Regional diet and isotopic niche of predatory fish following a regime shift in Lake Huron

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Abstract

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Lake Huron's food web has experienced drastic changes in response to multiple stressors including declines in offshore productivity, decreased trophic transfer efficiency and a transformation of the benthic food web. However, how these changes have affected the diets and isotopic niches of predatory fish is largely unexplored. My diet study analysed stomach contents from five predatory fish species (lake trout, lake whitefish, chinook salmon, rainbow trout, and walleye) from the Ontario waters of Lake Huron. My isotopic study focused on lake trout and lake whitefish, based on community concerns that recovering lake trout are competing with or consuming lake whitefish. By contrast, I found that lake whitefish were a minimal component of lake trout diets, and the diet and isotopic overlap between these two species was low overall, but varied regionally. Both the dietary and isotope analyses reflect the high regional diversity of energy sources used by predatory fish.

Keywords: Regime shift; predator-prey; isotopic niche; Lake Huron; regional energy sources; food web

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Chapter 1: General Introduction

This thesis aims to describe the interactions between lake whitefish and lake trout in Lake Huron from a western science perspective. I am part of an interdisciplinary team that is in partnership to better understand interactions between lake whitefish and lake trout using a two-eyed seeing approach that looks to both Indigenous Ecological Knowledge (IEK) and western science knowledge. In the spirit of a true two-eyed seeing approach, the impetus for this research as well as the research hypotheses being addressed originated from members of Saugeen Ojibway Nation (SON). Beginning with the development of the research proposal that led to this project and continuing through to the writing of this thesis and beyond, the project team including members and representatives of SON have frequently engaged in knowledge transfer, team building, and communications activities. My role, since I joined the team in 2021, is as one of the western science researchers, although I have had the opportunity to engage and communicate with SON members and the broader interdisciplinary research team including staff of the Ontario Ministry of Natural Resources and Forestry (MNRF). The results I will share are from a western science perspective, and are thus, only part of the story. Further insights about the broader two-eyed seeing project can be found in a documentary made by the project team (A Two-Eyed Seeing Approach to Food Web Dynamics and Fish Interactions In Lake Huron - YouTube) and will be forthcoming through reports and publications that will be produced in the future as the project progresses.

The research I present in this thesis focuses on the past two decades, a time of profound change in Lake Huron's food web. These ecological changes have occurred in response to multiple stressors including climate change and invasive species. Among the more influential disruptors are the invasive dreissenid mussels, which spread quickly throughout the Great Lakes (except Lake Superior) after first being observed in 1988 in the St. Clair River (Hebert et al. 1989). Dreissenid mussels, which include zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostiformus bugensis*) mussels, have been implicated in many of the changes impacting multiple trophic levels on the Great Lakes by intercepting and shunting nutrients towards the nearshore, altering the energy available to offshore regions (Hecky et al. 2004). These food web changes are suggestive of a "regime shift" (Barbiero et al. 2018; Rudstam et al. 2020), where the ecosystem transitions from one state to another, often associated with disturbance (Scheffer and Carpenter, 2003). Additionally, the trophic transfer efficiency in Lake Huron has been reduced, where the proportion of energy transferred from lower trophic levels to upper trophic levels is lower than in all other Great Lakes (Stewart et al. 2018). This, along with decreased prey fish abundance, has been associated with changes to condition, growth and abundance for predatory fish (He et al. 2016; Borgeson et al. 2020).

One of the fish species most affected is the lake whitefish (*Coregonus clupeaformis*). Lake whitefish support large commercial fisheries in the Great Lakes and annual harvests from Lake Huron alone averaged 3.2 million kg between 2005 and 2010 (Gobin et al. 2015). Nevertheless, in the last 30 years whitefish abundance has been declining (Cottrill et al. 2020). In most areas of Lake Huron, whitefish biomass peaked in

1996, and has been decreasing or at very low levels since (Mohr and Ebener, 2005; Cottrill et al. 2020). Though fishing effort was reduced lake-wide, these declines can be largely attributed to reductions in recruitment; population indices of ages 1-3 have declined from 2001 onwards to well below the long-term average , where some year classes went unobserved entirely (Cottrill et al. 2020). Shifts in lake whitefish depth distribution and diet have also been reported, as a historically important prey item, *Diporeia* spp., has essentially disappeared and lake whitefish have since transitioned to eating more invasive dreissenid mussels (Pothoven and Nalepa, 2006; Rennie et al. 2009). Increased dreissenid mussel consumption has implications for lake whitefish health including reductions in growth rates, condition factor and altered maturation schedules (Rennie et al. 2009; Pothoven and Madenjian, 2013). These changes in growth and maturation, combined with observed population declines could alter the sustainable harvest of lake whitefish, making this a high-priority issue for fisheries managers from both the US and Canada.

Lake whitefish are an essential part of the culture, sovereignty, food, and identity of the Saugeen Ojibway Nation (SON), and are a highly valued species in the commercial fishery (Gobin et al. 2023; Almack et al. 2023). On the Saugeen (Bruce) Peninsula, the Saugeen Ojibway Nation, comprising members from two sister First Nations, the Chippewas of Nawash Unceded First Nation and Chippewas of Saugeen First Nation, have harvested fish and wildlife throughout their traditional territory since time immemorial. The declines in lake whitefish abundance have negatively impacted the SON commercial fishing economy and is a serious concern to members of the community (Almack et al. 2023). Understanding potential causes of lake whitefish declines is a priority to SON members and leadership. While there are several potential causes of the declines, a specific concern from SON is that increasing populations of lake trout, now heavily supplemented by stocking, are negatively impacting lake whitefish through predation or competition for food or resources. SON harvesters have noted increased occurrence of lake whitefish in lake trout stomachs as well as behavioural and physical differences between stocked lake trout and the lake trout that existed historically (Almack et al. 2023).

Lake trout (*Salvelinus namaycush*), the historic top predator in the Great Lakes, are now in a decades-long recovery following the 1940's collapse related to colonial overharvest by the commercial fishing industry and parasitism by sea lamprey (*Petromyzon marinus*; Eshenroder et al. 1995). Lake trout have been stocked into Lake Huron since the 1970's for rehabilitation (Eshenroder et al. 1995), and by 2010, basin-wide wild recruitment was documented (He et al. 2012). While populations of lake trout are still well below the fish management objectives for the lake, widespread natural reproduction in the main basin exceeded 40% annually in 2018 and achieved the criteria to reduce stocking; fish to be stocked in the main basin of Lake Huron were subsequently reallocated and were stocked in the North Channel and Georgian Bay (Lenart et al. 2020). SON community members expressed their concerns regarding ecosystem impacts of stocking predators into a lake with decreased productivity, as such stocking can be regarded as interference with natural processes (Gobin et al. 2023).

The issue of lake trout and lake whitefish interactions is complex and requires input from multiple sources of knowledge, including Indigenous Ecological Knowledge (IEK) held by SON members gained from living and fishing in Lake Huron and Georgian Bay through many generations. For understanding complex systems, utilizing a "two-eyed seeing approach", where one eye focuses on IEK and the other on quantitative scientific (Western) knowledge allows for information exchange and the co-production of knowledge (Martin, 2012). This MSc thesis represents the Western science part of the larger two-eyed seeing project that brings together SON, the Ontario Ministry of Natural Resources and Forestry, and academic partners to examine the interactions between lake trout and lake whitefish. The IEK component of the study includes interviews with members of SON using a map-based approach where knowledge holders in the community share stories and provide information about changes in the Lake Huron ecosystem, changes in fish populations including shifts in diet and distribution and impacts or shifts in the fishery. The specific IEK portion of the study is not reported on here, as learnings from the interviews with knowledge holders will be shared in upcoming reports and publications. However, as noted earlier, the project itself was developed with input from SON and the research project objectives arose from SON member concerns (Gobin et al. 2023; Almack et al. 2023), thus elements of IEK have been implicitly included from the project's earliest stages. Future community workshops are being planned where learnings from the two knowledge systems will be brought together to gain a more holistic and broad understanding of the interactions between lake trout and lake whitefish and the ecosystem changes in Lake Huron. I encourage readers of my thesis to seek out future products from our research project that are focused on the Indigenous Ecological Knowledge component of this two-eyed seeing study for a more holistic understanding of the interactions between lake trout and lake whitefish.

The primary objective of the two-eyed seeing study is to investigate the potential role of lake trout in the declines of lake whitefish. The western science component of the study aims to describe the diets and isotopic niches of lake trout and lake whitefish in order to determine the extent to which lake trout are consuming lake whitefish, or if there are overlaps in diet or isotopic niche that may indicate the potential for competition for food sources. Both species have undergone substantial changes in the past 20 years, and to date, minimal research has been conducted in quantifying interactions between lake trout and lake whitefish. The main component of my thesis is divided up into two data chapters, one focussing on fish diets and the other focusing on stable isotope analysis of fish scale samples.

