niche width suggested a diverse diet. Brandt (1986) found that during the spring, Brown Trout in Lake Ontario have a diverse diet consisting more of insects and sculpin species, while they have a narrow dietary suite in the summer feeding on Alewife and Rainbow Smelt. Invertebrates were not enumerated in salmonid diets in this study, and although rare, may have contributed to increased isotopic niche width. An allometric shift was observed in Brown Trout, as length increased, $\delta^{15}N$ increased. Larger individuals may be preying upon more Round Gobies and smaller individuals may be preying on Alewife, as the Round Goby $\delta^{15}N$ value can be approximately 1‰ higher than Alewife $\delta^{15}N$ values. Brown Trout catch decreases with distance from shore with catch nearly zero at three kilometres from shore (Olson et al., 1988). Niche area and overlap suggests that this species inhabits environments most related with the nearshore, as well as the offshore. Here, Brown Trout could prey easily upon Alewife in the nearshore and offshore and on Round Goby while they inhabit the nearshore during the summer.

Lake Trout were predicted to have the largest niche based on previous diet analyses (Brandt, 1986; Rand & Stewart, 1998; Rush et al., 2012). Instead, Lake Trout had the same niche size as Coho Salmon but Lake Trout inhibit a much different niche as this species had no isotopic overlap with the other salmonids. Diet reconstruction indicated that adult Lake Trout consume mainly Alewife, Rainbow Smelt and Round
Goby in that relative order. Rush et al. (2012) also determined that Lake Trout are feed primarily on two prey sources (i.e., Alewife and Round Goby) and Slimy Sculpin contribute on average <5% to the diet. Sculpin spp. contributed little to the Lake Trout diet analyzed nearly thirty years ago (Brandt, 1986). Lake Trout are a hypolimnetic species (Dryer, 1966; Hansen et al., 1995), which probably accounted for this species high δ¹⁵N values. Hodell & Schelske (1998) found that Lake Ontario deep water sedimentary organic matter had δ¹⁵N values between 7 and 8‰ since about the 1960’s, as higher δ¹⁵N values result from benthic nutrient cycling (Mulholland et al., 2000). Therefore offshore benthic prey (e.g., sculpins, Rainbow Smelt) as found in Mumby et al. (Chapter 2), were found to have elevated δ¹⁵N values. Therefore, nitrogen enrichment from consuming these fishes would result in high δ¹⁵N values in Lake Trout. Adult Lake Trout are also cannibalistic (Dietrich et al., 2006), which could have accounted for higher δ¹⁵N values. The carbon (δ¹³C) linear regression analysis suggested that smaller adults are probably more nearshore and/ or benthic while larger adults are situated further offshore and/ or more pelagic.

As predicted from our hypothesis, Rainbow Trout feed across trophic positions due to a narrow δ¹³C range but broad δ¹⁵N range. Yuille et al. (2015) found similar results with Rainbow Trout. The Rainbow Trout niche was the largest of the salmonids which suggested that they have a diet consisting of a large diversity of prey which follows from previous diet data collected (Brandt, 1986). Alewife contributed to >85% of the Rainbow Trout diet, the most of the salmonids, followed by Round Goby. Both in the spring and summer, Alewife have contributed close to 100% of the Rainbow Trout diet, followed by Rainbow Smelt (Rand & Stewart, 1998). Rainbow Smelt abundance in Lake Ontario has declined drastically (Holden & Connerton, 2015). Round Goby appears to have replaced
Rainbow Smelt in the Rainbow Trout diet. The large niche area of this species could be explained by allometric patterns over length. As the fork length increased, $\delta^{13}C$ decreased and $\delta^{15}N$ increased. Stable isotope values suggest that larger individuals feed at higher trophic positions further offshore than smaller Rainbow Trout. The offshore movement of Rainbow Trout is consistent with the thermal bar formation during the spring (Stewart & Bowlby, 2009). Larger Rainbow Trout over smaller individuals probably follow the thermal bar to the offshore during the spring to feed mainly on Alewife. Smaller individuals may be situated further inshore where they possibly feed on Round Gobies and possibly invertebrates during the summer.

