Food web metrics of piscivorous predators in the Lake-Huron Erie Corridor using stable isotopes

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FOOD WEB METRICS OF PISCIVOROUS PREDATORS IN THE LAKE HURON-ERIE CORRIDOR USING STABLE ISOTOPES

by

Brent Nawrocki

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

Windsor, Ontario, Canada

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DETERMINING FOOD WEB METRICS OF PISCIVOROUS PREDATORS IN THE LAKE HURON-ERIE CORRIDOR USING STABLE ISOTOPES

By

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September 1, 2015
DECLARATION OF ORIGINALITY

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ABSTRACT

The Laurentian Great Lakes are home to a high biodiversity of freshwater piscivorous predators; however the trophic role of these species is poorly understood. Using stable isotopes of carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N), I examined trophic position, niche widths and overlap of piscivorous predators across three sites in the Lake Huron-Erie Corridor (HEC). Trophic position (TP) was determined by $\delta^{15}$N, while habitat utilization was measured using $\delta^{13}$C. Across all sites and species, mean trophic position ranged from 4.0 to 5.1, were highest for Longnose Gar (Lepisosteus osseus), and lowest for Northern Pike (Esox lucius). Bowfin (Amia calva) had a larger niche width and low overlap with other predators across site, while Longnose Gar and Northern Pike had the smallest niche widths and high interspecific overlap. Variation in TP, niche width and overlap suggested different foraging behaviour, trophic interactions, and more complex food web structure in the HEC than previously believed.
DEDICATION

I dedicate this thesis to my parents, Bernie and Dorothy, for being my biggest cheerleaders, and to Maghen Ajing Quadrini. Your friendship is unmatched.
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CHAPTER 1

GENERAL INTRODUCTION

Food web ecology

Trophic ecology is the study of feeding relationships between species within communities or ecosystems. Accurate descriptions of feeding relationships are essential to a wide range of ecological concepts, allowing for greater understanding of the roles that species occupy in their environment. One of the most rudimentary concepts in characterizing trophic ecology of species is the ‘food cycle’, which was first proposed by Pierce et al., 1912. The ‘food cycle’ was defined as a series of trophic relationships linking predator and prey species that are dependent upon a primary food source (Pierce et al., 1912). The concept of the ‘food cycle’ was later refined to that of a ‘food web’ by Charles Elton to accommodate more complex trophic interactions between and amongst predator and prey species in order to monitor energy flow through ecosystems (Elton, 1927).

Within food webs, a series of food chains have traditionally been used to classify species based upon their feeding habits (Elton, 1927; Lindeman, 1942). Food chains encompassed the range of possible energy transfer paths within an ecosystem, and were further categorized into trophic levels (Lindeman, 1942). Primary producers occupy the lowest trophic level in a food chain, facilitating energy and non-biological carbon through consumption by herbivores and eventually predators (Lindeman, 1942). An increase in trophic level correlates to both a decrease in biomass and a loss of energy, where the least amount of biomass is seen at the highest trophic level occupied by top predators (Elton, 1927). However, while food chains were able to provide an explanation as to the rate of contribution of energy from one trophic level to another, they oversimplified carbon flow across trophic levels and underestimated complex omnivorous
relationships that exist in the natural environment (Burns, 1989). We can relate food webs, food chains and trophic levels, through the concept of trophic structure or trophic position (TP), which is a continuous measurement of prey consumption by a predator, accurately quantifying omnivory and predators that consume prey from multiple trophic levels, ultimately minimizing the oversimplification of trophic relationships (Paine, 1988; Vander Zanden & Rasmussen, 1996).

However, while TP allows for the determination of feeding complexity, it does not provide information on interspecific diet comparisons. To examine interspecific trophic interactions, the concept of niche was first proposed by Joseph Grinnell in 1917, where it was defined as the sum of habitat requirements and behaviours that allow a species to persist (Grinnell, 1917). Elton further elaborated upon Grinnell’s definition by proposing that functional niche is dependent upon the distribution of resources and competitors (Elton, 1927), while G. Evelyn Hutchinson proposed the n-dimensional hyper volume, known as the realized niche, which takes into consideration both ecosystem parameters as well distribution of resource and predators (Hutchinson, 1957).

Elton also theorized that food webs were the biological process responsible for regulating species populations and communities, and are further understood through niche (Elton, 1927; Bersier, 2007). Ecological models have shown that food webs that exhibit a low occurrence of functional redundancy are characterized by weak trophic interactions, and are important in stabilizing existing trophic structure (McCann, 1998). The concept of functional redundancy assumes that species have similar niches in ecosystems, and are therefore functionally interchangeable with negligible adverse impacts on ecosystem function (Rosenfield, 2002). Understanding functional redundancy is further complicated by ontogenetic shifts, seasonal
changes in species abundance and intraguild predation (Ben-David et al., 1997; van Leeuwen et al., 2013) and these mechanisms need to be considered in studies that quantify food web structure (Persson & De Roos, 2012). Furthermore, a decrease in biodiversity can result in stronger trophic interactions and a higher degree of functional redundancy, increasing the likelihood for systems to undergo destabilizing dynamics and collapses (i.e. trophic cascades) (McCann, 2000). The evaluation of functional niche can be used as an empirical tool to predict the occurrence of functional redundancy, in an effort to understand interspecific food web dynamics (Rosenfield, 2002).

Piscivorous predators, which occupy the highest trophic levels within a food web, consume prey of high trophic levels (Domingo et al., 2012). Within ecosystems, these predators generally have different niches, which allow for dynamic trophic relationships between predators and prey (Polis et al., 1989). Understanding how piscivorous predators co-exist as a result of different feeding strategies will provide greater insight into food web structure and a more accurate estimation of trophic position at upper trophic levels within a food web. These trophic relationships amongst higher trophic level predators help maintain biodiversity and decrease the likelihood of trophic cascades, while also being responsible for top-down control in trophic pyramids (Lindeman, 1942; Ritchie & Johnson, 2009). Understanding the niches and feeding habits of higher trophic level species will promote a greater understanding of ecosystem dynamics, community structure, and the potential for functional redundancy (Hairston et al., 1960; Elmhagen et al., 2010).

Trophic position and niche, which are both quantitative measurements, have traditionally been used to understand the role of higher trophic level predators within a food web by measuring the energetic relevance of consumption of multiple prey items (Duffy et al., 2005;
Parnell et al., 2013; Vander Zanden et al., 1997). Niche, TP, and food web structure are often quantified using stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N) (Newsome et al., 2007). Traditional methods such as observation of foraging and stomach content analysis have also been used to estimate TP and dietary niche by providing an instantaneous “snapshot”, yet these methods can be unreliable due to sampling bias, mastication of prey, rare feeding events, variable digestion rates, and empty stomachs (Hyslop, 1980; Polito et al., 2011; Woodward & Hildrew, 2001). Stable isotopes are advantageous due to their ability to provide an integrated characterization of the diet of a species across different periods of time as well as providing insight into carbon sources (Newsome et al., 2007). However, stable isotopes are susceptible to variation within species- and tissue-specific turnover rates as well as varying discrimination factors, and temporal variation (Bond & Jones, 2009).

**Stable isotopes in trophic ecology**

Stable isotopes are elements that exist in multiple forms, having the same amount of protons and electrons, but different amounts of neutrons in the nucleus, allowing for mass-dependant isotopic fractionation (Peterson & Fry, 1987). Isotopes of an element are classified based off their atomic mass as ‘heavy’ or ‘light’, where heavy isotopes are usually less abundant in the natural environment (Fry, 2007). Changes in the abundance of stable isotopes in the environment are a result of isotopic fractionation due to kinetic reactions of isotopes (Biegeleisen, 1965). Light isotope bonds are more easily broken which allows for a faster isotope fractionation rate than heavy isotope bonds due to greater potential energy and requiring less energy for atoms to move apart and for bonds to break (Fry, 2007). Molecules containing lighter isotopes are more readily broken down and excreted than molecules containing heavy isotopes allowing for these molecules to act as chemical tracers that can be ecologically insightful into
estimating feeding behaviour and carbon sources (Fry, 2007). In quantifying the change in ratio of heavy to light isotopes, tissues are measured against a standard and calculated using the equation \( \delta X = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 1000 \), where \( R_{\text{sample}} \) is represented by the ratio of the heavy to light isotope and \( R_{\text{standard}} \) represents the ratio of heavy to light isotopes in an internationally accepted standard. Less negative values indicate an increase in the ratio of heavy to light isotopes from the standard and more negative values indicate a decrease in the ratio of heavy to light isotopes in relation to the standard.

Stable isotopes of nitrogen have traditionally been used to provide an estimate of TP, where \( \delta^{15}N \) in an organism is enriched relative to that of its diet items (DeNiro & Epstein, 1981), and thus larger \( \delta^{15}N \) is indicative of a species that feeds at higher trophic levels (Michener & Lajtha, 2007). This stepwise increase in \( \delta^{15}N \) with each trophic level is called a diet-tissue discrimination factor (DTDF), and quantifies the difference in \( \delta^{15}N \) between an organism and its diet (Caut et al., 2009). A DTDF of +3.4‰ between trophic levels has traditionally been used to understand the relationship between increasing \( \delta^{15}N \) and trophic levels (Minagawa & Wada, 1984; Vander Zanden and Rasmussen, 2001; Post, 2002). However, a number of recent papers have found DTDF decreases with increasing \( \delta^{15}N \) in the diet of a species (herein referred to as “scaled DTDF”); providing less truncated TP estimates of higher trophic level species (Overmyer et al., 2008; Caut et al., 2009; Hussey et al., 2014).

The turnover of stable isotopes, particularly when an animal switches diet, has to be taken into consideration when studying TP as they are influenced by the range of values in diet, anabolic tissue growth and replacement of the tissue of interest (i.e. isotopic routing) (MacAvoy et al., 2005). Turnover rates are tissue-dependant and a function of metabolic activity and protein composition, where a greater turnover rate is generally seen in plasma and liver tissue, while a
slower rate is present in muscle tissue and bone (DeNiro & Epstein, 1981; MacAvoy et al., 2005; Newsome et al., 2007). Understanding that variable tissue turnover rates reflect the tissue metabolic rate, and that DTDF is not consistent across species or tissues, is important in the accurate estimation of TP and ultimately the role of piscivorous predators in an ecosystem through the use of stable isotope analysis (MacAvoy et al., 2005). However, a meta-analysis was performed to calculate a scaled DTDF that addresses variable turnover rates for different species and ecosystems for white muscle tissue, finding a decrease in $\Delta^{15}N$ between trophic levels with increasing dietary $\delta^{15}N$ (Caut et al., 2009; Hussey et al., 2014; Overmyer et al., 2008).

While stable isotopes of nitrogen are associated with diet characterization in a food web, stable isotopes of carbon ($\delta^{13}C$) quantify the sources of primary production within an ecosystem, and are defined by a nutrient, or carbon, source (Fry, 2007). In aquatic systems, these carbon isotopes produce a broad and continuous range of isotopic signatures due to differing photosynthetic pathways in primary producers as well as variable rates of air-water gas exchange of carbon dioxide at the boundary layer (Emerson, 1975; Fry, 2007). Pelagic primary producers (or phytoplankton) are isotopically lighter and depleted in Carbon-13 relative to nearshore or benthic primary producers and macrophytes because phytoplankton experience less boundary layer effects due to their high ratio of surface area to volume, their dispersion and their turbulent environment (Fry, 2007). $\delta^{13}C$ has a negligible increase (<1‰) in stepwise enrichment between trophic levels, allowing consumers and primary producers to have comparable values, which assists in the estimation of consumer diets as it relates to nearshore and offshore feeding (Kelly et al., 2012). This negligible increase in carbon is also important in proper baseline selection for TP calculation, as baseline species characterize differing basal $\delta^{13}C$ and $\delta^{15}N$ values for different food webs (e.g. littoral or pelagic zones in freshwater lakes) (Post, 2002).
Both $\delta^{15}$N and $\delta^{13}$C can be used in conjunction to quantify the isotopic niche width of a species in order to better understand how different species co-exist with respect to feeding strategies while also providing further insight into food web structure. Evaluating ecological niches using stable isotopes can be valuable in quantifying variation in resource and habitat use, at both an individual and population level, allowing for a greater understanding of how top predators partition resources and habitats (Newsome et al., 2007). Niche overlap can be indicative of resource competition or an abundance of prey items and is seen through similar interspecific $\delta^{15}$N and $\delta^{13}$C values (Zalewski et al. 2014). Larger interspecific isotopic variation implies a reduced estimate of overlap in isotopic niche space and suggests diet specialisation or functional redundancy within a system (Araújo et al., 2011).

**Piscivorous Predators in a Great Lakes connecting channel**

The Laurentian Great Lakes is a highly productive series of interconnected freshwater lakes that provide diverse habitats and supports a high biodiversity of freshwater fish species (Environmental Protection Agency, 2005; Lapointe, 2014). These lakes are linked together by a series of great river systems, known as the Great Lakes Connecting Channels, that have undergone, and continue to undergo substantial ecological changes such as the introduction of aquatic invasive species (AIS), eutrophication, habitat reduction and climate change (Environmental Protection Agency, 2005). The feeding ecology of top predators in the HEC are generally understudied, and include: Walleye (*Sander vitreus*), Northern Pike (*Esox Lucius*), Muskellunge (*Esox masquinongy*), Largemouth Bass (*Micropterus salmoides*), Longnose Gar (*Lepisosteus osseus*) and Bowfin (*Amia calva*). While these predators may appear to occupy similar TPs and are often categorized into TP = 4.0, their diets exhibit a high degree of variability and are thought to not be functionally similar (Rosenfield, 2002; Krause et al., 2003).
In other freshwater systems, Walleye, Longnose Gar, and Muskellunge are believed to feed in benthopelagic regions (Bozek et al., 1999; Campbell et al., 2009), while Bowfin, Largemouth Bass and Northern Pike often feed in productive littoral habitats with extensive macrophyte growth, anoxic conditions and an abundance of aquatic invertebrates and centrarchids (Mundahl et al., 1998; Venturelli & Tonn, 2006; Hodgson et al., 2008; Corkrum, 2010). While these predators differ in prey item consumption, they also exhibit different feeding strategies; Bowfin and Longnose Gar are believed to be piscivorous generalists in other systems (Schneider, 2002; Koch et al., 2009; McGrath, 2010), while Walleye and Largemouth Bass have been known to exhibit both generalist and specialist behaviour (Keast 1979; Winemiller & Taylor, 1987; Bowlby et al., 1991). Northern Pike are considered to be opportunistic feeders, where feeding opportunities and seasonal changes in prey abundance, not prey size, are considered to be the main determinant of diet (Broughton, 2001; Harvey, 2009). Likewise, diet of Muskellunge is believed to change with respect to season, opportunistically consuming prey of higher trophic levels in the spring and lower trophic level, more abundant prey in the fall (Bozek et al., 1999).