My thesis also includes a regional component, as Lake Huron is very complex and each of the geologically distinct basins have physical and biological differences (Rudstam et al. 2020; Warner et al. 2009). There are gradients of productivity in the lake that could have important effects of prey availability and predator abundances (Eberts et al. 2017; Fetzer et al. 2017). The extent to which stressors have cumulatively impacted Lake Huron also varies across the lake (Riseng et al. 2018; Dai et al. 2019). Declines in commercial fishing yields of lake whitefish are more pronounced in southern Georgian Bay and the northern and central areas of the main basin, suggesting regional variation in the extent to which drivers are influencing population dynamics (Cottrill et al. 2020). Additionally, commercial catches of lake trout were lower in the North Channel and Georgian Bay than in the main basin, and the majority of natural reproduction for lake trout was found to be in the northern main basin (Lenart et al. 2020). Prey densities are also known to differ regionally; for example, the North Channel has low levels of calcium, resulting in low habitat suitability for dreissenid mussels (Therriault et al. 2012; Kirkendall et al. 2021), perhaps facilitating the continued survival of an important prey item of lake whitefish, *Diporeia* spp. in this part of the lake. Regions of the lake also have differing prey fish densities; for example, rainbow smelt were found in higher densities in the North Channel, and bloater were more concentrated in the main basin (O'Brien et al. 2023). As the abundance and diversity of prey and predators varies across the lake, I felt it was important to include this spatial factor by dividing the Ontario waters of the lake into five regions: the North Channel, Georgian Bay, and northern, central and southern areas of main basin. The SON traditional territory is within the central main basin and southwestern Georgian Bay regions identified here.

Chapter 2 used dietary analysis on stomachs collected between 2004 and 2019 to determine to what extent lake whitefish are consumed by lake trout, and the degree to which their consumption of lake whitefish by lake trout is related to region, season or predator size. This time period of 2004-2019 was selected as 2004 is considered to be the beginning of the post-regime shift era. Additionally, lower ecosystem productivity and high numbers of invasive species have reduced the native prey resources available to both lake whitefish and lake trout in Lake Huron. This chapter also included the analyses of other fish predator diets, including walleye (*Sander vitreus*), chinook salmon (*Oncorhynchus tshawytscha*), and rainbow trout (*Oncorhynchus mykiss*), populations of which are of ecological significance and of interest to fisheries managers. Both chinook salmon and rainbow trout are non-native species that have been stocked into Lake Huron (Borgeson et al. 2020). I used three main methods to describe and compare the diets: proportion of prey by biomass, an index of relative importance and a Schoener overlap index (Pinkas et al. 1971; Schoener, 1970). My findings will contribute to the overall understanding of post regime shift diets of several important predators in Lake Huron, as well as provide an indication of whether there is potential for interactions between lake trout and lake whitefish.

Chapter 3 focused on stable isotope analysis to calculate the size and width of lake trout and lake whitefish niches, which allows better understanding of the sources of energy in the diets of these fishes. Isotopic niches can help describe the energetic sources used by a species and their relative position in a food web using ratios of the stable forms of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$), respectively. I used several metrics to describe and compare the isotopic niche characteristics of lake trout and lake whitefish, including carbon and nitrogen means and ranges, as well as niche size and relative overlap of lake trout and lake whitefish niches, which can be used to indicate potential for competition. I also calculated the enrichment of lake trout $\delta^{15}N$ compared to lake whitefish to consider the scope for lake trout predation of lake whitefish. These isotope metrics will provide a greater understanding of the energetic sources of—and relationship between—lake trout and lake whitefish in Lake Huron.

I have quantified the diets of five important species in this comprehensive study including more than 18,500 stomachs following a regime shift which had resulted in profound changes to the food web. My examination of isotopic niches of lake trout and lake whitefish provides important insight into the ecology of these important species. A study of this scale describing fish diets and isotopic niches across Lake Huron has not been previously examined and is important given the suite of changes that have occurred in Lake Huron.

Chapter 2: Regional predatory fish diets following a regime shift in Lake Huron

2.1 Abstract

Over the past 20 years, the Lake Huron ecosystem has undergone unprecedented change, including a reduction in offshore productivity, prey fish collapse, and transformation of the benthic food web. Yet, little is known about how these changes have affected the diet of key fish species. In this study, I used 18,543 stomach samples collected between 2004-2019 to characterize the diet of five key species: lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), chinook salmon (*Oncorhynchus tshawytscha*), rainbow trout (*Oncorhynchus mykiss*), and walleye (*Sander vitreus*), collected from the Ontario waters of Lake Huron including the North Channel, Georgian Bay and the main basin. Specifically, I described regional diets using an index of relative importance and diet biomass proportions, and determined the Schoener diet overlap index between the five predators. I found that invasive species dominated the diets of fishes examined; lake whitefish diets were dominated by dreissenid mussels in the southern main basin and by round goby (*Neogobius melanostomus*) in the central main basin. Chinook salmon had a highly uniform diet of rainbow smelt (*Osmerus mordax*) and coregonines, contributing to the high levels of diet overlap with lake trout, especially in the North Channel. My study demonstrates that while invasive species are pervasive in the diets of predatory fish lake-wide, there remains a significant degree of unexplained regional variation when considering the impacts of recent ecosystem changes on food webs, particularly when devising management strategies aimed at balancing predator and prey populations.

2.2 Introduction

Over the past two decades, the Lake Huron food web has experienced drastic changes across multiple trophic levels in response to anthropogenic stressors, such as climate change and invasive species. These include declines in offshore productivity (Hecky and DePinto, 2020) and changes to lower food webs (Barbiero et al. 2018). While efforts to control phosphorus in the 1970’s were successful in avoiding eutrophication of the upper Great Lakes, recent re-oligotrophication has resulted in lower spring total phosphorus levels in Lake Huron than those observed in Lake Superior, historically the most oligotrophic of the Laurentian Great Lakes (Barbiero et al. 2012; Rudstam et al. 2020). The size of the Lake Huron spring phytoplankton bloom has also been dramatically reduced (Barbiero et al. 2019), and summer zooplankton community biomass has been reduced to less than one third of the biomass reported between 1997-2002 (Rudstam et al. 2020). Seasonal chlorophyll maxima now occur in the fall instead of the spring, and the altered structure of the zooplankton community featuring fewer cladocerans and an increased proportion of calanoid copepods more closely resembles that of Lake Superior (Barbiero et al. 2012). These lower food web changes are suggestive of a “regime shift” (Barbiero et al. 2018; Rudstam et al. 2020), where the ecosystem transitions from one state to another, often associated with disturbance (Scheffer and Carpenter, 2003)

Invasive dreissenid mussels, acting as ecosystem engineers, have been implicated in many of the recent ecosystem changes in Lake Huron through their ability to intercept and shunt nutrients towards the nearshore, altering the transport of particulates to offshore regions (Hecky et al. 2004). Benthic prey communities changed following dreissenid establishment, including dramatic declines and spatial contractions of *Diporeia* spp.*,* a formerly dominant member of the benthic food web and a key link between primary production and fish production (Pothoven and Nalepa, 2006). Of the two major species of dreissenids, quagga mussels (*Dreissena bugensis*) can tolerate and spawn in colder temperatures than zebra mussels (*Dreissena polymorpha*), and the expansion of quagga mussels is associated with loss of *Diporeia* from progressively deeper sites from 2001-2007 (French et al. 2009). Once the most abundant offshore prey fish in Lake Huron, the invasive alewife (*Alosa pseudoharengus*) underwent a population collapse in 2003, with biomass decreasing by up to 99%, and have shown no signs of recovery since (Bence et al. 2008; Riley et al. 2008, 2020). The alewife collapse has been linked to decreased lower trophic level production, high mortality during the extremely cold winter of 2002-2003, and increased predation mortality from chinook salmon (Barbiero et al. 2011; Dunlop and Riley, 2013; He et al. 2015). Following the alewife collapse, prey fish biomass was also greatly reduced and has remained low since 2010, having decreased to only 20% of the mean abundance estimate reported between 1976 to 1996 (Riley et al. 2010). These shifts in the prey community have raised concerns regarding the size of the forage base and its ability to support predatory fish including lake trout (*Salvelinus namaycush*), chinook salmon (*Oncorhynchus tshawytscha*), and walleye (*Sander vitreus*), populations of which continue to fluctuate in response to stocking, population recovery, and wild recruitment (Roseman et al. 2014). Recoveries of lake trout and walleye in some areas and the declines of chinook salmon, a dominant predator since the 1980s, represent relatively recent changes in the food web (Johnson et al. 2015; Dobiesz et al. 2005) that could have implications for prey fish populations and predator diets. Stocking rates of salmonids have occasionally been adjusted in consideration of prey fish abundance (Dobiesz et al. 2005; Borgeson et al. 2020). However, with increased wild reproduction of chinook salmon, for example, managers will have less ability to control predation pressure as in the past through management actions such as alterations in stocking (Bence et al. 2008). Collectively, many of these outlined changes are associated with the regime shift in Lake Huron that occurred between 2002 and 2004, likely associated with the dreissenid invasion in the early 1990's (Hecky et al. 2004). Food web changes include the major decline in primary productivity in 2003 (Barbiero et al. 2009), the collapse of the predominant alewife fishery by 2004 (Bence, 2008), as well as the substantial biomass decrease of the offshore prey fish community (Riley et al. 2020).