Isotopic overlap was highest among salmon species over a range of -21‰ to -22‰ for $\delta^{13}C$ and 15.5‰ to 16.5‰ for $\delta^{15}N$ as indicated on the isotopic bi-plot. Yuille et al. (2015) suggested that a common prey source was driving the high overlap of salmonids in Lake Ontario. Alewife was observed to be the predominant prey item consumed by all salmonids and this likely accounted for the high isotopic niche overlap and similar trophic positions among the species. The Pacific salmonids and Atlantic Salmon had diets composed of >70% Alewife suggesting they prefer Alewife relative to the other prey species. Chinook Salmon compose a majority of the salmonid biomass in Lake Ontario and consume a large amount of the Alewife biomass an annual basis (Murry et al., 2010), therefore having a disproportionate effect on Alewife predation compared to other salmonid species. The preference for Alewife in the diets of Lake Ontario salmonids has changed little since the 1980’s (Brandt, 1986), as this is mostly probably due to the large abundance of Chinook Salmon in the lake (Connerton et al., 2009). Although the contribution of Alewife to has remained high in the diet, Rainbow Smelt has declined in the diet.
Rainbow Smelt were found as the third most prevalent diet item in the salmonids, other than Lake Trout, where the smelt were the second most prevalent prey in the diet. This was probably due to the large decline of Lake Ontario Rainbow Smelt population (Holden & Connerton, 2015) and invasion of Round Goby (Mills et al., 2003). Round Goby was detected as a secondary prey item, especially in Brown Trout. The migration of Round Gobies to the nearshore during the spring and summer (Miller, 1986), is likely increasing the risk to this species in the shallows. The majority of Round Goby predation possibly occurred during the spring before Pacific salmonids and Atlantic Salmon migrate to preferred cooler, offshore waters for the summer (Scott & Crossman, 1973; Haynes et al., 1986; Stewart & Bowlby, 2009). Rush et al. (2012) speculated that higher $\delta^{13}C$ values in Lake Trout resulted from Round Goby predation and therefore had a high reliance on nearshore carbon. Brown Trout have a high reliance on nearshore carbon due to the high estimated proportion of Round Goby in their diet and since Round Goby were found to have higher $\delta^{13}C$ values than other forage fishes. Deepwater and Slimy Sculpin were found in low dietary proportions in the salmonid diet with consumption most pronounced in Lake Trout, Atlantic Salmon, and Coho Salmon, with the 95% creditable interval reaching approximately 0.05. Sculpin spp. have been found in Coho Salmon stomachs but only in the spring while Lake Trout consume sculpin species in both the spring and summer (Brandt, 1986). Coho and Atlantic Salmon are confined to the nearshore during the spring because of non-preferred colder waters in the offshore, when Alewife are less readily available. Alewife have been reported to inhabit the offshore for an extended period of time in the spring (O’Gorman et al., 2000). In turn, Coho and Atlantic Salmon could be actively preying on benthic prey (i.e., Round Goby) more frequently in the spring before the arrival of Alewife.
Differences in diet and niche may be a reflection of where salmonids are found in the epilimnion. The consumption of Alewife probably occurred in different thermal optimums/vertical depths, as suspected by Yuille et al. (2015). Chinook Salmon tend to inhabit shallower bathymetric depths than Rainbow Trout in the spring (Stewart & Bowlby, 2009). Coho Salmon individuals have been detected to confine movements within the upper reaches of the epilimnion (Ogura & Ishida, 1992), therefore overlapping both Rainbow Trout and to a greater extent, Chinook Salmon vertical depths (Stewart & Bowlby, 2009). Niche width suggested that Coho Salmon occupied shallower bathymetric depths, which perhaps increased the amount of time Coho Salmon interacted with the benthic habitat.

Lake Ontario Pacific salmonids may have fed on Alewife in different areas of the epilimnion, thus partitioning resource use spatially. Vertical depths of Lake Ontario Atlantic Salmon are not known, although Atlantic Salmon feed close to the surface in the other systems (Hansen & Quinn, 1998), where Alewife are common. The Atlantic Salmon diet and niche suggested that they probably co-inhabit bathymetric depths similar to that of Pacific salmonids and but were also found to inhabit their own unique niche space further offshore (i.e., deeper bathymetric depths). Mixing models suggest that the diet of Atlantic Salmon was similar to Coho Salmon, suggesting that both species inhabit shallower bathymetric depths.

