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Tanya E. Fendler
University of Windsor

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Impact of Partial Migration, Ontogeny, and Species Invasions on Lake Sturgeon Feeding Ecology in the Huron Erie Corridor

By

Tanya E. Fendler

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University of Windsor

Windsor, Ontario, Canada

Impact of Partial Migration, Ontogeny, and Species Invasions on Lake Sturgeon Feeding Ecology in the Huron Erie Corridor

By

Tanya Fendler

APPROVED BY:

____
D. M. Higgs
Department of Biological Sciences

____
H. J. MacIsaac
Great Lakes Institute for Environmental Research

____
D. W. Hondorp, Co-Advisor
U.S. Geological Survey

____
A. T. Fisk, Advisor
Great Lakes Institute for Environmental Research

23 April 2018

DECLARATION OF CO-AUTHORSHIP

I. CO-AUTHORSHIP

I hereby declare that this thesis incorporates a submitted manuscript that is result of joint research. S. T. Kessel provided analyzed acoustic telemetry data and H. Pettitt-Wade provided data analysis of prey samples for chapter two. Both J. A. Chiotti and D. Gorsky contributed to chapters 2 and 3 with sample collection and aging analyses. T. E. Pitcher contributed resources and access to many contacts needed to complete this project. In all chapters, both A. T. Fisk and D. W. Hondorp provided consultation and resources needed to complete this research. In all cases, the key ideas, primary contributions, stable isotope data analysis, interpretation, and writing are a product of my work.

I am aware of the University of Windsor Senate Policy on Authorship and I certify that I have properly acknowledged the contribution of other researchers to my thesis, and have obtained written permission from each of the co-authors to include the above material in my thesis.

I certify that, with the above qualification, this thesis, and the research to which it refers, is the product of my own work.

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ABSTRACT

Research surrounding lake sturgeon (*Acipenser fulvescens*) feeding ecology in the Great Lakes is dated compared to other aspects of their ecology, despite their threatened status. Recent research has demonstrated migration polymorphisms in lake sturgeon from the Lake Huron-to-Lake Erie corridor (HEC), but dietary links are lacking in this system. This knowledge gap led to the question of whether or not lake sturgeon feeding ecology varies both temporally and spatially within the HEC. We found adult lake sturgeon were generalist feeders in this system. After the round goby (*Neogobius melanostomus*) invasion, differences in isotopic niches were observed across age-classes. Mean stable isotopes were similar across migration behaviours and location, however niche sizes ranged from 3.1‰ to 8.5‰. Findings suggest diet estimates of lake sturgeon are not transferable across study sites. This interdisciplinary approach of combining movement and feeding ecology can be applied to other species and other study systems.

DEDICATION

This thesis is dedicated to my parents, Jürgen and Elizabeth; your love, encouragement, and advice have guided me every step of the way.

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I am foremost thankful to my dedicated supervisors, Aaron Fisk and Darryl Hondorp for their constant encouragement, helpful revisions, support for new project ideas, and above all, taking me on as one of their students.

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TABLE OF CONTENTS

4. GENERAL DISCUSSION

LIST OF TABLES

Chapter 2

Chapter 3

LIST OF FIGURES

Chapter 1

Chapter 2

Chapter 3

CHAPTER 1

GENERAL INTRODUCTION

Food Web Ecology

Food chains are a linear sequence of energy transferred to each organism as one consumes the other. Food chains are made up of producers and consumers; producers are heterotrophs that use solar radiation to produce their own food, and consumers gain their energy by feeding on either producers or other consumers. The higher up a consumer is on a food chain, the more energy is lost to the environment; this inefficiency limits the length of most food chains as well as explains why fewer organisms occupy each successive level. Most species feeding relationships are more complex than solely consuming one prey item (omnivory) and thus food webs are a more accurate representation of feeding relationships than food chains (Paine, 1988).

Food webs, comprised of several food chains, are a complex network of interactions among organisms within a community and were first described in Elton (1927). It was proposed that highly complex food webs consisting of few strong and many weak interactions are highly stable and thus less prone to species invasions and population oscillations (Elton, 1958; Paine, 1980; McCann et al., 1998). For example, 28 million pathways were estimated in the food web connecting Cape fur seals (*Arctocephalus pusillus pusillus*) to Cape hakes (*Merluccius spp.*; Yodzis, 1998), a human harvested fish. Originally, Yodzis was asked if culling cape fur seals in South Africa would increase the hake harvest, but he ultimately found that controlling fur seal populations would increase numbers of other predators.

Today, we live in the era of the Anthropocene, a period in which human activity has a dominating effect on climate and the environment. Within this era, and likely driven by humans, is the sixth largest extinction event in history (Stephen et al., 2004).

Overharvesting, habitat fragmentation, and the introduction of invasive species have all contributed to species extinction and are all pressures on food webs. In Daniel Pauly's *Fishing Down Marine Food Webs* (1998), humans overharvested the top trophic levels of the marine food web (ie: tuna) and eventually had to look for other sources of food from lower trophic levels (anchovies). In contrast to removal, the addition of species into a community can impact food webs. For example, largemouth bass (*Micropterus salmoides*) was released into a system where lake trout (*Salvelinus namaycush*) was the top predator. Lake trout was subsequently shifted to a lower trophic level due to competition for prey resources with largemouth bass (Vander Zanden, 1999).

The conditions surrounding the study of food webs make it difficult to quantify the entire set of feeding relations possible in a community. Observational methods to study feeding relationships are difficult in nature because feeding events are rare, time consuming, and environmental conditions can make studying problematic. Stomach content analysis of consumers and stable isotope analysis are two alternative methods to studying food webs, each with their own list of pros and cons. Additionally, while the "web" remains, new species can be added and old ones can disappear, making them even more difficult to study (Elton, 1927). However, it is important to study food webs to promote a better understanding of ecosystem dynamics and community infrastructure in midst of the Anthropocene.

Feeding Ecology and Stable Isotopes

Feeding ecology is the study of consumer-resource relationships between different organisms in a food web. Joseph Grinnell (1917) first coined the term "niche", defined as the sum of habitat requirements and behaviours that allow a species to persist. These niches can be modeled using the Hutchinsonian niche, which is made up of two parts: a fundamental niche and a realized niche (Hutchinson, 1957). The fundamental niche is the area where a species can survive and reproduce, while the realized niche is an area where fitness is higher and takes into consideration predation and competition. The X and Y axes of this model, which usually incorporates biotic and abiotic factors that affect a species' survival, can be modified to incorporate factors that influence a species feeding ecology.

Stable isotopes, most commonly carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), have been used in many ecological studies (Vander Zanden & Rasmussen, 2001; Bearhop et al., 2004; Brush et al., 2012), are elements with an extra neutron that make it possible to compare the ratios from light to heavy isotopes in a mass spectrometer because they travel different distances through a magnetic field (Fry, 2007); these differences in isotopic composition are linked to food source. In freshwater lakes, $\delta^{13}C$ is an indicator of whether an individual is feeding on more littoral or pelagic foods (Fry, 2007). These isotopic compositions will typically be higher the more near-shore (littoral) they feed, which comes from macrophytes and algae, whereas an offshore $\delta^{13}C$ comes from the production of phytoplankton – both these groups having a different photosynthetic pathway (France, 1995). In comparison, $\delta^{15}N$ is correlated with trophic level because an organism will use ^{14}N more readily than ^{15}N from its tissues and ^{15}N will accumulate up the food chain (Hussey et al., 2012).

Using stable isotope analysis (SIA) is beneficial over stomach content because it provides information on diet over a time scale of weeks to years depending on the tissue, as compared to the species' digestion time, usually < 24 hours. Stomach content analysis either requires sacrificing the subject or an invasive stomach pumping method (Hakala & Johnson 2004; Parra & Jedensjo, 2014), consequently making stable isotope method more practical when studying species at risk. However, baseline data is necessary to place individuals within a food web based on isotopic compositions due to the possible effects of spatial and temporal variation (Post, 2002).

Lake Sturgeon Morphology, Ecology, and History

Lake Sturgeon are a long-lived, cartilaginous fish that are native to the Laurentian Great Lakes (hereafter the Great Lakes). Historical records from Great Lakes fisheries report individuals captured were over 2m in length and weighed over 100 kg (Van Oosten, 1956). Lake sturgeon are potamodromous and migrate for both feeding and spawning purposes (Schueller & Hayes, 2010). They are intermittent spawners and usually reach sexual maturity between ages 12-15 for males and 18-27 for females (Peterson et al., 2007). Although mostly consisting of a cartilaginous skeleton, they are armored with bony plates called scutes and boney pectoral fins. Their pectoral fin spines grow in patterns consistent with tree rings, which have been used as a method for aging sturgeon for approximately 100 years (Bruch et al., 2009). These spines also record environmental conditions, such as changes in nitrogen and carbon stable isotopes, and are a non-lethal way of obtaining this data from lake sturgeon.

Lake sturgeons primarily feed on benthic invertebrates that are found using a variety of sensory receptors (Auer, 2007). They forage by feeling along the bottom of lakes and rivers for prey using four barbels and sucking them up with a protractible mouth (Vecsei & Peterson 2004). Prey sources are then crushed against a cartilaginous palate (Priegel & Wirth, 1974). Although benthic macroinvertebrates are the dominant prey source (Peterson et al., 2007), lake sturgeon diet varies temporally and spatially (Beamish et al., 1998, Guilbard et al., 2007). For example, adult lake sturgeon in Oneida Lake fed mainly on Zebra Mussels, while lake sturgeon from the Niagara River fed predominantly on round gobies (Jackson et al., 2002; Jacobs et al., 2017).

Lake sturgeon, now protected in all U.S states and Canadian provinces bordering the Great Lakes, were once abundant throughout the Great Lakes but have since declined to historically low levels due to overfishing and habitat fragmentation (Auer, 1996). In the early 1800s, lake sturgeon were considered a bycatch species, however, it was not until they were commercially targeted for their caviar in the 1880s that their population drastically declined (Auer & Dempsey, 2013). Additionally, river habitats were being dredged and dammed to build cities and shipping channels and support the growing population, thus affecting lake sturgeon spawning sites and migration routes (Auer & Dempsey, 2013). Intermittent spawning and late maturity make lake sturgeon particularly sensitive to overfishing and habitat fragmentation (Auer, 1996; St. Pierre & Runstrom 2004). Although fishing regulations have been implemented in Canada and the U.S, lake sturgeon have been slow to recover. In an effort to increase the lake sturgeon population, artificial spawning reefs were constructed in the Detroit River in 2004 and utilized by 2009 (Roseman et al., 2011). At present, lake sturgeon are listed as vulnerable in Minnesota and Wisconsin; threatened in Ontario (Canada), Michigan and New York; endangered in Illinois, Ohio and Indiana; and critically imperiled in Pennsylvania (see Figure 1.1).

Invasive Species in the Laurentian Great Lakes

Invasive species are defined as an animal, plant, or fungus species introduced outside of its native range that has become widespread and dominant in that new range (Colautti & MacIsaac, 2004). In the Great Lakes, invasive species have caused a number of economic and ecologic effects. For example, in 2012 U.S Fish and Wildlife Service reported over 400 species are at risk due to competition with and predation by invasive species, and costs the region 200 million U.S dollars annually in management. The successful establishment of these invasive species is partly due to the similarities between the new habitat and their native range, the Ponto-Caspian region of Europe (Kornis et al., 2012); many invaders were introduced through discharge of ballast water of transoceanic vessels (Reid & Orlova, 2002). However, these species can also have beneficial effects on native species in their environment, for instance small-bodied invasive species have become prey for larger-bodied native species (Vander Zanden et al., 1999).

Invasive species introduction and proliferation has resulted in their assimilation into local food webs through predator-prey interactions. As such, Dreissenid mussels and round goby have caused a multitude of ecological effects in the Great Lakes in part through alterations to the food web dynamics of native species (Ozersky et al., 2012). Dreissenid mussels were first discovered in Lake Erie in 1986 and became well-established in the Great Lakes by 1989 (Griffiths et al., 1991). Round goby was first documented in the St. Clair River in 1990 and by 1999 were well-established in the Great Lakes (Walsh et al., 2007). Dreissenid mussels filter feed for plankton and thus pelagic carbon and round goby feed on Dreissenid mussels. Native benthic-feeding fish feed on

Dreissenid mussels and round goby, and in some instances, these species constitute a large proportion of their diets. For example, adult lake sturgeon in Lake Ontario now feed primarily on Dreissenid mussels and round goby (Auer & Dempsey, 2013; Jacobs et al., 2017).

Study System

Research took place within the Lake Huron-to-Lake Erie Corridor (HEC) which is comprised of the St. Clair River, Lake St. Clair, and the Detroit River. The St. Clair River flows 64 km south from Lake Huron to Lake St. Clair. Lake St. Clair is a relatively shallow lake, averaging 3.4m deep and shipping channels 8.2m deep (Leach, 1991), with a highly urbanized shoreline (U.S Army Corps of Engineers, 2004). Finally, the Detroit River flows 44 km from Lake St. Clair to Lake Erie. The HEC is a known migration route of lake sturgeon and contains current spawning habitats (Roseman et al., 2011; Hondorp et al., 2014). This major connecting channel has remained unobstructed by barriers such as dams, allowing lake sturgeon to feed and move liberally and thrive as one of the healthiest populations (Thomas & Haas, 2002). Recent research found migration polymorphisms, different migration behaviours, exists among lake sturgeon within this connecting channel (Kessel et al., 2017) and was thus chosen for our research to determine potential sub-populations of lake sturgeon based on their foraging ecology.

Chapters and Objectives

The objective of my thesis is to quantify lake sturgeon feeding ecology, a largely overlooked aspect of lake sturgeon ecology, across migration behaviours categorized by

Kessel et al. (2017), age-classes, and through two major invasive species invasions (Dreissenids and round goby). The thesis consists of two research chapters, both used $\delta^{13}C$ and $\delta^{15}N$ in fin spines collected from 1991 to 2014. Of these samples, 56 were collected from Lake St. Clair, 90 from the Detroit River, and 56 from St. Clair River, for a total of 202 samples to quantify food ecology, in particular using isotopic niche, a measure of dietary niche. Lake sturgeon fin spines grow radially and were used to categorize them into age-classes. These spines are also a non-lethal way of gaining information about their relative environmental conditions through its chemical composition altered by their diet and this composition remains inert in the bone and thus was used for this study.

Chapter 2 – Isotopic niches of lake sturgeon with different migration behaviours within and between rivers and lakes

The main objective of this chapter is to determine whether lake sturgeon feeding ecology varies on the spatial scale within the HEC, and examined the following hypotheses:

H_1: Isotopic niches of lake sturgeon within the HEC will show a high degree of niche overlap across capture locations.

H_2: Isotopic niches of lake sturgeon will vary both by migration behaviour and by location in which they migrated to, likely due to the variation in prey richness and abundance.

H_3: Diet estimates of lake sturgeon will show high preference towards benthic invasive species, possibly due to their high abundance in the HEC.

Chapter 3 – Isotopic Niches of Lake Sturgeon Pre- and Post- Dreissenid Mussel and Round Goby Invasions

The main objective of this chapter is to determine if lake sturgeon feeding ecology varies on the temporal scale, examining the following hypotheses:

H_1: Lake sturgeon isotopic niches will reflect their increased predation on the invasive round goby and Dreissenid mussels, increasing their trophic position and use of the pelagic energy pathways (Figure 1.2).

H_2: Isotopic niches of lake sturgeon will vary ontogenetically, likely due to size-specific constraints.

References

Auer, N.A., (1996). Importance of Habitat and Migration to Sturgeons with Emphasis on Lake Sturgeon. *Canadian Journal of Fisheries and Aquatic Sciences*, *53*(1), 152–160.

Auer, N.A., & Dempsey, D. (2013). *The Great Lake Sturgeon*. East Lansing, MI: Michigan State University Press.

Beamish, F.W.H., Noakes, D.L.G., & Rossiter, A. (1998). Feeding Ecology of Juvenile Lake Sturgeon, *Acipenser fulvescens,* in Northern Ontario. *The Canadian Field-Naturalist, 112*(3), 459–468

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., & MacLeod, H. (2004). Determining Trophic Niche Width: *A Novel Approach Using Stable Isotope Analysis. Journal of Animal Ecology, 73*(5), 1007–1012.

Brush, J.M., Fisk, A.T., Hussey, N.E., & Johnson, T.B. (2012). Spatial and Seasonal Variability in the Diet of Round Goby (Neogobius melanostomus): Stable Isotopes Indicate that Stomach Contents Overestimate the Importance of Dreissenids. *Canadian Journal of Fisheries and Aquatic Sciences*, *69*(3), 573–586.

Bruch, R.M., Campana, S.E., Davis-Foust, S.L., Hansen, M.J., & Janssen, J. (2009). Lake Sturgeon Age Validation using Bomb Radiocarbon and Known-Age Fish. *Transactions of the American Fisheries Society, 138*(2), 361 – 372.

Colautti, R. I., & MacIsaac, H. J. (2004). A Neutral Terminology to Define ‘Invasive’ Species. *Diversity and Distributions, 10*(1), 135 – 141.

Elton, C.S. (1927). *Animal Ecology*. New York, NY: The MacMillan Company.

Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*. Chicago, IL: University of Chicago Press.

France, R. L. (1995). Carbon-13 Enrichment in Benthic Compared to Planktonic Algae, Foodweb Implications. *Marine Ecology Progress Series, 124*(1), 307–312.

Fry B. 2007. *Stable Isotope Ecology*. Baton Rouge, LA: Springer.

Griffiths, R.W., Schloesser, D.W., Leach, J.H., & Kovalak, W.P. (1991). Distribution and Dispersal of the Zebra Mussel (*Dreissena polymorpha*) in the Great Lakes Region. *Canadian Journal of Fisheries and Aquatic Sciences, 48*(8), 1381–1388.

Grinnell, J. (1917). The Niche-Relationships of the California Thrasher. *The Auk, 34*(4), 427–433.

Guilbard, F., Munro, J., Dumont, P., Hatin, D., & Fortin, R. (2007). Feeding Ecology of Atlantic Sturgeon and Lake Sturgeon Co-Occuring in the St. Lawrence Estuarine Transition Zone. *American Fisheries Society Symposium, 56*(1), 85–104.

Hakala, J. P. & Johnson, F. D. (2004). Evaluation of a Gastric Lavage Method for Use on Largemouth Bass. *North American Journal of Fisheries Management, 24*(1), 1398–1403.

Hondorp, D.W., Roseman, E.F., Manny, B.A., Seelbach, P.W., Newman, K.R., & Strach, R.M. (2014) An Ecological Basis for Fish Habitat Restoration in the Huron-Erie Corridor. *Journal of Great Lakes Research, 40*(1), 23–30

Hussey, N.E., MacNeil, M.A., Olin, J.A., McMeans, B.C., Kinney, M.J., Chapman, D.D., & Fisk, A.T. (2012). Stable Isotopes and Elasmobrachs: Tissue Types, Methods, Applications and Assumptions. *Journal of Fish Biology, 80*(5), 1449–1484.

Hutchinson, G. E. (1957). Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology, 22*(1), 415–427.

Jackson, J.R., VanDeValk, A.J., Brooking, T.E., vanKeeken, O.A., & Rudstam, L.E. (2002). Growth and Feeding Dynamics of Lake Sturgeon, Acipenser fulvescens, in Oneida Lake, New York: Results from the First Five Years of a Restoration Program. *Journal of Applied Ichthyology, 18*(1), 439–443.

Jacobs, G.R., Bruestle, E.L., Hussey, A., Gorsky, D., & Fisk, A.T. (2017). Invasive Species Alter Ontogenetic Shifts in the Trophic Ecology of Lake Sturgeon (*Acipenser fulvescens*) in the Niagara River and Lake Ontario. *Biological Invasions, 19*(1), 1533–1546.