**Study system**

The research for my MSc. project took place in the Detroit River and the southeastern basin of Lake St. Clair. The Detroit River and Lake St. Clair comprise the lower portion of the Huron-Erie Corridor (HEC) and link the Great Lakes Huron and Erie, serving as an important economical and wildlife migration route (Baustian et al., 2014; Hondorp et al., 2014). Lake St. Clair has an average depth of 3.4m, a natural maximum depth of 6.3m and a navigational shipping channel depth of 8.2m (Leach, 1991), while the Detroit River has an average depth range of 6.4-8.8m (Hondorp et al., 2014). The lower Huron-Erie corridor is a shallow and
productive connecting channel with regular seasonal changes in water temperature, but not in annual flow regime (Hondorp et al., 2014). There is also a great amount of anthropogenic shoreline modification along the Detroit River and Lake St. Clair, leading to a decrease in littoral organic detritus and vegetation (Radomski & Goeman, 2001; Lapointe, 2014). Most importantly, the system supports a wide biodiversity and a large number of top predator fish species that have been known to possess seasonal shifts in diet compared to most temperate freshwater systems, thus making it an ideal system for comparing higher trophic level predator interactions as they vary with season and site (Leach, 1991; Perga & Gerdeaux, 2005; Corkrum, 2010). Due to the relatively large amount of predator species and complex trophic relationships that exist in this freshwater system, it is likely that functional redundancy is not relevant in the trophic structure of the Huron-Erie corridor food web (Rosenfield, 2002).

**Chapters and Objectives**

The overall objective of my thesis is to contribute to our understanding of top predator fish species in the HEC, an area that has largely been neglected for food web studies and will be composed of two research chapters. The first is an examination of trophic structure through TP calculation of piscivorous predators Largemouth Bass, Longnose Gar, and Northern Pike in the lower Lake Huron-Erie Corridor. The second quantifies dietary niche widths of higher trophic level predators using stable isotopes to quantify inter-specific seasonal and spatial niche overlap and examine potential competition and habitat partitioning.

*Chapter 2 – Revisiting trophic position of the top predator guild in the Huron-Erie corridor of the Laurentian Great Lakes*
The objectives of this chapter are to quantify TPs of freshwater top predator fish species and overall food chain lengths in the lower Huron-Erie corridor. TP is calculated using stomach content analysis and stable isotopes. The use of a conventional DTDF as well as a proportionate DTDF from Hussey et al., 2014 will be used to estimate TP (Minagawa & Wada, 1984; Post, 2002); these estimates will be compared and contrasted against dietary TP estimates to assess if conventional stable isotope methods provide a reduced estimate of food chain length and trophic position of top predator species.

The hypotheses to be tested in this chapter include:

H$_1$: Top predatory fish in the HEC will exhibit a greater range in TP and overall food chain length than currently believed.

H$_2$: Scaled DTDF will provide consistently greater TP estimates than the conventional constant DTDF.

Chapter 3 – Diet, Niche Width and Overlap of Top Predators in the lower Huron-Erie corridor

The objectives of this chapter are to quantify isotopic niche width and overlap of top predatory fish species in the lower Lake Huron-Erie corridor across season and site. Isotopic niche widths of predators are estimated using both carbon and nitrogen stable isotopes (Parnell et al., 2013).

The hypotheses to be tested in this chapter include:

H$_1$: Isotopic niche widths of top predators will show a low degree of overlap.

H$_2$: Isotopic niches of predatory fish species will vary by season and site, possibly due to changing prey diversity and biomass.
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CHAPTER 2

REVISITING TROPHIC POSITION OF A PISCIVOROUS PREDATOR GUILD IN THE HURON-ERIE CORRIDOR OF THE LAURENTIAN GREAT LAKES
Introduction

Understanding the trophic position and diet of fish species in an ecosystem that continues to experience constant anthropogenic stressors is important for correctly characterizing food web structure and function, and ultimately in ecosystem management, particularly as it pertains to commercial and recreational fish stocks (Layman et al., 2007). This is particularly important for higher trophic level species, where anthropogenic driven changes in abundance or trophic interactions can facilitate trophic cascades, leading to altered food webs and ecosystem services (Layman et al., 2007). For example, the decline of Atlantic cod (*Gadus morhua*) in the northwest Atlantic Ocean caused a trophic cascade and altered trophic linkages, leading to changes in community structure as well as declines in fish stocks and commercial profit (Frank et al., 2005).

The Laurentian Great Lakes is an economically important ecosystem that supports a $7 billion annual commercial and recreational fishery predominantly focusing on higher trophic level fish species (Landsman et al., 2011). In comparison to most temperate freshwater systems, this ecosystem is defined by complex predator-prey interactions and high fish biodiversity (Crossman & Cudmore, 1998; Lapointe, 2014) and thus provides a model system for studying freshwater top predators. Moreover, the Great Lakes have long been subjected to increasing human population, urbanization, industrialization, and exploitation, including anthropogenic-mediated stressors such as toxic chemicals, e.g. organophosphate flame retardants (OPE) (Venier et al., 2014), aquatic invasive species, e.g. Round Goby (*Neogobius melanostomus*) (Jude et al., 1992), and over-harvesting of fish species, e.g. Walleye (*Sander vitreus*) (Baustian et al., 2014). The persistence of these stressors has led to and is continuing to lead to changes in ecosystem structure and function (Pikitch et al., 2004).
In the Great Lakes, there exists a variety of high trophic level fish species that are believed to stabilize trophic structure and community composition (Turshak, 2013). However, many of these predators, such as Longnose Gar (*Lepisosteus osseus*) and Northern Pike (*Esox lucius*) are understudied and little is known regarding their diet preferences and feeding strategies and how these vary over time and space. In other freshwater systems, Longnose Gar are known to be primarily piscivorous due to their needle-nose mouth morphology, yet exhibit generalist foraging tactics (McGrath, 2010), and consume smaller prey even when they attain a larger size (Haase, 1969). Northern Pike are considered to be opportunistic predators, with prey availability and seasonal changes in prey abundance considered to be the main determinants of diet rather than prey size (Beaudoin et al., 1999; Hurley, 2008). In comparison, Largemouth Bass (*Micropterus salmoides*) are relatively well studied and are known to exhibit both generalist and specialist feeding tactics depending on location, and consume a wide variety of prey, ranging from crayfish to *Cyprinidae* spp. (Keast, 1978; Winemiller & Taylor, 1987).

Trophic position (TP), a continuous measure of a consumer’s feeding habits that accounts for the consumption of prey across trophic levels (i.e. omnivory), provides a standardized ecological metric on relative diet and species interactions across ecosystems (Paine, 1988; Vander Zanden & Rasmussen, 1996). Estimates of TP have traditionally been calculated through stomach content analysis of proportional diet contributions; however this method can be subject to biases associated with misidentification of prey, rare feeding events, empty stomachs, uneven digestion rates of prey, e.g. soft-bodied vs hard-shelled, and disproportional estimates of diet based off weight and sample numbers (Hyslop, 1980). Stomach content analysis also requires large sample numbers, which can be difficult to acquire and may not be ethical, especially for rare or endangered species. As well, TP calculated from stomach content data often combines
many diverse species into a single functional group that can result in inaccurate estimates, and
oversimplify food web structure (Hussey et al., 2011). This may be the case in the Great Lakes,
where a wide range of fish species are generally assumed to feed at the same TP (Rasmussen et
al., 1990; Vander Zanden & Rasmussen, 1996; Vander Zanden et al., 1997). Determining an
accurate TP for a species or population is important for providing insights on species interactions
and energy flow, knowledge of which is necessary for an ecosystem-based approach to
monitoring and remediation of aquatic systems (Pikitch et al., 2004). It is also important to
understand if and why the TP of a species varies over space; particularly in large systems like the
Great Lakes where biodiversity and environmental characteristics are spatially heterogeneous
(Lapointe, 2014).

Over the past three decades, the use of nitrogen stable isotopes ($\delta^{15}$N) to estimate TP has
become a well-established method (Fry, 2007; Peterson & Fry, 1987). Most applications of
stable isotopes to quantify TP employ a constant diet tissue discrimination factor (DTDF), most
commonly 3.4‰, which reflects the expected change in $\delta^{15}$N between a prey and consumer and
provides a means to estimate TP of a population or species when compared to a baseline, usually
a lower TP species (Minagawa & Wada, 1984; Peterson & Fry, 1987, Vander Zanden &
Rasmussen, 1999). However, recent laboratory studies have demonstrated a strong linear
relationship where DTDF ($\Delta^{15}$N) decreases with increasing $\delta^{15}$N in food consumed (Caut et al.,
2008; Overmyer et al., 2008; Dennis et al. 2010), consequently a scaled DTDF approach to
estimating TP has been proposed to account for this inverse relationship (Hussey et al. 2014).

Additionally, stable isotopes of carbon ($\delta^{13}$C) are used to determine the sources of
primary production and ultimately the food web a consumer feeds within (Peterson & Fry, 1987).
Similar to $\delta^{15}$N, $\delta^{13}$C fractionates between trophic levels, but at a more conservative rate (0.47 ±
1.23‰ in freshwater ecosystems) and this needs to be considered when selecting an appropriate baseline species to estimate TP (Vander Zanden & Rasmussen, 2001; Post, 2002). If expected fractionation of $\delta^{13}$C between a predator and baseline is not evident, it suggests the species are feeding in different food webs, which often have different $\delta^{15}$N values, and can lead to erroneous TP estimates (Post, 2002).

The objective of this study was to quantify and examine differences in TP and ultimately trophic structure of three freshwater piscivorous predators (Longnose Gar, Largemouth Bass, and Northern Pike) across three sites in the Lake Huron-Erie Corridor in the Great Lakes. We calculated TP using stable isotopes baseline based on appropriate $\delta^{13}$C fractionation between previously estimated trophic levels of predator and baseline species. Finally, we compare and contrast TP estimates for these three freshwater predators using (i) stomach content data, (ii) a constant DTDF ($TP_{\text{Additive}}$) in a traditional additive isotope framework, and (iii) a scaled DTDF ($TP_{\text{Scaled}}$) within a narrowing isotope framework. We hypothesize that the $TP_{\text{Scaled}}$ of these species will have greater variability due to diverse feeding behaviours documented from diet data among these predator species from other systems and spatially heterogeneous prey assemblages within the HEC, suggesting more complex trophic structure in freshwater ecosystems than previously assumed.

**Methodology**

*Sample Collection*

Study species were collected at three sites in the Lake Huron-Erie corridor of the Laurentian Great Lakes; around Peche (~42.35°N, -82.93°W) and Grass Islands (42.22°N, -
83.11°W) in the Detroit River, and Mitchell’s Bay, located in the Northeastern Basin of Lake St. Clair (~42.48°N, -82.42°W) in the spring (20 April – 20 June, 2014).

Fish species were captured using trap nets, fyke nets, angling, seine nets, and a single anode boat electrofisher with a direct current (DC) of 4.0A and a pulse frequency of 30-60 Hz. All fish were euthanized with an overdose of tricaine methanesulfonate (MS-222). For each fish, morphometric measurements including total length (Longnose Gar size range: 53-75cm, Largemouth Bass: 25-42cm, Northern Pike: 50cm-70cm) and weight were taken and ~5 g of muscle tissue was sampled anterior to the dorsal fin and stored frozen until analyzed for stable isotopes. Whole stomachs were removed and preserved in 95% ethanol to prevent enzymatic degradation, and frozen until stomach content analysis (Carreon-Martinez et al., 2011).

Stomach Content Analysis and Standardized Trophic Position based on dietary proportions

Individual cumulative frequency rarefactory curves based on stomach content data were calculated for each predator at each site to determine both prey item diversity (75% and 95% confidence) within the diet of each predator to inform whether stomach sample sizes adequately described the diet of the species for accurate TP_{SCA} (dietary TP) calculation (Table 2.1) (Colwell, 2006). Curves that plateaued at or near the asymptote value were considered to adequately describe the diet. Each diet item was identified to the lowest possible taxonomic level and percentage frequency of occurrence (%F; the percent occurrence of a particular prey species across all stomachs), percentage by number (%N; the proportion of a prey species relative to all prey species) and percentage by weight (%W; the percent weight contribution of a species across total mass of all prey species) within all stomachs of a particular predator at each site were
calculated. The Index of Relative Importance (IRI) (Hyslop, 1980; Cortes, 1997) was then determined and expressed on a percent basis (%IRI) (Cortes et al., 1996), using the equation

\[ IRI = (%N \times %W) + %F \] (1)

and

\[ \%IRI_i = \frac{100 \cdot IRI_i}{\sum_{i=1}^{n} IRI_i} \] (2)

To calculate a standardized TP estimate for each species based on stomach content data, we used the following equation (3) (Cortes, 1999)

\[ TP_{SCA} = 1 + (\sum_{i=1}^{x} \%IRI_i \times TP_i) \] (3)

where previously estimated TPs of prey items (TP\(_i\)) (McLeod et al., 2015; Vander Zanden et al., 1997), as well as proportional %IRI values for each corresponding prey item (%IRI\(_i\)) and are surmised for each predator at each site. Unidentifiable material present in the stomachs of predators was not included in IRI, %IRI or TP\(_{SCA}\) calculations.

**Carbon and Nitrogen Stable Isotope Analysis**

All fish muscle tissue samples were lyophilized at -48 °C and 133 \( \times 10^3 \) mbar for 48h, ground by hand, and lipid-extracted using a 2:1 chloroform:methanol mixture (Bligh and Dryer 1959). Following lipid extraction, ~400-600 \( \mu \)g of sample per individual was weighed into tin cups. The carbon and nitrogen isotopic composition of each sample were determined using a Delta V Advantage Thermoscientific continuous flow mass spectrometer (Thermo Electron Corporation, Bremen, Germany) coupled to a 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA). Stable isotope values are reported as per mil (\( \delta \)) and were calculated using the equation:

\[ \delta X = \left( \frac{R_{sample}}{R_{standard}} - 1 \right) \times 1000 \] (4)
where X represents $^{13}$C or $^{15}$N and R is represented by $^{13}$C:$^{12}$C and $^{15}$N:$^{14}$N. Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (AIR) were used as standard reference materials for carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N), respectively. Analysis precision was assessed by examining variation in replicate tissue samples (every 10th sample was run in triplicate), all were within the acceptable ±0.2‰ standard deviation range (0.1‰ for $\delta^{13}$C and 0.1‰ for $\delta^{15}$N, n=30), and values for internal laboratory standards run after every 12 samples (NIST 1577c and internal lab standard tilapia (Oreochromus spp.) muscle (both n=221)), which were < 0.2‰ for $\delta^{13}$C and < 0.2‰ for $\delta^{15}$N. Accuracy was assessed by certified NIST standards analyzed during the same time as sample; $\delta^{15}$N values were within 0.1 ‰ (NIST 8573), -0.4‰ (NIST 8548), and <0.01‰ (NIST 8549), and for $\delta^{13}$C within 0.2‰ (NIST 8542) and -0.1‰ (NIST 8573) of certified values.