The consumption of Alewife by Lake Trout and Brown Trout possibly occurred in different vertical depths than other salmonids. Lake Trout in Lake Ontario were most abundant within a few metres below the thermocline while Brown Trout were most abundant in the thermocline and a few metres above and near the surface (Olson et al., 1988). Lake Trout have been recorded to move above the thermocline (Scott &
Crossman, 1973; Olson, 1988). This area of the water column is probably where Lake Trout consume the highest percentage of Alewives in their diet. Little data has been published on Brown Trout habitat use in the Great Lakes, but the higher δ¹³C values suggest that Brown Trout feed more in the nearshore than other salmonids. Olson et al. (1988) observed Brown Trout occupied habitats closest to the shore. Therefore, Brown Trout probably consumed both nearshore and offshore Alewife, in which the partitioning of Alewife was much greater in the offshore epilimnion area due to the overlap of the Brown Trout isotopic niche with the other salmonids. Olson et al. (1988) showed that resource overlap between Lake Trout and Brown Trout was moderate but overlapped on all three variables (food – presumably Alewife, and both horizontal and vertical niche use).

Summary

Diet reconstruction detected that the consumption of Alewife was driving the high isotopic niche overlap between the salmonids in Lake Ontario. Niche area analysis indicated that Chinook Salmon have a narrow diet while Rainbow Trout have a wide dietary suite of prey. Brown Trout were found to have a high degree of isotopic distinctness from all other salmonids as Round Goby composed a third of its diet. Negative correlation between δ¹³C values and fish length of Chinook and Coho Salmon indicate that smaller individuals may have a preference for nearshore areas while larger fish may prefer offshore areas. Lake trout were hypothesized to have a generalist diet, but consumed only Alewife, Rainbow Smelt, and Round Goby. Restoration of Atlantic Salmon to Lake Ontario may be difficult because all salmonids must share a limited supply of Alewife to sustain their growth. However, Atlantic Salmon niche space was somewhat unique indicating that they may be able to partition resources in time and space.
in such a way to coexist with other salmonids. Using both niche area and diet, Lake Ontario salmonids excluding Lake and Brown Trout probably co-habitat similar vertical depths in and above the thermocline. The results gathered from this study showed that the salmonid SEA$_C$ placement on the isotopic bi-plot is highly influenced by Alewife. Round Goby is now present in salmonid diets and has replaced Rainbow Smelt as the second most prevalent diet item.
3.5 References


Table 3.1. Estimated diet of Lake Ontario salmonids based on gut contents (percentage based on prey occurrence and estimated prey item contributions [mean (5% credible interval, 95% credible interval)] via SIAR.