Kessel, S.T., Hondorp, D.W., Holbrook, C.M., Boase, J.C., Chiotti, J.A., Thomas, M.V., Wills, T.C., . . . Krueger, C.C. (2017). Divergent Migration Within Lake Sturgeon (*Acipenser fulvescens*) Populations: Multiple Distinct Patterns Exist Across an Unrestricted Migration Corridor. *Journal of Animal Ecology, 87*(1), 259–273.

Kornis, M. S., Mercado-Silva, N. & Vander Zanden, M. J. (2012). Twenty Years of Invasion: a Review of Round Goby *Neogobius melanostomus* Biology, Spread and Ecological Implications. *Journal of Fish Biology, 80*(1), 235–285

Leach, J. H. (1991). Biota of Lake St. Clair: Habitat Evaluation and Environmental Assessment. *Hydrobiologia, 219*(1), 187–202.

McCann, K., Hastins, A., & Huxel, G.R. (1998). Weak Trophic Interactions and the Balance of Nature. *Nature, 395*(1), 794–798.

Ozersky, T., Evans, D.O., & Barton, D.R. (2012). Invasive Mussels Alter the Littoral Food Web of a Large Lake: Stable Isotopes Reveal Drastic Shifts in Sources and Flow of Energy. *PLOS one. 7*(12), e51249. doi:10.1371/journal.pone.0051249.

Paine, R.T. (1980). Food Webs: Linkage, Interaction Strength and Community Infrastructure. *Journal of Animal Ecology, 49*(6), 666–685.

Paine, R. T. (1988). Food Webs: Road Maps of Interactions or Grist for Theoretical Development? *Ecology, 69*(1), 1648–1654.

Parra, G. J. & Jedensjö, M. (2014), Stomach Contents of Australian Snubfin (*Orcaella heinsohni*) and Indo-Pacific Humpback Dolphins (*Sousa chinensis*). *Marine Mammal Science, 30*(1), 1184–1198.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., & Torres, F. J. (1998). Fishing Down Marine Food Webs. *Science, 279*(5352), 860–863.

Peterson, D.L., Vecsei, P., & Jennings, C.A. (2007). Ecology and Biology of the Lake Sturgeon: a Synthesis of Current Knowledge of a Threatened North American *Acipenseridae*. *Reviews in Fish Biology and Fisheries. 17*(1), 59–76.

Post, D.M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology, 83*(3), 703–718.

Priegel, G.R., & Wirth, T.L. (1974). *The lake sturgeon: it's life history, ecology and management*, Madison, WI: Wisconsin Department of Natural Resources Publication.

Reid, D. F., & Orlova, M. I. (2002). Geological and Evolutionary Underpinnings for the Success of Ponto-Caspian Species Invasions in the Baltic Sea and North American Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences, 59*(1), 1144–1158.

Roseman, E. F., Manny, B., Boase, J., Child, M., Kennedy, G., Craig, J., Soper, K., & Drouin, R. (2011). Lake Sturgeon Response to a Spawning Reef Constructed in the Detroit River. *Journal of Applied Ichthyology, 27*(1), 66–76.

Schueller, A. M., & D. B. Hayes. (2010). Sensitivity of Lake Sturgeon Population Dynamics and Genetics to Demographic Parameters. *Transactions of the American Fisheries Society, 139*(1), 521–534.

St. Pierre, R., & Runstrom, A. (2004). *Acipenser fulvescens* [The IUCN Red List of Threatened Species]. Retrieved from http://www.iucnredlist.org/details/223/0.

Steffen, W., Sanderson, A., Tyson, P.D., Jäger, J., Matson, P.A., Moore III, B., Oldfield, F., . . . Wasson, R. J. (2004) *Global Change and the Earth System: A Planet Under Pressure*. Berlin, Germany: The IGBP Book Series.

Thomas, M. V., & Haas, R. C. (2002). Abundance, Age Structure, and Spatial Distribution of Lake Sturgeon, *Acipenser fulvescens*, in the St. Clair System. *Journal of Applied Ichthyology, 18*(1), 495–501.

U.S Army Corps of Engineers (2004). *St. Clair River and Lake St. Clair Comprehensive Management Plan*. Retrieved from http://www.lre.usace.army.mil/Portals/69/docs/PPPM/PlanningandStudies/ApprovedReviewPlans/SCRLSCfinal2.pdf

Vander Zanden, M.J., Casselman, J.M., & Rasmussen, J.B. (1999). Stable Isotope Evidence for the Food Web Concequence of Species Invasions in Lakes. *Nature. 401*(1), 464–467.

Van Oosten, & Eschmeyer, P. H. (1956). *Biology of Young Lake Trout (Salvelinus namaycush) in Lake Michigan.* U.S Fish and Wildlife Research Report 42.

Vander Zanden, M.J., & Rasmussen, J.B. (2001). Variation in δ^{15}N and δ^{13}C Trophic Fractionation: Implications for aquatic food web studies. *Limnology and Oceanography, 46*(8), 2061–2066.

Vecsei, P. & Peterson, D.L. (2004) Sturgeon Ecomorphology: a Descriptive Approach. In: G. T. O. LeBreton, F. W. H. Beamish, R. S. McKinley (Eds.), *Sturgeons and Paddlefish of North America* (103–133). Dordrecht, The Netherlands: Kluwer Academic Publishers.

Walsh, M.G., Dittman, D.E., & O'Gorman, R. (2007). Occurrence and Food Habits of the Round Goby in the Profundal Zone of Southwestern Lake Ontario. *Journal of Great Lakes Research*, *33*(1), 83–92.

Yodzis, P. (1998) Local Trophodynamics and the Interaction of Marine Mammals and Fisheries in the Benguela Ecosystem. *Journal of Animal Ecology, 67*(1), 635–658.

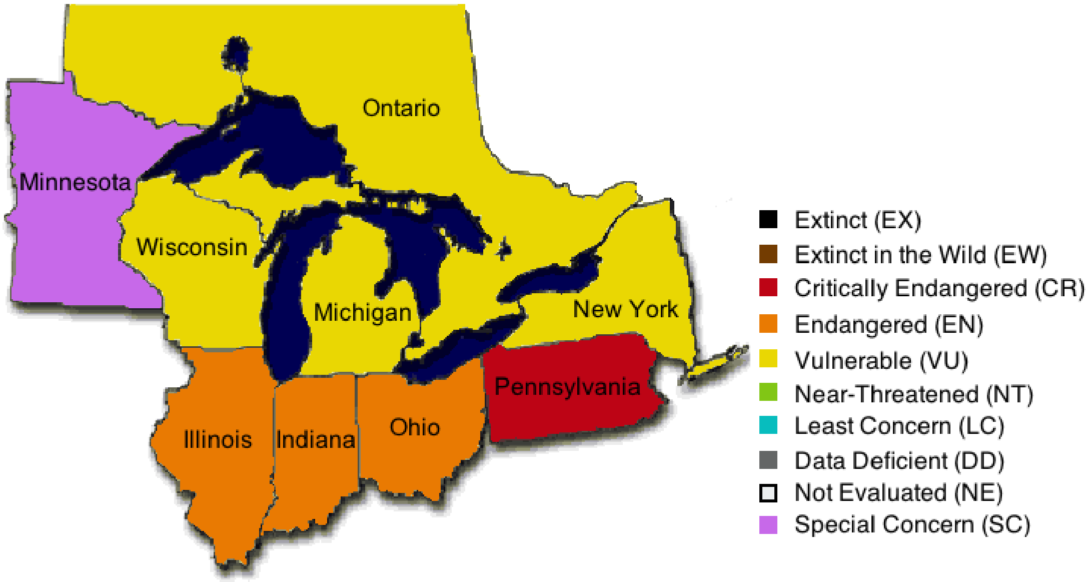

Figure 1.1 Conservation status of lake sturgeon in each bordering U.S. state and Canadian province as of August 2016. Data was collected from U.S. Geological Survey, U.S Fish and Wildlife Service, and Ontario Ministry of Natural Resources and Forestry.

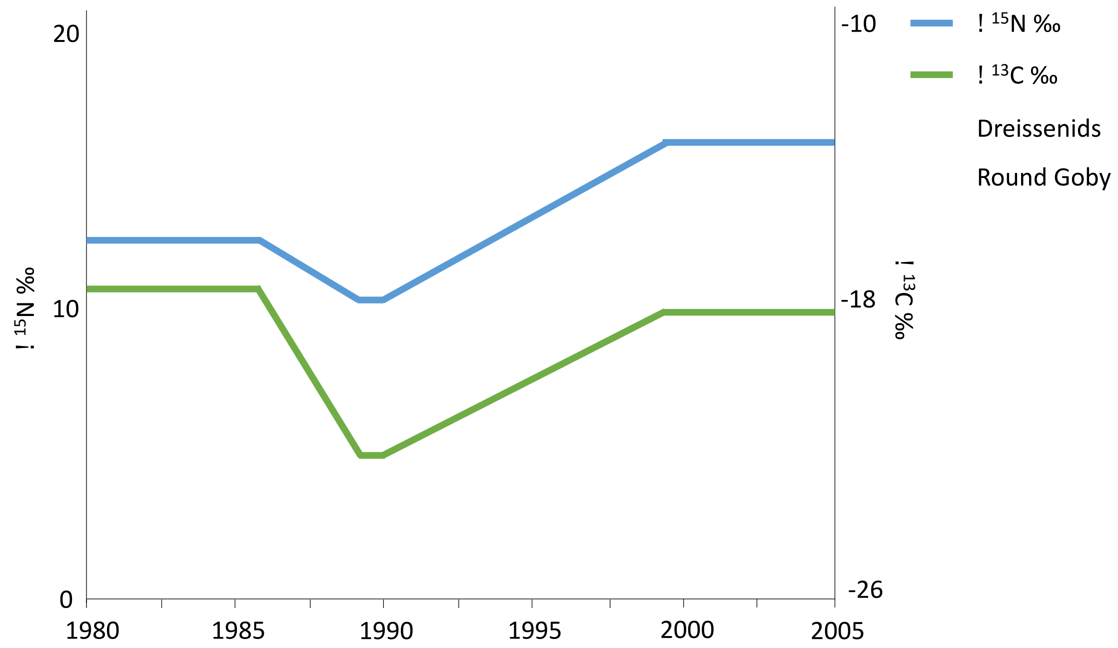

Figure 1.2 Conceptual model depicting the hypothesized effect Dreissenids and round gobies have on δ^{13}C and δ^{15}N in fin spines of lake sturgeon. The shaded areas represent the time in which the invasive species were first discovered to when they were considered widespread and dominant in the Huron Erie Corridor.

CHAPTER 2

ISOTOPIC NICHES OF LAKE STURGEON WITH DIFFERENT MIGRATION BEHAVIOURS WITHIN AND BETWEEN RIVERS AND LAKES

Introduction

Partial migration occurs when individuals in a population migrate while others remain residents and has been demonstrated across a variety of taxa (Grist et al., 2017; Quinn et al., 2017; Tshipa et al., 2017). Competitive release and trophic polymorphism, i.e., different feeding strategies, have both been shown in populations that have partial migration (Chapman et al., 2012). For example, Näslund (1991), demonstrated in a lab setting that some individuals of Arctic char (*Salvelinus alpinus*) migrate out of an area when fed smaller rations, thus reducing intraspecific competition. In the common roach (*Rutilus rutilus*), partial migration was related to resource, or trophic polymorphism, through intrapopulation variation in dietary preferences (Bolnick et al, 2003). Understanding feeding ecology across partially migrant fish populations is important for management and conservation, particularly for commercially important or threatened species.

Lake sturgeon (*Acipenser fulvescens*) have been shown to exhibit partial migration (Rusak & Mosindy 1997, Boase et al., 2011, Kessel et al., 2017). Although lake sturgeon are intermittent spawners, long-term data analysis of their migration behaviour have only recently been analyzed. In the Lake Huron-Lake Erie corridor, that includes connecting rivers and a much smaller Lake St. Clair, lake sturgeon showed five distinct migratory behaviours that differed with respect to when and for how long river habitats were used (see Kessel et al., 2017). River resident were defined as lake sturgeon that spend all or the majority of years in rivers with short duration lake trips, while those that spent the majority of years in lakes with short duration river trips were classified as lake dominant migrants. The other migratory behaviours include two forms of seasonal migrants, where every year lake sturgeon migrate into lakes in the winter and rivers in the summer, or visa versa, and lake skippers, where lake sturgeon consistently move between two lakes with the same pattern.

Lake sturgeon were once abundant throughout the Great Lakes, but due to overfishing and habitat fragmentation in the late 1800s, their populations dropped to 1% of their historic numbers (Pollock et al., 2014). Today, lake sturgeon are considered vulnerable and endangered in U.S states and the Canadian province bordering the Great Lakes. Efforts to recover lake sturgeon populations include re-building spawning reefs, restrictions on catch-and-release recreational fishing, and stocking programs (Peterson et al., 2007). While lake sturgeon recovery and research increased over the past few decades, little is known about their foraging ecology, particularly the influence of varying migration behaviours among sub-populations. Foraging and habitat use are tightly linked aspects of ecology that should be considered together to inform conservation and restoration efforts of threatened species, including the lake sturgeon (Jackson et al., 2002; McCabe et al., 2006; Gerig et al., 2011).

Lake sturgeon feeding ecology varies spatially, however is not as current compared to other aspects of their ecology (Pollock et al., 2014). Boase et al. (2011) found that mayfly (*Ephemeroptera spp*.) density was a predictor of lake sturgeon presence or absence in Lake St. Clair but a feeding link was not established; however, the feeding link from mayflies to crayfish to lake sturgeon was made in the Saskatchewan River (Phillips, unpublished data, In: Pollock et al., 2014). Lake sturgeon in Lake Winnebago fed mainly on Chironomids (Choudhury et al., 1996), round goby was their dominant prey in the Niagara River (Jacobs et al., 2017), and in general, Guilbard et al.

(2007) found their diet varied spatially in the St. Lawrence River. Given this variability, it is important to understand spatial variation in lake sturgeon diet to ensure future anthropogenic stressors do not impact vital prey resources (Pollock et al., 2014).

The Lake Huron-to-Lake Erie Corridor (HEC) is a historically known spawning ground of lake sturgeon (Auer, 1996) and has remained unobstructed by barriers, such as dams, that can impede spawning. Although its rivers were dredged to create shipping channels, lake sturgeon are able to move and feed freely through the lake and river habitats of the HEC. Thomas & Hass (2002) have documented that lake sturgeon in this area are considered one of the healthiest populations within the Great Lakes. Within the HEC are many variable habitats like the eutrophic Lake Erie or the shallow Lake St. Clair, which vary chemically and physically (i.e. chlorophyll-*a* concentrations, spring rate of warming, flow, etc.) both within and across lakes (Wang et al., 2015). Thus, the abundance and species composition of sturgeon prey varies spatially due to diversity in the physical habitat, and furthermore feeding opportunities may differ between migrant and river-resident individuals. Importantly, Smith and Baker (2005) noted that some systems may provide all resources needed for lake sturgeon to complete their lifecycle, consistent with a residency migration strategy. Additionally, residency may occur when individuals do not have enough energy accumulated to both invest in gonad/egg production and migrate out of the system (Chapman et al., 2012).

Although diet in a species at risk is difficult to quantify because of concerns about collection, stable isotopic niche provides a non-lethal method to quantify relative habitat and resource partitioning among or within populations (Chapman et al., 2012). In freshwater lakes, $\delta^{13}C$ is an indicator of littoral or pelagic location foraging and $\delta^{15}N$ is correlated with trophic position because it increases up the food chain (Cabana & Rasmussen, 1996; Fry, 2007). Using stable isotopes to quantify niche differences is beneficial over stomach content because it provides information over a time scale of weeks to years depending on the tissue. Stomach content only provides dietary data within the species' digestion period and often requires sacrificing the subject or an invasive stomach pumping method to gain information (Brush et al., 2012; Hakala & Johnson 2004, Parra & Jedensjo, 2014). Lake sturgeon fin spines grow radially and its chemical composition remains inert, and are thus a non-lethal way of gaining dietary information through isotopes (Jacobs et al., 2017).

The purpose of this study was to determine if capture location or migration behaviour are better predictors of lake sturgeon food habits, using the HEC population as a model. A combination of acoustic telemetry (Kessel et al., 2017) and stable isotope analyses in fin spines were used to test if adult lake sturgeon isotopic niche, a measure of dietary niche, varies 1) across capture location, 2) across locations in which they migrated, and 3) among migration strategies. We expect isotopic niches of lake sturgeon will vary depending on where they migrated and spend a majority of their time, given differences between river and lake habitats. An additional objective was to compare dietary proportions of lake sturgeon that remained within and between the St. Clair and Detroit Rivers. Common prey of lake sturgeon, determined using previous dietary studies on lake sturgeon, were thus also analyzed for stable isotopes.

Methods

Study Site and Lake Sturgeon Capture and Handling

Lake Sturgeon were captured from the Detroit River (n = 52) and the St. Clair River (n = 50) between years 2012 and 2014 (Figure 2.1) using six setlines constructed of a 91m diamond braid rope mother line with 50 snews (drop lines) joined at ~1.5m intervals. Each snew consisted of a 40cm number 36 tarred nylon twine, a net snap with swivel, and a Kirby size 4 hook, which was baited with previously frozen and thawed whole round gobies (*Neogobius melanostomus*). Setlines were set in the afternoon and recovered the next morning. Captured live lake sturgeon were hoisted aboard the research vessel using a landing net where total length, weight, and sex (when possible) were recorded. A sample of the leading-edge pectoral fin spine was removed, placed in a labelled paper envelope to be air-dried back at the lab for stable isotope and age analyses. As well, acoustic transmitters (VEMCO model V16-6L, 95mm in length, ~10-year battery life) were implanted into the peritoneal cavity as previously described by Hondorp et al. (2015). Following surgery and biopsy, sturgeon were released back to the river where they were caught.

Stable Isotope Analysis

Pectoral fin spines of lake sturgeon were first cross-sectioned using a low speed IsoMet saw to approximately 3mm thickness. Cross-sections were then drilled using a 5000 Sherline vertical milling machine at the edge of the spine, which is the location of most recent growth, and therefore reflects the most recent feeding history. To ensure isotopic niches were influenced by ontogenetic differences (Jacobs et al., 2017), drilled cross-sections were checked to confirm each drilled hole was a representation of the feeding history of individuals over the age of 15. Because aging fin spines become increasingly inaccurate over the age of 14 (Bruch et al., 2009), we accounted for this by grouping the drill points into a single age-class of ≥ 15. Powdered fin spine samples from drilling were weighed (600-800μg) into tin capsules, and $\delta^{13}C$ and $\delta^{15}N$ were determined using a Finnigan MAT Deltaplus mass spectrometer (Thermo Finnigan, San Jose, CA, USA) equipped with a 4010 elemental analyzer (Costech Instruments, Valencia, CA, USA).

Common prey of lake sturgeon were analyzed for $\delta^{15}N$ and $\delta^{13}C$; these included round gobies, logperch (*Percina caprodes*), zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*), mud snails (*Neotaenioglossa Hydrobiidae*), two types of amphipods (*Echinogammarus ischnus and Gammarus fasciatus*), Chironomid larvae (*Chironomidae spp*.), and crayfish (*Cambaridae spp*.). These were chosen based on dietary studies conducted on lake sturgeon in other regions of the Great Lakes. Round gobies and all macroinvertebrates were collected between years 2011 and 2013 from five sites within the St. Clair and Detroit Rivers (Table 2.1, Figure 2.1). Round gobies were collected using a bag seine net, angling and minnow traps, and macroinvertebrates were collected using a ponar sampler (see Pettitt-Wade et al., 2016). Logperch were collected from the Detroit River by USFWS using minnow traps in Fall 2017.

All fish muscle and invertebrate samples were freeze-dried for 48h and crushed into a fine powder using scissors. Invertebrates were lipid extracted by adding 2mL of 2:1 chloroform:methanol to a subsample, vortexed for 30s, and left in a 30°C water bath for 24h. The supernatant was carefully poured off, the vial with subsample refilled with 2mL of solvent, vortexed, poured off again, and left in the lab under a fume hood until dry (>24h) before weighing. Fish muscle and spine tissue were not lipid extracted due to low lipid content (Post et al., 2007). Fish muscle and macroinvertebrates were weighed into tin cups at 400 – 600 and 600 – 800 μg, respectively, before being run for stable isotopes as per lake sturgeon samples described above.