**Trophic Position estimates using Stable Isotopes**

Trophic position was first calculated using a constant, additive discrimination framework and the commonly used DTDF value of 3.4‰ (Minagawa & Wada, 1984; Vander Zanden et al., 1997; Cabana & Rasmussen, 1996);

$$TP_{additive} = \frac{\delta^{15}N_{predator} - \delta^{15}N_{baseline}}{3.4} + TP_{baseline} \quad (5)$$

where $TP_{baseline}$ represents literature estimates of baseline species trophic position (Keast & Walsh, 1968; Scott & Crossman, 1973; Marsh & Douglas, 1997; Vander Zanden et al., 1997; Froese & Pauly, 2000; McLeod et al., 2015)

Following the more recent scaled, narrowing discrimination framework, that accounts for varying DTDFs through assuming a proportional decrease in $\Delta^{15}$N between consumer and prey with increasing consumer $\delta^{15}$N (Hussey et al. 2014), TP was calculated as follows;

$$TP_{scaled} = \frac{\log(\delta^{15}N_{lim} - \delta^{15}N_{baseline}) - \log(\delta^{15}N_{lim} - \delta^{15}N_{TP})}{k} + TP_{baseline} \quad (6)$$
where $\delta^{15}N_{lim}$ represents the rate at which $^{15}$N and $^{14}$N uptake equals the rate of $^{15}$N and $^{14}$N excretion respectively (resulting in no net change in $\delta^{15}$N between consumer and prey, $\Delta^{15}$N = 0), and $k$ represents the rate at which $\delta^{15}N_{TP}$ approaches $\delta^{15}N_{lim}$ per TP increment. Both $\delta^{15}N_{lim}$ and $k$ were determined through meta-analysis of literature values reported for fish and were 21.93 and 0.14 respectively (Hussey et al., 2014).

**Baseline-Consumer Carbon Ratio**

For both equations (5) and (6), we used $\delta^{15}$N values of different $^{1^0}$ (trophic level ~ 2) and $^{2^0}$ (trophic level ~ 3) baseline species that reflected expected $\delta^{13}$C fractionation between presumed trophic levels of consumer and baseline (0.47 ± 1.23‰ per trophic level in freshwater systems) (Table 2.2). To determine the $\delta^{13}$C fractionation relationship between each predator and baseline species, a baseline-consumer Carbon ratio was calculated using the following equation:

$$Baseline - Consumer Carbon Ratio = \frac{\Delta\delta^{13}C_{consumer-baseline}}{\Delta LitTP_{consumer-baseline}} \times 0.47\%\text{O}$$

where $\Delta\delta^{13}C_{consumer-baseline}$ represents the difference between mean consumer and baseline $\delta^{13}$C values, and $\Delta LitTP_{consumer-baseline}$ is the difference between consumer and baseline literature TP values. The $\Delta\delta^{13}C_{consumer-baseline}$ is divided by 0.47‰ to obtain a ratio. Baseline species that result in a baseline-consumer Carbon ratio closer to 1 indicate that both consumer and baseline species feed within the same food web and are considered appropriate for use in predator TP estimation (Table 2.2).

**Data Analysis**

Trophic position estimates calculated using both a constant DTDF and a scaled DTDF were compared using Student’s paired t-test for each species separately. To assess the potential
influence of selected baseline species on TP estimation, individual ANOVAs (dependent factor: TP, independent factor: baseline species) were used to examine whether there were significant differences in TP when using different baselines using either a constant or scaled DTDF separately; an example of this sensitivity analysis is shown for Largemouth Bass in Table 2.3.

Because estimates of TP using the scaled approach did not differ among baseline species at each site following the above analysis (see Results), these values were used to examine spatial variation in TP across the three sampling sites (Peche Island, Grass Island and Mitchell’s Bay). Individual one-way analyses of covariance (ANCOVAs) were used for each species (dependent factor: TP; covariates: standard length, sex; independent factor: site) and Tukey’s post-hoc comparisons were used to compare difference in TP of each predator among sites. Residuals were tested for normality and homogeneity of variance using Shapiro-Wilks Test and Levene’s Test. Separate linear regression models were performed for each predator at each site to determine the correlation strength between TP and covariates (standard length, sex). All statistical analyses were performed using R (Version 0.98.1083, R Core Team, 2014) and statistical significance was set at α = 0.05.

Results

Diet from Stomach Contents

Of the 182 Longnose Gar, Largemouth Bass, and Northern Pike stomachs examined, 50% (n=92, Largemouth Bass, n=50; Longnose Gar, n=34; Northern Pike, n=8) contained identifiable prey items across the three sites. Stomach content data did not meet 95% dietary diversity based on rarefactory curves, but were well represented using 75% dietary diversity criteria (Table 2.1). Stomach contents of Northern Pike at Grass Island were not sufficient to
quantify 75% dietary diversity, and thus were not sufficient to determine TP_{SCA} (Table 2.1). Diets of Largemouth Bass, Longnose Gar, and Northern Pike varied interspecifically across all 3 sites; Longnose Gar consumed mainly insectivores such as Spottail Shiner (Notropis hudsonius) and zoobenthivores such as Spotfin Shiner (Cyprinella spiloptera) across sites, while Northern Pike mainly consumed piscivores and omnivores such as Yellow Perch (Perca flavescens) and Bluegill (Lepomis machrochirus). By %IRI, Largemouth Bass diet was not consistent across all 3 sites; crayfish (Humilis spp.) were major contributors to Largemouth Bass diet at both Grass Island and Peche Island, while Spottail Shiners were consumed at Grass Island and Mitchell’s Bay (Table 2.4). Longnose Gar stomach contents consisted of mainly Cyprinidae spp. across all 3 sites; Spottail Shiners were consumed at both Peche Island and Mitchell’s Bay, while Striped Shiners and Spotfin Shiners were consumed at Grass Island (Table 2.5). Bluegill were also a major contributor to Longnose Gar diet at both Grass Island and Mitchell’s Bay (Table 2.5). Northern Pike stomach contents were not consistent across all 3 sites; major contributors to Northern Pike diet at Peche Island included Common Carp (Cyprinus carpio), Pumpkinseed (Lepomis gibbosus), and Silver Bass (Morone chrysops) (Table 2.6). Northern Pike consumed mostly Bluegill and Round Goby (Neogobius melanostomus) at Grass Island, and consumed mainly Yellow Perch at both Grass Island and Mitchell’s Bay (Table 2.7).

**Trophic position based from diet proportions**

Reflecting stomach content data, TP_{SCA} estimates varied across all sites for both Longnose Gar and Largemouth Bass (Longnose Gar TP range: 3.3-4.0, Largemouth Bass TP range: 3.7-4.2), while TP of Northern Pike was similar between two sites, Peche Island and Grass Island (TP = 4.2) (Table 2.3).

**Trophic position based on an additive and scaled stable isotope framework**
TP_{Scaled} values did not differ, but there were significant differences for TP_{Additive} (ANOVA, P < 0.05), among the selected baselines, either ~TL=2 or TL=3 (ANOVA, P > 0.05), (Table 2.3). All TP ranges were greater when using a scaled DTDF as opposed to a constant DTDF (Figure 2.1). Using a scaled DTDF, Largemouth Bass had the greatest interspecific and intraspecific TP range at Mitchell’s Bay (TP range = 1.7 TLs) (Figure 2.1a), while Longnose Gar had the largest interspecific TP range at Peche Island (TP range = 2.3 TLs) (Figure 2.1b) and Grass Island (TP range = 1.5 TLs). TP estimates using the scaled approach were moderately higher and had a larger variation in range than those using a constant DTDF for most species and sites (Largemouth Bass: P <0.02 for all 3 sites, Northern Pike: P < 0.02 for all 3 sites) (Figure 2.2, Table 2.3); the only exception was Longnose Gar at Peche Island (TP_{Scaled} = 5.1, TP_{Additive} = 5.0; P = 0.38).

Species specific TP estimates

Mean TP estimates of all species were found to be significantly different across site (P < 0.02 for all species); Largemouth Bass TP estimates at Mitchell’s Bay and Peche Island did not differ (Tukey’s HSD, P = 0.61) but were significantly greater than Grass Island (Tukey’s HSD, Mitchell’s Bay-Grass Island, P = 0.01; Peche Island-Grass Island, P < 0.001). Longnose Gar TP values at Peche Island were significantly higher than Grass Island (Tukey’s HSD, P < 0.001) and Mitchell’s Bay (P <0.001), but no significant differences between Peche Island and Grass Island (P = 0.12). Northern Pike TP estimates at Mitchell’s Bay were significantly greater than Grass Island (Tukey’s HSD, P = 0.03), but Peche Island and Grass Island (P = 0.12) or Peche Island and Mitchell’s Bay (P = 0.45) did not differ. The interaction effect of total length and sex did not influence TP for Largemouth Bass, Longnose Gar, or Northern Pike (covariate: total length, P > 0.06 for all species, covariate: sex, P > 0.1 for all species). Linear regression showed no
correlation between TP estimates and total length at any site for Largemouth Bass, Longnose Gar, or Northern Pike (P > 0.06 for all species).

**Discussion**

Trophic position estimates are important for understanding trophic structure and energy-flow within food webs. Trophic position of three predatory fish species from the lower Great Lakes estimated using stable isotopes were greater than their generally perceived trophic level of four (Krause et al., 2003; Mason et al., 2002), suggesting food chain lengths in the Great Lakes may be longer than previously estimated. TPs also varied between the species and with site, although not sex or body length, suggesting greater trophic complexity within the upper trophic level guild of the Great Lakes. Importantly, all three predators showed larger intra- and inter-species ranges in TP estimates, with individuals feeding over 1 to 1.5 trophic levels. Species and site differences in TP were moderately higher when estimated using a scaled rather than a constant DTDF, while the scaled DTDF approach was more robust to different baseline species. These results refine our understanding of trophic roles of predatory fish in the Great Lakes and should be considered in food web modeling and management decisions.

Using the scaled DTDF approach, Largemouth Bass in the Huron-Erie corridor fed at a TP between 4.1 and 4.6, varying across the sites. Literature estimates of Largemouth Bass TP are in the lower half of this range (McLeod et al., 2015; Vander Zanden et al., 1997). A TP of > 4.0 seems likely for Largemouth Bass, given a predominantly fish diet and assuming most fish in the Great Lakes are at least TP = 3.0. For a fish to be at TP < 3.0, it would have to have a diet that is primarily primary production (i.e., algae) and the prey fish found in the Largemouth Bass were all > TP 2.7. As well, some species found in the stomachs were high trophic position species,
such as Northern Pike, although these were smaller juveniles. This is consistent with O’Brien (1979), who stated that due to large gape size and unique mouth morphology, Largemouth Bass are able to consume a wide variety of primary and secondary consumers across size ranges. The variation in TP estimates across sites as well as the lack of interaction effect with total body length suggests Largemouth Bass are generalists and are plastic in their diet preferences; however, this may also be due to individual specialization within the population. The feeding strategies of this species has been described as specialists (Keast, 1979), generalists (Winemiller & Taylor, 1987), and opportunists (Hodgson & Kitchell, 1987) across various sites, providing further reason to believe that foraging plasticity and TP values of Largemouth Bass are dependent on differences in ecosystems, and are likely due to prey availability (Hodgson et al., 2008).

Longnose Gar TP$_{Scaled}$ values in the Huron-Erie corridor were between 4.1 and 5.1, varying across sites, which differed from recent estimates for this species in this region (McLeod et al., 2015). Prey found in Longnose Gar stomachs had TP ≈3.0, however the majority of stomachs were empty at Peche Island, and possessed unidentifiable material, or were partially digested, thus not providing an accurate estimation of Longnose Gar diet and ultimately TP$_{SCA}$. Spatial variation in diet has been noted previously, where Longnose Gar have been characterized as opportunistic feeders, feeding in demersal, nearshore, and benthopelagic habitats in other systems, each possessing different species assemblages (McGrath et al., 2013; Robertson et al., 2008; Tyler et al., 1994). Additionally, the range in TP$_{Scaled}$ values suggests Longnose Gar feed on prey across multiple trophic levels; which suggests opportunistic or generalist feeding behaviour in the Great Lakes. Our findings were not consistent with McGrath et al. (2013), who found that prey type differed and prey size increased with increasing body length in Longnose
Gar (TL ranges: <60cm, 60-80cm, >80cm). Other studies have found that Longnose Gar consumed a variety of lower TL consumers such as *Cyprinidae* spp., *Clupeidae* spp., and *Fundulidae* spp. (Haase, 1969; McGrath, 2010).

Northern Pike TP_{Scaled} were more similar at all 3 sites (4.0-4.4) than either Largemouth Bass or Longnose Gar, suggesting that diet of this species is more consistent across sites in the Huron-Erie Corridor. Literature has reported conflicting results for Northern Pike; some studies show this species to feed primarily on Yellow Perch (*Perca flavescens*) in small lakes (Venturelli & Tonn, 2005), but others report a wide selection in prey consumption across different freshwater systems (Diana, 1979; Inskip, 1982); our stomach contents showed Northern Pike to consume many prey items, such as *Cyprinidae*, *Centrarchidae*, and invertebrates. Prey availability has been observed to be a factor driving Northern Pike feeding habits, suggesting an opportunistic feeding strategy, and may switch to diets of less energetically optimal prey items such as invertebrates, when other prey species are in low abundance or interspecific competition is high (Chapman & Mackay, 1990; Diana, 1979; Hurley, 2008; Venturelli & Tonn, 2005), including cannibalism when food density is low (Westers & Stickney, 1993). However, total length was found to not be a significant covariate of Northern Pike TP at any site, suggesting consumption of similar trophic level prey across body size and site.

Interspecific TP comparisons showed Longnose Gar had the highest TPs at Peche Island and Grass Island (TP range: 4.7-5.1), while Northern Pike had the lowest TPs at these sites (TP range: 4.0-4.2); these differences across species may be attributed to differences in foraging strategies, since Longnose Gar are predominantly piscivorous and consume higher trophic level (higher δ^{15}N values) prey such as *Cyprinidae* spp., *Fundulidae* spp., and *Clupeidae* spp. (Haase, 1969; McGrath, 2010). However, dietary plasticity of Largemouth Bass as well as opportunistic
feeding strategies of Northern Pike may result in lower TP estimates due to consumption of lower trophic level invertebrates such as *Humilis* spp. and *Chironomidae* spp. (Winemiller & Taylor, 1987). Unlike Largemouth Bass and Northern Pike, Longnose Gar are not invertivores and the diet of mainly fish likely explains the higher TP values (Hurley, 2008; McGrath et al., 2013). Largemouth Bass and Northern Pike $\delta^{13}C$ values were more representative of littoral feeding, while Longnose Gar had lower $\delta^{13}C$ values reminiscent of offshore feeding. The lower $\delta^{13}C$ values in Longnose Gar may suggest that there are fewer opportunities for invertivory in offshore areas, thus resulting in higher Longnose Gar TP values due to consumption of higher TL fish species.