Despite the profound changes that have occurred in Lake Huron's food web, there are relatively few studies of fish diets following the regime shift and none that we know of that examine diets across a broad spatial scale. An analysis of fish diets can yield useful information about linkages between species and the flow of energy in the food web and reveal how fish populations have responded to ecosystem changes (Hyslop, 1980). A notable study of fish diets in Lake Huron was conducted by Roseman et al. (2014), where piscivore diets in western Lake Huron in 2009-2011 were compared to the 1983-1986 diets described by Diana (1990). Roseman et al. (2014) found the native prey fish community had largely disappeared from the diets of lake trout, chinook salmon, rainbow trout (*Oncorhynchus mykiss*), and walleye in the 2009-2011 period. Overall, piscivores were more reliant on smaller and fewer alewife and rainbow smelt (*Osmerus mordax*) than they were previously, and the reduced body size of prey did not appear to be compensated by consuming more prey (Roseman et al. 2014). Chinook salmon were still highly reliant on alewife, despite the alewife collapse, and had a high proportion of empty stomachs. Predators also ate more insects and conspecifics than in the prior study, and the authors concluded these diet trends were indicative of chronic prey limitation (Roseman et al. 2014). While Roseman et al. (2014) effectively described piscivore diets following a period of profound change, the study focused on the western side of Lake Huron's main basin and was limited to fish sampled from anglers. To date, there are a lack of studies on fish diets across the Ontario waters of Lake Huron, which covers over 50% of the total lake area, including the North Channel and Georgian Bay.

The second-largest, and perhaps the most complex among the Laurentian Great Lakes, Lake Huron is unique as it is composed of three connected, but geographically distinct basins: the main basin, Georgian Bay, and the North Channel, each of which maintain physical and biological differences (Rudstam et al. 2018; Warner et al. 2009). Overall, Lake Huron is oligotrophic, with the exception of Saginaw Bay in the United States which is eutrophic, and the North Channel in Ontario waters which is considered mesotrophic (Ebener and Riley, 2018). Productivity gradients are mostly driven by climate, land forms, depth, and anthropogenic influences (Riseng et al. 2018). Nearshore areas, with elevated nutrients and water temperatures have greater species richness than open-water areas (Fetzer et al. 2017). More productive regions like Saginaw Bay (American waters), and portions of the North Channel and Georgian Bay can help sustain key offshore fish (Fielder et al. 2020). Lake Huron's basins support distinct fish communities; for example, acoustic surveys found bloater (*Coregonus hoyi*) biomass estimates in the main basin to be nearly twice as high as in the North Channel and nearly four times that in Georgian Bay (Riley et al. 2020). However, the shallower North Channel and Georgian Bay have consistently higher biomasses of pelagic fish overall, especially rainbow smelt, than in the main basin, and the shallower basins are likely important contributors to lake-wide fish production (Warner et al. 2009).

I focused on five species for which there was adequate diet information: lake trout, lake whitefish, walleye, chinook salmon, and rainbow trout. Populations of lake trout, the historic top predator in the lake, are in a decades-long recovery following their 1940's collapse associated with overfishing and parasitism by sea lamprey (Eshenroder et al. 1995; Lenart et al. 2020). Lake whitefish, a commercially fished species, are of immense cultural and economic importance in the Great Lakes region (Cottrill et al. 2020; Almack et al. 2023). Lake whitefish population abundances, commercial catches, growth, condition, and recruitment have undergone substantial declines during the post regime shift era (Fera et al. 2015; Gobin et al. 2016; Fera et al., 2017; Ebener et al. 2021). Associated with these declines in lake whitefish are reported changes in the species diet. For example, lake whitefish in South Bay, Lake Huron shifted from a focus on *Diporeia* to lower energy density dreissenid mussels (Rennie et al. 2009a). In recent years, lake whitefish have been consuming increasing numbers of round goby (*Neogobius melanostomus*) in the main basin (Pothoven and Madenjian, 2013). In a 70-year study of food web changes in South Bay, Lake Huron, lake whitefish showed shifts in their isotopic niche more so than any other fish species examined, indicating large changes in the feeding ecology of the species (Trumpickas et al. 2022). However, little is known about specific changes in lake whitefish diets across most regions of Lake Huron. While lake whitefish are not typically considered a predatory fish, the data set had sufficient samples for their diet analysis, and as lake whitefish diets have been found to contain more fish prey, their inclusion was important. Concerns have also been raised by Saugeen Ojibway Nation that stocking of lake trout has contributed to declines of lake whitefish through predation on or competition with lake whitefish (Gobin et al. 2023; Almack et al. 2023). Lake whitefish are an essential part of the culture, sovereignty, food, and identity of the Saugeen Ojibway Nation, and are a highly valued species in the commercial fishery (Gobin et al. 2023; Almack et al. 2023).

Populations of other predators have also experienced declines following the regime shift, including chinook salmon, which were originally stocked in the Great Lakes, in part, to control the non-native planktivores, rainbow smelt and alewife (Tody and Tanner, 1966). The recent population declines of both alewife and rainbow smelt likely contributed to lower abundance, growth, and condition of chinook salmon (Johnson and Gonder, 2013; Roseman and Riley, 2009). Rainbow trout, another introduced predator, did not show the same condition factor declines as chinook salmon following the alewife collapse (Borgeson et al. 2020). Rainbow trout have a diverse diet of invertebrates and fish species, which until recently had included alewife (Roseman et al. 2014). Like lake trout, walleye populations experienced declines in the 1940's - likely associated with habitat degradation, overfishing, and impacts of invasive species (Schneider and Leach, 1977). Predation of walleye fry by alewives was cited as the primary factor in the recruitment failures of walleye (Fielder et al. 2007), and the subsequent collapse of alewife has been associated with walleye recovery (Johnson et al. 2015). Walleye populations have seen recoveries in Saginaw Bay, however, the lake-wide yield is still well below the fish community objective established by management agencies on Lake Huron (Fielder et al. 2020). Additionally, walleye body condition in Saginaw Bay declined following a 1990 prey biomass decline and has not fully recovered (He et al. 2016). Alewife and rainbow smelt were the main component of walleye diets in the 1990's (Dobiesz, 2003), whereas more recently, rainbow smelt and round goby dominate walleye diets (Pothoven et al. 2017).

The overall objective of this study was to compare the post-regime shift diet of key fish species across the Ontario waters of Lake Huron, focusing on how diets of these five focal species vary among the lake's three basins. I did this by examining the stomach contents of over 18,500 fish collected between 2004-2019 as part of agency monitoring programs. With these data, I estimated an index of relative importance which provides an assessment of which prey items are the most significant overall to a species based on the frequency, number and volume of prey consumed (Pinkas et al. 1971). I also estimated Schoener's overlap index, which is a relative measure of the degree to which two species consume similar diets (Schoener, 1970). The index of relative abundance provides information on the importance of a prey item in the diet while Schoener's overlap index provides an indicator of the potential for resource competition between species. With decreased prey availability lake-wide, including the loss of alewife, there are concerns about increased competition for a more limited prey base among predators. For lake trout and lake whitefish where sample sizes were higher, I furthermore compared diets across different size classes, seasons, and time and provided an assessment of the extent of predation of lake trout on lake whitefish and the extent of diet overlap between lake trout and lake whitefish. To my knowledge, this is the most comprehensive assessment to date of fish diets in the Ontario waters of Lake Huron.

2.3 Methods

Fish stomachs were collected between 2004 and 2019 by the Upper Great Lakes Management Unit of the Ontario Ministry of Natural Resources and Forestry as part of their annual monitoring programs. Samples originated from sport fish (angler) programs, commercial fisheries sampling programs, and nearshore and offshore index netting surveys. Gill nets are the primary capture technique used by nearshore, offshore, and commercial fishing programs. Gill nets vary in mesh size according to target species, and range between 32 and 189 mm. Nearshore and commercial fishing programs also capture fish using trap nets, though these represent fewer total efforts.

Fish associated with the sport fish programs are caught by angling. Sampling events and catch densities vary by region based on survey schedules (Figure 2.1).

Stomachs were collected in all management districts in the Ontario waters of Lake Huron (Figure 2.1) including the North Channel, Georgian Bay, and the main basin. Fish stomachs were collected from several species considered to be of management relevance. At the beginning of the time series, lake trout and lake whitefish were the primary species from which stomachs were collected, however, other species were added over time. For the purposes of this study, I focused on five species for which there were adequate sample sizes across a broad spatial scale: lake trout, lake whitefish, chinook salmon, rainbow trout, and walleye (Table 2.1). Each individual stomach sampled from one of the focal species was given a unique stomach identification number which could be linked back to the capture information of the fish it was taken from, including date, time, and location of capture, as well as biological information such as length, weight, and age of the fish. Stomachs of lake trout, lake whitefish, and chinook salmon were annually sampled lake-wide and constitute a large proportion of the total samples. Rainbow trout and walleye stomachs were included in the analysis but represent fewer collection areas or are more limited in number (Table 2.1). Within each region, sample sizes of fewer than ten stomachs for each predator species were not included in the %W, IRI or overlap analyses.

Upon capture, fish total length and round weight were measured. Whole stomachs were removed and placed on ice in the field to slow degradation until samples could be frozen at the end of the field day. Sex and maturity status were assessed, and aging structures were removed in the field or at the end of the sampling day. Stomachs were removed from the freezer individually to be thawed 1-2 days prior to sampling. The thawed, full stomach was weighed, then emptied onto a clean petri dish, with care taken to remove all ingested material from the stomach lining. Once contents were emptied, the stomach was re-weighed. Organisms were broadly sorted into familial categories, then identified to the lowest taxon possible (Table A1.1), where key identification features were retained given the digestive state of the prey. Each grouping of common items was bulk-weighed and counted using uniform, distinguishing features (e.g., head capsule) rather than trying to reconstruct a prey item from pieces for a count. For prey fish that could be identified to species, individual wet weights and standard lengths of each prey item were recorded. Unidentified fish and invertebrate volumes, including pieces were reapportioned among identified species volumes based on the composition of identified fish or invertebrate prey species of the regional-level predator diets.