Stable isotope ratio values were expressed following the equation:

$$\delta X \text{ ‰} = (R_{SAMPLE} / R_{STANDARD} - 1) \times 1000$$

where X represents ^{13}C or ^{15}N and R represents the ratio of either $^{13}C{:}^{12}C$ or $^{15}N{:}^{14}N$ The mean analytical precision was 0.16‰ for $\delta^{15}N$ and 0.14‰ for $\delta^{13}C$ using four standards: NIST standard 1577c (bovine liver), an internal laboratory standard (tilapia muscle), certified USGS 41, and urea (n=88 for all); both values were under the acceptable 0.2‰. Equipment accuracy was checked throughout the sample analysis period based on NIST standards 8573, 8547, and 8574 for $\delta^{15}N$ and NIST standards 8542, 8573, and 8574 for $\delta^{13}C$ (n = 79 for all except n = 65 for NIST 8573); the mean differences from certified values were -0.13, -0.17 and -0.05‰ for $\delta^{15}N$ and -0.09, -0.06 and 0.05‰ for $\delta^{13}C$.

Acoustic telemetry

See Kessel et al. (2017) for details on acoustic telemetry. Briefly, acoustic receivers (Vemco 69kH, n=136) were strategically placed to monitor lake sturgeon movement within the HEC between 2012 and 2014; the array was altered slightly each year based on the previous year's data to improve efficiency (Figure 2.1). A rationalized detection efficiency of 100% was assumed, and a total of 268 lake sturgeon were tagged with V16 transmitters.

Individual lake sturgeon migratory or residence behaviours assessment methods were detailed in Kessel et al. (2017). In brief, lake sturgeon telemetry data were analyzed using Vemco VUE software with false detections and acoustic tag ID collisions identified and removed using the White-Mihoff Filtering Tool in the GLATOS package. Lake sturgeon were categorized using a agglomerative hierarchical cluster analyses into five migration behaviours: 1) seasonal movement patterns from rivers in the summer to lakes in the winter, 2) majority of year spent in lakes with short duration river trips, 3) majority of year spent in rivers with short duration lake trips, 4) seasonal movement patterns from lakes in the summer to rivers in the winter, and 5) individuals that utilize two lakes and one river with a consistent pattern. For this study, these five migration behaviours were grouped into three: river-resident (migration behaviour 3), seasonal migrant (migration behaviours 1, 4, and 5) and lake dominant migrant (migration behaviour 2) to address this study's objective. The three groups were combined into the single seasonal migrant group since our analysis of feeding ecology included an average across years, not seasons. Furthermore, we recognized a river-resident group, but residents of different rivers (e.g., Detroit vs. St. Clair) may or may not feed on the same prey.

In addition to migration behaviours, the location in which each lake sturgeon migrated was also analyzed. For this study, we used three discrete migration locations: 1) Detroit River to Lake Erie, 2) Detroit River to St. Clair River, and 3) St. Clair River to Lake Huron. The first category included lake dominant and seasonal migrant lake sturgeon that moved from Detroit river to Lake Erie. The second category incorporated Detroit and St. Clair River residents, seasonal migrants that moved from these two rivers to Lake St. Clair, and lake dominant migrants that remained in Lake St. Clair. These two rivers were grouped together since stable isotopes were not statistically different between rivers among sturgeon and prey. Finally, the third category contained lake dominant and seasonal migrant lake sturgeon that moved from the St. Clair River to Lake Huron.

Statistical analysis

Stable isotopes for lake sturgeon were separated in three ways: 1) based solely on capture location with no regard for migration behaviour, 2) migration location with no regard for capture or migration behaviour, and 3) migration behaviours with no regard for capture location; the latter two categorized by telemetry data in Kessel et al. (2017). Since the drilled point on each fin spine covered multiple years (multiple rings), we grouped three of Kessel's migration behaviours into one; both seasonal migration behaviours were grouped together along with individuals that utilized two lakes and one river, thus making three distinct migration behaviours: lake dominant migrant, seasonal migrant, and river-resident. Seasonal migrants return to spawning rivers annually, whereas lake dominant migrants return to spawning rivers at frequencies less than once per year.

A Shapiro-Wilk test for normality and a Levene's test to verify homogeneity of variances were used to assess assumptions of parametric statistics, however they were not normally distributed, and a non-parametric Kruskal-Wallis test was used to compare stable isotopes between capture site, migration location, and migration behaviour.

Diet proportion estimates of the lake sturgeon sub-population that migrated within and between the St. Clair and Detroit Rivers was calculated with a Bayesian modelling framework in the package SIMMR (Parnell et al., 2013); this package runs a MCMC model and provides a probability of diet proportions using a DTDF and the means and SDs of potential prey isotopes from the system. Prey data from the St. Clair and Detroit

Rivers were combined along with literature isotope values of key prey items of lake sturgeon in the HEC. Since there is no diet-tissue discrimination factors (DTDFs) for lake sturgeon fin spine, we calculated our own using stomach content and fin spine isotope results from Jacobs et al. (2017). They found round gobies made up 86% by weight of lake sturgeon stomach content in the Niagara River. We then calculated the difference between the stable isotope values of lake sturgeon fin spines and round goby muscle, for a DTDF of +1.4 and +2.1 for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Isotopic niches were quantified using $\delta^{13}C$ and $\delta^{15}N$ data and the SIBER (Stable Isotope Bayesian Ellipses in R) analysis package in R. The Standard Ellipse Area (SEA_B) are calculated through a set of 10 000 iterations from the Markov chain Monte Carlo (MCMC) simulation; the mean and covariance are used to construct the ellipse which represents 40% of the simulated data, a conservative realized niche (Jackson et al., 2011; Guzzo et al., 2013). Comparable to bootstrapping, SEA_C Bayesian estimates adjust for differences in sample sizes and accounts for the influence of outliers. Area and overlap of each ellipse among lake sturgeon categories was calculated using SIBER.

All statistical analyses were completed using R version 3.4.1.

Results

Comparing stable isotopes of lake sturgeon and prey

Stable isotopes in lake sturgeon did not differ among capture and migration groups, and no significant differences were found between $\delta^{13}C$ and $\delta^{15}N$ across capture locations, migration locations, and migration behaviours (Table 2.1). Although not statistically different, the lake sturgeon population that remained within and between the

Detroit River and the St. Clair River had the highest δ^{13}C (-17.3 ± 1.2; mean ± SD) and the population that migrated from St. Clair River to Lake Huron had the lowest (-18.2 ± 2.1; Table 2.1). The highest δ^{15}N was seen in the population of lake sturgeon that migrated from Detroit River to Lake Erie (12.3 ± 1.5) and the lowest was seen in the population of river-residents (10.8 ± 1.0; Table 2.1).

All prey sources showed an increase in δ^{15}N from a low in Lake Huron to a high in Lake Erie, except in G. *fasciatus* (Table 2.1). Zebra mussels from Lake Huron and Lake Erie had the lowest δ^{15}N value (2.8 ± 0.5) and the lowest δ^{13}C value (-24.7 ± 0.5), respectively (Table 2.1). The highest δ^{15}N value came from round gobies in Lake Erie (14.6 ± 1.5), and in three of the four locations had higher mean δ^{15}N than lake sturgeon from the St. Clair and Detroit Rivers.

Diet proportions based on stable isotopes

Based on stable isotopes in fin spine tissue, adult lake sturgeon that migrated within and between the Detroit River and St. Clair River fed across a large variety of prey (Figure 2.2). Adult lake sturgeon showed wide variation in stable isotopes among individuals, ranging from -22.1 to -14.3 for δ^{13}C and 8.8 to 14.8 for δ^{15}N (Figure 2.2). Diet estimate proportions ranged from 9.9% to 13.4% for individual items (Figure 2.3); the lowest contributor was crayfish and the highest was E.*ishmus*.

Isotopic niche

Lake sturgeon categorized solely by capture location, regardless of migration behaviour, had high isotopic niche overlap; the St. Clair River population had 80% overlap with the Detroit River population, but only 60% of Detroit River overlapped with St. Clair (Table 2.2, Figure 2.4).

Isotopic niche overlap varied among individuals with different migration patterns (Table 2.2, Figure 2.4). Both the St. Clair River to Lake Huron population and the population that remained within and between the Detroit River and the St. Clair River had 22% niche overlap with the population that migrated from Detroit River to Lake Erie. The population that remained within and between the Detroit River and the St. Clair River had high overlap (76%) with the population that migrated from St. Clair River to Lake Huron. River-resident population had complete isotope niche overlap (100%) with the lake dominant migrant population.

Detroit River-collected lake sturgeon had a larger isotopic niche area than St. Clair River (Figure 2.5a). Isotopic niche area increased from the Lake Erie to HEC to Lake Huron sub-populations, when breaking data into migration location (Figure 2.5b). The lake dominant sub-population had the largest isotopic niche, followed by seasonal migrant and river resident, within the migration behaviour sub-populations (Figure 2.5c).

Discussion

Lake sturgeon isotopic niches of fin spines had high overlap across migration locations and behaviours, however they were unique in size. This high overlap could be due to the low resolution in stable isotopes among prey sources, which contributed to the approximate equal proportions of prey sources found in this system in diet mixing models. But taken together, stable isotopes indicated a generalist feeding behaviour of lake sturgeon in the HEC. Disparity in niche sizes across migration locations and behaviours suggests trophic polymorphism may drive varying migration strategies, and has implications for management and recovery strategies, but further fine scale assessment of diet and feeding are required.

Similar isotopic niches between St. Clair River and Detroit River lake sturgeon populations represent comparable resource use, foraging behaviour, or prey availability between the two sub-populations categorized by capture location. There was a slightly lower δ^{13}C in the Detroit River isotopic niche, which is similar to differences in prey from the Detroit River and Lake Erie. These categories do not incorporate the migratory polymorphism of lake sturgeon in this system described in Kessel et al. (2017), which could account for the larger niche sizes. Habitat use and foraging are related elements of an organism's ecology (Jackson et al., 2002) and once considered together, show differences in niche sizes of lake sturgeon from the HEC.

The isotopic niche of the Detroit River to Lake Erie migrant sub-population had higher δ^{15}N than the other two sub-populations, which corresponds with higher δ^{15}N in prey from Lake Erie, and indicates feeding at a higher trophic position. This niche was also smallest of the sub-populations, suggesting a more specialist behaviour (Bolnick et al., 2003), although it could indicate that the baseline isotope values in Lake Erie are more confined then the other locations. The sub-population of lake sturgeon that migrated between St. Clair River and Lake Huron had a larger niche area that pulled towards a lower δ^{13}C, which did not correspond with the prey sampled at that location. It is important to note however that Lake Huron only had three prey sources quantified for isotopes, likely masking the importance of other benthic prey to this sub-population. Nevertheless, Lake Huron was the only location where mean δ^{15}N of round gobies was lower than lake sturgeon, which may imply they are of greater importance to the lake sturgeon population that migrates from St. Clair River to Lake Huron than the other sub-populations analyzed, and similarly to Niagara River population (Jacobs et al., 2017). Thus, we recommend future studies analyze the abundance, diversity, and stable isotopes of benthic macroinvertebrate populations across Lake Huron in order to incorporate other potential prey sources into future lake sturgeon diet analyses.

The population that migrated within and between the St. Clair and Detroit Rivers had a larger niche area than the river-resident population, potentially caused by the lake sturgeon feeding in Lake St. Clair. Lake sturgeon that forage in Lake St. Clair either consume different prey types or similar prey with different isotope values (Oviedo & Angerbjörn, 2005). Lake St. Clair is similar in both depth, climate, and anthropogenic stressors as its two connecting rivers (U.S Army Corps of Engineers, 2004), but has a larger surface area and provides overwintering habitat for species from other tributaries (ie: Thames River). Prey migrating from the other tributaries into Lake St. Clair may provide lake sturgeon with different prey resources or prey with different isotope values, likely causing the difference in niche size.

The river-resident population had the smallest niche size, suggesting that lake sturgeon that remain within rivers year-round may be more selective for prey, have a smaller prey base, and/or stable isotopes in the prey base have a smaller range of values. With high abundance and diversity of both native and invasive invertebrates in the HEC and low lake sturgeon numbers (Pollock et al. 2014), higher selectiveness in river-resident lake sturgeon is possible. In bluegill sunfish, individuals became increasingly selective for larger daphnia when prey abundance increased (Gibson, 1983). Our work can be further extended to include an analysis of prey species composition and abundance in the HEC in order to understand the amount of selectiveness river-resident lake sturgeon may be performing.

The lake dominant migrant population does not consider which lake they spend the majority of time, likely resulting in this sub-population’s large niche area. Both the large area in St. Clair River to Lake Huron population and the difference in δ^{15}N between them and the Detroit River to Lake Erie population accounts for this largest niche area of lake dominant migrants. Lake sturgeon inhabit both deep water and littoral zones of Lake Erie and Lake Huron (Bunnell et al., 2014), presumably causing the increased variation in isotopes.

Discrete sizes in isotopic niches across migratory locations and behaviours suggests that trophic polymorphism may play a role in the HEC lake sturgeon population’s feeding ecology. Chapman et al. (2012) suggested that there are four main causes of the evolution of partial migration: body size and physiological tolerance, predation risk, competitive release, and trophic polymorphism. Since we solely used adult lake sturgeon categorized over 1000mm TL, both predation risk and physiological constraints causing the migration polymorphism is unlikely. The competitive release hypothesis is also unlikely since invasive species are abundantly high in the HEC and lake sturgeon are still vulnerable with low population numbers, making trophic polymorphism the likely driver of migratory polymorphisms in lake sturgeon. However, we also acknowledge that trophic polymorphism may not be the driver of migration polymorphisms, but alternatively a consequence from it.

Our research is the first to use intraspecific variations in migration behaviours to study diet differences, however, stable isotopes have commonly been used in ecological studies to identify migration behaviours (Hesslein et al., 1991; Cerling et al., 2006; Trueman et al., 2012). For example, Nelson et al. (1989) document migration patterns of common smelt (*Retropinna retropinna*) using δ^{13}C and δ^{15}N stable isotopes from otoliths. In our study, the use of δ^{13}C and δ^{15}N stable isotopes would not have been effective in determining the migration strategies of lake sturgeon in this system since there were no significant differences in isotopes across behaviours, only disparity in niche sizes. The HEC has an abundance of zebra mussels, which couple benthic and pelagic habitats (Ackerman et al., 2001), likely causing similarities in isotopes across migration locations and behaviours. Additionally, Lake St. Clair is similar in depth to the connecting rivers (U.S Army Corps of Engineers, 2004), which further explains the similarity among migration groups.

Stable isotopes of lake sturgeon fin spines determined that both round gobies and zebra mussels were proportionally comparable to other prey sources analyzed to the diet of lake sturgeon. Still, it is important to note that lake sturgeon diet is spatially diverse, and our findings are unique compared to other recent research on lake sturgeon diet from other locations within the Great Lakes. In Guilbard et al. (2007), adult lake sturgeon from the St. Lawrence River fed mainly on Gammarids, but this varied by season and location. Additionally, Smith et al. (2016) found that fish-based protein was the main diet source of lake sturgeon from Rainy River, and the population from the Niagara River fed predominately on round gobies (Jacobs et al., 2017). Our efforts to quantify diet using isotopes are confounded because a diet tissue discrimination factor for lake sturgeon, or any sturgeon, fin spines generated through controlled lab studies is lacking.

Within and between the Detroit River and St. Clair River, lake sturgeon fed equally across prey sources sampled within the system; this could be representative of a generalist foraging behaviour or individual generalists within an area with low resolution in $\delta^{13}C$ and $\delta^{15}N$ among species (Bolnick et al., 2011). We incorporated key prey items found in other studies (ie: Chironomids and amphipods) but they were not of high importance for lake sturgeon that migrated within and between the Detroit and St. Clair Rivers. These variations in diet further support the spatial diversity of lake sturgeon diet within the Great Lakes (Beamish *et al.* 1998; Guilbard *et al.* 2007). For example, in the Niagara River, 86% of the stomach content identified in adult lake sturgeon were round gobies (Jacobs et al., 2017), much higher than in our study.

Lake sturgeon from the HEC exhibited high intraspecific variation in dietary preference, suggesting they are individual specialists in a generalist population. Since this analysis was conducted on lake sturgeon that remained within and between the St. Clair and Detroit Rivers, locational differences are unlikely the cause of the disparity. In being the healthiest population in the Great Lakes (Thomas & Haas, 2002), having resource use heterogeneity may reduce future intraspecific competition (Bolnick et al., 2003). Generalist populations are often more stable in a changing environment (Marvier et al., 2004) and given that this system is highly urbanized and subjected to environmental stressors (U.S Army Corps of Engineers, 2004), this sub-population may be well adapted to survive. For example, Devictor et al. (2008) looked at multiple species across different degrees of fragmented and disturbed habitats and found that the more specialist a species was, the stronger it was affected by fragmented and disturbed habitats, likely due to the loss of a key prey species. Although competition tends to be higher in generalists, generalist densities usually increase compared to specialists (Abrams, 2007).

Our study used literature values of δ^{13}C and δ^{15}N for some species in the diet models, but there were no values for other macroinvertebrates from Lake Huron. This was problematic since the largest isotopic niche was seen in lake sturgeon that migrate from St. Clair River to Lake Huron. This high intraspecific variation could mean two things: this population exhibits trophic polymorphism (i.e., feed on different items), or they feed on similar prey but in different habitats of Lake Huron. This further extends the need for a detailed stable isotope study to be conducted on macroinvertebrates in Lake Huron.

Our use of stable isotopes to study diet and trophic niche is transferable to other lake sturgeon populations, other sturgeon species, and other sensitive species or species at risk, where analyzing gut content may be impractical. For example, the shortnose sturgeon (*Acipenser brevirostrum*) is another species at risk like the lake sturgeon (Kynard, 1997). SIA on non-lethal tissue samples would allow for diet estimates without harming a protected species. Additionally, smaller fish are more susceptible to mortality via stomach pump (Hartleb & Moring, 1995; Kamler & Pope, 2001), and thus stable isotope methods for dietary analyses is more appropriate.

Our interdisciplinary approach can be used on other species that exhibit intrapopulation variations in migration behaviours. For example, male and female walleye (*Sander vitreus*) migrate to different locations of Lake Erie but the driver was unidentified (Raby et al.,2018). By combining Raby et al., (2018) telemetry data with stable isotope analysis, variations in feeding ecology across migration locations can be explored in walleye.

In summary, our research supports the spatially diverse foraging ecology of lake sturgeon and the need for current dietary data to aid in the conservation of populations within the Great Lakes. By understanding vital prey resources of lake sturgeon, better management strategies can be implemented for each sub-population as well as prevent future anthropogenic stressors from impacting their important prey. Because of the generalist feeding behaviour of adult lake sturgeon in the HEC, it may be beneficial to restore other genetically similar populations with offspring from the HEC population since they may be more resilient to stressors. Furthermore, while invasive species outcompete native species, they also represent a new prey resource for local species. The generalist foraging behaviour of lake sturgeon may be the reason why they are the healthiest population in the Great Lakes.

References

Abrams, P. A. (2007) Specialist-Generalist Competition in Variable Environments; The Consequences of Competition between resource. In D. A. Vasseur & K. S. McCann (Eds.), *The Impact of Environmental Variability on Ecological Systems* (133–157). Dordrecht, The Netherlands: Springer.

Ackerman, J.D., Loewen, M.R., & Hamblin, P.F. (2001) Benthic–Pelagic Coupling over a Zebra Mussel Reef in Western Lake Erie. *Limnology and Oceanography, 46*(4), 892–904.

Auer, N.A. (1996). Importance of Habitat and Migration to Sturgeons with Emphasis on Lake Sturgeon. Ca*nadian Journal of Fish and Aquatic Science, 53*(1), 152–160.