With the exception of Longnose Gar at Peche Island, scaled and constant DTDF methods produced different estimates of TP for all three fish species. More specifically, TP calculated using the scaled approach were higher and showed a greater range between species than estimates using the constant DTDF; similar results were found at higher trophic levels in a comparison of scaled and constant DTDFs in two marine ecosystems (Hussey et al. 2014). The lack of correlation between TP estimates and body length suggests consumption of prey from multiple trophic levels, resulting in varied TP values (Hussey et al., 2014). Additionally, the use of muscle tissue provided a long-term integrated assessment of diet, and suggests that high TP values for predators are driven by consistent consumption of higher trophic level prey, however this may be driven by individual specialization within a population or discrete habitat use that contain different prey assemblages, which could further explain large ranges in TP values (Fry, 2007; Newsome et al., 2009). Given the scaled approach produced TP estimates that did not differ when different baseline species at different trophic positions were used but the constant DTDF did, suggests the scaled approach is more robust to variation in the TP and $\delta^{15}N$ values of
the baseline species. This consistency in $T_{P, \text{Scaled}}$ estimates is important to consider in field studies using stable isotopes, where it is often difficult to standardize baseline species across ecosystems and the geographic distribution of species (Vander Zanden & Rasmussen, 1999) as well as seasonal variation in $\delta^{13}C$ and $\delta^{15}N$ values of both consumers and baselines that can confound absolute TP estimates (Perga & Gerdeaux, 2005; Post, 2002; Woodland et al., 2012).

Using the scaled approach showed greater differences and range in TP values between the predator species than previously suggested. This decompression of TPs and longer food chain lengths, which has been observed in marine systems using the same stable isotope assessment (Hussey et al. 2014), provides evidence of less functional redundancy in the predators of the Great Lakes, which is also supported by variation in predator $\delta^{13}C$ values which may be attributed to discrete habitat utilization. Additionally, there was no consistency to which method, scaled or additive, was more similar to literature based or dietary TP estimates; most literature estimates of TP are based on stomach contents. Adequate stomachs were sampled to show 75% dietary diversity and thus, the majority of consumed prey items. The lack of stomach content data can lead to erroneous TP estimates due to omission or misidentification of prey items, and thus is more prone to error in comparing more robust estimations of TP using stable isotopes.

The use of an appropriate baseline to determine trophic position using stable isotopes is critical as it pertains to $\delta^{13}C$ in ecosystems. Species that have different $\delta^{13}C$ values fed in different habitats, habitats that can have very different $\delta^{15}N$ values that confound TP estimates. In most cases, we were able to find a suitable baseline species that had appropriate $\delta^{13}C$ values that reflected $\delta^{13}C$ fractionation of 0.47‰ between trophic levels (Vander Zanden & Rasmussen, 2001; Post, 2002; McCutchan et al., 2003; Caut et al., 2009). The use of different primary and secondary consumers as baseline species (in comparison to primary producers) decreased the
likelihood of seasonal variation in $\delta^{13}$C due to slow isotopic turnover rates in white muscle tissue of these species, ultimately providing TP estimates that were more comparable to predator muscle tissue over a similar time period (Caut et al., 2009; Buchheister & Latour, 2008). Furthermore, in a system with high biodiversity, it was important to consider multiple baseline species that were not all taxonomically related since we aimed to quantify absolute trophic positions rather than shifts in diet due to seasonal changes (Post, 2002). However, the use of Zebra mussels (Dreissena polymorpha) as an isotopic baseline to estimate Longnose Gar TP at Peche Island was not reflective of accurate $\delta^{13}$C fractionation between trophic levels likely due to seasonal fluctuations in dissolved aquatic nitrates (Gustafson et al., 2007).

Larger variation in TP estimates using a scaled DTDF suggest compression and oversimplification of higher trophic level predators when using a constant DTDF, which typically derive similar TPs of approximately 4.0 for these piscivorous predators. This compression of TPs and food chain length, which has been observed in marine systems using a constant DTDF or stomach contents (Hussey et al. 2014), suggests interspecific competition, and functional redundancy in top predators of the Great Lakes is significant; although there is some habitat separation based on $\delta^{13}$C values which may be due to individual specialization or discrete intra-specific habitat use. This partitioning of resources and lack of redundancy indicated in this study through $TP_{Scaled}$ estimates has implications for understanding ecosystem dynamics and management decisions. More specifically, the need for accurate TPs can influence fisheries management decisions, the monitoring of contaminants, and setting human consumption guidelines (Link, 2002; Burkhard et al., 2013). With the possibility for continuing environmental regime shifts and climate change, accurate TP estimates need to be sensitive to change (seasonal,
spatial) and must incorporate uncertainty in order to make inferences about ecosystems as it relates to changing species assemblages and overfishing (Link, 2002).

Acknowledgments

We thank C. Lee, A. Weidl, J.Nix, and J. Mumby for assistance in the field, A.J. Hussey for guidance on stable isotope analysis, and K. Wellband and D. Yurkowski for help with R Studio. This research was funded by an NSERC Discovery Grant to A.T.F. and the Alex S. Davidson Great Lakes Stewardship to B.N.
References


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McGrath, P. E. 2010. The Life History of Longnose Gar (Lepisosteus Osseus), an Apex Predator in the Tidal Waters of Virginia. Williamsburg, VA: College of William and Mary, School of Marine Science.


### Table 2.1
Stomach content sample size needed to provide 75% and 95% measures of diversity based on cumulative frequency rarefactory curves of stomach contents for each species and site (Colwell, 2006). N/A was assigned to species that had a linear relationship between number of stomachs and diversity, and did not plateau. Species that were denoted with (*) represent adequate stomach contents to estimate dietary diversity (at either 75% or 95% diversity), and is determined by the presence and frequency of prey items.

<table>
<thead>
<tr>
<th>Species</th>
<th>n (# of stomachs)</th>
<th>Diversity asymptote value</th>
<th>Diversity value (75% diversity)</th>
<th>n (# of stomachs for 75% diversity)</th>
<th>Diversity value (95% diversity)</th>
<th>n (# of stomachs for 95% diversity)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Peche Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largemouth Bass</td>
<td>35</td>
<td>9.8</td>
<td>5.7</td>
<td>21*</td>
<td>6.2</td>
<td>45</td>
</tr>
<tr>
<td>Longnose Gar</td>
<td>6</td>
<td>5.2</td>
<td>3.9</td>
<td>11</td>
<td>4.7</td>
<td>24</td>
</tr>
<tr>
<td>Northern Pike</td>
<td>12</td>
<td>6.9</td>
<td>2.7</td>
<td>11*</td>
<td>2.8</td>
<td>23</td>
</tr>
<tr>
<td><strong>Grass Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largemouth Bass</td>
<td>30</td>
<td>6.2</td>
<td>4.6</td>
<td>11*</td>
<td>5.9</td>
<td>23*</td>
</tr>
<tr>
<td>Longnose Gar</td>
<td>31</td>
<td>8.1</td>
<td>6.1</td>
<td>12*</td>
<td>7.7</td>
<td>27*</td>
</tr>
<tr>
<td>Northern Pike</td>
<td>16</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td><strong>Mitchell’s Bay</strong></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largemouth Bass</td>
<td>15</td>
<td>5.4</td>
<td>4.1</td>
<td>13*</td>
<td>5.2</td>
<td>27</td>
</tr>
<tr>
<td>Longnose Gar</td>
<td>30</td>
<td>12.0</td>
<td>9.0</td>
<td>19*</td>
<td>11.4</td>
<td>41</td>
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<tr>
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<td>7</td>
<td>2.8</td>
<td>2.1</td>
<td>3*</td>
<td>2.7</td>
<td>8</td>
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</tbody>
</table>
Table 2.2 Stable isotopes (mean ± 1 SE) and estimated trophic position (TP\textsubscript{Scaled}) of predators and baseline species used to calculate trophic position for each high trophic level species at each site. Baseline species were selected based on a stepwise increase of 0.47‰ ± 1.23 per trophic level (Vander Zanden and Rasmussen, 2001; Post, 2002; McCutchan et al., 2003; Caut et al., 2009).

<table>
<thead>
<tr>
<th>Predator species</th>
<th>n</th>
<th>Lit TP\textsubscript{SCA}</th>
<th>δ\textsuperscript{13}C</th>
<th>δ\textsuperscript{15}N</th>
<th>Baseline</th>
<th>n</th>
<th>Lit Base TP\textsubscript{SCA}</th>
<th>δ\textsuperscript{13}C</th>
<th>δ\textsuperscript{15}N</th>
<th>Baseline-consumer Carbon ratio\textsuperscript{a}</th>
<th>TP\textsubscript{Scaled}</th>
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</thead>
<tbody>
<tr>
<td><strong>Peche Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largemouth Bass (Micropterus salmoides)</td>
<td>31</td>
<td>4.2\textsuperscript{1}</td>
<td>-16.9 ±0.3</td>
<td>14.4 ±0.2</td>
<td>Yellow bullhead (Ameirius natalis)</td>
<td>5</td>
<td>3.3\textsuperscript{2,3}</td>
<td>-17.4 ±0.4</td>
<td>10.6 ±0.6</td>
<td>1.0</td>
<td>4.6</td>
</tr>
<tr>
<td>Longnose Gar (Lepisosteus osseus)</td>
<td>6</td>
<td>4.0\textsuperscript{4}</td>
<td>-19.4 ±0.6</td>
<td>15.5 ±0.5</td>
<td>Zebra mussel (Dreissenia polymorpha)</td>
<td>1</td>
<td>2.0\textsuperscript{1}</td>
<td>-22.7 ±0.2</td>
<td>5.5 ±0.10</td>
<td>3.5</td>
<td>5.1</td>
</tr>
<tr>
<td>Northern Pike (Esox lucius)</td>
<td>18</td>
<td>4.2\textsuperscript{1,4}</td>
<td>-17.1 ±0.2</td>
<td>14.0 ±0.2</td>
<td>Shorthead Redhorse</td>
<td>5</td>
<td>3.1\textsuperscript{3,5}</td>
<td>-17.9 ±0.2</td>
<td>10.7 ±0.3</td>
<td>0.97</td>
<td>4.2</td>
</tr>
<tr>
<td><strong>Grass Island</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Largemouth Bass</td>
<td>27</td>
<td>4.2</td>
<td>-16.2 ±0.3</td>
<td>14.8 ±0.2</td>
<td>Rock Bass (Ambloplites rupestris)</td>
<td>6</td>
<td>3.4\textsuperscript{4}</td>
<td>-16.6 ±1.1</td>
<td>13.0 ±0.3</td>
<td>1.0</td>
<td>4.1</td>
</tr>
<tr>
<td>Longnose Gar</td>
<td>26</td>
<td>4.0</td>
<td>-18.3 ±0.3</td>
<td>15.2 ±0.2</td>
<td>Emerald Shiner (Notropis atherinoides)</td>
<td>8</td>
<td>2.9\textsuperscript{4}</td>
<td>-18.7 ±0.7</td>
<td>10.0 ±0.3</td>
<td>0.77</td>
<td>4.7</td>
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<td>Northern Pike</td>
<td>10</td>
<td>4.2</td>
<td>-16.6 ±0.4</td>
<td>14.8 ±0.1</td>
<td>Pumpkinseed</td>
<td>5</td>
<td>3.3\textsuperscript{3,6}</td>
<td>-17.3 ±1.4</td>
<td>13.0 ±0.5</td>
<td>1.65</td>
<td>4.0</td>
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<tr>
<td><strong>Mitchell's Bay</strong></td>
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<tr>
<td>Largemouth Bass</td>
<td>12</td>
<td>4.2</td>
<td>-16.8 ±0.7</td>
<td>15.4 ±0.3</td>
<td>Pumpkinseed</td>
<td>6</td>
<td>3.3</td>
<td>-17.4 ±0.5</td>
<td>12.7 ±0.4</td>
<td>1.42</td>
<td>4.4</td>
</tr>
<tr>
<td>Species</td>
<td>Sample Size</td>
<td>Mean ± SD</td>
<td>Mean ± SD</td>
<td>Δ(^{13})C_(consumer - baseline)</td>
<td>ΔLitTP_(consumer - baseline)</td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>Longnose Gar</td>
<td>27</td>
<td>4.0 ± 0.3</td>
<td>16.2 ± 0.2</td>
<td>-18.6 ± 0.3</td>
<td>16.2 ± 0.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bluegill (Lepomis machrochirus)</td>
<td>5</td>
<td>3.2 ± 0.7</td>
<td>13.6 ± 0.3</td>
<td>-18.6 ± 0.7</td>
<td>13.6 ± 0.3</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Northern Pike</td>
<td>7</td>
<td>4.2 ± 0.3</td>
<td>15.4 ± 0.2</td>
<td>-16.9 ± 0.3</td>
<td>15.4 ± 0.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td>6</td>
<td>3.3 ± 0.5</td>
<td>12.7 ± 0.4</td>
<td>-17.4 ± 0.5</td>
<td>12.7 ± 0.4</td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
</tbody>
</table>

\(^a\)Baseline-consumer Carbon ratio - 

\[ \frac{\Delta^{13}C_{\text{consumer - baseline}}}{0.47\%} = \frac{\Delta\text{LitTP}_{\text{consumer - baseline}}}{\Delta^{13}C_{\text{consumer - baseline}}} \]

1. Vander Zanden et al., 1997
3. Froese & Pauly, 2000
4. McLeod et al., 2015
5. Scott & Crossman, 1973
Table 2.3 Stable isotopes (mean ± 1 SE) and trophic position (mean ± SD) estimates of Largemouth Bass (*Micropterus salmoides*) using different baseline species at Peche Island, Grass Island, and Mitchell’s Bay. ANOVAs were used to determine whether the use of different baseline species showed significant intraspecific differences in trophic position using either a trophic position with a narrowing DTDF (TP\textsubscript{Scaled}) or a constant DTDF (TP\textsubscript{Additive}), significant differences are denoted with (*).