Prey types that contributed >2% to any species diets in any region were individually included in the overlap and diet diversity analyses. For data visualization purposes, prey types were grouped with similar taxa to create a simplified legend common to all five species. For example, any unshelled invertebrate prey were grouped into the category “Other Invertebrates” (Table A1.1). Quagga and zebra mussels were grouped into “Dreissenids”. All other bivalves and gastropods that were not a dreissenid mussel were grouped into “Mollusca”. The *Coregonus spp.* category grouped identifiable coregonines including lake whitefish, cisco, and deepwater chub. The deepwater chub category included bloater and any deepwater cisco species (i.e, shortjaw cisco) that could be identified with enough detail to distinguish them from cisco and lake whitefish. To distinguish between coregonines we used mouth morphology when possible, in the absence of an intact or distinguishable mouth area, gill raker counts and fin ray counts were used. The *Coregonus spp.* category also included "Unidentifiable Coregonines"; individual prey items that were identifiable to the genus *Coregonus* but not to species (Figure A1.2)

Large sample sizes for lake trout and lake whitefish allowed for more detailed diet analysis. Lake trout and lake whitefish diets were evaluated by predator body length, season, and year. Prey items were included in the plots if their contribution was >2% of the diet of lake trout or lake whitefish for data visualization. Seasons were identified as: winter (January, February, March), spring (April, May, June), summer (July, August, September) and autumn (October, November, December), all from the first of the earliest month to the final day of the last month listed. Further details about prey categories used can be found in Table A1.1.

Data Analysis

All data collected for this project were entered and maintained in a Microsoft Access database and subsequently analyzed using the statistical software program R version 4.2.3 (R Core Team, 2023).

For each species, I calculated the percentage by biomass (%W) of each prey type. Total weights of each prey species were summed by individual fish, then grouped by predator species and by region. This percent weight metric reflects the energetic contributions of prey to the predator.

I used the %W values to calculate Shannon diversity indices, which I used to compare the diversity of the diets across regions and species. This method was also used by Woodard et al. (2021), and uses the equation:

$$\Sigma_i P_i \log_{10} P_i$$

Where P_i was the proportion of the biomass that the i-th diet item composed of the total biomass of prey for that species and region.

For each species, I calculated the index of relative importance (IRI; Pinkas et al. 1971), which reveals which prey items are contributing to diet the most, providing a different perspective than an examination of diet by biomass, the latter of which can be easily skewed by small numbers of large-bodied fish consumed as prey. In addition to prey contributions by weight, IRI also incorporated the proportion of predators that consumed each prey item, as well as the number of prey types consumed. This reflected the contributions of small but numerous prey as well as representation of the prey types that were consistently eaten by a proportion of the consumer population. While contributions of prey by weight are important for understanding bioenergetics, using IRI allows for a more holistic understanding of what prey items contributed to the diet

(Hart et al. 2002). The IRI index summarizes and identifies the important components of the diet and does not include unidentified prey items.

Calculating IRI requires an estimate of the percent weight (%W, the contributed weight of a prey species in proportion to combined weight of all prey consumed), the percent number (%N, the proportion of the count of a particular prey item relative to all counted items), and percentage by frequency of occurrence (%F, the percentage of predators which consumed that specific prey item out of the total number of fish that had consumed any prey). IRI was then calculated both as an index and as a percentage as in Pinkas (1971) as follows,

$$\mathrm{IRI} = (\%\mathrm{N} + \%\mathrm{W}) \times \%\mathrm{F}$$

and

$$\%\mathrm{IRI}_i = \frac{100\ \mathrm{IRI}_i}{\sum_{i=1}^{n}\ \mathrm{IRI}_i}$$

To investigate dietary overlap between predator species, Schoener's index, α (Schoener, 1970) was calculated using the equation:

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} \llbracket\, \left|P_{x_i} - P_{y_i}\right| \quad \rrbracket\right)$$

where *i* represents one prey item, and *P* is the proportion of the prey item *i* in the diet of *x* and *y*, with *x* and *y* each representing a different predator species, paired for comparison. The proportional biomass of unique prey types was used to calculate the

Schoener overlap index. Schoener's overlap index produces a single α value of overlap between two species and ranges between 0 (no overlap) and 1 (complete overlap). Overlap values greater than 0.6 (60%) are considered significant, though not necessarily indicative of competition without investigating abundance of the prey resource (Schoener, 1970; Jacobs et al. 2010). Regional pair-wise comparisons of all predator species were conducted.

For the five focal species, I calculated %W and IRI and compared Schoener's overlap index for each species pair combination for each basin of Lake Huron. For lake trout and lake whitefish, I had enough data to also examine these metrics by season, consumer length bin, and by sampling year. Length bins for lake whitefish grouped fish that were <200mm in total length, and every 100 mm up to 601-700 mm. For lake trout, the smallest bin of fish was <300 mm in total length, and every 100 mm up to 801-900 mm.

I performed G tests to determine if there are differences in the frequency of empty stomachs by species depending on region, and subsequent pairwise G tests to identify between which regions there were differences. Significance was based on Bonferroni corrected critical P-value (Pcrit; 0.00833) to minimize the chance of false significance, or Type I error. I used linear models to detect if there were changes over time in the proportion of empty stomachs by species by region, with a significance value of $p < 0.05$. Additionally, I used linear modelsto compare the prevalence of fish in general and round gobies in particular in the diets of lake whitefish, and if the average size of sampled lake whitefish or lake trout increased over time.

2.4 Results

Of the 18,543 stomachs included in my analysis of the five key predators, 69% (12,863) had contents, with the frequency of empty stomachs ranging annually between 17-47% (Figure 2.2). There were no significant changes in the percentage of empty stomachs over time for chinook salmon, lake trout, walleye, or lake whitefish (Figure 2.2). Emptiness rates of rainbow trout stomachs decreased significantly over time (adjusted $R^2 = 0.769$,$F(1,7)= 27.57$, $p< 0.05$). Emptiness rates differed by region for chinook salmon ($G= 67.94$, $df= 3$, $p < .001$) and the ratio of empty to non-empty stomachs was significantly higher in Georgian Bay than in other regions determined with post-hoc pairwise G tests, ($p < .001$). Walleye had higher proportions of empty stomachs in the southern main basin ($G= 36.724$, $df= 3$, $p<.001$) than in the central main basin, Georgian Bay and the North Channel (all $p< .01$).

Among the five study species, there were 621,744 individual prey items recorded across seventy-one identified prey types (i.e., taxa). Sixty-eight taxa were represented in Georgian Bay, many more taxa than the other regions which had between 45-54 species each. However, the number of predator stomachs sampled was also much higher in Georgian Bay than elsewhere.

The proportion of unidentifiable diet items by volume varied by species, ranging from 21% to 55% of diets, with rainbow trout and walleye diets having the lowest and highest proportion of unknown items, respectively (Figure A1.3). All species had unidentified fish, invertebrates, and organic matter as stomach contents.

Diet by % biomass (%W)

Between species, diets of predators varied, and in all areas, each predator ate numerous prey types (Figure 2.3). Rainbow trout and lake whitefish had the most diverse diets of the five species based on the Shannon diversity index (Table A1.2), and consumed prey from 40 and 43 taxa, respectively. Lake trout and chinook salmon diets had the lowest diet diversity with most of their diet consisting of a single species—rainbow smelt—which made up 68 and 88% of the diet by biomass, respectively (Figure A.1.3). Fish prey constituted over 99% of the lake trout diet and 96% of the chinook salmon and walleye diet by biomass. All key predator species consumed round goby. For species whose diets contained higher volumes of invertebrate prey (lake whitefish and rainbow trout), *Bythotrephes* spp. contributed 8 and 10% to the lake-wide biomass, respectively.

Diets of the five species varied by region (Figure 2.3). Diets of chinook salmon contained a high biomass of rainbow smelt, the highest occurring in the North Channel (94%) and the lowest in the southern main basin (78%). Chinook salmon diets had *Coregonus* spp. as the second most common prey type (6-8% of the diet biomass), except for in Georgian Bay, where round goby and *Bythotrephes* consumption exceeded that of *Coregonus* spp. For chinook salmon, lake trout, and walleye, consumption of *Coregonus* spp. was the highest in the southern main basin (7, 18, and 34% respectively). The southern main basin had the highest diversity index values for lake trout and included alewife, deepwater chub, gizzard shad, and round goby in addition to rainbow smelt and *Coregonus* spp. Of the identifiable coregonines within the *Coregonus* spp. category, deepwater chub were consumed in higher volumes by lake trout and walleye in the southern main basin than elsewhere. For lake trout, lake whitefish, and walleye, consumption of round goby was the highest in the central main basin (39, 72 and 77% of biomass respectively), and the lowest in the North Channel. For rainbow trout, the regional consumption of round goby differed from the other predators, where the highest proportion of round goby in the diet was in the North Channel; proportions there were over seven times higher than those from the central main basin. Lower sample sizes might have biased indices of diet diversity in some cases, notably walleye in the central main basin and rainbow trout in the North Channel. Lake whitefish diets were the most diverse in the North Channel and Georgian Bay, and less diverse in the central and southern main basins (Table A1.2). Dreissenid mussels dominated the diets of the lake whitefish from the southern main basin (71%), where the diets were the least diverse among regions. The lake whitefish diet from the North Channel was 79% invertebrates, with amphipods, *Diporeia* spp., invertebrates, and molluscs each with >9% of the total diet biomass. Lake whitefish diet in the other regions was also mostly invertebrate-based, other than the central main basin where fish constituted 71% of the diet.