<table>
<thead>
<tr>
<th>Species</th>
<th>Prey Item</th>
<th>Gut Content</th>
<th>Estimated Prey Item Proportions</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic Salmon</td>
<td>Alewife</td>
<td>N/A</td>
<td>0.78 (0.71, 0.85)</td>
</tr>
<tr>
<td>(gut n= 0)</td>
<td>Rainbow Smelt</td>
<td>N/A</td>
<td>0.05 (0.00, 0.12)</td>
</tr>
<tr>
<td>(isotope n= 41)</td>
<td>Round Goby</td>
<td>N/A</td>
<td>0.14 (0.06, 0.21)</td>
</tr>
<tr>
<td></td>
<td>Deepwater Sculpin</td>
<td>N/A</td>
<td>0.02 (0.00, 0.04)</td>
</tr>
<tr>
<td></td>
<td>Slimy Sculpin</td>
<td>N/A</td>
<td>0.02 (0.00, 0.05)</td>
</tr>
<tr>
<td>Chinook Salmon</td>
<td>Alewife</td>
<td>0.96</td>
<td>0.74 (0.71, 0.76)</td>
</tr>
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<td>(gut n= 54)</td>
<td>Rainbow Smelt</td>
<td>0.04</td>
<td>0.12 (0.08, 0.16)</td>
</tr>
<tr>
<td>(isotope n= 289)</td>
<td>Round Goby</td>
<td>0.00</td>
<td>0.13 (0.10, 0.16)</td>
</tr>
<tr>
<td></td>
<td>Deepwater Sculpin</td>
<td>0.00</td>
<td>0.01 (0.00, 0.01)</td>
</tr>
<tr>
<td></td>
<td>Slimy Sculpin</td>
<td>0.00</td>
<td>0.01 (0.00, 0.02)</td>
</tr>
<tr>
<td>Coho Salmon</td>
<td>Alewife</td>
<td>1.00</td>
<td>0.73 (0.65, 0.80)</td>
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<td>(gut n= 9)</td>
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<td>0.02 (0.00, 0.05)</td>
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<tr>
<td></td>
<td>Slimy Sculpin</td>
<td>0.00</td>
<td>0.02 (0.00, 0.05)</td>
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<tr>
<td>Brown Trout</td>
<td>Alewife</td>
<td>0.83</td>
<td>0.69 (0.61, 0.76)</td>
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<td>(gut n= 27)</td>
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<td>0.01 (0.00, 0.04)</td>
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<td>(isotope n= 47)</td>
<td>Round Goby</td>
<td>0.17</td>
<td>0.29 (0.21, 0.36)</td>
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<td></td>
<td>Deepwater Sculpin</td>
<td>0.00</td>
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<tr>
<td></td>
<td>Slimy Sculpin</td>
<td>0.00</td>
<td>0.01 (0.00, 0.02)</td>
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<tr>
<td>Lake Trout</td>
<td>Alewife</td>
<td>0.72</td>
<td>0.56 (0.52, 0.60)</td>
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<tr>
<td>(gut n= 140)</td>
<td>Rainbow Smelt</td>
<td>0.08</td>
<td>0.22 (0.14, 0.29)</td>
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<td>(isotope n= 127)</td>
<td>Round Goby</td>
<td>0.18</td>
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<td></td>
<td>Deepwater Sculpin</td>
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<tr>
<td></td>
<td>Slimy Sculpin</td>
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<tr>
<td>Rainbow Trout</td>
<td>Alewife</td>
<td>0.92</td>
<td>0.86 (0.81, 0.91)</td>
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<td>(gut n= 25)</td>
<td>Rainbow Smelt</td>
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<td>0.01 (0.00, 0.03)</td>
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<tr>
<td>(isotope n= 126)</td>
<td>Round Goby</td>
<td>0.08</td>
<td>0.12 (0.07, 0.16)</td>
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<tr>
<td></td>
<td>Deepwater Sculpin</td>
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<td>0.00 (0.00, 0.01)</td>
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<tr>
<td></td>
<td>Slimy Sculpin</td>
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<td>0.01 (0.00, 0.01)</td>
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</tbody>
</table>
Table 3.2. Fork length (mm), stable isotopes ratios (mean ± SE) and C/N ratio of adult (>300 mm) Atlantic Salmon, Chinook Salmon, Coho Salmon, Brown Trout, Lake Trout, and Rainbow Trout collected from Lake Ontario between April to December 2013. Atlantic Salmon collected from 2008 to 2011, and 2013. Predators were lipid extracted, prey non-lipid extracted. Total length used for prey.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Length (mm)</th>
<th>δ¹³C Mean ± SE</th>
<th>δ¹⁵N Mean ± SE</th>
<th>C/N ratio Mean ± SE</th>
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</thead>
<tbody>
<tr>
<td><strong>Predator</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Atlantic Salmon</td>
<td>41</td>
<td>551 ± 8.32</td>
<td>-22.0 ± 0.10</td>
<td>16.0 ± 0.07</td>
<td>*3.3 ± 0.02</td>
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<tr>
<td>Chinook Salmon</td>
<td>289</td>
<td>700 ± 11.78</td>
<td>-22.1 ± 0.03</td>
<td>16.2 ± 0.02</td>
<td>3.4 ± 0.01</td>
</tr>
<tr>
<td>Coho Salmon</td>
<td>42</td>
<td>596 ± 12.62</td>
<td>-21.9 ± 0.06</td>
<td>16.1 ± 0.10</td>
<td>3.3 ± 0.02</td>
</tr>
<tr>
<td>Brown Trout</td>
<td>47</td>
<td>517 ± 15.19</td>
<td>-21.4 ± 0.11</td>
<td>15.8 ± 0.08</td>
<td>3.4 ± 0.02</td>
</tr>
<tr>
<td>Lake Trout</td>
<td>127</td>
<td>589 ± 10.04</td>
<td>-21.8 ± 0.05</td>
<td>17.5 ± 0.05</td>
<td>3.4 ± 0.01</td>
</tr>
<tr>
<td>Rainbow Trout</td>
<td>126</td>
<td>593 ± 8.35</td>
<td>-22.0 ± 0.05</td>
<td>15.6 ± 0.07</td>
<td>3.4 ± 0.02</td>
</tr>
<tr>
<td><strong>Prey</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alewife</td>
<td>802</td>
<td>140 ± 1.41</td>
<td>-24.1 ± 0.04</td>
<td>12.6 ± 0.04</td>
<td>4.0 ± 0.03</td>
</tr>
<tr>
<td>Rainbow Smelt</td>
<td>355</td>
<td>110 ± 1.48</td>
<td>-23.6 ± 0.02</td>
<td>15.0 ± 0.07</td>
<td>3.5 ± 0.01</td>
</tr>
<tr>
<td>Round Goby</td>
<td>448</td>
<td>90 ± 1.53</td>
<td>-21.8 ± 0.09</td>
<td>13.6 ± 0.06</td>
<td>3.4 ± 0.01</td>
</tr>
<tr>
<td>Deepwater Sculpin</td>
<td>223</td>
<td>126 ± 1.69</td>
<td>-24.7 ± 0.06</td>
<td>16.9 ± 0.04</td>
<td>4.1 ± 0.06</td>
</tr>
<tr>
<td>Slimy Sculpin</td>
<td>209</td>
<td>97 ± 1.34</td>
<td>-24.6 ± 0.05</td>
<td>16.6 ± 0.05</td>
<td>3.8 ± 0.04</td>
</tr>
</tbody>
</table>