<table>
<thead>
<tr>
<th>Baseline</th>
<th>n</th>
<th>δ\textsuperscript{13}C (±SE)</th>
<th>δ\textsuperscript{15}N (±SE)</th>
<th>Lit TP\textsubscript{SCA}</th>
<th>TP\textsubscript{Scaled} ± SD</th>
<th>P</th>
<th>TP\textsubscript{Additive} ± SD</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Peche Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow bullhead (<em>Ameirius natalis</em>)</td>
<td>5</td>
<td>-17.4 ± 0.4</td>
<td>10.6 ± 0.6</td>
<td>3.3\textsuperscript{1,2}</td>
<td>4.6 ± 0.4</td>
<td>4.4 ± 0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shorthead Redhorse (<em>Moxostoma macrolepidotum</em>)</td>
<td>5</td>
<td>-17.9 ± 0.2</td>
<td>10.7 ± 0.3</td>
<td>3.1\textsuperscript{1,2,3}</td>
<td>4.4 ± 0.3</td>
<td>0.09</td>
<td>4.2 ± 0.3</td>
<td>&lt;0.01*</td>
</tr>
<tr>
<td>Chironomid larvae</td>
<td>8</td>
<td>-17.4 ± 0.3</td>
<td>7.2 ± 0.1</td>
<td>2.3\textsuperscript{4}</td>
<td>4.4 ± 0.4</td>
<td>4.4 ± 0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spottail Shiner (<em>Notropis hudsonius</em>)</td>
<td>8</td>
<td>-18.4 ± 0.7</td>
<td>10.2 ± 0.4</td>
<td>2.7\textsuperscript{4}</td>
<td>4.3 ± 0.4</td>
<td>4.1 ± 0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Grass Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock Bass (<em>Ambloplites rupestris</em>)</td>
<td>6</td>
<td>-16.6 ± 1.1</td>
<td>13.0 ± 0.3</td>
<td>3.4\textsuperscript{4}</td>
<td>4.1 ± 0.3</td>
<td>3.9 ± 0.2</td>
<td></td>
<td>0.04*</td>
</tr>
<tr>
<td>Pumpkinseed (<em>Lepomis gibbosus</em>)</td>
<td>5</td>
<td>-17.3 ± 1.4</td>
<td>13.0 ± 0.5</td>
<td>3.3\textsuperscript{2,4}</td>
<td>4.0 ± 0.3</td>
<td>3.8 ± 0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spottail Shiner</td>
<td>10</td>
<td>-15.3 ± 0.1</td>
<td>10.7 ± 0.2</td>
<td>2.7\textsuperscript{4}</td>
<td>4.1 ± 0.3</td>
<td>3.9 ± 0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Mitchell’s Bay</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td>6</td>
<td>-17.4 ± 0.5</td>
<td>12.7 ± 0.4</td>
<td>3.3\textsuperscript{2,3,5}</td>
<td>4.4 ± 0.4</td>
<td>4.1 ± 0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Yellow Perch (<em>Perca flavescens</em>)</td>
<td>11</td>
<td>-17.8 ± 0.2</td>
<td>13.2 ± 0.2</td>
<td>3.7\textsuperscript{6}</td>
<td>4.6 ± 0.4</td>
<td>4.3 ± 0.3</td>
<td></td>
<td>0.02*</td>
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<tr>
<td>Zebra mussel (<em>Dreissena polymorpha</em>)</td>
<td>10</td>
<td>-27.6 ± 0.4</td>
<td>8.2 ± 0.2</td>
<td>2.2\textsuperscript{6}</td>
<td>4.6 ± 0.4</td>
<td>4.3 ± 0.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Marsh & Douglas, 1997  
2Froese & Pauly, 2000  
3Scott & Crossman, 1973  
4McLeod et al., 2015
5Keast & Walsh, 1968
6Vander Zanden et al., 1997
Table 2.4 Stomach content analysis of Largemouth Bass (*Micropterus salmoides*) across three sampling sites. Prey number (%N), prey frequency (%F), and prey weight (%W) were all used to calculate an Index of Relative Importance (%IRI) (see methods for details). The three largest contributors to consumer diet were highlighted for each site, based on %IRI values.

<table>
<thead>
<tr>
<th>Species</th>
<th>Trophic Guild</th>
<th>Literature TP</th>
<th>Grass Island (n=8)</th>
<th>Peche Island (n=25)</th>
<th>Mitchell's Bay (n=13)</th>
<th>%N</th>
<th>%F</th>
<th>%W</th>
<th>%IRI</th>
<th>%N</th>
<th>%F</th>
<th>%W</th>
<th>%IRI</th>
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<tr>
<td>Invertebrates</td>
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<td></td>
<td>2.5[^1]</td>
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<td>28.6</td>
<td>13.8</td>
<td>4.1</td>
<td>18.4</td>
<td>28.6</td>
<td>20.0</td>
<td>5.6</td>
<td>25.8</td>
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<tr>
<td>Spottail Shiner</td>
<td>Omnivorous zoobenthos</td>
<td>2.7[^4]</td>
<td>8.1</td>
<td>5.9</td>
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<td>2.9</td>
<td>7.1</td>
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<td>3.2</td>
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<tr>
<td>(Notropis hudsonius)</td>
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<td></td>
<td>2.7[^4]</td>
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<td>20.0</td>
<td>23.5</td>
<td>38.3</td>
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<tr>
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<td>2.5[^1]</td>
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<td>0</td>
<td>9.5</td>
<td>6.9</td>
<td>1.8</td>
<td>3.2</td>
<td>21.2</td>
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<td>22.2</td>
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<tr>
<td>(Luxilus chrysocephalus)</td>
<td>Insectivores[^2,3]</td>
<td></td>
<td>2.9[^4]</td>
<td>2.7</td>
<td>2.9</td>
<td>1.8</td>
<td>1.2</td>
<td>2.4</td>
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<tr>
<td>Emerald Shiner</td>
<td></td>
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<td>2.5[^1]</td>
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<td>6.1</td>
<td>6.7</td>
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<td>(Notropis atherinoides)</td>
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<td>3.4</td>
<td>1.9</td>
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<td>2.9</td>
<td>19.6</td>
<td>32.1</td>
<td>6.1</td>
<td>13.3</td>
<td>14.8</td>
<td>10.5</td>
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<tr>
<td>(Labidesthes sicculus)</td>
<td>Zoobenthivores[^2]</td>
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<td>10.3</td>
<td>1.8</td>
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<td>Crayfish</td>
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<td>3.0[^1]</td>
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<td>20.4</td>
<td>59.8</td>
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<td>(Humilis spp.)</td>
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<td>13.3</td>
<td>14.8</td>
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<td>6.9</td>
<td>2.4</td>
<td>0.7</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(Neogobius melanostomus)</td>
<td>Omnivore[^3]</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Yellow Perch</td>
<td></td>
<td></td>
<td>4.2[^1,4]</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2.4</td>
<td>3.4</td>
<td>9.1</td>
<td>1.6</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(Perca flavescens)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Northern Pike (juvenile)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>(Esox lucius)</td>
<td>Piscivores[^2]</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

[^1]: Grass Island (n=8)
[^2]: Insectivores
[^3]: Omnivore
[^4]: Peche Island (n=25)
[^5]: Mitchell's Bay (n=13)
[^6]: Brook Silverside (Labidesthes sicculus)
[^7]: Black Bullead (Ameiurus melas)
[^8]: Round Goby (Neogobius melanostomus)
\( a \text{%N} = \text{Determined as the proportion of a particular prey species relative to all prey species.} \\
\text{b}\text{%F} = \text{Determined as the percent occurrence of a particular prey species across all stomachs.} \\
\text{c}\text{%W} = \text{Determined as the percent weight contribution of a species across total mass of all prey species within all stomachs.} \\
\text{d}\text{%IRI} = \text{Percent Index of Relative Importance is determined through the contribution of %N, %F, and %W (see methods for details).} \\
\text{1} \text{Vander Zanden et al., 1997} \\
\text{2} \text{Uzarski et al., 2005} \\
\text{3} \text{Bhagat et al., 2007} \\
\text{4} \text{McLeod et al., 2015} \\
\text{5} \text{Keast, 1968} \\
\text{6} \text{Keast, 1985} \\
\text{7} \text{Turner, 1966} \\
\text{8} \text{Brush et al., 2012}
Table 2.5 Stomach content analysis of Longnose Gar (*Lepisosteus osseus*) across three sampling sites. Prey number (%N), prey frequency (%F), and prey weight (%W) were all used to calculate an Index of Relative Importance (%IRI) (see methods for details). The three largest contributors to consumer diet were highlighted for each site, based on %IRI values.

<table>
<thead>
<tr>
<th>Species</th>
<th>Trophic Guild</th>
<th>Literature TP</th>
<th>Grass Island (n=12)</th>
<th>Peche Island (n=3)</th>
<th>Mitchell's Bay (n=14)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Invertebrates</td>
<td></td>
<td></td>
<td>%N&lt;sup&gt;a&lt;/sup&gt; %F&lt;sup&gt;b&lt;/sup&gt; %W&lt;sup&gt;c&lt;/sup&gt; %IRI&lt;sup&gt;d&lt;/sup&gt;</td>
<td>%N %F %W %IRI</td>
<td>%N %F %W %IRI</td>
</tr>
<tr>
<td>Spottail Shiner</td>
<td>Insectivores&lt;sup&gt;2,3&lt;/sup&gt;</td>
<td>2.7&lt;sup&gt;4&lt;/sup&gt;</td>
<td>12.5 16.7 5.5 9.8</td>
<td>0 0 0 0</td>
<td>16.1 35.7 16.4 50.00</td>
</tr>
<tr>
<td><em>Notropis hudsonius</em></td>
<td></td>
<td>2.5&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>42.9 33.3 52.5 34.7</td>
<td>0 0 0 0</td>
</tr>
<tr>
<td>Striped Shiner</td>
<td>Insectivores&lt;sup&gt;3&lt;/sup&gt;</td>
<td>2.5&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>42.9 33.3 52.5 34.7</td>
<td>0 0 0 0</td>
</tr>
<tr>
<td><em>Luxilus chrysocephalus</em></td>
<td></td>
<td>2.7&lt;sup&gt;5,6&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>6.5 14.3 4.1 6.5</td>
<td>3.2 6.5 7.1 6.5</td>
</tr>
<tr>
<td>Brook Silverside</td>
<td>Insectivores&lt;sup&gt;3&lt;/sup&gt;</td>
<td>2.7&lt;sup&gt;5,6&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>6.5 14.3 4.1 6.5</td>
<td>3.2 6.5 7.1 6.5</td>
</tr>
<tr>
<td><em>Labidesthes siculus</em></td>
<td></td>
<td>2.7&lt;sup&gt;5,6&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>6.5 14.3 4.1 6.5</td>
<td>3.2 6.5 7.1 6.5</td>
</tr>
<tr>
<td>Black Bullhead</td>
<td>Insectivores&lt;sup&gt;3&lt;/sup&gt;</td>
<td>2.7&lt;sup&gt;5,6&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>6.5 14.3 4.1 6.5</td>
<td>3.2 6.5 7.1 6.5</td>
</tr>
<tr>
<td><em>Ameiurus melas</em></td>
<td></td>
<td>2.7&lt;sup&gt;5,6&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>6.5 14.3 4.1 6.5</td>
<td>3.2 6.5 7.1 6.5</td>
</tr>
<tr>
<td>Spottfin Shiner</td>
<td>Zoobenthivores&lt;sup&gt;2&lt;/sup&gt;</td>
<td>2.5&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6.3 8.3 8.5 4.0</td>
<td>42.9 66.7 46.8 65.3</td>
<td>0 0 0 0</td>
</tr>
<tr>
<td><em>Cyprinella spiloptera</em></td>
<td></td>
<td>2.5&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6.3 8.3 8.5 4.0</td>
<td>42.9 66.7 46.8 65.3</td>
<td>0 0 0 0</td>
</tr>
<tr>
<td>Crayfish</td>
<td>Zoobenthivores&lt;sup&gt;2&lt;/sup&gt;</td>
<td>2.5&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6.3 8.3 8.5 4.0</td>
<td>42.9 66.7 46.8 65.3</td>
<td>0 0 0 0</td>
</tr>
<tr>
<td><em>Humilis spp.</em></td>
<td></td>
<td>2.5&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6.3 8.3 8.5 4.0</td>
<td>42.9 66.7 46.8 65.3</td>
<td>0 0 0 0</td>
</tr>
<tr>
<td>Bluegill</td>
<td>Omnivores&lt;sup&gt;2&lt;/sup&gt;</td>
<td>3.2&lt;sup&gt;4&lt;/sup&gt;</td>
<td>6.3 8.3 44.2 36.5</td>
<td>0 0 0 0</td>
<td>3.3 7.1 33.5 11.3</td>
</tr>
<tr>
<td><em>Lepomis macrolepis</em></td>
<td></td>
<td>3.2&lt;sup&gt;4&lt;/sup&gt;</td>
<td>6.3 8.3 44.2 36.5</td>
<td>0 0 0 0</td>
<td>3.3 7.1 33.5 11.3</td>
</tr>
<tr>
<td>Largemouth Bass</td>
<td></td>
<td>3.3&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
<td>3.2 7.1 5.4 2.6</td>
</tr>
<tr>
<td>(juvenile)</td>
<td></td>
<td>3.3&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
<td>3.2 7.1 5.4 2.6</td>
</tr>
<tr>
<td><em>Micropterus salmoides</em></td>
<td></td>
<td>3.3&lt;sup&gt;1&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
<td>3.2 7.1 5.4 2.6</td>
</tr>
<tr>
<td>Northern Pike</td>
<td>Piscivores&lt;sup&gt;2,3&lt;/sup&gt;</td>
<td>4.2&lt;sup&gt;1,4&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
<td>3.2 7.1 0.2 1.1</td>
</tr>
<tr>
<td>(juvenile)</td>
<td></td>
<td>4.2&lt;sup&gt;1,4&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
<td>3.2 7.1 0.2 1.1</td>
</tr>
<tr>
<td><em>Esox lucius</em></td>
<td></td>
<td>4.2&lt;sup&gt;1,4&lt;/sup&gt;</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
<td>3.2 7.1 0.2 1.1</td>
</tr>
<tr>
<td>Yellow Perch</td>
<td></td>
<td>3.7&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6.3 8.3 27.2 9.2</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
</tr>
<tr>
<td>(Perca flavescens)</td>
<td></td>
<td>3.7&lt;sup&gt;1&lt;/sup&gt;</td>
<td>6.3 8.3 27.2 9.2</td>
<td>0 0 0 0</td>
<td>0 0 0 0</td>
</tr>
</tbody>
</table>
\( \%N \) = Determined as the proportion of a particular prey species relative to all prey species.

\( \%F \) = Determined as the percent occurrence of a particular prey species across all stomachs.

\( \%W \) = Determined as the percent weight contribution of a species across total mass of all prey species within all stomachs.

\( \%\text{IRI} \) = Percent Index of Relative Importance is determined through the contribution of \( \%N \), \( \%F \), and \( \%W \) (see methods for details).

1 Turner, 1966
2 McLeod et al., 2015
3 Keast, 1968
4 Keast, 1985
5 Vander Zanden et al 1997
Table 2.6 Stomach content analysis of Northern Pike (*Esox lucius*) across three sampling sites. Prey number (%N), prey frequency (%F), and prey weight (%W) were all used to calculate an Index of Relative Importance (%IRI) (see methods for details). The three largest contributors to consumer diet were highlighted for each site, based on %IRI values.