Invasive species comprised over 50% of the diet of all fish species examined except for lake whitefish in the North Channel (33%) and northern main basin (41%). Lake whitefish diets were 97% invasive species in the southern main basin and 95% invasive species in the central main basin. These were primarily dreissenid mussels in the southern main basin (59%) and round goby in the central main basin (72%).

Rainbow smelt, round goby, dreissenid mussels, and *Bythotrephes* were invasive species commonly consumed by the key predators, and along with alewife and gizzard shad, 86% of the collective biomass of identified prey in this study was of invasive origin.

Index of relative importance (IRI)

The IRI varied regionally for each predator and the same overall trends were noted as for percent biomass (%W) in the diversity of prey types in the fish diets (Figure 2.4). For example, the IRI of lake whitefish showed a larger range of important prey items than the IRIs of the other species, and lake whitefish from different basins had different important items. Amphipods (including deepwater *Diporeia* spp.) in the diets of lake whitefish were important in the North Channel but not elsewhere. Mollusca were the most important lake whitefish diet item in the northern main basin, and just minimally so in the central and southern main basins. The most important items for lake whitefish in the central and southern main basins were round goby and dreissenid mussels, respectively. The IRI of lake whitefish from Georgian Bay showed that *Bythotrephes* and insects were the most important prey, followed by molluscs, dreissenids, and round goby.

The IRI of chinook salmon was dominated by just two species, rainbow smelt and *Bythotrephes*. *Bythotrephes* had very high IRI scores for chinook salmon in Georgian Bay, central and southern main basins (93, 98 and 57%), and were consumed by 5 – 18% of chinook salmon. The importance of *Bythotrephes* in the diet of chinook salmon and rainbow trout was higher using IRI than using %W. The IRI of *Bythotrephes* in rainbow trout diets exceeded that of round goby and insects combined, as between 29-33% of rainbow trout consumed *Bythotrephes* regionally and *Bythotrephes* exceeded 80% of the number of prey consumed by rainbow trout in all three regions.

Rainbow smelt had the highest IRI values in both lake trout and walleye diets in all areas except the central main basin where round goby was the most important diet item for these two predators. For both lake trout and walleye, alewife were less important using IRI than by using %W, because so few individuals (<5%) of either species ate alewife and by numbers, alewife were less than 1% of the total prey count. Similarly, lake whitefish represented up to 5% of the diet of lake trout by biomass in the central main basin but were of very low importance using IRI; this was because < 1 % of lake trout (4 /993) consumed lake whitefish and of the total number of prey items consumed by lake trout, few were lake whitefish (4 /9,238 items).

Schoener overlap index

There was regional variation in the degree of diet overlap between species (Figure 2.5). The northern main basin only had sufficient sample sizes for the comparison of lake trout and lake whitefish, where the overlap index was low (23.7%). Lake trout and lake whitefish overlap was low overall (8.5-17.6% in the North Channel, Georgian Bay, and southern main basin), though higher in the central main basin (39.7%).

Lake trout and chinook salmon had the most overlap among species across all regions of the lake indicating that, overall, these species relied on many of the same sources of energy in the food web. Overlap between lake trout and chinook salmon was significant (ie. >60%) in three of the four regions compared, and highest in the North Channel (94.2 % overlap), followed by Georgian Bay (78.2%), and southern main basin (61.8%). The only other significant diet overlap was between walleye and lake trout in the central main basin (60.1%). Generally, lake whitefish had the least amount of overlap with other species, especially with chinook salmon (5.0 – 8.5 %) in all regions.

Diet overlap indices were similar among regions, with one significant pairing occurring within each region (Figure 2.5). Georgian Bay had higher indices of overlap between rainbow trout and walleye (54.6%) than elsewhere as well as between rainbow trout and lake whitefish (48.6%). Of the 10 pairings in the central main basin, six had overlap indices of less than 30%, and just one was significant (walleye with lake trout) with an overlap value of just over 60%. The relatively high overlap between walleye and lake trout was consistent across regions, significantly overlapping in the central main basin, and having nearly significant overlap in the North Channel and the southern main basin.

Detailed trends for lake trout and lake whitefish

As total length increased in lake trout, the diet became more diverse across all regions (Figure 2.6a). Larger bodied fish like burbot, lake whitefish, and gizzard shad were consumed by the largest lake trout, and smaller lake trout showed the highest reliance on rainbow smelt. There were differences by region in the prey types eaten by the largest lake trout. Even within the main basin, the largest lake trout ate more burbot in the north, lake whitefish in the central region, and gizzard shad in the south. Alewife contributed consistently among size classes of lake trout in Georgian Bay. Across basins, round goby were eaten by all size classes of lake trout in all basins, though their biomass contribution increased with lake trout size in the central main basin but decreased with size in Georgian Bay. These were replaced by a decrease in the proportion of rainbow smelt and an increase in the proportion of alewife in these two basins, respectively.

Lake whitefish consumed a higher biomass of round goby as they increased in length in all basins, but especially in Georgian Bay and the central main basin (Figure 2.6b). Sampled lake whitefish increased in size over time, including in the central main basin ($R^2 = 0.025$, $F(1,268)= 7.93$, $p<0.05$) and Georgian Bay ($R^2 = 0.010$, $F(1,1381)= 15.1$, $p<0.001$), where lake whitefish increasingly consumed round goby over time (Figure 2.7b). The proportion of lake whitefish consuming fish in the central main basin significantly increased between 2004 to 2019 (R^2 0.388, $F(1,9) = 7.351$ $p < 0.05$) and had exceeded 20% since 2011. Lake whitefish also had increased proportions of round goby in their diets over time when controlling for body size. The largest fish (501-700mm) had an increased biomass proportion of round goby in their diet from 2004-2019 ($R^2 = 0.462$, $F(1,9) = 9.596$ $p < 0.05$).

Generally, dreissenid mussel proportion in the diet increased with size of lake whitefish size and were comparatively rare in diets of lake whitefish that were <300 mm in total length. Within the main basin, where dreissenids contributed the most to lake whitefish diet, all sizes consumed them but the proportion was still lower in smaller individuals (<300 mm). In the North Channel, dreissenid mussels were only found in the stomachs of the largest lake whitefish and were not detected in smaller lake whitefish. In the North Channel, the consumption of *Diporeia spp*. was much greater for smaller lake whitefish and dropped off entirely with increasing lake whitefish length.

There were some subtle trends in lake trout diets by season (Figure A1.4). As winter and fall had smaller sample sizes, or were not sampled at all for some regions, detection of detailed trends was difficult. *Coregonus* consumption by lake trout tended to be the highest in the fall, especially noticeable in the North Channel and southern main basin. In three of the four regions where lake whitefish were a detectable part of the lake trout diet, they contributed more during the spring than during the summer. In the northern main basin, consumption of lake whitefish by lake trout was higher in the summer versus the spring. Gizzard shad were only consumed in the winter in the southern main basin and almost exclusively by lake trout >600 mm total length.

Lake whitefish seasonal diet patterns revealed higher consumption of *Bythotrephes* in the summer and fall compared to the winter and spring (Figure A1.4). Dreissenid mussels were consumed slightly more in spring than in summer in the main basin, making up 88% of the spring biomass in the southern main basin. In the North Channel, where fewer dreissenids were consumed, the spring diet of lake whitefish had a higher contribution from molluscs. In the North Channel and the northern main basin, deep water amphipods were consumed slightly more by lake whitefish in the summer than other seasons.

Lake trout diets varied among years (Figure 2.7a). In Georgian Bay, the consumption of alewife by lake trout decreased from a relative high in 2007 (72% of the diet) to less than 10% annually since 2016. In the central and southern main basins, the biomass of round goby consumed was variable. Round goby were detected in lake trout diets in the earliest years of the diet study, and averaged 44% of diet biomass in the central main basin and 17% in the southern main basin between 2005 and 2010. Consumption of round goby by lake trout dropped in 2013 (< 6 % for either region) and increased again in 2017-2018 (> 27 % for both regions). In the southern main basin, lake trout consumed deepwater chub (cisco species other than *Coregonus artedi*) at an increasing rate since 2012. Rainbow smelt consumption by lake trout across regions was fairly consistent, especially in the North Channel where it remained the primary food source through 2019 (87-99% of the diet biomass). Most of the burbot consumed by lake trout occurred in the recent years in the central main basin, but in the early years in Georgian Bay. Consumption of lake whitefish by lake trout was mostly found in the first few years of the study with only two samples occurring since 2009.