Beamish, F.W.H, Noakes, D.L.G, & Rossiter, A. (1998). Feeding Ecology of Juvenile Lake Sturgeon, *Acipenser fulvescens,* in Northern Ontario. *The Canadian Field Naturalist, 112*(1), 459–468.

Boase, J. C., Diana, J. S., Thomas, M. V., & Chiotti, J. A. (2011). Movements and Distribution of Adult Lake Sturgeon from their spawning site in the St. Clair River, Michigan. *Journal of Applied Ichthyology, 27*(1), 58–65.

Bolnick, D.I., Svanback, R., Fordyce, J. A., Yang, L.H., Davis, J.M., Hulsey, C.D., & Forister, M.L. (2003). The Ecology of Individuals: Incidence and Implications of Individual Specialisation. *American Naturalist, 161*(1), 1–28.

Bruch, R.M., Campana, S.E., Davis-Foust, S.L., Hanen, M.J., & Janssen, J. (2009). Lake Sturgeon Age Validation Using Bomb Radiocarbon and Known-Age Fish. *Transactions in American Fisheries Society, 138*(1), 361–372.

Brush, J.M., Fisk, A.T., Hussey, N.E., & Johnson, T.B. (2012). Spatial and Seasonal Variability in the Diet of Round Goby (*Neogobius melanostomus*): Stable Isotopes indicate that Stomach Contents Overestimate the Importance of Dreissenids. *Canadian Journal of Fisheries and Aquatic Science, 69*(3), 573–586.

Bunnell, D.B., R.P. Barbiero, S.A. Ludsin, C.P. Madenjian, G.J. Warren, D.M. Dolan, T.O. Brenden, . . . B.C. Weidel. (2014). Changing Ecosystem Dynamics in the Laurentian Great Lakes: Bottom-Up and Top-Down Regulation. *BioScience 64*(1), 26–39.

Cabana, G. & Rasmussen, J. B. (1996) Comparison of Aquatic Food Chains using Nitrogen Isotopes. *PNAS, 93*(1), 10844–10847.

Cerling, T.E., Wittemyer, G., Rasmussen, H.B., Vollrath, F., Cerline, C.E., Robinson, T.J., & Douglas-Hamilton, I. (2006). Stable Isotopes in Elephant Hair Document Migration Patterns and Diet Changes. *PNAS, 103*(2), 371–373.

Chapman, B.B., Hulthén, K., Brodersen, J., Nilsson, P.A., Skov, C., Hansson, L.-A, & Brönmark, C. (2012). Partial Migration in Fishes: Causes and Consequences. *Journal of Fish Biology, 81*(1), 456–478.

Choudhury, A., Bruch, R., & Dick, T.A. (1996). Helminths and Food Habits of Lake Sturgeon *Acipenser fulvescens* from the Lake Winnebago System, Wisconsin. *The American Midland Naturalist, 135*(2), 274–282.

Devictor, V., Julliard, R., & Jiguet, F. (2008), Distribution of Specialist and Generalist Species Along Spatial Gradients of Habitat Disturbance and Fragmentation. *Oikos, 117*(1), 507–514.

Fry, B. (2007). *Stable Isotope Ecology*. Baton Rouge (LA): Springer.

Gerig, B., Moerke, A., Greil, R., & Koproski, S. (2011). Movement Patterns and Habitat Characteristics of Lake Sturgeon (*Acipenser fulvescens*) in the St. Marys River, Michigan, 2007-2008. *Journal of Great Lakes Research, 37*(2), 54–60.

Gibson, R. M. (1983). Visual Abilities and Foraging Behaviour of Predatory Fish. *Trends in Neurosciences, 6*(1), 197–199.

Grist, H., Daunt, F., Wanless, S., Burthe, S.J., Newell, M. A., Harris, M.P., & Reid, J.M. (2017). Reproductive Performance of Resident and Migrant Males, Females and Pairs in a Partially Migratory Bird. *Journal of Animal Ecology, 86*(5), 1010–1021.

Guilbard, F., Munro, J., Dumont, P., Hatin, D., & Fortin, R. (2007). Feeding Ecology of Atlantic Sturgeon and Lake Sturgeon Co-Occurring in the St. Lawrence Estuarine Transition Zone. *American Fisheries Society Symposium, 56*(1), 85–104.

Guzzo, M., Haffner, G., Legler, N., Rush, S., & Fisk, A. (2013). Fifty years later: Trophic Ecology and Niche Overlap of a Native and Non-Indigenous Fish Species in the Western Basin of Lake Erie. *Biological Invasions, 15*(8), 1695–1711.

Hakala, J.P. & Johnson, F. D. (2004). Evaluation of a Gastric Lavage Method for use on Largemouth Bass. 2004. *North American Journal of Fisheries Management, 24*(4), 1398–1403.

Hartleb, C.F., & Moring, J.R. (1995). An Improved Gastric Lavage Device for Removing Stomach Contents from Live Fish. *Fisheries Research,24*(3), 261–265.

Hesslein, R.H., Capel, M.J., Fox, D.E., & Hallard, K.A. (1991) Stable Isotopes of Sulfur, Carbon, and Nitrogen as Indicators of Trophic Level and Fish Migration in the Lower Mackenzie River Basin, Canada. *Canadian Journal of Fisheries and Aquatic Sciences, 48*(1), 2258–2265

Hondorp, D.W., Holbrook, C.M., & Krueger, C.C. (2015). Effects of Acoustic Tag Implantation on Lake Sturgeon *Acipenser fulvescens*: Lack of Evidence for Changes in Behavior. *Animal Biotelemetry, 3*(44), doi:10.1186/s40317-015-0085-0

Jacobs, G.R., Bruestle, E.L., Hussey, A., Gorsky, D., & Fisk, A.T. (2017). Invasive Species Alter Ontogenetic Shifts in the Trophic Ecology of Lake Sturgeon (*Acipenser fulvescens*) in the Niagara River and Lake Ontario. *Biological Invasions, 19*(1), 1533–1546.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing Isotopic Niche Widths Among and Within Communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology, 80*(3), 595–602.

Kamler, J.F., & Pope, K.L. (2001). Nonlethal Methods of Examining Fish Stomach Contents. *Reviews in Fisheries Science,9*(1), 1–11.

Kessel, S.T., Hondorp, D.W., Holbrook, C.M., Boase, J.C., Chiotti, J.A., Thomas, M.V., Wills, T.C., . . . Krueger, C.C. (2017). Divergent Migration Within Lake Sturgeon (Acipenser fulvescens) Populations: Multiple Distinct Patterns Exist Across an Unrestricted Migration Corridor. *Journal of Animal Ecology, 87*(1), 259–273.

Kynard, B. (1997). Life History, Latitudinal Patterns, and Status of the Shortnose Sturgeon, *Acipenser brevirostrum*. *Environmental Biology of Fishes, 48*(1-4), 319–334.

Marvier, M., Kareiva, P., & Neubert, M. G. (2004). Habitat Destruction, Fragmentation, and Disturbance Promote Invasion by Habitat Generalists in a Multispecies Metapopulation. *Risk Analysis, 24*(1), 869–878.

McCabe, D.J., Beekey, M.A., Mazloff, A., & Marsden, J.E. (2006). Negative Effect of Zebra Mussels on Foraging and Habitat use of Lake Sturgeon (*Acipenser fulvescens*). *Aquatic Conservation: Marine and Freshwater Ecosystems, 16(*1), 493–500.

Näslund, I. (1991). Effects of Temperature, Season, and Feeding Conditions on the Rheobehaviour Behaviour of Two Stocks of Landlocked Arctic Char. *Nordic Journal of Freshwater Research, 66*(1), 108–114.

Nelson, C.S., Northcote, T.G., & Hendy, C.H. (1989). Potential Use of Oxygen and Carbon Isotopic Composition of Otoliths to Identify Migratory and Non-Migratory Stocks of the New Zealand Common Smelt: a Pilot Study. *New Zealand Journal of Marine Freshwater Research, 23*(1), 337–344.

Oviedo, F. & Angerbjorn, A. (2005). Resolving Temporal Variation in Vertebrates Using Naturally Occurring Stable Isotopes. *Oecologia, 144*(1), 647–58.

Parra, G. J., & Jedensjo, M. (2014). Stomach Contents of Australian Snubfin (*Orcaella heinsohni*) and Indo-Pacific Humpback Dolphins (*Sousa chinensis*). *Marine Mammal Science, 30*(3): 1184–1198.

Peterson, D.L., Vecsei, P., & Jennings, C.A. (2007). Ecology and Biology of the Lake Sturgeon: a Synthesis of Current Knowledge of a Threatened North American *Acipenseridae*. *Reviews in Fish Biology and Fisheries, 17*(1), 59–76.

Pettitt-Wade, H. (2016). *Niche Breadth and Invasion Success*. (Doctoral dissertation). Retrieved from The University of Windsor. (http://scholar.uwindsor.ca/cgi/viewcontent.cgi?article=6759&context=etd)

Pollock, M. S., Charr, M., Kreitals, N. M., & Phillips, I. D. (2014). Review of a Species in Peril: What We Do Not Know About Lake Sturgeon May Kill Them. *Environmental Reviews, 23*(1), 30–43.

Post, D.M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology, 83*(3), 703–718.

Post, D. M., Layman, C. A., Arrington, D. A., Takimoto, G., Quattrochi, J., & Montaña, C. G. (2007). Getting to the Fat of the Matter: Models, Methods and Assumptions for Dealing with Lipids in Stable Isotope Analyses. *Oecologia*, *152*(1), 179–189.

Quinn, T. P., Bond, M. H., Brenkman, S. J., Paradis, R., & Peters, R. J. (2017). Re-Awakening Dormant Life History Variation: Stable Isotopes Indicate Anadromy in Bull Trout Following Dam Removal on the Elwha River, Washington. *Environmental Biology of Fishes*, *100*(12), 1659–1671.

Raby, G.D., Vandergoot, C.S., Hayden, T.A., Faust, M.D., Kraus, R.T., Dettmers, J.M., Cooke, S.J., . . . Krueger, C.C. (2018). Does Behavioural Thermoregulation Underlie Seasonal Movements in Lake Erie Walleye? *Canadian Journal of Fisheries and Aquatic Sciences, 75*(3), 488–496.

Rusak, J.A & T. Mosindy. (1997). Seasonal Movements of Lake Sturgeon in Lake of the Woods and the Rainy River, Ontario. *Canadian Journal of Zoology, 74*(1), 383–395.

Smith, K.M., & Baker, E.A. (2005) Characteristics of Spawning Lake Sturgeon in the Upper Black River, Michigan. *North American Journal of Fisheries Management, 25*(1), 301–307.

Smith, A., Smokorowski, K., Marty, J., & Power, M. (2016) Stable Isotope Characterization of Rainy River, Ontario, Lake Sturgeon Diet and Trophic Position. *Journal of Great Lakes Research, 42*(2), 440–447.

Thomas, M. V., & Haas, R. C. (2002). Abundance, Age Structure, and Spatial Distribution of Lake Sturgeon, *Acipenser fulvescens,* in the St Clair System. *Journal of Applied Ichthyology*, *18*(1), 495–501.

Trueman, C.N., MacKenzie, K.M., & Palmer, M.R. (2012). Identifying Migrations in Marine Fishes Through Stable-Isotope Analysis. *Journal of Fish Biology, 81*(2), 826–847.

Tshipa, A., Valls-Fox, H., Fritz, H., Collins, K., Sebele, L., & Mundy, P., Chamaillé-Jammes, S. (2017). Partial Migration Links Local Surface-Water Management to Large-Scale Elephant Conservation in the World's Largest Transfrontier Conservation Area. *Biological Conservation*, *215,* 46–50.

U.S Army Corps of Engineers (2004). *St. Clair River and Lake St. Clair Comprehensive Management Plan*. Retrieved from

Wang, L., Riseng, C. M., Mason, L. A., Wehrly, K. E., Rutherford, E. S., McKenna, J. E., . . . Coscarelli, M. (2015). A Spatial Classification and Database for Management, Research, and Policy Making: The Great Lakes Aquatic Habitat Framework. *Journal of Great Lakes Research*, *41*(2), 584–596.

Table 2.1 Stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) in lake sturgeon fin spines (median) and potential prey species (mean ± 1 SD) collected from the locations within the Lake Huron-to-Lake Erie corridor. Lake sturgeon isotopes were additionally separated into the location they migrated to and by their migration behaviour using telemetry data analyzed in Kessel *et al*. (2017). Species denoted with a superscript letter are isotope values from previous literature.

Prey Source	Lake Huron			St. Clair River			Detroit River			Lake Erie		
	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N	n	δ^{13}C	δ^{15}N
Round Goby	30	-18.9 ± 0.7	7.9 ± 0.5	40	-18.1 ± 1.8	11.6 ± 0.6	63	-19.5 ± 2.7	12.0 ± 1.6	30	-20.6 ± 1.1	14.6 ± 1.5
Logperch	–	–	–	0	–	–	4	-19.2 ± 2.0	10.2 ± 1.0	–	–	–
Zebra Mussel	6	-21.3 ± 0.3	2.8 ± 0.5	30	-19.9 ± 2.2	7.6 ± 0.4	36	-24.4 ± 3.6	9.5 ± 2.3	20	-24.7 ± 0.5	11.8 ± 0.3
Quagga Mussel	24	-21.0 ± 1.4	3.0 ± 0.9	0	–	–	11	-20.4 ± 1.0	7.4 ± 0.9	10	-21.8 ± 1.1	10.8 ± 0.8
Chironomids	–	–	–	–	–	–	1[a]	-20.5	8.5	18[b]	-19.3 ± 1.1	10.9 ± 1.2
E. *ishmus*	–	–	–	–	–	–	10[a]	-17.6 ± 0.6	8.8 ± 0.3	4[b]	-19.6 ± 1.6	10.2 ± 0.5
Mud Snails	–	–	–	2[a]	-16.1 ± 0.3	7.9 ± 0.6	–	–	–	–	–	–
G. *fasciatus*	–	–	–	3	-16.9 ± 0.2	11.1 ± 1.2e^{-2}	–	–	–	5[b]	-16.8 ± 1.0	9.1 ± 1.0
Crayfish	–	–	–	5	-16.2 ± 0.5	6.8 ± 1.2	–	–	–	–	–	–
Lake Sturgeon	–	–	–	44	-17.4	11.1	47	-17.9	11.4	–	–	–
Migration Location	Combined Capture Locations											
Detroit R. to L. Erie	9	-17.8	12.4									
Detroit R. to St. Clair R.	54	-17.4	10.9									
St. Clair R. to L. Huron	28	-18.0	11.4									
Migration Behaviour	Combined Capture Locations											
Lake Dom. Migrant	46	-18.0	11.2									
Seasonal Migrant	23	-17.7	11.6									
River-Resident	22	-17.4	10.9									

[a] Pettitt-Wade (2016)
[b] Campbell et al. (2009)

Table 2.2 Overlap in isotopic niche (%) based on niche size (‰^{2}) and SEA$_C$ (‰^{2}) for lake sturgeon collected from two locations in the Lake Huron-to-Lake Erie corridor for a) St. Clair River and Detroit River capture locations, b) St. Clair and Detroit River split into their migration location from analyzed telemetry data, and c) categorized into lake dominant migrant, seasonal migrant, and river-resident migration behaviours. Groupings in the leftmost column are used to read percent overlap values; for example, the St. Clair River population niche overlaps 80% with the Detroit River population niche.

a)

Capture Location	St. Clair R.	Detroit R.	Niche Size (‰^{2})	SEA$_C$ (‰^{2})
St. Clair R.	–	80	5.4	5.3
Detroit R.	60	–	7.2	7.1

b)

Migration Location	Detroit R. to L. Erie	Detroit R. to St. Clair R.	St. Clair R. to L. Huron	Niche Size (‰^{2})	SEA$_C$ (‰^{2})
Detroit R. to L. Erie	–	36	55	3.3	3.2
Detroit R. to St. Clair R.	22	–	76	5.3	5.2
St. Clair R. to L. Huron	22	49	–	8.3	8.1

c)

Migration Behaviour	Lake Dom. Migrant	Seasonal Migrant	River-Resident	Niche Size (‰^{2})	SEA$_C$ (‰^{2})
Lake Dom. Migrant	–	52	36	8.7	8.5
Seasonal Migrant	77	–	37	5.9	5.7
River-Resident	100	69	–	3.2	3.1

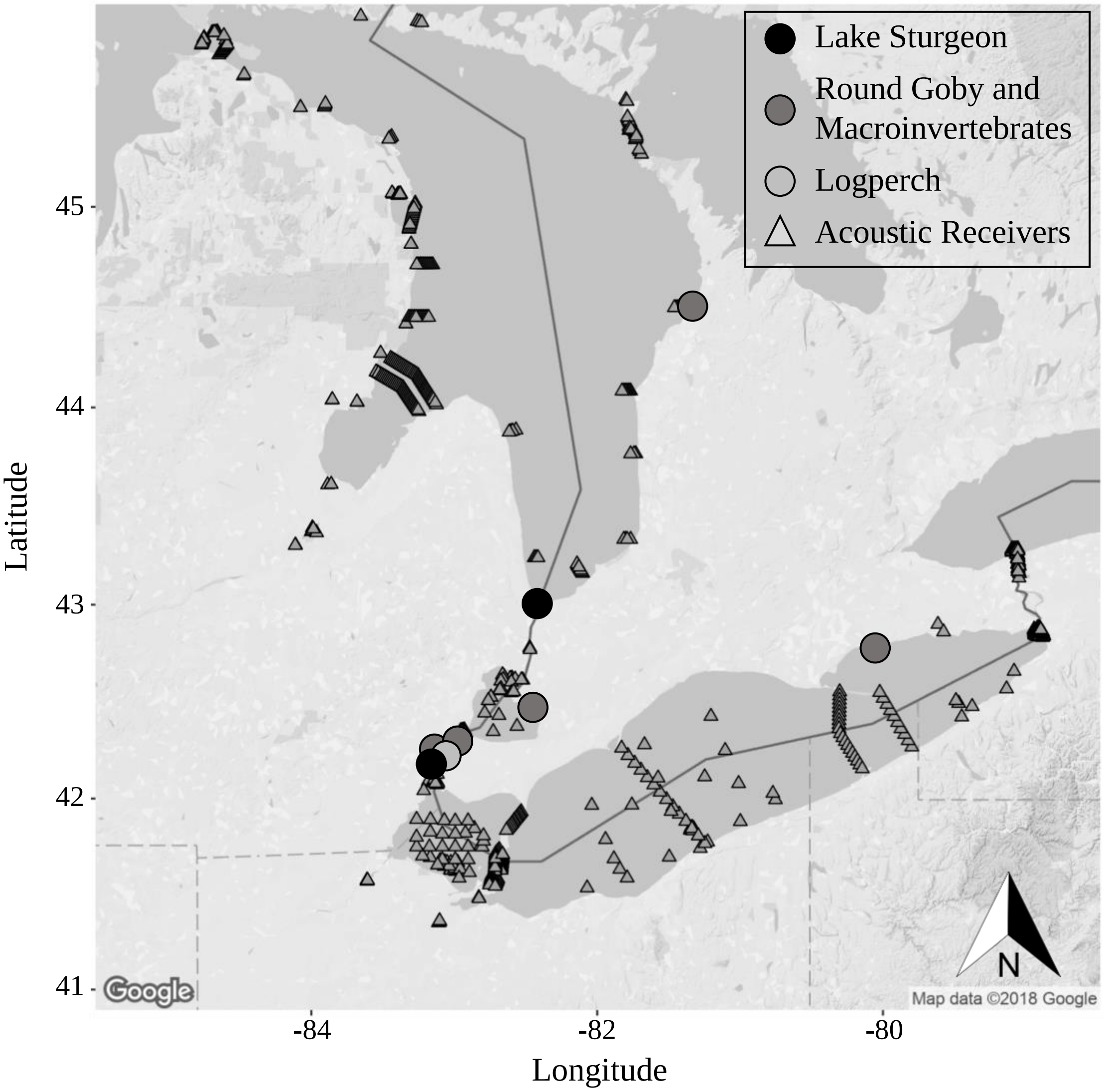

Figure 2.1 Sampling sites for lake sturgeon, round gobies, logperch, and other macroinvertabrates (circles) within the Lake Huron-to-Lake Erie corridor collected from 2011 to 2017. Acoustic receivers (triangles) are also depicted on the map and were deployed during years 2012 to 2014.