<table>
<thead>
<tr>
<th>Species</th>
<th>Trophic Guild</th>
<th>Literature TP</th>
<th>Grass Island (n=8)</th>
<th>Peche Island (n=10)</th>
<th>Mitchell's Bay (n=7)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>%N</td>
<td>%F</td>
<td>%W</td>
</tr>
<tr>
<td>Invertebrates</td>
<td></td>
<td>2.5¹</td>
<td>12.5</td>
<td>12.5</td>
<td>0.2</td>
</tr>
<tr>
<td>Invertebrates</td>
<td>Omnivorous zoobenthivores¹</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spottail Shiner</td>
<td>Insectivores²,³</td>
<td>2.7²</td>
<td>12.5</td>
<td>12.5</td>
<td>0.3</td>
</tr>
<tr>
<td>Common Carp</td>
<td>Insectivores²</td>
<td>2.5¹</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Bluegill</td>
<td>Omnivores²</td>
<td>3.2³</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Common Carp</td>
<td>Omnivores²</td>
<td>3.1⁴</td>
<td>12.5</td>
<td>12.5</td>
<td>57.5</td>
</tr>
<tr>
<td>Pumpkinseed</td>
<td>Omnivores²</td>
<td>3.3⁵</td>
<td>12.5</td>
<td>12.5</td>
<td>10.7</td>
</tr>
<tr>
<td>Round Goby</td>
<td>Omnivores²</td>
<td>3.2⁶</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Silver Bass</td>
<td>Piscivores²,³</td>
<td>3.5¹</td>
<td>12.5</td>
<td>12.5</td>
<td>28.7</td>
</tr>
<tr>
<td>Yellow Perch</td>
<td>Piscivores²,³</td>
<td>3.7¹</td>
<td>12.5</td>
<td>12.5</td>
<td>0.6</td>
</tr>
</tbody>
</table>

¹%N = Determined as the proportion of a particular prey species relative to all prey species.

²%F = Determined as the percent occurrence of a particular prey species across all stomachs.
\%W = Determined as the percent weight contribution of a species across total mass of all prey species within all stomachs.
\%IRI = Percent Index of Relative Importance is determined through the contribution of \%N, \%F, and \%W (see methods for details).

1Vander Zanden et al., 1997
2Uzarski et al., 2005
3Bhagat et al., 2007
4McLeod et al., 2015
5Maitland & Campbell, 1992
6Froese & Pauly, 2000
7Keast & Walsh, 1968
8Brush et al., 2012
Figure 2.1 Trophic position estimates of (a) Largemouth Bass (*Micropterus salmoides*), (b) Longnose Gar (*Lepisosteus osseus*), and (c) Northern Pike (*Esox lucius*) at Peche Island, Grass Island, and Mitchell’s Bay in the Huron-Erie corridor. Black circles represent TP$_{Scaled}$ (±1 SD) estimates, open circles represent TP$_{Constant}$ (±1 SD) estimates, and black triangles represent dietary TP values. Significant differences between mean TP$_{Scaled}$ and TP$_{Additive}$ were denoted with (*) for each species and site.
Figure 2.2 Trophic position estimates of Northern pike (*Esox Lucius*), Longnose Gar (*Lepisosteus osseus*) and Largemouth Bass (*Micropterus salmoides*) from the Huron-Erie corridor using both a scaled DTDF and a constant DTDF. Northern pike are represented by squares, Longnose Gar (*Lepisosteus osseus*) by triangles, and Largemouth Bass (*Micropterus salmoides*) by circles. Black data points denote species from Mitchell’s Bay, light grey represents Peche Island and dark grey points represent Grass Island.
CHAPTER 3

NICHE WIDTH AND OVERLAP OF PISCIVOROUS PREDATORS IN THE LOWER LAKE HURON-ERIE CORRIDOR
Introduction

The importance of quantifying niches, trophic interactions, and resource partitioning in biological communities has long been recognized in both marine and freshwater communities (Bearhop et al., 2004; Newsome et al., 2007). However species abundances, functional feeding groups, and trophic guilds within food webs vary seasonally and spatially, leading to potential changes in ecosystem structure and function, and complicate our understanding of food webs (Layman et al., 2007). Occupied niche space suggests habitat and resource use, and suggests competition for resources when two species occupy similar niche space (Elton, 1927; Hutchinson, 1957). Quantifying niche space and overlap between species across temporal and spatial scales is often implemented to understand dynamic changes in trophic interactions and resource partitioning (Schmidt et al., 2009). Understanding trophic interactions, resource and habitat use by way of niche characterization in food webs allows for the greater capacity for species monitoring and restoration, as well as improving existing food web models (Link, 2002).

The Laurentian Great Lakes is a complex freshwater ecosystem with high fish species diversity, complicated by the extirpation of a number of native species e.g. Shortjaw cisco (*Coregonus zenithicus*) and Kiyi (*C. kiyi*) (Stockwell et al., 2010), and the introduction of non-native fish species, e.g. Round Goby (*Neogobius melanostomus*), due to human-mediated transport (Jude et al., 1992). The Great Lakes possess complex predator-prey interactions and high biodiversity of piscivorous predator fish, providing a model system for studying resource partitioning and niche overlap between freshwater fish species (Hoyle et al., 2012; Lapointe, 2014). This system is also economically important for both U.S.A. and Canada, generating approximately $7 billion annually in commercial and recreational fisheries (Landsman et al., 2011). Moreover, the Great Lakes have been subjected to a variety of anthropogenic stressors
due to the large human population, resulting in the release of toxic chemicals, e.g. organophosphate flame retardants (OPE) (Venier et al., 2014), habitat degradation and fragmentation (Hurly & Christie, 1977; Krieger et al., 1992; Lapointe, 2014), and over-harvesting of fish species, e.g. Lake Sturgeon (*Acipenser fulvescens*) (Benson et al., 2003).

There are a variety of higher trophic level fish species that are believed to vary in habitat and resource utilization in the Great Lakes, however the majority of these are understudied and their ecological role is not well understood (Turshak et al., 2013), including Longnose Gar (*Lepisosteus osseus*), Northern Pike (*Esox lucius*), Largemouth Bass (*Micropterus salmoides*), Bowfin (*Amia calva*), Walleye (*Sander vitreus*), and Muskellunge (*Esox masquinongy*). In other freshwater systems, Bowfin, Largemouth Bass, and Northern Pike are known to utilize similar nearshore habitats characterized by dense macrophytic growth, low oxygen concentrations, and a greater abundance of aquatic invertebrates (Mundahl et al., 1998; Benturelli & Tonn, 2006; Hodgson et al., 2008), compared to Walleye, Muskellunge, and Longnose Gar that utilize similar pelagic habitats, characterized by low aquatic invertebrate abundance and less macrophytic growth (Bozek et al., 1999; Campbell et al., 2009; Corkrum, 2010). Bowfin and Largemouth Bass have been found to exhibit great dietary plasticity, consuming a variety of prey items in nearshore environments (Keast, 1979; Winemiller & Taylor, 1987; Mundahl et al., 1998), compared to Northern Pike and Muskellunge, which have been described as opportunistic, where seasonal changes in prey abundance are believed to determine diet composition (Bozek et al., 1999; Venturelli & Tonn, 2006; Harvey, 2009). Longnose Gar and Walleye have been described as primarily piscivorous generalists, consuming a variety of species such as *Cyprinidae* spp. and *Fundulidae* spp. (Bowlby et al., 1991; McGrath, 2010; McGrath et al., 2013).
To understand the variation in resource and habitat utilization amongst higher trophic level species, isotopic niche width can be quantified using carbon ($\delta^{13}$C) and nitrogen ($\delta^{15}$N) stable isotopes (Bearhop et al., 2004). Carbon stable isotopes identify primary production sources within an ecosystem, differing across habitat types from nearshore areas that have higher $\delta^{13}$C than pelagic areas (Fry, 2007). Nitrogen stable isotopes have traditionally been used to estimate TP, increasing at a known rate between prey and predator (DeNiro & Epstein, 1981).

Recent studies have aimed to quantify a species or population’s niche using stable isotopes (Layman et al., 2007; Jackson et al., 2011). Isotopic niches, which are measured as stable isotope coordinates, have been quantified through the total area (TA) or convex hull around the outermost data points in an isotopic bi-plot providing a metric of the habitat use and diet of a population (Layman et al., 2007). However TA is sensitive to outliers and small sample sizes, often resulting in overestimation of isotopic niche. A more robust estimate of isotopic niche, standard ellipse area (SEA), accounts for the influence of outliers and small sample sizes and encompasses the core isotopic niche (represented by a fraction of total area, e.g. 40% of the spread of isotope values) (Jackson et al., 2011). Standard ellipse area values can be used for geometric calculations of interspecific isotopic niche overlap, providing insight into potential functional redundancy and competition for resources through positioning of ellipses (Guzzo et al., 2013). Additionally, SEA can be further refined through statistical estimates using Bayesian statistics to estimate SEA, providing a robust estimate of isotopic niche that can be compared using likelihood-based estimates, and can be used to make inferences regarding interspecific habitat and resource utilization (Jackson et al., 2011).

The objective of this study was to understand niche width and overlap, competition for resources, and functional redundancy of top predator fish species (Bowfin, Longnose Gar,
Largemouth Bass, Northern Pike, Muskellunge, and Walleye) on both a seasonal and spatial scale using stable isotopes. We examine both the size of isotopic niche as well as the degree of overlap between species and hypothesize that due to seasonal fluctuations in prey density and location in the Great Lakes (Corkrum, 2010; Hoyle et al., 2012; Lapointe, 2014), the degree of overlap will vary seasonally for each species. Additionally, due to different feeding habits and habitat utilization observed in these species across other freshwater ecosystems, we hypothesize that isotopic niche width and overlap will vary across species.

**Methodology**

*Sample Collection*

Study species were collected at two sites in the Lake Huron-Erie corridor of the Laurentian Great Lakes; Peche Island (~42.35°N, -82.93°W) in the Detroit River, and Mitchell’s Bay, which is located in the Northeastern Basin of Lake St. Clair (~42.48°N, -82.42°W) in the spring (20 April – 20 June, 2014) and fall (20 September – 14 November, 2014).

Fish were captured using a combination of trap, fyke, seine nets, and a single anode boat electrofisher with a direct current (DC) of 4.0A and a pulse frequency of 30-60 Hz. All fish were euthanized with tricaine methanesulfonate (MS-222) and morphometric measurements (standard and total length, weight) were taken, and a ~5 g sample of muscle tissue were removed anterior to the dorsal fin and frozen until analyzed for stable isotopes.

*Stable Isotope Analysis*

All samples were lyophilized at -48 °C and 133 × 10³ mbar for ~48h, ground by hand, and lipid-extracted using a 2:1 chloroform:methanol mixture (Bligh and Dryer 1959). Samples were then weighed into tin cups (sample mass 400-600 μg), and carbon and nitrogen isotopic
compositions were determined with a Delta V Advantage Thermoscientific continuous flow mass spectrometer (Thermo Electron Corporation, Bremen, Germany) equipped with a 4010 Elemental Combustion System (Costech Instruments, Valencia, CA, USA). Stable isotope values are reported as per mil (δ) and calculated using the equation:

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

where X represents $^{13}$C or $^{15}$N and R is represented by $^{13}$C:$^{12}$C and $^{15}$N:$^{14}$N. Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (AIR) were used as standard reference materials for carbon (δ$^{13}$C) and nitrogen (δ$^{15}$N), respectively. Analytical precision was assessed by examining variation in replicate tissue samples (every 10th sample was run in triplicate), all were within the acceptable ±0.2‰ standard deviation range (0.1‰ for δ$^{13}$C and 0.1‰ for δ$^{15}$N, n=30), and values for internal laboratory standards were run after every 12 samples (NIST 1577c and internal lab standard tilapia (Oreochromus spp.) muscle (both n=221), which were < 0.2‰ for δ$^{13}$C and < 0.2‰ for δ$^{15}$N. Accuracy was assessed by certified NIST standard analyzed during the same time as sample δ$^{15}$N values were within 0.1 ‰ (NIST 8573), -0.4‰ (NIST 8548), and <0.01‰ (NIST 8549), and δ$^{13}$C within 0.2‰ (NIST 8542) and -0.1‰ (NIST 8573) of certified values.

**Isotopic niche size and overlap**

All statistical analysis was performed using the statistical software package ‘R’ (RStudio, Version 0.98.1083, R Core Team, 2014). Prior to statistical analysis, all data were determined to be normal and equal in variance using Shapiro-Wilks tests and Levene’s test, respectively. Individual t-tests for each species found no significant differences in δ$^{13}$C or δ$^{15}$N between the two seasons, eliminating season as a factor and allowing all samples to be grouped
by site (Peche Island or Mitchell’s Bay) (see results, Table 3.1). Due to inconsistent baseline species collected at each site, we could not compare differences in predator isotopic niche widths between sites. To compare isotopic composition between species at each site, multivariate analysis of variance (MANOVA) was used for each site to assess if $\delta^{13}$C and $\delta^{15}$N varied between species (dependent variables: $\delta^{13}$C and $\delta^{15}$N, independent variable: species). If the MANOVA results indicated significant differences between the species within a site (Peche Island or Mitchell’s Bay) univariate ANOVA models with Tukey’s post-hoc comparisons were used to compare the CV (Canonical Variables) scores (CV1 and CV2) of each predator species, to determine which species differed.

To estimate the ecological niche space occupied by each predator species at a given site, we generated isotopic niche ellipses using the SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) analysis package in R Studio. The standard ellipse area (SEA) of each predator was estimated using the $\delta^{13}$C and $\delta^{15}$N isotope values to generate ellipses that represented the core isotopic niche, which encompasses 40% of the spread of data along both axes; the SEA values were then corrected to minimize potential biases related to sample size using the equation from Jackson et al. (2011), to generate a corrected Standard Ellipse Area estimate ($SEA_C$) and the area of isotopic niche overlap between each predator was quantified for each site (Peche Island or Mitchell’s Bay) and expressed as % between each predator combination (Guzzo et al., 2013).

A Bayesian model was used to estimate each standard ellipse area over 10,000 iterations ($SEA_B$; Jackson et al. 2011). These models determined mean $SEA_B$ values and the 50, 75, and 95% Bayesian credibility intervals (BCI) for each species. Pairwise likelihood comparisons of the $SEA_B$ values were made between species to report the proportion of simulations showing a
difference in the size of the isotopic niches through likelihood-based estimates of size. The use of SEA_C gives insight into the positioning and orientation of ellipse area, while SEA_B provides a robust estimate of isotopic niche size.

**Results**

At Peche Island, Bowfin had the highest standard deviation for both δ^{13}C (-16.8 ± 2.1) and δ^{15}N and the lowest mean δ^{15}N (13.5 ± 1.3), while Longnose Gar had the highest δ^{15}N (15.8 ± 1.1) (Table 3.1). Walleye had the lowest δ^{13}C (-20.1 ± 1.1) and Bowfin had the highest δ^{13}C (Figure 3.1). At Mitchell’s Bay, Bowfin had the largest standard deviation for both δ^{13}C and δ^{15}N values, as well as the lowest mean δ^{13}C (-21.7 ± 2.3) and δ^{15}N (14.3 ± 1.3) values. Northern Pike had the largest mean δ^{13}C value (-17.5 ± 1.1), while Largemouth Bass had the largest mean δ^{15}N value (16.4 ± 1.1) (Figure 3.2).

Species-specific t-tests revealed no significant differences in either δ^{13}C or δ^{15}N between seasons at both Peche Island and Mitchell’s Bay for all species (all P > 0.06), allowing us to remove collection season as a factor in the analysis (Table 3.1). MANOVAs for each site revealed there to be significant differences in δ^{13}C and δ^{15}N between species (Peche Island: Wilk’s λ = 0.38, P < 0.001; Mitchell’s Bay: Wilk’s λ = 0.37, P < 0.001). Further comparisons of the CV axes for each site indicated that there were significant differences among fish species for both CV1 and CV2 at both Peche Island (ANOVA, F_{2,174} = 21.5, P < 0.01) and Mitchell’s Bay (ANOVA, F_{2,122} = 19.8, P < 0.01; see Table 3.2).