*Only 2013 samples used, no C:N ratio data available for 2008 to 2011 samples.
Table 3.3. Linear regression analysis of stable isotope (C and N) values against fork length (FL, mm) for each salmonid species collected in Lake Ontario. P-values ≤ 0.05 (i.e., significant) are shown with regressions. The equation is as follows $\delta X = \beta \times FL \pm \alpha$, where $\alpha$ = intercept and $\beta$ = slope.

<table>
<thead>
<tr>
<th>Species</th>
<th>$\delta^{13}$C $\alpha$</th>
<th>$\delta^{13}$C $\beta$</th>
<th>$\delta^{13}$C $R^2$</th>
<th>$\delta^{13}$C p-value</th>
<th>$\delta^{15}$N $\alpha$</th>
<th>$\delta^{15}$N $\beta$</th>
<th>$\delta^{15}$N $R^2$</th>
<th>$\delta^{15}$N p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic Salmon</td>
<td>N/A</td>
<td>N/A</td>
<td>0.023</td>
<td>0.34</td>
<td>N/A</td>
<td>N/A</td>
<td>0.050</td>
<td>0.16</td>
</tr>
<tr>
<td>Chinook Salmon</td>
<td>-21.154</td>
<td>-0.0013</td>
<td>0.342</td>
<td>&lt;0.001</td>
<td>N/A</td>
<td>N/A</td>
<td>0.001</td>
<td>0.52</td>
</tr>
<tr>
<td>Coho Salmon</td>
<td>-20.579</td>
<td>-0.0022</td>
<td>0.196</td>
<td>&lt;0.01</td>
<td>N/A</td>
<td>N/A</td>
<td>0.006</td>
<td>0.61</td>
</tr>
<tr>
<td>Brown Trout</td>
<td>N/A</td>
<td>N/A</td>
<td>0.034</td>
<td>0.22</td>
<td>14.567</td>
<td>0.0023</td>
<td>0.217</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Lake Trout</td>
<td>-21.227</td>
<td>-0.001</td>
<td>0.053</td>
<td>&lt;0.01</td>
<td>N/A</td>
<td>N/A</td>
<td>0.005</td>
<td>0.43</td>
</tr>
<tr>
<td>Rainbow Trout</td>
<td>-21.018</td>
<td>-0.0016</td>
<td>0.077</td>
<td>&lt;0.01</td>
<td>12.153</td>
<td>0.0058</td>
<td>0.446</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>
Table 3.4. Overlap in isotopic niche (%) based on SEA$_C$, SEA$_{C'}$ ($\%^{2}$) and calculated trophic position (TP) for each salmonid species collected from Lake Ontario in 2013. Atlantic Salmon collected from 2008 to 2011 and in 2013. Rows represent how similar species are with another species (e.g., Atlantic Salmon covers 96% of the Chinook Salmon niche) while columns represent how distinct species are from one another (e.g., only 53% of the Atlantic Salmon niche overlaps with Chinook Salmon, therefore 47% of the Atlantic Salmon niche width is distinct from Chinook Salmon).