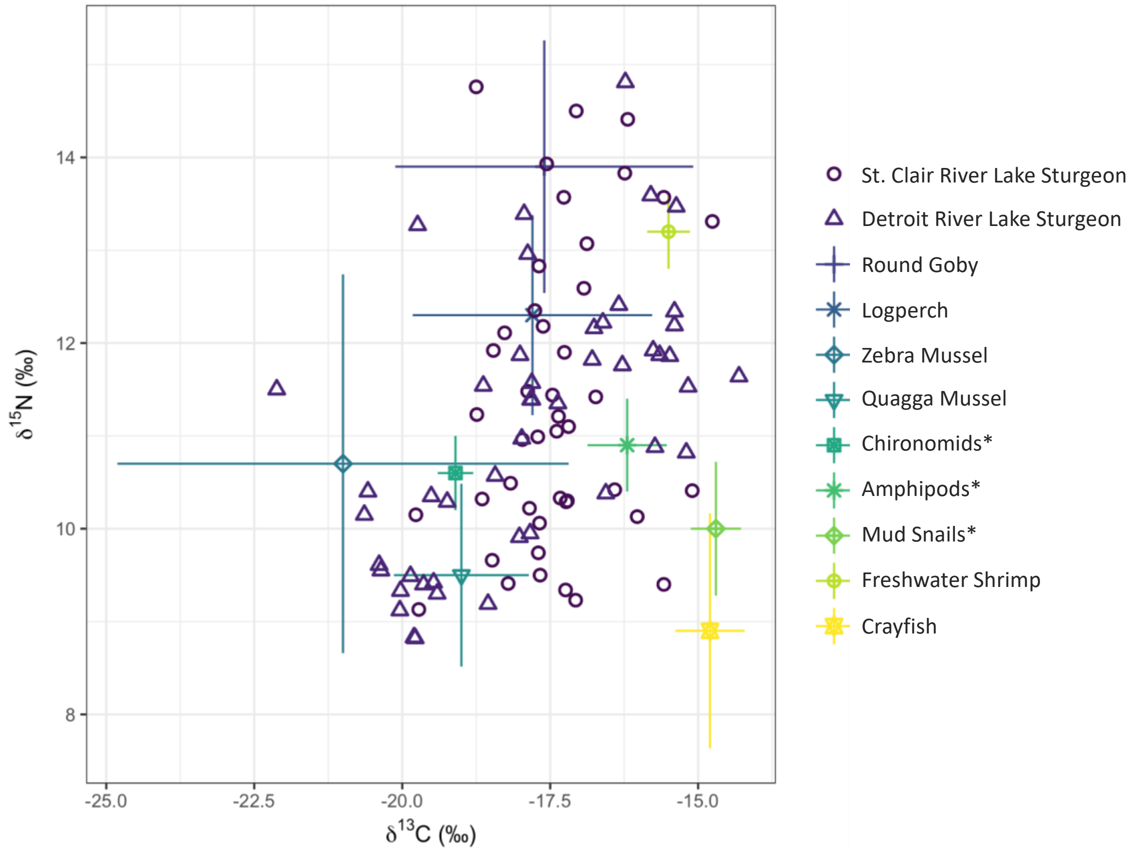

Figure 2.2 Values of $\delta^{13}C$ and $\delta^{15}N$ in individual lake sturgeon fin spine tissue, round goby and logperch muscle, and common invertebrate whole body (mean +/- SD) from the St. Clair and Detroit Rivers. Lake sturgeon isotopes were corrected using the calculated DTDF of +1.4 and +2.1 for $\delta^{13}C$ and $\delta^{15}N$, respectively. (*) denotes literature values from Pettitt-Wade (2016).

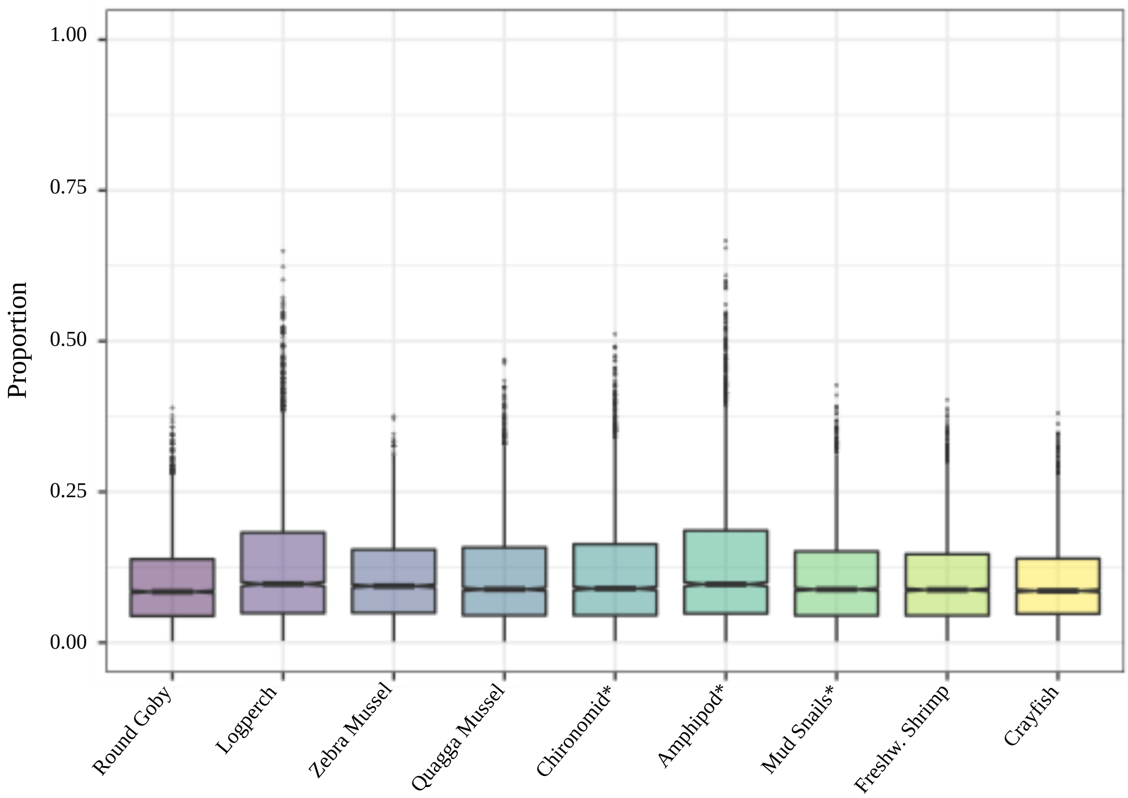

Figure 2.3 Diet proportion estimates (median and quartiles) of lake sturgeon using δ^{13}C and δ^{15}N that migrate within and between the St. Clair and Detroit Rivers determined by running an MCMC model in SIMMR. Error bars serve as the 10th and 90th percentiles. *Pettitt-Wade (2016).

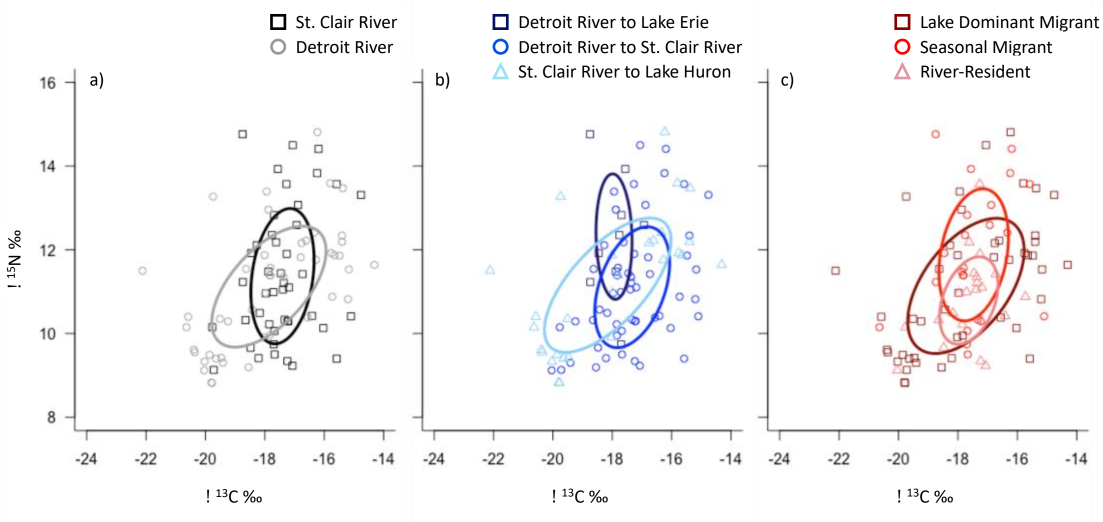

Figure 2.4 Isotopic niche areas of lake sturgeon fin spine tissue, ellipses represent a conservative realized niche (40% of the data): a) St. Clair River and Detroit River capture locations, b) St. Clair and Detroit River split into their migration location from analyzed telemetry data, and c) categorized into lake dominant migrant, seasonal migrant, and river-resident migration behaviours. Both b and c migration categorizations are based on telemetry data analyzed by Kessel et al (2017).

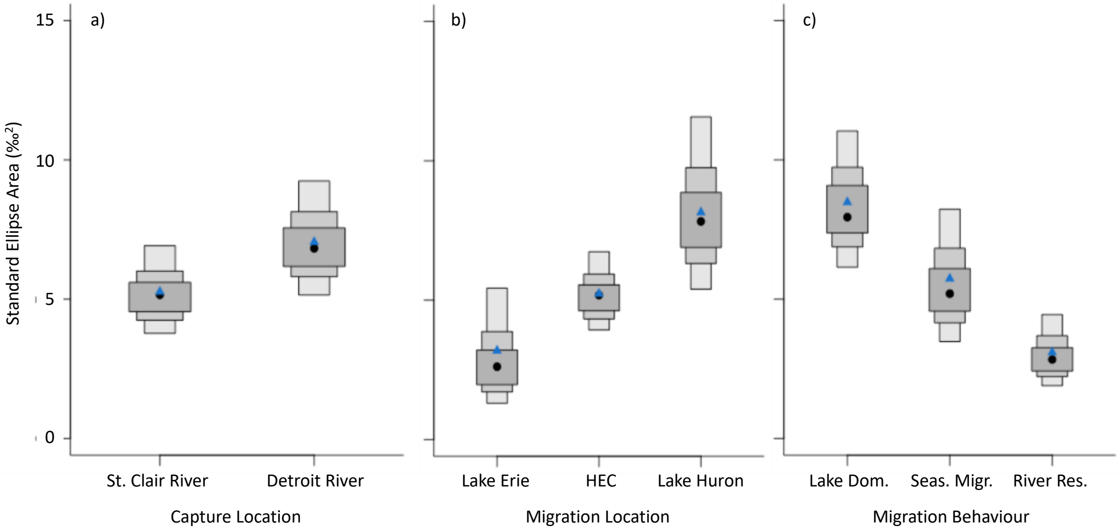

Figure 2.5 Density plots of Bayesian credibility intervals (BCIs) for standard ellipses area (SEA_B) of lake sturgeon stable isotopes. The black dots represent mean SEA_B, the blue triangles represent SEA_C, and the grey blocks represent BCIs of 50, 75 and 95%. a) St. Clair River and Detroit River capture locations. b) movement locations of lake sturgeon from St. Clair River and Detroit River. c) lake dominant migrant, seasonal migrant, and river-resident migration behaviours of lake sturgeon individuals. Both the middle and right panel migration categorizations are based on telemetry data analyzed by Kessel et al (2017).

CHAPTER 3

ISOTOPIC NICHES OF LAKE STURGEON PRE- AND POST- DREISSENID MUSSEL AND ROUND GOBY INVASIONS

Introduction

The introduction and proliferation of invasive species in aquatic ecosystems has resulted in their integration into local food webs through predator-prey interactions, both as small-bodied invasive species that can be consumed by larger predatory native species (Vander Zanden et al., 1999) or as invasive predators that consume native prey (Flecker & Townsend, 1994). Dreissenid mussels (*Dreissena polymorpha D. rostriformis bugensis*) and round gobies (*Neogobius melanostomus*) are important invaders of the Laurentian Great Lakes that have caused a multitude of ecological effects including alterations to the food webs and prey of native predators (Ozersky et al., 2012).

The invasive round goby and zebra mussel were first documented in the Great Lakes in the Lake Huron-to-Lake Erie Corridor (HEC), which consists of St. Clair River, Lake St. Clair, and Detroit River. Zebra mussels were found in Lake Erie in 1986, becoming well established in the Great Lakes by 1989 (Griffiths et al., 1991; Carlton, 2008). Round goby was first documented in the St. Clair River in 1990, and by 1999 were well-established at many places throughout the Great Lakes (Walsh et al., 2007). Native benthic-feeding fish feed on Dreissenid mussels and round goby, and in some instances, these species constitute a large proportion of their diets (Jacobs et al., 2017).

Lake sturgeon are benthic generalists capable of feeding on invasive species, and adult lake sturgeon appear to feed primarily on Dreissenid mussels and round goby (French, 1993; Auer & Dempsey, 2013; Jacobs et al., 2017). Despite lake sturgeon's life history traits that make them sensitive to anthropogenic stressors (Auer, 1996; St. Pierre & Runstrom, 2004), their long lifespan (up to 150 years) make them an ideal study species when looking historic trends in benthic food web connectivity (Peterson et al., 2007). Although mostly consisting of a cartilaginous skeleton, lake sturgeon are armored with bony plates called scutes and boney pectoral fins. Lake sturgeon fins grow radially, and fin ray sections have been used as a method for aging sturgeon (Bruch et al., 2009). Because fin ray tissue incorporates chemicals from consumed prey, fin rays also provide a non-lethal way to quantify chronological changes in sturgeon feeding ecology. The rays' radial growth makes it possible to determine a lake sturgeon's isotopic niche, a measure of dietary niche, at specific ages and within specified time periods, such as before or after the introduction of invasive species. In other words, fin rays can be used to reconstruct the historical diet of lake sturgeon.

An advantage of stable isotope analysis (SIA) over stomach content analysis for determining diet or feeding ecology is that SIA provides a picture of animal food habits integrated over time spans of weeks to months, which is more relevant to understanding invasive species impacts on food webs than the snap-shot view of animal diet provided by stomach content analysis. For sturgeon, stomach content analysis also requires an invasive stomach pumping method or sacrificing the subject (Hakala & Johnson, 2004; Parra & Jedensjo, 2014), which is undesirable when studying species at risk, such as the lake sturgeon.

Stable isotopes, commonly $\delta^{13}C$ and $\delta^{15}N$, are used to assess feeding ecology of organisms, including Great Lakes fish (Bearhop et al., 2004; Brush et al., 2012; Colborne et al., 2013). In freshwater systems, $\delta^{13}C$ provides insights on carbon sources or habitat used (e.g., pelagic vs littoral) and $\delta^{15}N$ provides a quantitative measure of trophic position (Cabana & Rasmussen, 1996; Fry, 2007). Stable isotopes can also be used to calculate an isotopic niche, which have been used to understand the role a species plays in communities or ecosystems (Vander Zanden et al., 1997; Parnell et al., 2013). However, baseline stable isotope data is necessary to place individuals within an isotopic niche due to the possible effects of spatial and temporal variation (Post, 2002); by having an appropriate baseline, trophic position and carbon source can be inferred.

Invasive species can further impact ontogenetic, or size-specific diet shifts, both in invaded fish species and in native species through predation of invasive species. In Lake Ontario, lake sturgeon (*Acipenser fulvescens*) ontogenetic diet shifts to higher trophic levels increased at faster rate following the round goby invasion (Jacobs et al., 2017). Whether similar diet shifts have occurred in other Great Lakes populations, such as the one in the HEC, is unknown. The HEC population of lake sturgeon is of particular interest since it was the first exposed to round gobies and Dreissenid mussels, which are now an important food resource for many benthic predators, including lake sturgeon (Kornis et al., 2012; Jacobs et al., 2017). Lake sturgeon are benthic generalists, however their diet can vary both spatially and temporally and thus dietary information should be assessed in each population.

The purpose of this study was to determine if and how feeding ecology of juvenile, sub-adult, and adult lake sturgeon in the HEC has changed following invasions of Dreissenid mussels and round goby. Quantifying lake sturgeon feeding ecology in this system will provide information about changes in distribution and abundance of prey for this population. Our study differs from Jacobs et al. (2016) in five distinct ways: Our analysis focuses on the HEC population of lake sturgeon, we analyzed dietary data from the pre- Dreissenid time period, we included lake sturgeon over 14 years old, we incorporated a baseline, and we studied population niche size and overlap. Since lake sturgeon diet varies spatially (Pollock et al., 2014), it's important to analyze feeding behaviour across populations. Dreissenids were included in our study since they couple benthic and pelagic carbon and have become a part of lake sturgeon diet (Jackson et al., 2002). Lake sturgeon on average reach sexual maturity between ages 15 to 27 and by incorporating a third age-class that migrates to spawn and forage, different stable isotope values are likely to be seen. Adding a baseline to our study allows us to ensure that changes in isotopes over time are due to dietary shifts and not environmental changes (Post, 2002). Finally, niches can be used to understand adaptability and generalist/specialist behaviours (Broennimann et al., 2007; Quevedo et al., 2009).

Given the proliferation of Dreissenid mussels and round goby in the HEC, and the Jacob et al. (2017) study in Lake Ontario, we hypothesize they have become the dominant prey of lake sturgeon and increased their use of the pelagic energy pathway via the mussels, and trophic position through consumption of round gobies (Figure 1.2). We predict that both juvenile and adult lake sturgeon fed on similar prey types before the Dreissenid and round goby invasions; after these invasions, we expect that lake sturgeon under age five (< 700mm TL) continue to feed on their historic prey as well as round goby, but not Dreissenids because they lessen the availability of juveniles' preferred prey (McCabe et al., 2006), while invasive species became the dominant prey of lake sturgeon five years and older (≥ 700mm TL; see French, 1995; Auer & Dempsey, 2013; Jacobs et al. 2017). To address this, we measured δ^{13}C and δ^{15}N in lake sturgeon at three locations within the HEC (Detroit River, Lake St. Clair, and Detroit River). These sites were chosen to reflect the population and potential sub-population of lake sturgeon in the HEC. To put the sturgeon isotopes in perspective, δ^{13}C and δ^{15}N were measured in invasive prey (round gobies, zebra mussels, and quagga mussels) and mayflies from the HEC as a baseline. The mayflies were historical samples, covering a time period from 1977 to 2014, to provide a temporal baseline.

Methods

Study Site and Sample Collection

Lake sturgeon were captured via setlines from three sites within the HEC (Figure 3.1) by United States Fish and Wildlife Services (USFWS) and Ontario Ministry of Natural Resources and Forestry (OMNRF) from years 1991 to 2014. Captured lake sturgeon were measured for total length, weight, and a section of the leading-edge pectoral fin ray was stored in a labelled paper envelope and archived for age and stable isotope analyses. Of these sections, 56 were collected from Lake St. Clair, 90 from the Detroit River, and 56 from St. Clair River, for a total of 202 samples.

Round gobies and Dreissenid mussels were captured from four sites within the HEC between 2011 and 2013 (Figure 3.1). Round gobies were collected using minnow traps, bag seine nets, and angling methods; Dreissenid mussels were collected via a ponar sampler per Pettit-Wade et al. (2016). Round gobies were euthanized, and both round gobies and Dreissenid mussels were bagged on ice until stored in the laboratory freezer. These samples were later thawed, and boneless, skinless muscle samples were dissected from the round gobies, and the soft tissue from the Dreissenid mussels were separated from the shells for stable isotope analysis.