*Isotopic niche width and overlap*

Separate SIBER models for Peche Island and Mitchell’s Bay found the highest SEA_C values, i.e. ellipse areas, were Bowfin (Peche Island SEA_C = 8.54 %o^2; Mitchell’s Bay SEA_C =
9.37 ‰) and differed by <1 ‰ (Table 3.3, Fig 3.1b & 3.2b). Bowfin also had the largest CR at both Peche Island (4.4 ‰) and Mitchell’s Bay (4.7 ‰) (Table 3.3). The lowest SEA_C and CR varied by site and species; Northern Pike at Peche Island (CR = 1.8‰; SEA_C = 1.76 ‰) and Longnose Gar at Mitchell’s Bay (CR = 1.6‰; SEA_C = 1.70 ‰). Northern Pike also had the lowest NR range at both Peche Island and Mitchell’s Bay (0.9‰) (Table 3.3). Area of isotopic niche overlap at Peche Island was greatest for Northern Pike compared to Bowfin (100% overlap) and Largemouth Bass (84%) as well as between Muskellunge and Longnose Gar (71%) (Table 3.4, Figure 3.1b). Longnose Gar at Mitchell’s Bay had the greatest amount of overlap with Largemouth Bass (71%) and Walleye (42%), while Bowfin had no niche area overlap with any predator except Walleye (14%) (Table 3.4, Figure 3.2b).

Across the SIBER model simulations of ellipse areas (SEA_B), Bowfin had the highest mean SEA_B (± 95% BCI) values at both sites (Peche Island SEA_B = 8.41 ± 3.30 ‰; Mitchell’s Bay SEA_B = 8.19 ± 2.47 ‰). Additionally, the Bowfin SEA_B values at both sites were higher than all other predators in 99% of the 10,000 simulations (Table 3.5; Fig. 3.1c & 3.2c). The lowest mean SEA_B (± 95% BCI) values at Peche Island were found for Northern Pike (SEA_B = 1.89 ± 0.55 ‰) and were smaller than all other predators in 68% of the simulations (Table 3.5; Fig. 3.1c). Longnose Gar had the lowest SEA_B values at Mitchell’s Bay (SEA_B = 1.89 ± 0.61 ‰) and had smaller area estimates than all other predators in 75% of simulations (Table 3.5, Fig. 3.2c).

**Discussion**

In this study, stable isotopes of white muscle tissue were used to model isotopic niches, a proxy for the resource niche of species, across multiple piscivorous predators from two sites.
within the Huron-Erie Corridor. No evidence of seasonal variation in $\delta^{13}C$ and $\delta^{15}N$ values between spring and fall for any of the species sampled at either Peche Island or Mitchell’s Bay. However, there was varying interspecific isotopic niche sizes and degrees of overlap between the six species, suggesting less habitat and diet partitioning between these species in the lower Great Lakes than previously believed (e.g. Mason et al., 2002).

The absence of seasonal variation in $\delta^{13}C$ and $\delta^{15}N$ at either Mitchell’s Bay or Peche Island using white muscle tissue suggests similar foraging strategies for each species across much of the year. This seasonal consistency may be attributed to access to either the same prey items over time or to different prey items that occupy similar foraging roles and, therefore, indistinguishable isotopic compositions (Oviedo & Angerbjörn, 2005). Additionally, the similar values between spring and fall sampling period may be related to the rate of isotope turnover in white muscle tissue. The relatively slow turnover of white muscle (isotopic turnover rate $\approx$ several months; Boecklen et al., 2011) compared to other tissues, e.g. liver, provides the best estimate of whole season isotopic niche for freshwater piscivorous predators because it is not influenced by short-term variations in feeding habits, or rare feeding events (Newsome et al., 2007; Perga & Gerdeaux, 2005), but this may also limit the ability to detect changes over the sampling period used in this study, therefore tissue selection may be dependent on the scientific question being asked.

At both Peche Island and Mitchell’s Bay, Bowfin had the greatest isotopic niche width of all the species sampled, suggesting potential dietary plasticity or intraspecific competition leading to individual specialisation (Araújo et al., 2011; Bolnick et al., 2011). The comparatively small isotopic niche width for Muskellunge at Peche Island may signify a predominantly piscivorous diet in offshore areas (lower $\delta^{13}C$), signifying that lower trophic level (lower $\delta^{15}N$)
invertebrates and young-of-year fish may not be major contributors to Muskellunge diet. Likewise, the wide and high-positioned $\delta^{15}$N range and narrow $\delta^{13}$C range in Longnose Gar and Walleye isotopic niches at Peche Island could suggest consumption of higher trophic level prey in predominantly offshore areas. The wide $\delta^{13}$C ranges in isotopic niche widths of Largemouth Bass, Northern Pike, and Bowfin at Mitchell’s Bay suggest more varied habitat use, while the NR ranges for these species are narrower and could signify consumption of similar trophic-level prey. Overall, the variability in the isotopic niches inhabited by the piscivorous predators provides indicators that there may be a greater degree of niche partitioning occurring within the HEC than previously thought.

These similar isotopic niche widths for each species at Peche Island and Mitchell’s Bay represent similar resource use or feeding behaviour at a population level across site (Bearhop et al., 2004). However, with the exception of Northern Pike and Largemouth Bass, the shape and placement of ellipses in isotopic niche space differed for many species at Mitchell’s Bay, suggesting differential habitat and resource use by each predator, or differences in lake morphology and ultimately the isotopic landscape between Peche Island and Mitchell’s Bay. The wetlands in Mitchell’s Bay contain a greater amount of terrestrial carbon input, resulting in lower $\delta^{13}$C and a greater scale in primary production sources relative to Peche Island, which has a smaller $\delta^{13}$C scale and a lower amount of terrestrial carbon and organic terrestrial detritus likely due to increased anthropogenic stressors and shoreline modification (Lapointe, 2014; Leach, 1991). Furthermore, increased agricultural run-off in the watershed around Mitchell’s Bay may influence stable isotopes, resulting in a changed isotopic scale (Baustian et al., 2014; Staton et al., 2003). This difference in isotopic scale can facilitate different orientations and shapes of ellipses; however this does not necessarily suggest a different niche across sites, as differences in
isotopic baselines could lead to altered positioning of ellipses, and thus underestimation of functional redundancy (Jackson et al., 2011; Keough et al., 1996). The larger isotopic scale at Mitchell’s Bay may explain the larger CR for most species relative to Peche Island, and may suggest that terrestrial carbon inputs are relevant at Mitchell’s Bay.

Varying degrees of overlap between predator species, as well as differences in δ\(^{13}\)C and δ\(^{15}\)N values at Peche Island and Mitchell’s Bay suggest that complete functional redundancy across all piscivorous predators may not be occurring in the Great Lakes. By Hutchinson’s definition of niche, a large degree of overlap between species signifies same resource utilization and is a component of functional redundancy within ecosystems (Hutchinson et al., 1957; Rosenfield, 2002). At Peche Island, a division in resource and habitat use showed Bowfin, Largemouth Bass, and Northern Pike to have isotopic niche overlap, while these three species did not experience niche overlap with Muskellunge, Walleye, or Longnose Gar, which could suggest separate trophic guilds of piscivorous predators. However, this division in trophic guilds does not suggest intraguild competition or functional redundancy, as consumption of different prey in similar habitats with similar isotope signatures could lead to isotopic niche overlap. The higher δ\(^{15}\)N values, narrow CR, and ellipse area segregation for Longnose Gar, Muskellunge, and Walleye may be driven by a greater abundance of 1\(^{0}\) and 2\(^{0}\) consumers in offshore environments, while the greater ellipse areas and degree of overlap between Bowfin, Northern Pike, and Largemouth Bass may be due to increased invertebrate and young-of-year fish abundance in nearshore environments (Corkrum, 2010; Lapointe, 2014).

This similar pattern of niche overlap was not observed at Mitchell’s Bay, suggesting that trophic interactions amongst predators vary throughout the Great Lakes and may be due to different prey abundances or riparian zones (Hondorp et al., 2014; Lapointe, 2014; Pettitt-Wade
et al., 2015). The lack of Bowfin niche overlap at Mitchell’s Bay with most predators suggests differential prey consumption, and is supported by stomach contents at Mitchell’s Bay as well as literature in other freshwater systems, showing a great amount of crayfish consumption, while crayfish were not present in the stomachs of any other predator (Jordan & Arrington, 2014; Nawrocki & Fisk, unpublished data). Additionally, reduced niche overlap between Walleye and all other predators may suggest a lack of competition with other predators, and may be due to offshore (pelagic) feeding, as evident by lower δ13C.

While there are few diet studies on the majority of these piscivorous predators in the Great Lakes, studies in other temperate freshwater systems have found comparable results. Muskellunge have been known to consume higher trophic level prey, e.g. Yellow Perch (Perca flavescens) and White Sucker (Catastomus commersoni) when available (Bozek et al., 1999), while Bowfin are documented to consume a wide variety of prey as a response to changes in prey abundances as well as increasing environmental stressors, however they consume greater proportions of crayfish (Humilis spp.) when available (Jordan & Arrington, 2001; Mundahl et al., 1998). Likewise, Largemouth Bass have been classified as exhibiting specialist, generalist, and opportunistic behaviour (Keast, 1979; Winemiller & Taylor, 1987), ultimately demonstrating dietary plasticity in relation to seasonal and spatial availability of prey (Hodgson et al., 2008). Longnose Gar have been observed to consume predominantly fish species (McGrath, 2010; McGrath et al., 2013), including higher trophic level prey fishes, agreeing with our findings of a large NR for Longnose Gar at Peche Island. In contrast to many of the other species that seem to show high levels of littoral foraging, Walleye have been described as piscivorous specialists utilizing the more open pelagic regions of freshwater lakes (Hoyle et al., 2012). The varied feeding habits and prey item selection of piscivorous predators in other freshwater systems
supports a lack of functional redundancy and needs to be considered a possibility in the Great lakes.

Additional studies on isotopic niches of piscivorous predators and their prey may be important to further understand feeding behaviour and trophic interactions within the Great Lakes. Community metrics derived from stable isotopes cannot be independently used to this end, because they provide an integrated assessment of diet over a long period of time and may be confounded by isotopic routing (Kelly & Martinez del Rio, 2010; Layman et al., 2007). The wide isotopic niche of species like Bowfin and Largemouth Bass could be representative of a generalist population, or could suggest individual specialisation, while smaller isotopic niches (e.g. Muskellunge, Northern Pike) could represent individual generalist behaviour within a population represented by low variance in both δ¹³C and δ¹⁵N, or could suggest a population of specialists feeding on one specific prey type (Bolnick et al., 2011; Eloranta et al., 2013). Additional isotopic niche metrics such as measuring mean nearest neighbour distance (MNND) and standard deviation of nearest neighbour distance (SDNND) have been proposed to further quantify functional redundancy through understanding clustering of data on isotopic bi-plots (Abrantes et al., 2014; Layman et al., 2007), however the spread of data does not necessarily suggest functional redundancy as stable isotopes are non-descript in identifying prey item contribution to consumer diet. Furthermore, interspecific niche overlap may not suggest competition, and may be a result of co-existence through shared habitat use, diurnal feeding habits, or prey availability (Harvey et al., 2012). To further understand these differences, candidate prey items and stable isotope mixing models (e.g. SIAR; Jackson et al. 2010) would be necessary to further develop these theories, and would provide insight into relative contributions of prey within consumer diets (Semmens et al., 2013). Additionally, the use of another isotope,
such as $\delta^{34}\text{S}$, can discern differences in feeding as it relates to sedimentary detritus and differences in prey availability throughout the water column, where varying species $\delta^{34}\text{S}$ could suggest co-existence between predators (Croisetière et al., 2009).

Functional redundancy of piscivorous predators has been thought to be prevalent in the Great Lakes, resulting in the generalization of prey item selection and habitat use of piscivorous predators regardless of species (Krause et al., 2003). However, this study showed inter-specific differences in isotopic metrics (niche width and overlap), suggesting a lack of functional redundancy and varied habitat and resource use in the HEC. These weak trophic interactions, as depicted by varying niche width and overlap, are important in maintaining ecosystem stability and biodiversity (McCann, 1998). Furthermore, the variation in niche isotopic variation observed here is consistent with Elton’s description of niche and Hutchinson’s n-dimensional hyper volume niche theory, which predicts species niches must differ in some aspect or competition will persist until one group is excluded from a given niche when resources are limited, resulting in extirpation or a sudden change in niche (Bolnick, 2001; Elton, 1927; Hutchinson 1957). A greater understanding of trophic interactions, and ultimately food web structure, are required in the face of continued anthropogenic stressors in an environmentally and economically important ecosystem such as the Great Lakes.

Acknowledgements

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McGrath, P. E. 2010. The Life History of Longnose Gar (Lepisosteus Osseus), an Apex Predator in the Tidal Waters of Virginia. Williamsburg, VA: College of William and Mary, School of Marine Science.


Table 3.1 Stable isotopes (mean ± 1 SD) of predator species collected in spring and fall 2014 at Peche Island and Mitchell’s Bay in the Lake Huron and Erie Corridor. Values of $\delta^{13}$C and $\delta^{15}$N did not vary across season and were grouped into a single data set.

<table>
<thead>
<tr>
<th>Species</th>
<th>Peche Island</th>
<th>Mitchell’s Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>$\delta^{13}$C</td>
</tr>
<tr>
<td>Bowfin (Amia calva)</td>
<td>23</td>
<td>-16.8 ($\pm$ 2.1)</td>
</tr>
<tr>
<td>Largemouth Bass (Micropterus salmoides)</td>
<td>43</td>
<td>-16.8 ($\pm$ 1.5)</td>
</tr>
<tr>
<td>Longnose Gar (Lepisosteus osseus)</td>
<td>11</td>
<td>-19.2 ($\pm$ 1.0)</td>
</tr>
<tr>
<td>Muskellunge (Esox masquinongy)</td>
<td>25</td>
<td>-19.1 ($\pm$ 0.8)</td>
</tr>
<tr>
<td>Northern Pike (Esox lucius)</td>
<td>41</td>
<td>-16.9 ($\pm$ 1.0)</td>
</tr>
<tr>
<td>Walleye (Sander vitreus)</td>
<td>38</td>
<td>-20.1 ($\pm$ 1.1)</td>
</tr>
</tbody>
</table>
Table 3.2 Mean canonical variable (CV) values from separate post-hoc ANOVAs at Peche Island and Mitchell’s Bay for predator species. Superscript letters A, B, and C represent similarities between CV axes of predator species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Peche Island</th>
<th>Mitchell’s Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>CV1</td>
<td>CV2</td>
</tr>
<tr>
<td>Bowfin (Amia calva)</td>
<td>-0.07\textsuperscript{A}</td>
<td>0.42\textsuperscript{A}</td>
</tr>
<tr>
<td>Largemouth Bass (Micropterus salmoides)</td>
<td>-0.03\textsuperscript{B}</td>
<td>0.50\textsuperscript{B}</td>
</tr>
<tr>
<td>Longnose Gar (Lepisoteus osseus)</td>
<td>-0.05\textsuperscript{A,B}</td>
<td>0.53\textsuperscript{B}</td>
</tr>
<tr>
<td>Muskellunge (Esox masquinongy)</td>
<td>-0.07\textsuperscript{A}</td>
<td>0.49\textsuperscript{B,C}</td>
</tr>
<tr>
<td>Northern Pike (Esox lucius)</td>
<td>-0.05\textsuperscript{A,B}</td>
<td>0.46\textsuperscript{A,B,C}</td>
</tr>
<tr>
<td>Walleye (Sander vitreus)</td>
<td>-0.11\textsuperscript{C}</td>
<td>0.44\textsuperscript{A,C}</td>
</tr>
</tbody>
</table>
Table 3.3  SEA_C values (‰^2) as well as carbon (δ13C) and nitrogen (δ15N) ranges (‰) of SEA_C for predator species at Peche Island and Mitchell’s Bay. SEA_C values represent the core isotopic niche (40% of the spread of data) of δ13C and δ15N values.