<table>
<thead>
<tr>
<th>Species</th>
<th>Atlantic Salmon</th>
<th>Chinook Salmon</th>
<th>Coho Salmon</th>
<th>Brown Trout</th>
<th>Lake Trout</th>
<th>Rainbow Trout</th>
<th>SEA$_{C}$ ($%^{2}$)</th>
<th>Trophic Postion (TP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic Salmon</td>
<td>---</td>
<td>96</td>
<td>75</td>
<td>35</td>
<td>0</td>
<td>50</td>
<td>1.0</td>
<td>4.0</td>
</tr>
<tr>
<td>Chinook Salmon</td>
<td>53</td>
<td>---</td>
<td>52</td>
<td>17</td>
<td>0</td>
<td>30</td>
<td>0.6</td>
<td>4.0</td>
</tr>
<tr>
<td>Coho Salmon</td>
<td>65</td>
<td>81</td>
<td>---</td>
<td>34</td>
<td>0</td>
<td>40</td>
<td>0.9</td>
<td>4.0</td>
</tr>
<tr>
<td>Brown Trout</td>
<td>42</td>
<td>36</td>
<td>47</td>
<td>---</td>
<td>0</td>
<td>33</td>
<td>1.2</td>
<td>3.9</td>
</tr>
<tr>
<td>Lake Trout</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>---</td>
<td>0</td>
<td>0.9</td>
<td>4.2</td>
</tr>
<tr>
<td>Rainbow Trout</td>
<td>67</td>
<td>74</td>
<td>62</td>
<td>37</td>
<td>0</td>
<td>---</td>
<td>1.4</td>
<td>3.9</td>
</tr>
</tbody>
</table>
Figure 3.1. Lake Ontario salmonid and prey sampling sites completed using 12 different transects (six in the USA and six in Canada) and seven creel survey locations (all in Canada) in 2013. Creel survey locations represented by stars and transects represented by arrows. Transect length and direction represented by arrow length and position.
Figure 3.2. Stable isotope bi-plot (isoscape) of the isotopic niches of Lake Ontario Atlantic Salmon, Chinook Salmon, Coho Salmon, Brown Trout, Lake Trout and Rainbow Trout collected in 2013. Atlantic Salmon collected from 2008 to 2011 and in 2013. Thick circles enclose standard (40%) ellipse areas (SEA) for all species with Atlantic Salmon represented by a long dashed grey circle, Chinook Salmon by a long dashed black circle, Coho Salmon by a solid black circle, Brown Trout by a dot dashed black circle, Lake Trout by a dotted dashed grey circle and Rainbow Trout by a solid grey circle. Individual data points (light grey) are represented by squares for Atlantic Salmon, x’s for Chinook Salmon, crosses for Coho Salmon, stars for Brown Trout, circles for Lake Trout, and inverted triangles for Rainbow Trout.
4.1 Summary

It is important to understand the intra and interactions within and between organisms, not only to provide general information on the trophic structure within an ecosystem but also to gain knowledge into the isotopic niche width and overlap, and diet using quantitative measurements. The overall goal of this work was to examine the isotopic niche and diet of the Lake Ontario salmonids (Atlantic Salmon *Salmo salar*, Chinook Salmon *Oncorhynchus tshawytscha*, Coho Salmon *Oncorhynchus kisutch*, Brown Trout *Salmo trutta*, Lake Trout *Salvelinus namaycush*, and Rainbow Trout *Oncorhynchus mykiss*) and whether the salmonid niches are influenced by the trophic ecology of their prey, the forage fish (Alewife *Alosa pseudoharengus*, Rainbow Smelt *Osmerus mordax*, Round Goby *Neogobius melanostomus*, Deepwater Sculpin *Myoxocephalus thompsonii*, and Slimy Sculpin *Cottus cognatus").

The analysis in chapter two estimated the isotopic niche and overlap to determine habitat use and diet of forage fish species using $^{15}$N and $^{13}$C isotopes as tracers. Variation in the isotope values in relation to fish size, bathymetric depth, and region was also examined. The forage fish community provides the food resources for salmonid predators which in turn support valued recreational fisheries and native fish restoration programs. This research improved our understanding of the ecology of forage fish in Lake Ontario. Of particular interest was determining the response of the prey community to recent invasions by the Round Goby and populations declines in both populations of Deepwater
Sculpin and Rainbow Smelt. By quantifying the isotopic niche and examining variation in isotope values of these species, several conclusions were reached. To a large extent Lake Ontario forage fishes were estimated to have unique isotopic niches, both in area and overlap, except for the sculpin species (Deepwater and Slimy Sculpin) which had high isotopic overlap with each other. Niche area determined that forage fish diet ranged from a select few prey to a wide range of prey with Round Goby encompassing the largest niche area and the sculpin spp. and Rainbow Smelt had the smallest. Discrete regional subpopulations based on stable isotope values were suggested for Alewife, Rainbow Smelt and Round Goby. Spatial and temporal changes in the $\delta^{15}$N and $\delta^{13}$C values in smaller Alewife were much more variable compared to larger Alewife across the lake compared in which larger Alewife $\delta^{15}$N values varied little across space and time. Temporal changes in Rainbow Smelt $\delta^{15}$N values with length were greater than $\delta^{13}$C for this species with most isotopic variability occurring only in the spring.