Mayfly nymphs (*Hexagenia spp.*) were collected as a baseline species, using ponar samplers from sites within Lake St. Clair and the Detroit River from 1977 to 2014 by USGS (Figure 3.1). They were washed through a 0.65mm mesh screen and preserved in either formaldehyde or ethanol per Krieger et al. (1996) and finally analyzed for δ^{13}C and δ^{15}N. This species was used for baseline isotope data because it has a known trophic position of 2 and has been collected since before the Dreissenid invasions from the HEC. A total of 31 samples were ran for SIA, each consisting of five homogenized whole-body mayfly nymphs from the same year and sample site. Long term preservation using ethanol had no effect on δ^{15}N in ants (Tillberg et al., 2006), and Sarakinos et al. (2002) found no significant difference when using samples preserved with 4% formaldehyde and 90% ethanol on δ^{13}C and δ^{15}N in mud shrimp (*Crangon septemspinosa*), therefore preservation effects were assumed to be negligible.

Stable Isotope Analysis

The lake sturgeon fin rays were cross-sectioned and drilled using a 5000 Sherline vertical milling machine at three specific points on the spine, which represent three age-classes of that individual's life history (ages 1 to 4, 4 to 14, and 15+) for stable isotope analysis (δ^{13}C and δ^{15}N). Three experts from USFWS aged these drilled cross-sections to ensure each drilled hole was within the age-classes defined above and to determine the approximate year(s) of that drill hole. Round goby muscle tissue and Dreissenid mussel soft tissue were freeze-dried for 48h and crushed into a fine powder using scissors. Dreissenid mussel soft-tissue was lipid extracted using methods described in (Pettitt-Wade et al., 2016); lipid extraction was not done on fish muscle and ray tissue since they have low lipid content. Drilled fin ray tissue, powdered round goby muscle, Dreissenid mussel soft tissue and baseline samples were weighed (400–800µg) into tin cups and δ^{13}C and δ^{15}N were determined using a Finnigan MAT Deltaplus mass spectrometer

(Thermo Finnigan, San Jose, CA, USA). Stable isotope ratio values were expressed using the following equations:

$$\delta X \text{ ‰} = (R_{\mathrm{SAMPLE}} / R_{\mathrm{STANDARD}} - 1) \times 1000$$

where X represents ^{13}C or ^{15}N and R represents the ratio of either ^{13}C:^{12}C or ^{15}N:^{14}N. Mean analytical precision was estimated using four standards: NIST standard 1577c (bovine liver), an internal laboratory standard (tilapia muscle), certified USGS 41, and urea (n=88 for all). Equipment accuracy mean differences from certified values were -0.13, -0.17 and -0.05‰ for $\delta^{15}N$ and -0.09, -0.06 and 0.05‰ for $\delta^{13}C$, which was checked throughout the sample analysis period using NIST standards 8542, 8573, and 8574 for $\delta^{13}C$ and NIST standards 8573, 8547, and 8574 for $\delta^{15}N$ (n = 79 for all except n = 65 for NIST 8573).

Statistical analyses

Lake sturgeon stable isotope data was assigned to one of three size/age classes: 1) juvenile: 20 – 650 mm TL, ages 0 – 4; 2) sub-adult: 700 – 1150mm TL, ages 5 – 14; and 3) adult: > 1000mm in TL at age 15 and up. These age-classes were also chosen because they represent distinct size ranges according to Michigan's DNR and cover the age/size range over which ontogenetic changes in diet were expected (Boase et al., 2014). Sturgeon aged 15 and older were combined because aging fin rays becomes imprecise over the age of 14 (Bruch et al., 2009) and male sturgeon reach sexual maturity on average between ages 15 – 20 and females between 20 – 25. To assess the impact of Dreissenid and the round goby invasions, data from each age-class was separated into three time frames: 1) pre-invasion (<1988); 2) post-zebra mussel and pre-round goby (1990 – 1998); and 3) post-round goby (>1999).

Stable isotope Bayesian ellipses in R (SIBER) package was used to estimate the isotopic niche of lake sturgeon within each age-class and invasion time frame using $\delta^{13}C$ and $\delta^{15}N$ to generate standard ellipse areas (SEA_C). SEA_C displays the core 40% of the measured data as a conservative realized niche (Jackson et al., 2011; Guzzo et al., 2013). Size and overlap were estimated using Bayesian modelling that ran 10,000 iterations of the measured SEA (SEA_B; Jackson et al., 2011).

A Shapiro-Wilks and Levenes test was conducted on $\delta^{13}C$ and $\delta^{15}N$ and confirmed normal distribution and equal variance. Linear regressions were constructed for each stable isotope variable versus time in years. Because there were significant trends in $\delta^{13}C$ and $\delta^{15}N$ in mayfly over time, we corrected lake sturgeon values to reflect ecosystem changes in stable isotopes using the mayfly regressions. Davies' tests were employed to test for a change in slope by year in the linear regression. The linear regressions were then segmented at the point of inflection using the segmented package in R. Differences in $\delta^{13}C$ and $\delta^{15}N$ were evaluated by MANOVA across year and age-class, and a post-hoc Tukey Test was run if significant differences from the MANOVA existed. All statistic calculations were completed in R version 3.4.1 (R Core Team, 2017).

Results

Stable isotopes across age-classes

Lake sturgeon variations in diet, depicted as mean $\delta^{13}C$ and $\delta^{15}N$ varied in significance across age-classes and invasion history time periods (Table 3.1). Values of $\delta^{13}C$ did not differ across age-classes during the pre-invasions stage, but were lower in the post Dreissenid and pre- goby stage (Table 3.1). Differences in $\delta^{13}C$ among age-classes were observed in the post- invasion stage, with adults having the lowest values. Adult $\delta^{15}N$ was significantly lower than $\delta^{15}N$ in juveniles and adults in the post-round goby time frame (Table 3.1). Of the invasive species, zebra mussels had the lowest $\delta^{13}C$ (–22.2 ± 0.4) and round gobies had the highest (–19.0 ± 0.2; Table 3.1). Quagga mussels had the lowest $\delta^{15}N$ (7.4 ± 0.2) and round gobies had the highest (11.8 ± 0.2; Table 3.1).

Isotopic niche

The lake sturgeon populations within the pre-Dreissenid and post-Dreissenid Pre-round goby invasion time periods had high overlap (Figure 3.2), but invasion time period 2 had differences in variance (SEA; Table 3.2). The population from the post-round goby invasion time period displayed a decrease in $\delta^{15}N$ from high in juveniles to low in adults, with a niche overlap of only 2% (Table 3.2). All three age-classes from this time period had relatively similar sizes (5.7‰^{2}, 5.4‰^{2}, and 5.9‰^{2}; Figure 3.2).

Temporal trends in stable isotopes

Both $\delta^{13}C$ and $\delta^{15}N$ increased over time in the baseline species, mayfly nymphs (Figure 3.3). Raw values of $\delta^{13}C$ and $\delta^{15}N$ for lake sturgeon did not exhibit a similar increase over time as the baseline species (Figure 3.3), meaning there was a temporal trend in isotopes not seen in lake sturgeon. All $\delta^{13}C$ and $\delta^{15}N$ linear regressions were significant across all age-classes of lake sturgeon after being corrected for mayfly nymph baseline (Table 3.3).

Using the Davies' test, juvenile and sub-adult lake sturgeon had a significant change in slope in $\delta^{13}C$ at year 1988 (<0.05; p-value). Those same age-class populations had a significant change in slope in $\delta^{15}N$ at year 1994 and 1991, respectively (<0.05; Figure 3.4). The second half of the $\delta^{13}C$ segmented linear regressions shifted towards a more littoral carbon source and the second half of the δ^{15}N segmented linear regressions showed an increasing trend towards a higher trophic position over time.

Discussion

Lake sturgeon isotopic niches had high overlap across age-classes before round goby invasion, including periods when Dreissenids had invaded, but much less overlap after the round goby invasion. Low overlap across age-class may have resulted from size-dependant predation risk and foraging capability associated with smaller body size (Werner and Gilliam, 1984). The large and consistent niche sizes across size-classes and years, however, suggest an overall generalized foraging behaviour at every age-class, except the large size-class in the period after Dreissenid invasion and before round goby. Stable isotopes indicated a shift away from Dreissenid mussels, but towards round gobies in juvenile and sub-adult lake sturgeon after the goby invasion, likely making round goby an important prey item for younger age-classes.

We found evidence of similar resource use in lake sturgeon across age-classes before the Dreissenid invasion. Isotopic niches remained high in overlap after the Dreissenid and before the goby invasion, but the size of the adult age-class niche was smaller than juveniles and sub-adults. This high overlap suggests that either lake sturgeon are using the same resources across age-classes or they are feeding on prey that occupy a similar niche in different locations. Since lake sturgeon numbers were historically low a few decades ago (Hay-Chmielewski & Whelan, 1997), intraspecific competition is unlikely making similar resource use across age-classes possible.

After the round goby invasion, juvenile and subadult niches had little overlap with the adult age-class. Adult lake sturgeon had lower $\delta^{15}N$ and $\delta^{13}C$, suggesting that adult lake sturgeon feed on a more pelagic carbon source, but on lower trophic level prey than juveniles and sub-adults, potentially the result of predating on zebra mussels more heavily than round gobies. While juveniles may not forage in areas with an abundance of zebra mussels (McCabe et al., 2006) and consequently feed more prevalently on round gobies, our findings suggest that zebra mussels and other benthic invertebrates are more exploited by adult lake sturgeon. Intraspecific competition is likely not a factor influencing their ontogenetic niche shifts since lake sturgeon in the HEC are still considered below historic population sizes (Pollock et al. 2014). Since lake sturgeon did not travel great distances within the HEC (Kessel et al., 2017), we assumed the abundance of benthic invasive species in the HEC based on other studies (Priegel & Wirth, 1971; Auer, 1999). This abundance further supports that intraspecific competition for prey resources in the HEC is unlikely.

While mean $\delta^{13}C$ and $\delta^{15}N$ did not change in adults after the Dreissenid invasion, isotopic niches suggest Dreissenid mussels are contributing to adult lake sturgeon diet. Boase et al. (2014) found adult lake sturgeon inhabit areas with high zebra mussel densities, and while this is not a dietary link, it could mean that they are either feeding directly on zebra mussels or that they do not have higher preference for the macroinvertebrates that are less available in areas with abundant zebra mussels (McCabe et al., 2006). In Lake Oneida, Jackson et al. (2002) found large numbers of zebra mussels in the diet of lake sturgeon over 700mm TL, and similar sized lake sturgeon were in areas highly concentrated with zebra mussels in Lake St. Clair (Boase et al., 2014); while this size-class is part of our sub-adult age-class, we saw a shift towards a pelagic carbon signature and lower trophic level in our adults (1000+ mm TL).

Lake sturgeon showed large intraspecific ranges in $\delta^{13}C$ and $\delta^{15}N$, resulting in a wide population isotopic niche. This could be due to intrapopulation diet preferences or intrapopulation variation in habitat use composed of different prey (Smith & Skulason, 1996). Resource polymorphism in lake charr (*Salvelinus namaycush*) in Great Bear Lake was found, however morphological differences were associated with these varied feeding habits (Blackie et al., 2003). While lake sturgeon within the Huron-Erie Corridor do not exhibit morphological differences aside from length at different ages, resource polymorphism may be driven by other factors future projects could incorporate.

Values of $\delta^{13}C$ and $\delta^{15}N$ showed a significant increase over time in mayfly nymphs, suggesting a temporal ecosystem shift. Mayfly nymphs are an ecologically related species to lake sturgeon which we used to estimate temporal trends within the ecosystem. This trend may be reflective of eutrophication. Eutrophic ecosystems are considered highly productive, usually enriched with nitrogen and aquatic plants and algae (Chislock et al., 2013). Mayfly nymphs, being primary consumers (Brittain, 1982), will demonstrate an increased dependence on littoral carbon sources since plants and algae dominate a eutrophic system. However, lake sturgeon used an increasingly pelagic carbon source and decreasing trophic level, suggesting temporal trends in isotopes reflect changes in the diet of lake sturgeon. Additionally, each age-class had similar shifts in diet over time since they each showed the same trends.

Juvenile and sub-adult lake sturgeon did not reflect stable isotope values of Dreissenid mussels, indicating they are not as important to their diet as previously believed. Instead, an increase in $\delta^{13}C$ was seen in both these age-classes after zebra mussels were first discovered in the HEC. Previous studies in other areas of the Great Lakes that lake sturgeon under 700mm TL avoid foraging on zebra mussels (Jackson et al., 2002; Boase et al., 2014); our study supports these findings and others that concluded juvenile and sub-adult lake sturgeon avoid feeding on zebra mussels (Beamish et al., 1998; McCabe et al., 2006). Aside from zebra mussels lowering the availability of juveniles' preferred prey, Dreissenid mussels have a lower energy density than non-shelled macroinvertebrates (Johnson et al., 2005), likely driving avoidance in juvenile and sub-adult lake sturgeon since they have an increased energy cost for development.

While invasive species outcompete many native species for resources, they represent a new prey source of many local species (Jacobs et al., 2017; Pothoven et al., 2017; Happel et al., 2018). We found significant shifts toward a more fish-derived diet in juvenile and sub-adult lake sturgeon diet after round gobies were first discovered in the HEC. Evidence of lake sturgeon feeding on round gobies was similarly reported in in the Niagara River of Lake Ontario, where gut content revealed 86% of lake sturgeon total diet comprised of round gobies and stable isotopes of fin spines supported their diet results (Jacobs et al. 2017). In other species, walleye (*Sander vitreus*) captured from Lake Huron's main basin were feeding more prevalently on round goby and rainbow smelt (*Osmerus mordax*) than other potential prey items (Pothoven et al., 2017). Additionally, lake trout caught on the eastern shoreline of Lake Michigan consumed more round goby than other prey items based on gut content and fatty acids analyses (Happel et al., 2018).

It is important to study historic and present food web relationships in order to predict the impact of invasive species (Strayer et al., 2006) and better manage ecological restoration. This study quantified the historic and present trophic position and carbon source and the effects Dreissenid mussel and round gobies had on lake sturgeon in the HEC. Juvenile and sub-adult lake sturgeon may not have fed on Dreissenid mussels, but they did forage on round goby, and adult lake sturgeon showed a significant trend towards a more pelagic carbon source over time, complementing the signature of Dreissenid mussels. Not only do these invasive species contribute to the diet of a species at risk, but lake sturgeon of all age-classes may contribute in part to the resilience of an ecosystem to invasions by being native predators and acting as a biotic resistance.

References

Auer, N.A. (1996). Importance of Habitat and Migration to Sturgeons with Emphasis on Lake Sturgeon. *Canadian Journal of Aquatic Science, 53*(1), 152–160.

Auer, N.A. (1999). Population characteristics and movements of lake sturgeon in the Sturgeon River and Lake Superior. *Journal of Great Lakes Research*, *25*(1), 152–160.

Auer N, & Dempsey D. (2013). *The Great Lake Sturgeon*. East Lansing (MI): Michigan State University Press.

Beamish, F.W.H, Noakes, D.L.G, & Rossiter, A. (1998). Feeding Ecology of Juvenile Lake Sturgeon, *Acipenser fulvescens*, in Northern Ontario. *The Canadian Field Naturalist*, *112*(1), 459–468.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A., & MacLeod, H. (2004). Determining Trophic Niche Width: *A Novel Approach Using Stable Isotope Analysis*. *Journal of Animal Ecology*, *73*(5), 1007–1012.

Blackie, C.T., Weese, D.J., & Noakes, D.L.G. (2003). Evidence for Resource Polymorphism in the Lake Charr (*Salvelinus namaycush*) Population of Great Bear Lake, Northwest Territories, Canada. *Ecoscience, 10*(4), 509–514.

Boase, J.C., Manny, B.A., Donald, K.A.L., Kennedy, G.W., Diana, J.S., Thomas, M.V., & Chiotti, J.A. (2014). Habitat Used by Juvenile Lake Sturgeon (*Acipenser fulvescens*) in the North Channel of the St. Clair River (Michigan, USA). *Journal of Great Lakes Research*, *40*(2): 81–88.

Brittain, J.E. (1982). Biology of Mayflies. *Annual Review of Entomology, 27*, 119–147.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T., & Guisan, A. (2007). Evidence of Climatic Niche Shift During Biological Invasion. *Ecological Letters*, *10*(1), 701–709.

Bruch, R.M., Campana, S.E., Davis-Foust, S.L., Hansen, M.J., & Janssen, J. (2009). Lake Sturgeon Age Validation using Bomb Radiocarbon and Known-Age Fish. *Transactions of the American Fisheries Society*, *138*(2), 361–372.

Brush, J.M., Fisk, A.T., Hussey, N.E., & Johnson, T.B. (2012). Spatial and Seasonal Variability in the Diet of Round Goby (*Neogobius melanostomus*): Stable Isotopes

Indicate that Stomach Contents Overestimate the Importance of Dreissenids. *Canadian Journal of Fisheries and Aquatic Sciences, 69*(3), 573–586.

Cabana, G. & Rasmussen, J.B. (1996). Comparison of Aquatic Food Chains using Nitrogen Isotopes. *PNAS, 93*(1), 10844–10847.

Carleton, J.L. (2008). The Zebra Mussel *Dreissena polymorpha* Found in North America in 1986 and 1987. *Journal of Great Lakes Research, 43*(4), 770–773.

Chislock, M.F., Doster, E., Zitomer, R.A., & Wilson, A.E. (2013). Eutrophication: Causes, Consequences, and Controls in Aquatic Ecosystems. *Nature Education Knowledge, 4*(10).

Colborne, S. F., & Robinson, B. W. (2012). Effect of Nutritional Condition on Variation in δ^{13}C and δ^{15}N Stable Isotope Values in Pumpkinseed Sunfish (*Lepomis gibbosus*) Fed Different Diets. *Environmental Biology of Fishes, 96*(4), 543–554.

Flecker, A.R., & Townsend, C.R. (1994). Community-Wide Consequences of Trout in New Zealand Streams. *Ecological Applications, 4*(1), 798–807.

French, J. R. P. III., (1993). How Well can Fishes Prey on Zebra Mussels in Eastern North America. *Fisheries, 18*(1), 13–19.

Fry B. 2007. *Stable Isotope Ecology*. Baton Rouge, LA: Springer.

García-Berthou, E., & Moreno-Amich, R. (2000). Food of Introduced Pumpkinseed Sunfish: Ontogenetic Diet Shift and Seasonal Variation. *Journal of Fish Biology, 57*(1), 29–40.

Griffiths, R.W., Schloesser, D.W., Leach, J.H., & Kovalak, W.P. (1991). Distribution and Dispersal of the Zebra Mussel (*Dreissena polymorpha*) in the Great Lakes Region. *Canadian Journal of Fisheries and Aquatic Sciences, 48*(8), 1381–1388.

Guzzo, M., Haffner, G., Legler, N., Rush, S., & Fisk, A. (2013). Fifty Years Later: Trophic Ecology and Niche Overlap of a Native and Non-Indigenous Fish Species in the Western Basin of Lake Erie. *Biological Invasions, 15*(8), 1695–1711.

Hakala, J. P. & Johnson, F. D. (2004). Evaluation of a Gastric Lavage Method for Use on Largemouth Bass. *North American Journal of Fisheries Management, 24*(1), 1398–1403.

Happel, A., Jonas, J. L., McKenna, P. R., Rinchard, J., He, J. X., & Czesny, S. J. (2018). Spatial Variability of Lake Trout Diets in Lakes Huron and Michigan Revealed by

Stomach Content and Fatty Acid Profiles. *Canadian Journal of Fisheries and Aquatic Sciences, 75*(1), 95–105.

Hay-Chmielewski, E.M., & Whelan, G.E. (1997). Lake Sturgeon Rehabilitation Strategy. *Fisheries Division Special Report, 18*.