There were differences overtime in the diets of lake whitefish (Figure 2.7b), especially in the consumption of round goby. An increasing trend in diet biomass of round goby was especially prominent in the central main basin, exceeding 87% of the entire diet biomass in 2014-2016; similar trends were seen in Georgian Bay. Dreissenid mussels were a consistent contributor to lake whitefish diet in the southern main basin since 2005, ranging between 44-97% of the annual diet biomass. In Georgian Bay and central main basin, however, dreissenid mussel biomass in the diet of lake whitefish declined in 2015 and 2013, respectively. In the North Channel, deep-water amphipods were observed in the diet of lake whitefish intermittently, including in 2019 after 2 years of not being detected.

2.5 Discussion

In my comprehensive study of the stomach contents of fish collected across the Ontario waters of Lake Huron, I found that diets of the five focal species varied regionally, likely reflective of prey distributions and food web changes following a regime shift. Native species were relatively uncommon in fish diets, varying depending on predator species and region. Among the five predators, lake whitefish diets were the most diverse and differed substantially among regions, with diets containing higher proportions of native species In the North Channel and northern main basin. As such, lake whitefish diets in these northern regions of the lake may be more representative of historical lake whitefish diets. Conversely, lake whitefish diets in the central and southern main basin were dominated by invasive species. Dreissenid mussels were the predominant prey type for lake whitefish in the southern main basin, which has implications for condition and growth given the poor energy density of dreissenid mussels relative to native sources of prey such as *Diporeia* spp. (Rennie et al. 2009b, Pothoven and Madenjian, 2013). In the central main basin, round goby were the primary prey by biomass of lake whitefish, where they were also the dominant prey in the diets of lake trout and walleye. Overall, round goby were consumed by all five predators in all five regions examined. A major change to the prey fish community associated with the regime shift was the 2003 collapse of alewife populations, a previously common prey for predatory fish. In the near-absence of alewife, another non-native species, rainbow smelt were the dominant prey in the diet of chinook salmon and lake trout, which drove high levels of overlap between the two predators, especially outside of the main basin.

Invasive species were a prominent component of the diet of all species, with almost half of all fish with stomach contents containing at least one invasive prey item. Except for lake whitefish in the North Channel and northern main basin, fish diets were >50% invasive species by biomass. Regionally, fish in the central main basin had the highest occurrence of invasives in the diet, with all five predators having >80% of the diet biomass comprised of non-native species. Overall, the proportion of invasive species in the offshore prey fish community has continued to decline since a peak in 2005 (Riley et al. 2020), and native species like bloater have been reported to account for 90% of the main basins offshore prey fish biomass (O’Brien et al. 2023). Thus, it is surprising that piscivore diets continue to be made up of such high proportions of non-native species. This dominance of invasive species in the diet reflects the changes that have occurred in this dynamic food web, and the capacity of predators to consume novel prey. Individuals that had opportunistically switched to feeding on invasive species may have incurred a fitness advantage relative to those species that weren’t able to adapt to novel prey (Carlsson et al. 2009). However, invasive species are also associated with decreased biodiversity in ecosystems, and these simplified communities are even more vulnerable to future invasions and increased likelihood of system destabilization or collapse (McCann, 2000). Furthermore, while the inclusion of invasive species in the diet could indicate the resilience of these fish to adapt to a continually changing environment, the growth, health, and reproductive consequences to the consumer population remain to be fully explored. The results from this study provide insight into diet outcomes of key predators in an ecosystem prone to invasions.

Round goby were a prominent invasive prey species in my study, consumed by all five predators in all five regions. Overall, round goby made up the highest percentage of known diet biomass for rainbow trout and lake whitefish (37% and 29%;). For lake trout, lake whitefish, and walleye in the central main basin, round goby were the most important prey item using IRI, and contributed more to diet biomass than elsewhere, and influencing the high level of diet overlap between lake trout and walleye (Figure 2.5). Previous studies have also found that lake trout and walleye consumed more round goby in the central main basin than in the northern main basin and Saginaw Bay (Happel et al. 2022; Pothoven et al. 2017). Walleye and lake trout from western Lake Huron were found to rapidly shift their diets to include round goby following the alewife collapse during the regime shift (Fielder and Thomas, 2006; Dobiesz, 2003; Roseman et al. 2014). Predators in other systems have also quickly altered their diets to consume round goby, including cod (*Gadus morhua*) and perch (*Perca fluviatilis*) from the Baltic Sea, where, following their invasion in the 1980’s, gobies became the dominant prey type for both predators by 2006 (Almqvist et al. 2010). Round goby abundance in Lake Huron increased in 2021 compared to 2019-2020 in the main basin as estimated by bottom trawl surveys (O'Brien et al. 2023), though the robustness of these estimates are questionable because bottom trawls cannot sample in shallow or rocky areas where round gobies are often found (Ray and Corkum, 2001). The main basin might have more suitable habitat for round goby, which show a preference for rocky substrates as well as a proximity to pelagic habitats (Cooper et al. 2009). Further research is needed to evaluate the extent to which regional variation in predator diets are driven by preferences for particular prey items and/or prey distributions and availability.

The round goby prevalence in the diet of lake whitefish was notable, as prior to the 1980's, less than 0.1% of the diet biomass of lake whitefish in South Bay, Lake Huron was comprised of fish which were considered "incidental" (Ihssen et al. 1981). Lake Huron lake whitefish diet was historically dominated by amphipods, dipterans, and native molluscs (Ihssen et al. 1981, McNickle et al. 2006). Round gobies were first detected in Lake Huron in 1997 (Schaeffer et al. 2005) and showed a peak in their relative density as estimated by bottom-trawl surveys in 2003 yet were uncommon in lake whitefish stomachs before 2007 (Pothoven and Madenjian 2013). In the main basin, a shift towards piscivory by lake whitefish was also described by Pothoven and Madenjian (2013), who found the percentage of adult whitefish that had eaten fish increased from 10% in 2002-2006 to 20% in 2007-2011. While lake whitefish may have shown a period of transition towards consuming round gobies, lake trout consumed larger quantities of this novel prey item earlier in the time series. Specifically, diets of lake trout in the central main basin were 32% round goby biomass in 2005, the first year of this diet study in the region. Brownscombe and Fox (2013) describe a necessary learning period for predators to incorporate round gobies as novel prey. The physical resemblance of non-native prey to native prey species likely increases predation rates (Sih et al. 2010), and round goby in lakes Huron and Michigan have been observed outcompeting multiple sculpin species previously eaten by lake trout which have similar body forms and habitats as round goby (Lauer et al. 2004; Volkel et al. 2021; Eshenroder and Burnham-Curtis, 1999). The difference between lake trout and lake whitefish in their apparent learning period could be that lake trout were already eating a high proportion of prey fish, some of which resembled round goby, whereas lake whitefish ate mostly invertebrates and thus required more time to adjust to eating a prey fish that was very dissimilar to their native diet. Notably, lake whitefish body size was on average larger in recent years compared to the beginning of the time series, and sampled fish were older, likely related to fewer younger fish in the population as recruitment declined or due to density-dependent increases in growth as population abundance declined (Cottrill et al. 2020).Nonetheless, it is remarkable that in two regions of the lake, lake whitefish were able to eventually switch from an invertebrate-based diet to a diet dominated by a prey fish that has only been present in the lake for a little over 20 years.

Examining the diet of lake whitefish is particularly important given their widespread declines in lake whitefish abundance, biomass, recruitment, growth, and condition (Fera et al. 2015; Gobin et al. 2016; Fera, 2017; Cunningham and Dunlop, 2023). My study found that lake whitefish diets had greater diet diversity than the other key predators and that dominant prey types varied by region. Lake whitefish diets from the northern main basin and North Channel were more diverse and included higher proportions of native species than the other areas, for example including *Diporeia* spp. Prior to the dreissenid mussel invasion, *Diporeia* spp. contributed 82% of the stomach contents volume of lake whitefish in South Bay (Ihssen et al. 1981) and likely were important lake-wide (Nalepa et al. 2005). Conversely, in my study, *Diporeia* made up 2 and 12% of the lake whitefish diet biomass in the northern main basin and North Channel, respectively, and were not detectable elsewhere. *Diporeia* spp. dramatically declined and experienced a spatial contraction as dreissenid mussels spread across all of the Great Lakes except Lake Superior (Nalepa et al. 2005, Pothoven and Nalepa, 2006). The North Channel has low levels of calcium, resulting in very low habitat suitability for zebra mussels (Therriault et al. 2012; Kirkendall et al. 2021), perhaps facilitating the continued survival of *Diporeia* spp. in this part of the lake. Lake whitefish diets in the southern main basin were dominated by dreissenid mussels, 59% by weight and 90% of the IRI, likely reflecting higher dreissend densities in that region (Nalepa et al. 2015). Pothoven and Madenjian (2008) also observed a high rate of consumption of dreissenids by lake whitefish in the southern main basin. A shift from a typical pre-invasion diet dominated by *Diporeia* to a diverse post-invasion diet containing dreissenids resulted in an estimated 57% decrease in energy content (McNickle et al. 2006), as per gram, dreissenid mussels contain just 7% of the energy density of *Diporeia* (Hanson et al. 1997; Eggleton and Schramm, 2004). Consumption of the nutritionally poorer dreissenid mussels were associated with diminished condition, growth, and altered maturation schedules (Pothoven and Madenjian, 2013; Rennie et al. 2009b). The shift to round goby consumption in the central main basin and Georgian Bay could furthermore affect growth, potentially allowing lake whitefish to attain pre-dreissenid growth rates, though capture efficiency and mouth morphology may dampen this benefit (Pothoven and Madenjian, 2013). However, any potential benefits would likely be restricted to mature lake whitefish; of the lake whitefish in the dataset that consumed round goby, 97% were longer than 400mm or approximately 800g. Thus, we could expect regional variation in life history trends of lake whitefish based on the very different diets we observed across Lake Huron, with implications for recruitment and sustainable harvest rates.