Temporal changes in the $\delta^{15}$N values with length were also greater for Round Goby but varied by bathymetric depth. The $\delta^{15}$N values were always higher in Round Gobies collected in the offshore and much more variability in the $\delta^{15}$N values between the nearshore (<30 m) and offshore (>30 m) occurred during the spring and less during the summer. No regional subpopulations were detected for the sculpin spp. but $\delta^{15}$N increased with body size for Deepwater Sculpin and very slight seasonal changes in the $\delta^{15}$N values were observed for Slimy Sculpin.

The results of chapter two suggest partitioning of, and minimal competition for, dietary resources between forage fishes. Round Goby niche indicated that they have the largest prey base while the sculpin spp. and Rainbow Smelt consume a few select prey species. Rainbow Smelt and Round Goby had limited niche overlap probably because of
the common prey shared between both of these species (Evans & Loftus, 1987; Brush et al., 2012). The overlap between the sculpin spp. was most likely driven by dietary similarities, as the loss of *Diporeia* species in Lake Ontario caused Slimy Sculpin to switch to mainly consuming *Mysis relicta* (Walsh et al., 2008). Higher isotopic values were probably caused by benthic nutrient cycling in the offshore (Mulholland et al., 2000) and not necessarily a result of the fish feeding at a higher trophic level. The isotopic differences between small and large Alewives were likely caused by habitat differences while water stratification possibly drove the isotopic trends in Rainbow Smelt as habitat partitioning was evident in the spring when likely larger Rainbow Smelt fed in the pelagic and smaller individuals fed in the benthic. Round Goby migration to the nearshore during the spring (Lynch & Mensinger, 2012), was possibly influence variation in isotopic values in Round Goby. Ontogenetic shifts in diet were probably the influencing variation in isotopic values in Deepwater Sculpin.

There are three major conclusions from this work:

1. Limited resource sharing between forage fish as habitat preference influences diet.
2. Stable isotopes provide a method to infer diet generality or specificity via niche area determined by standard ellipses.
3. Nitrogen (δ\textsuperscript{15}N) over carbon (δ\textsuperscript{13}C) is driving the spatial and temporal isotopic trends in Lake Ontario, at least for the forage fishes.

Chapter three quantified the isotopic niche and overlap, and relative trophic position to determine habitat use and reconstructed the salmonid diet using the five major forage fishes of the six Lake Ontario salmonids using δ\textsuperscript{15}N and δ\textsuperscript{13}C. It was necessary to understand the niche and diet of these species as they serve as top predators in the offshore consuming large biomasses of forage fish and support an economically
important recreational fishery and native species restoration program. Peer-reviewed published diet data for most of these species dates before the arrival of Round Goby and Lake Ontario diet data does not exist for Atlantic Salmon. Results indicated that Lake Ontario salmonids co-inhabit mainly the offshore and Alewife was the main prey. Chinook Salmon niche was the smallest while Rainbow Trout had the largest niche. High niche exclusivity was present in Lake Trout, Brown Trout and Rainbow Trout, while the Chinook Salmon niche showed no niche exclusivity, in that nearly 100% of its niche was overlapped by other salmonids. Therefore, Chinook Salmon had the lowest niche partitioning of all salmonid species. The relative trophic position of the salmonids was estimated at approximately TP= 4. Round Goby was found to be a secondary prey item of many salmonids, especially in Brown Trout, followed by Rainbow Smelt.