Jackson J.R., Van DeValk A.J., Brooking T.E., van Keeken O.A., & Rudstam L.G. (2002). Growth and Feeding Dynamics of Lake Sturgeon, *Acipenser fulvescens*, in Oneida Lake, New York: Results from the First Five Years of a Restoration Program. *Journal of Applied Ichthyology, 18*(1), 439–443.

Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing Isotopic Niche Widths Among and Within Communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology, 80*(3), 595-602.

Jacobs, G.R., Bruestle, E.L., Hussey, A., Gorsky, D., & Fisk, A.T. (2017). Invasive Species Alter Ontogenetic Shifts in the Trophic Ecology of Lake Sturgeon (*Acipenser fulvescens*) in the Niagara River and Lake Ontario. *Biological Invasions, 19*(1), 1533–1546

Johnson, T.B., Allen, M., Corkum, L.D., & Lee, V.A. (2005). Comparison of Methods Needed to Estimate Population Size of Round Gobies (*Neogobius melanostomus*) in Western Lake Erie. *Journal of Great Lakes Research, 31*(1), 78–86.

Kornis, M. S., Mercado-Silva, N. & Vander Zanden, M. J. (2012), Twenty Years of Invasion: a Review of Round Goby *Neogobius melanostomus* Biology, Spread and Ecological Implications. *Journal of Fish Biology, 80*(1), 235–285.

Krieger, K. A., Schloesser, D. W., Manny, B. A., Trisler, C. E., Heady, S. E., Ciborowski, J. J. H., & Muth, K. M. (1996). Recovery of Burrowing Mayflies (Ephemeroptera: Ephemeridae: Hexagenia) in Western Lake Erie. *Journal of Great Lakes Research, 22*(2): 254–263.

McCabe, D. J., Beekey, M. A., Mazloff, A., & Marsden, J.E. (2006). Negative Effect of Zebra Mussels on Foraging and Habitat Use by Lake Sturgeon (*Acipenser fulvecens*). *Aquatic Conservation: Marine and Freshwater Ecosystems, 16*(1), 493–500.

Nilo, P., Tremblay, S., Bolon, A., Dodson, J., Dumont, P. & Fortin, R. (2006), Feeding Ecology of Juvenile Lake Sturgeon in the St. Lawrence River System. *Transactions of the American Fisheries Society, 135*(1), 1044–1055.

Ozersky, T., Evans, D.O., & Barton, D.R. (2012). Invasive Mussels Alter the Littoral Food Web of a Large Lake: Stable Isotopes Reveal Drastic Shifts in Sources and Flow of Energy. *PLOS one*. *7*(12): e51249. doi:10.1371/journal.pone.0051249.

Parnell, A. C., Phillips, D. L., Bearhop, S., Semmens, B. X., Ward, E. J., Moore, J.W., Jackson, A. L., . . . Inger, R. (2013). Bayesian Stable Isotope Mixing Models. *Environmetrics, 24*(6), 387–99.

Parra, G. J. & Jedensjö, M. (2014), Stomach Contents of Australian Snubfin (*Orcaella heinsohni*) and Indo-Pacific Humpback Dolphins (*Sousa chinensis*). *Marine Mammal Science, 30*(1), 1184–1198.

Peterson, D.L., Vecsei, P., & Jennings, C.A. (2007). Ecology and Biology of the Lake Sturgeon: a Synthesis of Current Knowledge of a Threatened North American *Acipenseridae*. *Reviews in Fish Biology and Fisheries, 17*(1), 59–76.

Pettitt-Wade H. 2016. *Niche Breadth and Invasion Success*. (Doctoral dissertation). Retrieved from The University of Windsor.

Pollock, M. S., Charr, M., Kreitals, N. M., & Phillips, I. D. (2014). Review of a Species in Peril: What We Do Not Know About Lake Sturgeon May Kill Them. *Environmental Reviews, 23*(1), 30–43.

Post, D.M. (2002). Using Stable Isotopes to Estimate Trophic Position: Models, Methods, and Assumptions. *Ecology, 83*(3), 703–718.

Pothoven, S. A., Madenjian, C. P., & Höök, T. O. (2017). Feeding Ecology of the Walleye (Percidae, *Sander vitreus*), a Resurgent Piscivore in Lake Huron (Laurentian Great Lakes) After Shifts in the Prey Community. *Ecology of Freshwater Fish, 26*(1), 676–685.

Priegel, G R. & Wirth, T.L., (1971). *The Lake Sturgeon: Its Life History, Ecology and Management*. Madison, WI: Wisconsin Department of Natural Resources, Publication 240.

Quevedo, M.R., Svanbäck, R., & Eklöv, P. (2009). Intrapopulation Niche Partitioning in a Generalist Predator Limits Food Web Connectivity. *Ecology, 90*(1), 2263–2274.

Sarakinos, H. C., Johnson, M. L., & Vander Zanden, J. (2002). A Synthesis of Tissue-Preservation Effects on Carbon and Nitrogen Stable Isotope Signatures. *Canadian Journal of Zoology, 80*(1), 381–387.

Smith, T.B., & Skulason, S. (1996). Evolutionary Significance of Resource Polymorphisms in Fishes, Amphibians, and Birds. *Annual Review of Ecology and Systematics, 27*(1), 111–113.

Strayer, D.L., Eviner, V.T., Jeschke, J.M., & Pace, M.L. (2006). Understanding the Long-Term Effects of Species Invasions. *Trends in Ecology & Evolution, 21*(11), 645–651.

St. Pierre, R., & Runstrom, A. (2004). *Acipenser fulvescens* [The IUCN Red List of Threatened Species]. Retrieved from http://www.iucnredlist.org/details/223/0.

Tillberg, C. V., McCarthy, D. P., Dolezal, A. G., & Suarez, A. V. (2006). Measuring the Trophic Ecology of Ants using Stable Isotopes. *Insectes Sociaux, 53*(1), 65–69.

Vander Zanden, M. J., Cabana, G., & Rasmussen, J. B. (1997). Comparing Trophic Position of Freshwater Fish Calculated Using Stable Nitrogen Isotope Ratios (d15N) and Literature Dietary Data. *Canadian Journal of Fish and Aquatic Sciences, 54*(1), 1142–1158.

Vander Zanden, M.J., Casselman, J.M., & Rasmussen, J.B. (1999). Stable Isotope Evidence for the Food Web Concequence of Species Invasions in Lakes. *Nature, 401*(1), 464–467.

Walsh, M.G., Dittman, D.E., & O'Gorman, R. (2007). Occurrence and Food Habits of the Round Goby in the Profundal Zone of Southwestern Lake Ontario. *Journal of Great Lakes Research, 33*(1), 83–92.

Werner, E. E., & Gilliam, J. F. (1984). The Ontogenetic Niche and Species Interactions in Size-Structured Populations. *Annual Review of Ecology and Systematics, 15*(1), 393–425.

Table 3.1 Stable isotopes (‰, mean ± 1 SE) of lake sturgeon fin spines across age-classes and invasion time periods, round goby, Dreissenid mussels, and mayfly nymphs collected from the Lake Huron–to–Lake Erie corridor. Superscript letters denote significant differences ($p<0.05$) within $\delta^{13}C$ or $\delta^{15}N$ determined by MANOVA.

	< 1988			**1990 – 1998**			**> 1999**		
Lake Sturgeon	**$\delta^{13}C$**	**$\delta^{15}N$**	**N**	**$\delta^{13}C$**	**$\delta^{15}N$**	**n**	**$\delta^{13}C$**	**$\delta^{15}N$**	**n**
Juvenile	-17.5 ± 0.1^{a}	10.9 ± 0.1^{zw}	88	-18.0 ± 0.2^{b}	11.3 ± 0.2^{z}	82	-17.3 ± 0.3^{ac}	13.0 ± 0.4^{x}	18
Sub–Adult	-17.7 ± 0.2^{ab}	11.9 ± 0.2^{y}	42	-18.4 ± 0.2^{b}	11.3 ± 0.2^{z}	46	-16.9 ± 0.2^{c}	12.3 ± 0.2^{y}	52
Adult	-17.2 ± 0.4^{ac}	12.0 ± 0.3^{y}	12	-18.2 ± 0.3^{b}	10.9 ± 0.4^{zw}	5	-18.0 ± 0.3^{b}	10.8 ± 0.3^{w}	33
Zebra Mussel	–	–	0	–	–	0	–22.4 ± 0.4	8.6 ± 0.3	72
Quagga Mussel	–	–	0	–	–	0	–20.4 ± 0.1	7.4 ± 0.2	35
Round Goby	–	–	0	–	–	0	–19.0 ± 0.2	11.8 ± 0.2	133
Mayfly Nymph	–25.2 ± 0.5	4.9 ± 0.7	7	–22.3 ± 0.3	6.1 ± 0.2	9	–23.0 ± 0.3	8.0 ± 0.4	15

Table 3.2 Overlap in isotopic niche (%) based on SEA$_C$, niche size (‰^{2}), and SEA$_C$ (‰^{2}) for lake sturgeon collected from three sampling locations within the Lake Huron-to-Lake Erie corridor. Rows show how similar lake sturgeon from one age-class is to those from another within time frames; for example, the niche of juvenile lake overlaps 50% with the niche of sub-adult lake sturgeon from before 1988. Columns show how distinct lake sturgeon from an age-class is to another; for example, 55% of the niche of juvenile lake sturgeon overlaps with the niche of sub-adult lake sturgeon under age 5 from before 1988 and thus 45% of the niche of juvenile lake sturgeon is unique from sub-adult lake sturgeon from before 1988.

	<1988			**1990 – 1998**			**>1999**		
Lake Sturgeon	Juvenile	Sub-Adult	Adult	Juvenile	Sub-Adult	Adult	Juvenile	Sub-Adult	Adult
Juvenile	–	50	39	–	60	16	–	62	2
Sub–Adult	55	–	70	67	–	16	65	–	20
Adult	39	64	–	100	88	–	2	18	–
SEAc (‰^{2})	4.3	3.9	4.3	4.9	4.4	0.8	5.7	5.4	5.9
Niche Area (‰^{2})	4.4	4.0	4.4	5.0	4.5	0.8	5.8	5.5	6.0

Table 3.3 Linear regression statistics of δ^{13}C and δ^{15}N for juvenile, sub-adult, and adult lake sturgeon, and mayfly nymphs from the HEC over time. Y-intercept and slope are denoted as b and *m*, respectively. First break refers to the linear regression from the first data point to the year when a significant shift in slope occurred. The second break refers to the linear regression from the year in which the significant shift in slope occurred to the last data point. In juveniles and sub-adults, the significant shift happened in 1994 and 1991 for δ^{15}N, respectively. In both those age-classes, the significant shift for δ^{13}C happened in 1988.

δ^{13}C

	Corrected Linear				First Break				Second Break			
	b	*m*	R^2	p-value	b	*m*	R^2	p-value	b	*m*	R^2	p-value
Lake Sturgeon												
Juvenile	73.9	$-4.7e^{-2}$	0.073	< 0.001	268	-0.11	0.31	< 0.001	-49.8	$1.5e^{-2}$	$2.5e^{-3}$	0.65
Sub–Adult	21.4	$-2.0e^{-2}$	0.021	< 0.01	456	-0.24	0.37	< 0.001	-149	$6.5e^{-2}$	0.1	< 0.001
Adult	175	$-9.8e^{-2}$	0.26	< 0.001								

δ^{15}N

	b	*m*	R^2	p-value	b	*m*	R^2	p-value	b	*m*	R^2	p-value
Lake Sturgeon												
Juvenile	149	$-7.0e^{-2}$	0.11	< 0.001	281	-0.14	0.19	< 0.001	-448	0.23	0.13	< 0.001
Sub–Adult	236	-0.11	0.32	< 0.001	337	-0.16	0.13	< 0.05	121	$-6.0e^{-2}$	$5.1e^{-2}$	<0.05
Adult	383	-0.19	0.59	< 0.001								

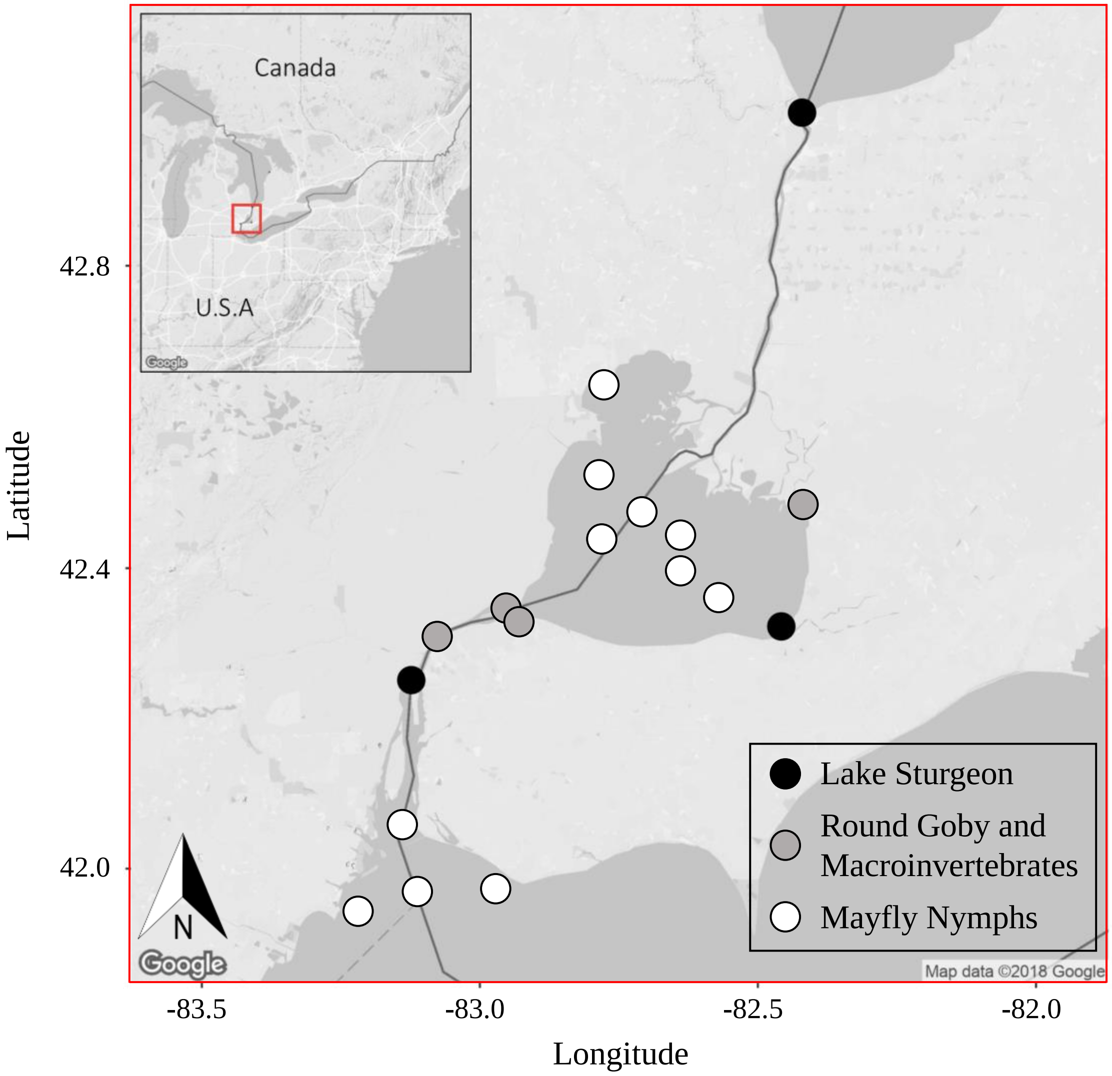

Figure 3.2 Sampling locations for lake sturgeon and mayfly nymphs from the Lake Huron-to-Lake Erie corridor. Lake sturgeon were collected from 1991 to 2014, mayfly nymphs from 1977 to 2014, and invasive species from 2011 to 2013.

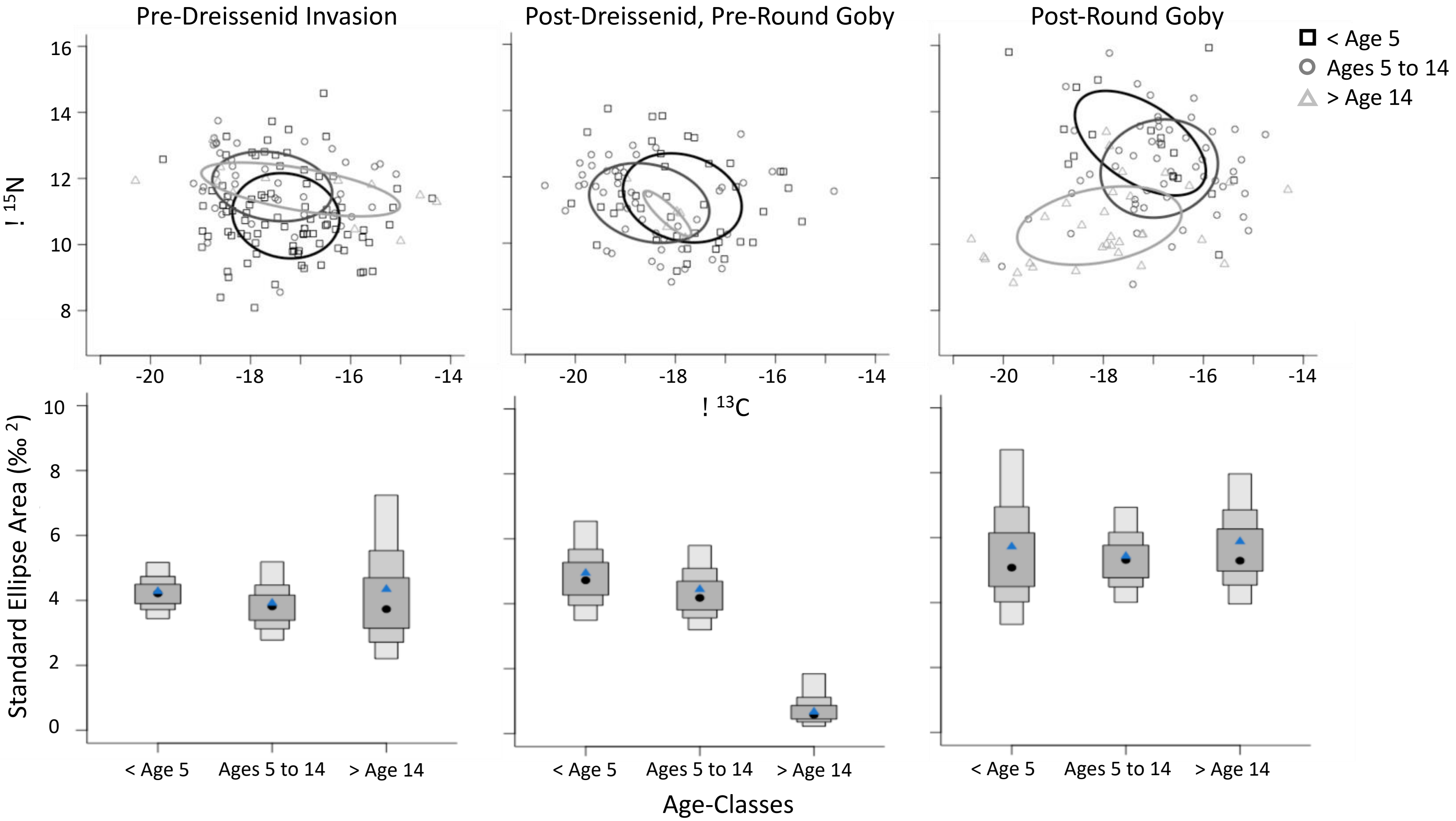

Figure 3.3 Isotopic niche areas and density plots of Bayesian credibility intervals (BCIs) for standard ellipses area (SEA_B) of lake sturgeon fin ray tissue collected from the HEC across times periods and age-classes. The black dots represent mean SEA_B, the blue triangles represent SEA_C, and the grey blocks represent BCIs of 50, 75 and 95%.