Another potential concern associated with a lake whitefish diet high in dreissenids is the potential for thiamine deficiency. Dreissenid mussels have been shown to have elevated levels of thiaminase (Tillitt et al. 2009), which could lead to thiamine deficiency and impaired recruitment in fish that consume them (Fisher et al. 1996). Thiaminase activities in zebra and quagga mussels were found to vary seasonally and spatially within the Great Lakes (Tillitt et al. 2009). Quagga mussels, for example, had the highest levels in the spring, followed by the summer and then fall (Tillitt et al. 2009). The implications for lake whitefish remain poorly understood, however, as thresholds for effects of low thiamine on embryos and larvae have not been established for the species. Furthermore, thiamine levels in lake whitefish eggs were the highest in Lake Huron and lower in Lake Superior (despite high and low abundances of dreissenids, respectively) and there appeared to be poor correspondence between dreissenids in the diet and thiamine levels in lake whitefish eggs (Riley et al. 2011). Further research may determine the implications of consuming a diet high in dreissenid mussels on thiamine levels and impaired recruitment in lake whitefish.

This study provides information on the potential for interactions between lake trout and lake whitefish. Saugeen Ojibway Nation (SON), comprised of two sister First Nations within the Saugeen (Bruce) Peninsula between Lake Huron's main basin and Georgian Bay, have expressed concern that the decline in lake whitefish can be attributed to predation by or competition with lake trout (Gobin et al. 2023, Almack et al. 2023). This study represents the Western science component of a collaborative two-eyed seeing project that brings together SON, the Ontario Ministry of Natural Resources and Forestry, and academic partners to use both Western science and Indigenous Ecological Knowledge (IEK) to better understand the interactions between lake trout and lake whitefish. Similar concerns have also been raised more broadly by commercial harvesters in lakes Huron and Michigan (Ebener et al. 2021). In my study, I found that while the degree of diet overlap between lake whitefish and lake trout was overall low, though there was variation among different regions of the lake. Diet overlap between lake trout and lake whitefish was higher in the central main basin than elsewhere (Figure 2.5), influenced by the common high levels of round goby consumption. The only other common prey items between lake trout and lake whitefish in this region were rainbow smelt and sticklebacks, which were only rarely eaten by lake whitefish.

Predation on lake whitefish by lake trout was also overall low. Lake whitefish contributed the most to lake trout diet in the central main basin, but only accounted for 5% of the diet biomass and with an IRI of 0.05 %. In the other four regions, lake whitefish as a proportion of lake trout diet biomass ranged between 0.4 and 1.1%. These findings were consistent with those from Roseman et al. (2014), who found lake whitefish comprised less than 1% of the diet biomass and were consumed by fewer than 1% of lake trout in the main basin of Lake Huron. None of the other predators in my study consumed any identifiable lake whitefish, and only consumed relatively small numbers of unknown coregonines. Notably, consumption of lake whitefish by lake trout increased with consumer length. For lake trout >800mm in total length, 19% of the diet biomass was lake whitefish, however, this biomass was from 2 individual lake whitefish. With the few lake whitefish that were eaten, and the small proportion of individual lake trout that preyed on lake whitefish, the IRI indicated that lake whitefish contributed minimally to the diet of lake trout. Also, most of the whitefish predation observed was for the earlier portion of the time series – 2009 or earlier. If lake trout predation was a primary cause of declining whitefish recruitment, we would expect to see continued predation on whitefish by lake trout. Notably, the sampling of lake trout and lake whitefish were biased towards summer (e.g, only 4% of stomachs were collected in the winter) so it is possible there are seasonal effects that were not detected. The largest lake trout sizes (>800 mm) were less represented and very large lake trout (>1000 mm) were virtually absent from the sampling. Predation by these rarer individuals on lake whitefish may occur at a higher rate and be more memorable among harvesters, leading to their concerns about the role of lake trout in the lake whitefish declines. Lake trout in the diet database were slightly larger on average in recent years compared to earlier years of the study, this increase may be related to improved body condition of lake trout after 2007 and through 2011 reported by He et al. following the alewife collapse, but body condition of lake trout was still lower than peak levels in the 1970's and 1980's (2016). Importantly, the relatively low rate of predation observed should be placed into the context of overall mortality of lake whitefish from sources outside of lake trout predation and requires further analysis.

My study found high levels of dietary overlap between chinook salmon and lake trout, the two top predators in Lake Huron, especially in the North Channel and Georgian Bay where both species heavily relied on rainbow smelt (Fig. 2.6 and 2.7). Rainbow smelt were the primary prey fish consumed by chinook salmon and exceeded 78% of the diet biomass in all regions. Diet overlap between predators is important when considering a changed environment with prey abundance concerns, like Lake Huron, because overlap can be associated with competition, which at high levels can leave individuals or species vulnerable to food limitation (Werner and Hall, 1979). However, without an analysis of chinook salmon and lake trout abundance versus abundance of all potential prey, it is not known whether the high diet overlap between these species is an indicator of competition (Jacobs et al. 2010). Diet similarity of lake trout and chinook salmon was also documented in an angler-caught predator diet study by Diana (1990) in the United States waters of Lake Huron's main basin, though in their study, alewife were abundant at the time and were a primary diet item. Given the crash of alewife in 2003 in Lake Huron (Riley et al. 2008; Bence et al. 2008; Dunlop and Riley, 2013), I found very little alewife in any of the fish diets, which is likely beneficial to species such as lake trout known to experience thiamine deficiency complex (or early mortality syndrome) when consuming alewife that are high in thiaminase (Fitzsimons et al. 2005; Johnson et al. 2015).

Of the species in my study, chinook salmon had the least variation in diet across regions of the lake with most of the diet consisting of rainbow smelt and some *Coregonus* spp. Lake trout diets were more diverse than chinook salmon, including higher biomass contributions by alewife, *Coregonus* spp., deepwater chub, and round goby. The diets of lake trout and chinook salmon were more diverse in the central and southern main basin, where they included more *Coregonus* spp., deepwater chub (includes bloater), round goby, and yellow perch (*Perca flavescens*) than elsewhere. As a result of a higher diet diversity in the southern and central main basin, diet overlap values were lower in these regions (42 and 62% respectively). Interestingly the highest population abundances of rainbow smelt occur in the North Channel and Georgian Bay (O’Brien et al. 2018), which is where lake trout and chinook salmon had higher levels of rainbow smelt consumption. The heavy reliance on rainbow smelt could negatively impact chinook salmon and lake trout growth and condition if adult rainbow smelt biomass continues to decline as it has since the 1990s (Riley et al. 2020). The regionally high overlap between top predators, lack of diet diversity, and declining biomass of the key prey item may warrant additional management attention when considering potential prey limitations.

An interesting finding of my study was the occurrence of often large numbers of *Bythotrephes*, another invasive species, in the diet of chinook salmon. In Georgian Bay and the central and southern main basins, 5-17% of sampled chinook salmon had eaten *Bythotrephes*, with an average consumption of 743 individual *Bythotrephes* each. Sheer numbers consumed and the proportion of fish that consumed *Bythotrephes* contributed to their overall importance (%IRI) in the chinook salmon diet; 36% in Georgian Bay and 34% in the central main basin (Figure 2.4). Roseman et al. (2014) reported similar findings in their study in western Lake Huron, with 21% of chinook salmon eating *Bythotrephes*. Jacobs et al. (2013) found *Bythotrephes* were often present in large numbers in chinook salmon diets, and with few or no other prey items in the stomach, indicating intentional rather than inadvertent consumption in Lake Michigan. Additionally, in my study, *Bythotrephes* in predator stomachs were counted using eye spots rather than the caudal spines that are largely indigestible (Parker Stetter et al. 2005), and thus should not be overrepresented in the diet. *Bythotrephes* were also the most important prey item for rainbow trout using the index of relative importance across the three sampled regions, and %W contributions were similar or higher than those reported by Roseman et al. from western Lake Huron fish (2014). *Bythotrephes* are relatively low in energetic value (1,674 J/g) compared to fish (4,240 J/g) or even other invertebrates like *Diporeia* (4,185 J/g; Pothoven and Madenjian, 2008). *Bythotrephes* are a nutritionally poor diet substitute for other pelagic prey (Parker Stetter et al. 2015), and as chinook salmon face potential prey limitation with the declines in prey fish populations, diets may not be sufficient to maintain body growth (Roseman and Riley, 2009; Johnson et al. 2010).