<table>
<thead>
<tr>
<th>Species</th>
<th>SEA_C (‰^2)</th>
<th>Carbon Range (CR) (‰)</th>
<th>Nitrogen Range (‰)</th>
</tr>
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<tbody>
<tr>
<td><strong>Peche Island</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bowfin <em>(Amia calva)</em></td>
<td>8.54</td>
<td>4.4</td>
<td>2.3</td>
</tr>
<tr>
<td>Largemouth Bass <em>(Micropterus salmoides)</em></td>
<td>4.38</td>
<td>2.9</td>
<td>1.4</td>
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<tr>
<td>Longnose Gar <em>(Lepisoteus osseus)</em></td>
<td>2.84</td>
<td>2.2</td>
<td>2.7</td>
</tr>
<tr>
<td>Muskellunge <em>(Esox masquinongy)</em></td>
<td>2.01</td>
<td>1.9</td>
<td>1.7</td>
</tr>
<tr>
<td>Northern Pike <em>(Esox lucius)</em></td>
<td>1.76</td>
<td>1.8</td>
<td>0.9</td>
</tr>
<tr>
<td>Walleye <em>(Sander vitreus)</em></td>
<td>3.42</td>
<td>1.9</td>
<td>2.4</td>
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<tr>
<td><strong>Mitchell’s Bay</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Bowfin</td>
<td>9.37</td>
<td>4.7</td>
<td>2.1</td>
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<tr>
<td>Largemouth Bass</td>
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<td>2.3</td>
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<tr>
<td>Longnose Gar</td>
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<td>1.6</td>
<td>1.4</td>
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<tr>
<td>Northern Pike</td>
<td>1.98</td>
<td>2.3</td>
<td>0.9</td>
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<tr>
<td>Walleye</td>
<td>4.15</td>
<td>2.9</td>
<td>1.7</td>
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Table 3.4 Area of overlap (%) between \( \text{SEA}_C \) values for predator species at Peche Island and Mitchell’s Bay. Percent overlap values are read with respect to the species in the leftmost column (e.g. 31% of Bowfin \( \text{SEA}_C \) overlaps with Largemouth Bass \( \text{SEA}_C \)).

<table>
<thead>
<tr>
<th>Species</th>
<th>Peche Island</th>
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<tr>
<td></td>
<td>Bowfin (%)</td>
<td>Largemouth Bass (%)</td>
<td>Longnose Gar (%)</td>
<td>Muskellunge (%)</td>
<td>Northern Pike (%)</td>
<td>Walleye (%)</td>
</tr>
<tr>
<td>Bowfin (Amia calva)</td>
<td>--</td>
<td>31</td>
<td>0</td>
<td>0</td>
<td>21</td>
<td>0</td>
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<td>Largemouth Bass (Micropterus salmoides)</td>
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<td>--</td>
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<tr>
<td>Longnose Gar (Lepisoteus osseus)</td>
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<td>--</td>
<td>51</td>
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<tr>
<td>Northern Pike (Esox lucius)</td>
<td>100</td>
<td>84</td>
<td>0</td>
<td>0</td>
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<td>Walleye (Sander vitreus)</td>
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<td>0</td>
<td>2</td>
<td>13</td>
<td>0</td>
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<tr>
<td></td>
<td>Bowfin (%)</td>
<td>Largemouth Bass (%)</td>
<td>Longnose Gar (%)</td>
<td>Muskellunge (%)</td>
<td>Northern Pike (%)</td>
<td>Walleye (%)</td>
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<td>Bowfin</td>
<td>--</td>
<td>0</td>
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<td>--</td>
<td>0</td>
<td>14</td>
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<td>Largemouth Bass</td>
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<td>--</td>
<td>27</td>
<td>--</td>
<td>18</td>
<td>7</td>
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<tr>
<td>Longnose Gar</td>
<td>0</td>
<td>71</td>
<td>--</td>
<td>--</td>
<td>12</td>
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<td>10</td>
<td>--</td>
<td>--</td>
<td>8</td>
</tr>
<tr>
<td>Walleye</td>
<td>31</td>
<td>8</td>
<td>17</td>
<td>--</td>
<td>4</td>
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</tr>
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</table>
Table 3.5 Likelihood estimates (%) to compare SEA$_B$ values (‰)$^2$ between predator species at Peche Island or Mitchell’s Bay. Likelihood estimates were measured as the probability of each species in the leftmost column having a larger SEA$_B$ value than the corresponding predator in every other column.

<table>
<thead>
<tr>
<th>Species</th>
<th>SEAB (‰)$^2$</th>
<th>Bowfin (%)</th>
<th>Largemouth Bass (%)</th>
<th>Longnose Gar (%)</th>
<th>Muskellunge (%)</th>
<th>Northern Pike (%)</th>
<th>Walleye (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Peche Island</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Bowfin (Amia calva)</td>
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<td>Largemouth Bass (Micropterus salmoides)</td>
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<td>99</td>
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<td>--</td>
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<td>94</td>
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<tr>
<td>Muskellunge (Esox masquinongy)</td>
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<td>15</td>
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<td>78</td>
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<tr>
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<td>6</td>
<td>32</td>
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<tr>
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<td>15</td>
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<td>97</td>
<td>99</td>
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<tr>
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<tr>
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<td>98</td>
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Figure 3.1 Isotopic niche area estimates at Peche Island showing (a) showing the mean ($\pm$ 1SD $\%$) of $\delta^{13}$C and $\delta^{15}$N values, (b) isotopic niche SEA$_C$ values ($\%$), and (c) density plots presenting the mean (SEA$_B$) and Bayesian credibility intervals (BCIs) of corrected SEA$_C$ values for Bowfin (Amia calva), Largemouth Bass (Micropterus salmoides), Longnose Gar (Lepisoteus osseus), Musklleunge (Esox masquinongy), Northern Pike (Esox lucius), and Walleye (Sander vitreus). Black dots in Figure 1.(c) correspond to mean SEA$_B$ values and the grey boxes represent BCIs of 50, 75 and 95%.
Figure 3.2 Isotopic niche area estimates at Mitchell’s Bay showing (a) showing the mean (± 1SD ‰) of δ^{13}C and δ^{15}N values, (b) isotopic niche SEA_C values (‰), and (c) density plots presenting the mean (SEA_B) and Bayesian credibility intervals (BCIs) of corrected SEA_C values for Bowfin (Amia calva), Largemouth Bass (Micropterus salmoides), Longnose Gar (Lepisosteus osseus), Northern Pike (Esox lucius), and Walleye (Sander vitreus). Black dots in Figure 1.(c) correspond to mean SEA_B values and the grey boxes represent BCIs of 50, 75 and 95%.
CHAPTER 4
CONCLUSION

Thesis Summary

The food web structure and trophic interactions of piscivorous predators is oversimplified in the Lake Huron-Erie Corridor (HEC), a system that has experienced a large amount of urbanization and associated anthropogenic stressors, which has led to changes in ecosystem function (Baustian et al., 2014; Pikitch et al., 2004). The overall goal of this project was to further understand the trophic ecology of piscivorous predator fish species in the Lake Huron-Erie Corridor (HEC) by determining trophic position (TP) and isotopic niche widths using stable isotopes of carbon (δ^{13}C) and nitrogen (δ^{15}N). The findings of this project help provide further insight into varied trophic roles (i.e. minimal functional redundancy) and trophic structure of piscivorous predators in the HEC.

Chapter 2

Chapter two determined TP variability across species and site using a scaled diet-tissue discrimination factor (DTDF) for Largemouth Bass (*Micropterus salmoides*), Longnose Gar (*Lepisosteus osseus*), and Northern Pike (*Esox lucius*), and addressed the importance of proper baseline selection for TP calculation based on discrimination of δ^{13}C between trophic levels. The use of a scaled DTDF was found to be more consistent in determining TP than a constant DTDF, allowing for different baseline species to be used to compare TP estimates across consumers. TP values were determined to be larger when using a scaled DTDF rather than a constant DTDF. These findings agree with Hussey et al., 2014, which showed a similar relationship between TP estimates using a scaled DTDF and constant DTDF in marine systems. Furthermore, TP values for all piscivorous predators varied significantly across site. Sex and body length were found to
not be significant co-variates in TP for any species, which does not agree with other diet studies that show ontogenetic shifts and diet selection sex differences of species in other shallow freshwater lakes (Campbell et al., 2009; Venturelli & Tonn, 2006; Willacker et al., 2013). Variation in TP values for Largemouth Bass and Longnose Gar were found to be driven by differences in prey item consumption, and are thought to be attributed to dietary plasticity due to the heterogeneous distribution of prey items through the Lake Huron-Erie Corridor (Corkurm, 2010; Lapointe, 2014), while the smaller TP range of Northern Pike may be due to opportunistic feeding strategies, where opportunistic consumption of prey across different trophic levels by individuals would result in comparable intrapopulation $\delta^{15}N$, ultimately showing a smaller TP range.

The results of this chapter suggest that food chain lengths in freshwater systems are longer than previously estimated, and that piscivorous predators in the HEC do not occupy the same trophic level of 4.0, ultimately demonstrating that trophic structure is more complex than previously believed (Krause et al., 2003). Furthermore, our results suggest that the use of a scaled DTDF is less sensitive to variation in baseline species (e.g. $1^{\circ}$ and $2^{\circ}$ consumers) for TP calculation, allowing for absolute TP values to be compared across species and site, without baseline $\delta^{15}N$ values influencing differences in TP values, ultimately preventing the truncated representation of higher trophic level predator feeding habits in the HEC. This study highlights the importance of selecting appropriate baseline species with respect to $\delta^{13}C$ fractionation to make accurate TP comparisons within food webs across species and locations, as well as how TP of piscivorous predators vary within the HEC. Mischaracterization of predator TP can confound our understanding of food web structure and ultimately influence management decisions, such as monitoring contaminants and setting human consumption guidelines (Pikitch et al., 2004).
Chapter three examined the spatial and seasonal variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Largemouth Bass, Longnose Gar, Northern Pike, Bowfin (Amia calva), Muskellunge (E. masquinongy), and Walleye (Sander vitreus) through the determination of isotopic niche width and overlap using carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotopes. Predator $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were found to not be significantly different with respect to season, suggesting similar foraging behaviour across seasons, or the consumption of seasonally abundant prey items with comparable isotopic signatures. The long isotopic turnover rate of white muscle tissue may not be representative of discernable isotopic differences between seasons; however white muscle is often used because it is not influenced by short-term changes in feeding habits, or rare feeding events (Newsome et al., 2007). Isotopic niche width estimates using Bayesian statistics revealed Bowfin to have the largest niche width at both Peche Island and Mitchell’s Bay, suggesting consumption of species that feed on different carbon sources and a variety of prey from different trophic levels. This is comparable to findings of a greater Bowfin niche breadth in Lake Ontario, where large ranges in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were observed (Zhang et al., 2012). Northern Pike and Longnose Gar had the smallest niche widths at Peche Island and Mitchell’s Bay respectively, which suggest a more focused foraging strategy. The small niche area of Northern Pike was not consistent with literature findings, which showed a wider range in $\delta^{13}\text{C}$ (Zhang et al., 2012), however stable isotope differences between the two systems could be attributed to varying isotopic scales. Furthermore, varying degrees of overlap in isotopic niche widths between species at Peche Island and Mitchell’s Bay suggest functional redundancy is not relevant and that there is differential resource and habitat utilization at these sites in the HEC.
There exists many higher trophic level fish species that are important to both commercial and recreational fisheries in the Great Lakes, however the trophic interactions and food web structure between these species is poorly understood and often generalized (Krause et al., 2003). Understanding the differences in isotopic niches of piscivorous predators is important for both species-level and ecosystem-based fisheries management, providing insight into both individual niche variation and higher trophic level community interactions across space and season (Fry, 2007; Link, 2002). The varying niche width areas and degree of overlap between species may suggest that piscivorous predators in the HEC employ different resource use and foraging strategies, ultimately filling different ecological roles in this ecosystem.

Conclusion

Future directions for this project involve the refinement of established food web metrics to further understand trophic interactions of piscivorous predators in the HEC. The use of multiple baselines when calculating TP can be important in characterizing different sources of primary production in an ecosystem, and should be considered in determining TP in food webs with large $\delta^{13}$C scales (Post, 2002). Additionally, the residency of piscivorous predators needs to be considered in future studies, as feeding from different habitats with unique $\delta^{13}$C may influence TP values. Furthermore, traditional stomach content analysis and collection of candidate prey items for stable isotope mixing models would provide insight into varying prey selection in consumer diets (Semmens et al., 2013). The use of an additional ecological tracer, such as $\delta^{34}$S which measures the flow of sedimentary detritus throughout a web, may further differentiate predator isotopic niches by eliminating evidence for competition as seen by niche overlap when using only $\delta^{13}$C and $\delta^{15}$N (Croistière et al., 2009).
The major conclusions of this project are that trophic positions of piscivorous predators in the HEC are less similar than previously estimated, and that differential utilization in diet items and habitat, as seen by varying niche width and interspecific overlap, suggest a lack of functional redundancy and greater trophic complexity in the HEC. The results of this study suggest that food web metrics such as TP and isotopic niche width can be valuable in differentiating resource and habitat utilization, as well as providing insight into differences in trophic interactions between piscivorous predators in the HEC.
References


Corkrum, L. D. 2010. Fishes of Essex County and Surrounding Waters. Windsor, ON: Essex County Field Naturalists’ Club.


VITA AUCTORIS

Brent Nawrocki was born in 1991 in Winsor, Ontario, Canada. He graduated from the University of Waterloo in 2013 with a B.Sc. in Honours Biology. He is currently a candidate for the M.Sc. degree in Environmental Science at the Great Lakes Institute for the Environmental Research, University of Windsor, Windsor, ON, Canada.