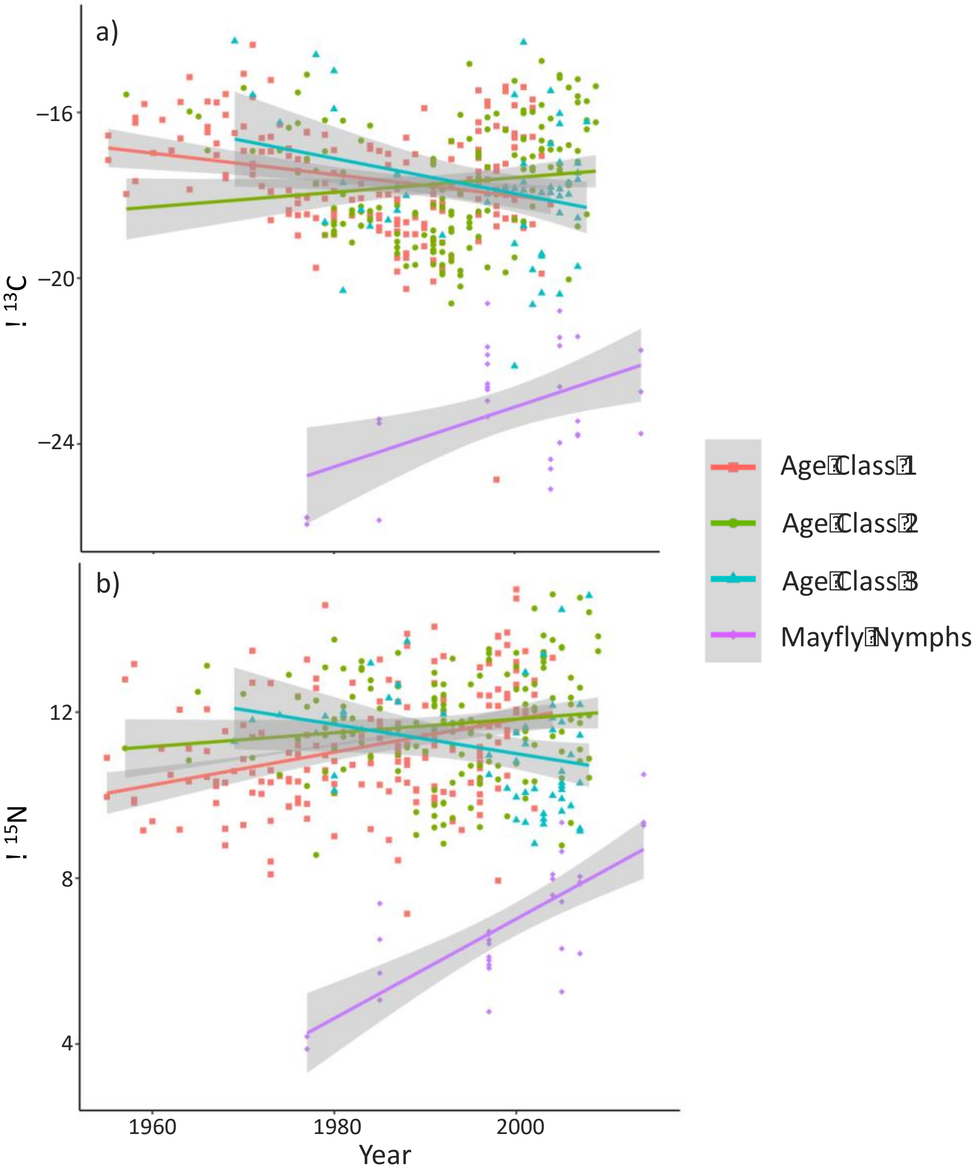

Figure 3.4 Temporal trends in raw δ^{13}C (a) and δ^{15}N (b) in fin spines of lake sturgeon by age-class from 1953 to 2009 in the HEC. Grey area represents 95% confidence region. Linear regressions were constructed for the mayfly nymph baseline as well as each age-class where age-class 1 = age 4 and less, age-class 2 = 5 to 14, and age-class 3 = 15+. R^2 and p-values for δ^{13}C were 0.075 and <0.01 for age-class 1, 0.020 and 0.083 for age-class 2, 0.082 and <0.05 for age-class 3, and 0.30 and <0.001 for mayfly baseline. R^2 and p-values for δ^{15}N were 0.10 and <0.001 for age-class 1, 0.018 and 0.1 for age-class 2, 0.099 and <0.05 for age class 3, and 0.63 and <0.001 for mayfly nymphs.

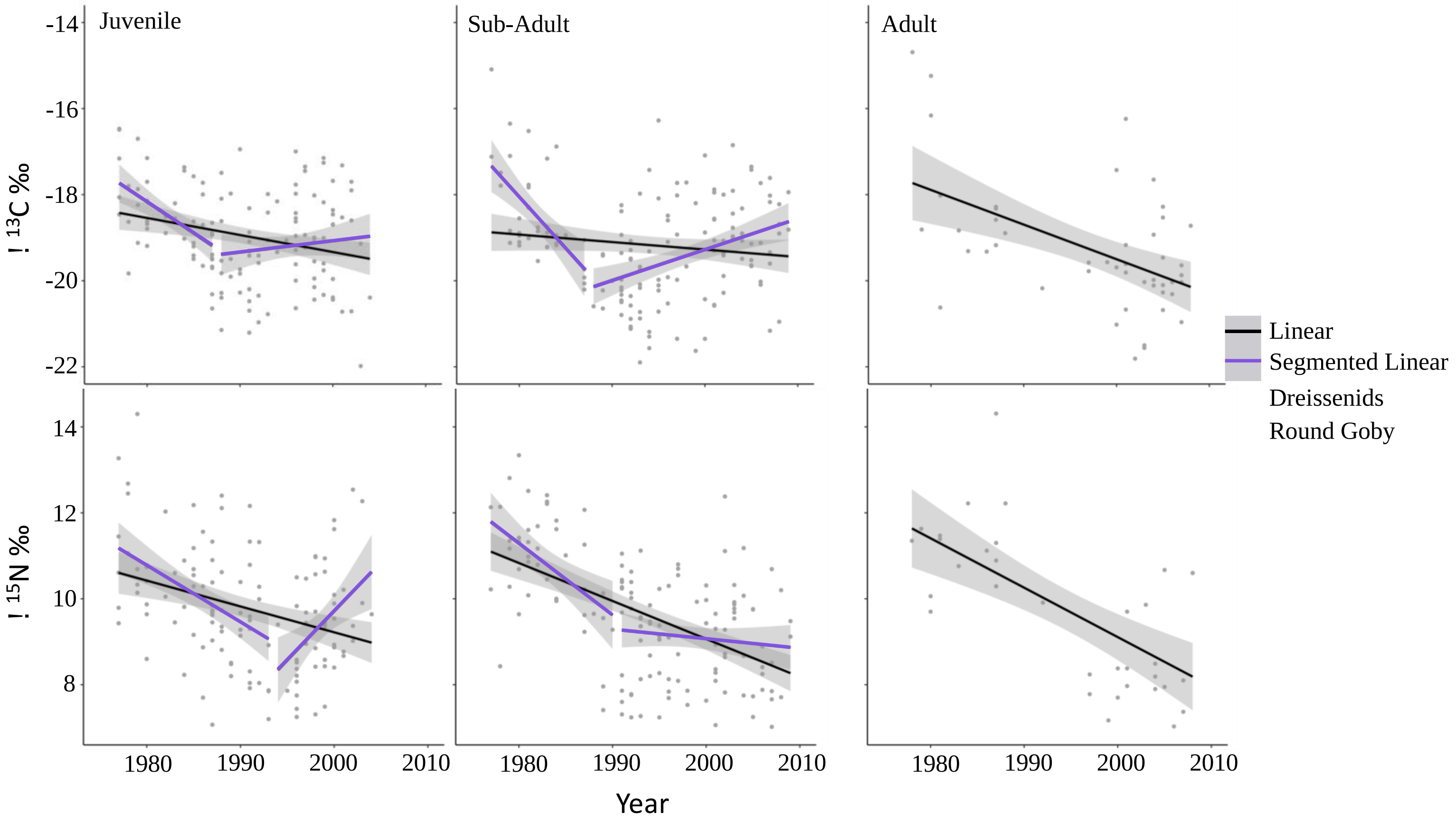

Figure 3.5 Scatterplot of δ^{13}C (panels a, b, and c) and δ^{15}N (panels d, e, and f) of lake sturgeon from 1977 to 2009 with both linear and segmented linear regressions and a 95% confidence region in grey. Lake sturgeon data was corrected for temporal trends in ecosystem using the mayfly baseline. Panels a) and d) (age-class 1, 4 and less), b) and e) (age-class 2, 5 to 14), and panels c) and f) (age-class 3, 15+). The shaded areas signify the time range when the invasive species were first discovered to when they were considered widespread and dominant.

CHAPTER 4

GENERAL DISCUSSION

Lake sturgeon feeding behaviour varies both spatially and temporally and thus dietary data is not transferable across locations. The Lake Huron–to–Lake Erie Corridor (HEC) is a major migration route and spawning ground of lake sturgeon (Auer et al., 1996; Roseman et al., 2011), but current dietary analyses are lacking for this species in this system. Our goal was to answer if lake sturgeon feeding ecology is impacted by partial migration, ontogeny, and species invasions within this system by quantifying stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$), trophic position (TP), and proportional diet estimates. Our findings provided information about intraspecific interactions across sub-populations of lake sturgeon categorized by migration behaviour, age-class, and invasion time period, adults' preferential prey items in this system, as well as information regarding the complex role invasive species play as a new prey resource.

Chapter Summaries

Chapter two analyzed isotopic niche size and overlap in adult lake sturgeon across different migration behaviours. It borrowed from the work of Kessel et al. (2017) to categorize lake sturgeon from two capture sites within the HEC into three distinct migratory behaviours and three discrete locations in which they migrated; the three migration behaviours are lake dominant migrant, seasonal migrant, and river-resident, and the three migration locations are St. Clair River to Lake Huron, within and between the St. Clair and Detroit Rivers, and Detroit River to Lake Erie. We further estimated proportional diet of lake sturgeon that migrated within and between the St. Clair and Detroit Rivers.

Isotopic niche size was largest in the lake dominant migrant sub-population, while river-residents were small in comparison. Upon separation into which lake they migrated to, the population that migrated from the Detroit River to Lake Erie had higher $\delta^{15}N$ than the population that migrated from St. Clair River to Lake Huron, as did the prey captured within each lake. Lake sturgeon that migrated to Lake Erie also had a smaller isotopic niche in comparison to the population that migrated to Lake Huron. Diet estimate and niche results showed lake sturgeon diet varied spatially. Despite their abundance, invasive species were equal contributors to adult lake sturgeon diet as other prey sources, suggesting a generalist behaviour within this system. Stable isotopes revealed discrete sub-populations of lake sturgeon by migratory locations and behaviours.

Chapter three examined temporal trends in juvenile, sub-adult, and adult lake sturgeon stable isotopes across three invasion time frames: pre-Dreissenid (<1988), post-Dreissenid and pre-round goby (1990–1998), and post-round goby (>1999). Archived pectoral fin spines of HEC lake sturgeon collected from 1991 to 2015, which include sub-populations, were sectioned across growth rings and analyzed for stable isotopes ($\delta^{15}N$ and $\delta^{13}C$). These data, along with key invasive prey, Dreissenid mussels (*Dreissena spp.)* and round goby (*Neogobius melanostomus*), provided a temporal assessment of feeding ecology of lake sturgeon at the individual and population level.

We observed differences in diet across age-classes after the round goby invasion and significant changes in slope of stable isotopes in juveniles and sub-adults after the Dreissenid and round goby invasions, suggesting juvenile and sub-adult lake sturgeon began feeding on round gobies, but avoided Dreissenid mussels. However, adult lake sturgeon isotopic signatures post-round goby suggests they are either feeding directly on zebra mussels or are not as restricted as their youth when foraging on other macroinvertebrates in high zebra mussel concentrated areas. While gobies may prey upon or outcompete small-bodied native fish, they potentially represent a new prey resource for native predators like lake sturgeon.

Conclusions

Temporal and spatial variations in lake sturgeon diet appeared in many ecological studies within the Great Lakes (Guilbard et al., 2007; Smith et al., 2016; Jacobs et al., 2017) and our research support these findings. Stable isotopes of lake sturgeon from the HEC conclude that dietary information is not transferable across populations. Furthermore, disparity in niche sizes across migration behaviour revealed discrete sub-populations within the HEC. With increasing anthropogenic stressors, it is important to study food web relationships – both historic and present – in order to best implement ecological restoration plans. Differing isotopes and niches of lake sturgeon at different ages suggest that they may require different management approaches within the HEC. Furthermore, adult lake sturgeon of different migration strategies had discrete niche sizes that require consideration before stocking arrangements.

New questions and future research on lake sturgeon diet arose from this project. Our work can be further extended to include an analysis of prey species composition and abundance in the HEC in order to understand the amount of preference lake sturgeon may be performing and support the trophic polymorphism hypothesis. Values of $\delta^{15}N$ and $\delta^{13}C$ differed in prey resources across capture sites, while mean isotope values remained similar in lake sturgeon that exhibit different migration behaviours. This suggests that certain prey (like the round goby) may be more abundant to lake sturgeon that migrate to Lake Huron, since it was the only location where $\delta^{15}N$ was lower in round goby than lake sturgeon. Because there was low resolution in stable isotopes among prey species from within and between the St. Clair and Detroit Rivers, adding a third stable isotope, such as $\delta^{34}S$ and collecting other non-lethal tissue samples, such as blood plasma and red blood cells, a more robust dietary analysis can be conducted.

Studies analyzing the diet tissue discrimination factor for lake sturgeon fin spines are lacking. In our study, we used values from Jacobs et al., (2017) to calculate the change in isotopes from round gobies to lake sturgeon fin spines since round gobies made up 86% of their stomach content. Stomach content only provides a “snapshot” of a species diet and tends to overestimate the importance of certain prey (Brush et al., 2012). Future projects could include a laboratory study where lake sturgeon are fed appropriate hatchery feed for a year and then analyze stable isotopes for that feed and the most recent age ring on lake sturgeon fin spines to calculate a more accurate DTDF.

Studies surrounding changes in diet with ecological shifts, such as human-induced invasions, have been well-documented (Becker & Beissinger, 2006; Jacobs et al., 2017; Blanke et al., 2018). Because these ontogenetic diet shifts in lake sturgeon include recent introductions, it’s important to study the complex role invasive species play as a new prey resource for this species at risk and potentially other local species. While invasive species outcompete many native species for resources, they represent a new prey source of many local species (Jacobs et al., 2017; Pothoven et al., 2017; Happel et al., 2018).

We provided information about the feeding ecology of a species for which standard gut content analysis is impractical. Our approach to studying diet composition and foraging niche is transferable to other lake sturgeon populations in the Great Lakes and other sturgeon species, such as the shortnose sturgeon (*Acipenser brevirostrum*), which is also anadromous (Gilbert, 1989). The shortnose sturgeon has a similar history as lake sturgeon in that they were both endangered due to overharvesting, habitat dredging, and pollution (Kynard, 1997). Stable isotope analysis of pectoral fin spines allows for dietary analysis of species at risk without further harming their already decimated population numbers.

Our approach is also transferable to other partially migratory species and species at risk. For example, Raby et al. (2018) found sex to be a determinant of when walleye migrated out, but why some individuals migrated further than others remained unexplained. Walleye are a long-lived species which are protected from anglers by length-limits on catch and spawning season closures. By implementing non-lethal stable isotope methods and utilizing Raby et al., (2018) telemetry data, a similar study could be done to answer if feeding opportunities are driving different migratory behaviours in walleye.

References

Auer, N.A. (1996). Importance of Habitat and Migration to Sturgeons with Emphasis on Lake Sturgeon. *Canadian Journal of Aquatic Science*, *53*(1), 152–160.

Becker, B. H., & Beissinger, S. R. (2006). Centennial Decline in the Trophic Level of an Endangered Seabird after Fisheries Decline. *Conservation Biology, 20*(1), 470–479.

Blanke, C., Chikaraishi, Y., & Vander Zanden, J. M. (2018). Historical Niche Partitioning and Long-Term Trophic Shifts in Laurentian Great Lakes Deepwater Coregonines. *Ecosphere, 9*(1), e02080. doi:10.1002/ecs2.2080

Brush, J.M., Fisk, A.T., Hussey, N.E., & Johnson, T.B. (2012). Spatial and Seasonal Variability in the Diet of Round Goby (Neogobius melanostomus): Stable Isotopes Indicate that Stomach Contents Overestimate the Importance of Dreissenids. *Canadian Journal of Fisheries and Aquatic Sciences, 69*(3), 573–586.

Guilbard, F., Munro, J., Dumont, P., Hatin, D., & Fortin, R. (2007). Feeding Ecology of Atlantic Sturgeon and Lake Sturgeon Co-Occuring in the St. Lawrence Estuarine Transition Zone. *American Fisheries Society Symposium, 56*(1), 85–104.

Happel, A., Jonas, J. L., McKenna, P. R., Rinchard, J., He, J. X., & Czesny, S. J. (2018). Spatial Variability of Lake Trout Diets in Lakes Huron and Michigan Revealed by Stomach Content and Fatty Acid Profiles. *Canadian Journal of Fisheries and Aquatic Science, 75*(1), 95–105.

Jacobs, G.R., Bruestle, E.L., Hussey, A., Gorsky, D., & Fisk, A.T. (2017). Invasive Species Alter Ontogenetic Shifts in the Trophic Ecology of Lake Sturgeon (*Acipenser fulvescens*) in the Niagara River and Lake Ontario. *Biological Invasions, 19*(1), 1533–1546.

Kessel, S.T., Hondorp, D.W., Holbrook, C.M., Boase, J.C., Chiotti, J.A., Thomas, M.V., Wills, T.C., . . . Krueger, C.C. (2017). Divergent Migration Within Lake Sturgeon (*Acipenser fulvescens*) Populations: Multiple Distinct Patterns Exist Across an Unrestricted Migration Corridor. *Journal of Animal Ecology, 87*(1), 259–273.

Kynard, B. (1997). Life History, Latitudinal Patterns, and Status of the Shortnose Sturgeon, *Acipenser brevirostrum*. *Environmental Biology of Fishes, 48*(1-4), 319–334.

Pothoven, S. A., Madenjian, C. P., & Höök, T. O. (2017). Feeding Ecology of the Walleye (Percidae, *Sander vitreus*), a Resurgent Piscivore in Lake Huron (Laurentian Great Lakes) After Shifts in the Prey Community. *Ecology of Freshwater Fish, 26*(1), 676–685.

Raby, G.D., Vandergoot, C.S., Hayden, T.A., Faust, M.D., Kraus, R.T., Dettmers, J.M., Cooke, S.J., . . . Krueger, C.C. (2018). Does Behavioural Thermoregulation Underlie Seasonal Movements in Lake Erie Walleye? *Canadian Journal of Fisheries and Aquatic Sciences, 75*(3), 488–496.

Roseman, E. F., Manny, B., Boase, J., Child, M., Kennedy, G., Craig, J., Soper, K., & Drouin, R. (2011). Lake Sturgeon Response to a Spawning Reef Constructed in the Detroit River. *Journal of Applied Ichthyology, 27*(1), 66–76.

Smith, A., Smokorowski, K., Marty, J., & Power, M. (2016) Stable Isotope Characterization of Rainy River, Ontario, Lake Sturgeon Diet and Trophic Position. *Journal of Great Lakes Research, 42*(2), 440–447.

VITA AUCTORIS

NAME:	Tanya E. Fendler
PLACE OF BIRTH:	Montreal, Quebec
YEAR OF BIRTH:	1992
EDUCATION:	M.Sc. Environmental Science (2018) Great Lakes Institute for Environmental Research University of Windsor Windsor ON, Canada
	B. Sc. Honours Biological Sciences (2015) Department of Biological Sciences University of Windsor Windsor ON, Canada