Results suggested that there is high potential for competition for shared (i.e., Alewife) resources mainly in the epilimnion but salmonids have adapted to incorporate benthic resources (i.e., Round Goby) into their diets. Niche area suggested that salmonid diets ranged from consuming a large suite of prey items to a select couple. The use of stable isotopes revealed that the changing ecology of these species may be through their life history strategies (i.e., ontogeny). Brown Trout likely obtain most of their carbon from nearshore environments due to the large percentage of Round Goby in its diet. There is possibly an allometric difference in Lake Trout, in that as this species grows, it likely obtains most of its diet from pelagic as opposed to benthic habitats. Atlantic Salmon restoration may prove difficult due to the large niche and diet overlap with the other species which means they will have to share limited food resources with other salmonids.
There are four major conclusions of this work:

1. There is high resource sharing between salmonids as most predation occurs in the offshore and is concentrated on Alewife.

2. Allometric variation in isotope values suggest smaller salmonids rely more on nearshore food resources than larger salmonids.

3. Using stable isotopes revealed that salmonids to differing extents consume Round Goby over Rainbow Smelt probably due to differences in prey abundances.

4. If the Alewife population was to collapse in Lake Ontario, salmonids with small niche areas would (i.e., Chinook Salmon) probably suffer and undergo population reduction.

4.2 Implications

This thesis has made substantial contributions to our knowledge of Lake Ontario salmonid and forage fish niche, trophic structure, diet and spatial and temporal variation in habitat use and diets among species. This study was unique to previous studies completed in the Great Lakes in that it was the largest stable isotope study completed in terms of single lake, single year sampling and data analyzation. This robust data set covered a large spatial scale, good seasonal coverage, used a proven modern technology (i.e., stable isotopes analysis), and examined many different predators and prey simultaneously. The large collection of prey allowed for complex analysis of the habitat use of the forage fish.

As well, this thesis improved our understanding of the Lake Ontario offshore predator-prey interactions in terms of fisheries management and restoration. This understanding could help lead in mitigating trophic cascades/trophic shifts which have
occurred in Lake Huron (Madenjian et al., 2013). Humans highly regulate the predator-prey interactions in Lake Ontario and in other Great Lakes (Dettmers et al., 2012), which impacts the ecosystem health of Lake Ontario. Imbalance of predator to prey biomass could result in changes to the top-down or bottom-up regulations. Further understanding the predator-prey interactions assist in the determination of the trophic transfer efficiency from the forage fish and salmonids.

It is important to understand how native and non-native species interact and how food webs respond to invasive species. Resource partitioning between abundant non-native salmonids and rare native salmonids raises concerns about salmonid interaction (Crawford, 2001). This situation could be suppressing the native salmonid populations, as non-native salmonids consume a large percentage of favoured forage fishes, leaving the native salmonids to spend additional energy to actively seek out prey. This in turn could cause native salmonids to shift their distribution to find the favoured forage fishes to prey upon. The offshore Lake Ontario food web responded quickly to the wave of invasive species like the Round Goby as this species has become a staple food stuff for the salmonids and provides another link in the food web. As well, salmonids could potentially influence Round Goby population dynamics through top-down controls.

Our study analyzed trophic structure and diet by using muscle tissue which represents an accumulated monthly isotopic outlook due to slower turnover rates (Thomas & Crowther, 2015). To observe weekly to daily changes in the isotopic values of these species (both prey and predator) we should further use liver and blood as by using these tissues we could detect swift changes in diet and habitat use (Buchheister & Latour, 2010). As well, the diet of the forage fish could be determined using stable isotopes values from prey (i.e., zooplankton, Mysids, etc.) to compare historical (pre 1990) diets to
current diets due to the large influx of invasive zooplankton to Lake Ontario since the 1990’s (Mills et al., 2005).

The results drawn from this study could have implications for the restoration of Bloater, which are currently being stocked into Lake Ontario. The isotopic niche area of this species is unknown in Lake Ontario. Bloater (*Coregonus hoyi*) is an important forage fish in Lakes Michigan and Huron salmonid diets (Jacobs et al., 2013; Roseman et al., 2014). Results show that there is little niche overlap between the forage fishes, but would Bloater occupy its own unique niche area or be completing for resources with other hypolimnetic dwelling forage fishes (e.g., Rainbow Smelt, sculpin spp.). Round Goby are a secondary prey item of nearly all Lake Ontario salmonids, probably due to the decline of Rainbow Smelt abundance (Holden & Connerton, 2015). If the decline of Rainbow Smelt continues and Bloater stocking is increased, Bloater will likely substitute into the salmonid diet, mainly Lake Trout over Rainbow Smelt.
4.3 References


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