A potential bias in my study, as in most diet studies, lies in the accuracy of prey identification, which is related to the state of digestion or body features of the prey (Carreon-Martinez et al. 2011). Prey size is positively correlated with residence time in the stomach (Chapman et al. 1989), thus large-bodied fish prey may be overrepresented when compared to small-bodied fish or soft-bodied invertebrates in gut contents (Hyslop, 1980). Additionally, food items like molluscs with digestion-resistant hard structures have prolonged residence time in a stomach, and therefore can be overrepresented compared to an organism that digests quickly (Walsh et al. 2007). In my study, I found a fairly large proportion of the diet was made up of unidentified prey items (for example, 55% of diet biomass for walleye and 35% for chinook salmon). My assumption is that those unidentified prey have a similar ratio to the stomach contents that were positively identified, however, this may not always be the case if certain prey were more readily identifiable based on their features or digestion rates. Further studies could employ the use of DNA barcoding applied to stomach contents to help reveal the biases in stomach content analysis, or to include measures of diet based on stable isotopes (Carreon-Martinez et al. 2011; Kelling et al. 2016; Mumby et al. 2018). Stable isotopes are coarse taxonomically but integrative over time compared to stomach contents, which are more precise taxonomically but specific over time, so each method offers tradeoffs in understanding the energetic sources used by individuals and populations.

Previous fish diet studies on Lake Huron have generally been limited to the US waters (i.e., western side) of the main basin (Roseman et al. 2014) or are focused on a particular consumer species (Pothoven and Madenjian, 2013; Pothoven et al. 2017; Happel et al. 2018). The regional variation found in fish diets across Lake Huron underscores the importance of including spatial stratification when conducting stomach content analyses. Regional prey usage can be used to inform bioenergetics or ecosystem models that help to understand predator/prey imbalance or explore the effects of management scenarios on fish populations (e.g., Dobiesz, 2003). This is particularly important considering the significant declines in productivity that have occurred in Lake Huron over the past 20 years (Rudstam et al. 2020; Barbiero et al. 2011). Continuing to assess predator populations and diets though long-term monitoring programs can be used to describe important linkages in the food web and can help quantify system-level responses to the broad ecological changes occurring in Lake Huron.

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Table 2.1. Numbers of fish with stomachs removed and contents identified for five fish species in Lake Huron. Regions are listed geographically from North to South; NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, SMB= southern main basin. Species names are abbreviated; CS= chinook salmon, LT= lake trout, LW= lake whitefish, RT= rainbow trout, WL= walleye.

	Region	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**
CS	NC						15	28	11	27	3	1					
	GB			2	5	2	23	6	1	182	18	142	196	376	323	346	348
	NMB							5									
	CMB			5	8	7	11	27	12	22	40	14	10	18	26	13	71
	SMB		12	10	2	29	37	13	4		6		1	3	1		1
LT	NC					22	69	64	213	89	171	105	197	147	136	72	69
	GB	65	23	106	63	59	72	133	168	98	202	153	323	275	743	624	676
	NMB				36	35	39	64	142	119	97	10	50	29		35	
	CMB		48	65	59	65	57	64	28	47	48	82	154	166	179	197	164
	SMB		42	89	64	112	27	12	263	35	67	67	55	60	18	84	46
LW	NC		32	22			58		64	110	220	99	143	124	32	56	57
	GB	1	36	56	103	61	141	215	121	162	198	113	98	71	31	42	33
	NMB		16		19	51	34	32	228	42	52	10	15	10	6	26	
	CMB	11	21	68	46	42	66	4	44	21	32	34	15	12	1	14	9
	SMB		41	158	91	106	33	1	257	80	58	93	61	73	60	106	41
RT	NC												31	17	2		1
	GB			1						2	1	35	74	54	41	72	24
	NMB																
	CMB							16		1	16	7	10	22	19	13	24
	SMB											2	1	1			
WL	NC						6				33	21	10	343	503	120	92
	GB						19	4	26	26	2	106	265	179	80	288	199
	NMB																
	CMB							3		1	2	2	3	32	9	4	6
	SMB						13	1	17	19	35	2	12	19	46	28	21

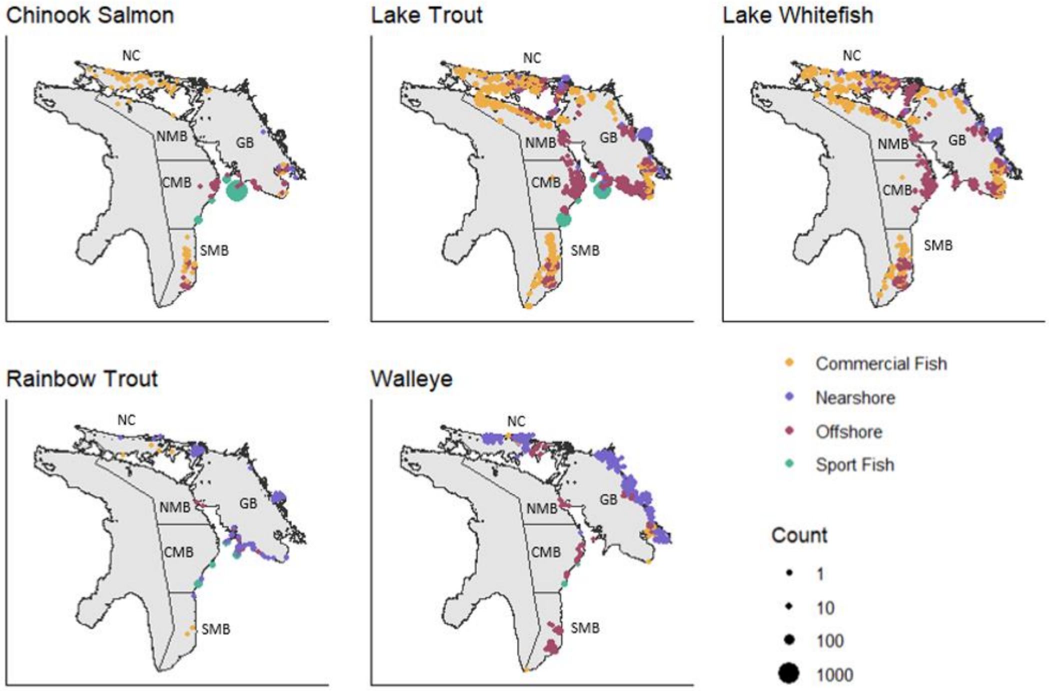

Figure 2.1. Map of Lake Huron showing catch locations by sampling program for fish stomachs used in the diet study. "Sport Fish" includes angling derbies, where fish are captured from a wider area and brought to a common location. The symbol size corresponds to sample size. Different regions are depicted including NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.

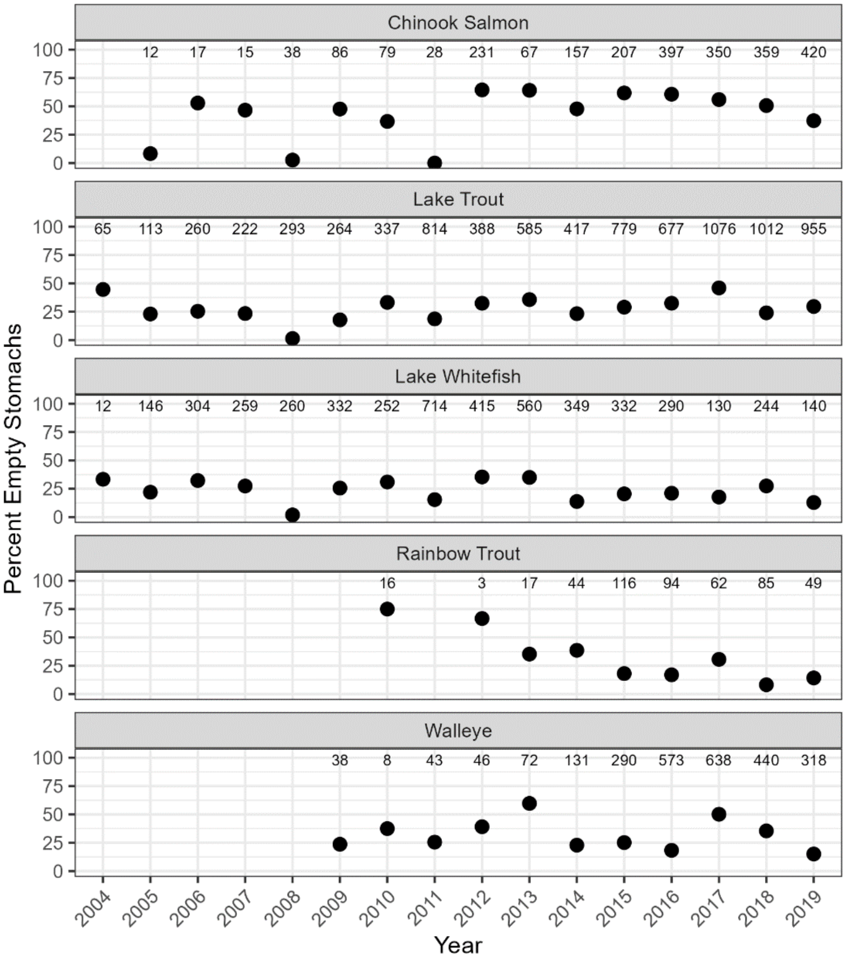

Figure 2.2. Proportion of empty stomachs by year. Proportions were calculated by grouping across regions by species (shown) and calculated again with regions separated. Different regions are depicted including NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.

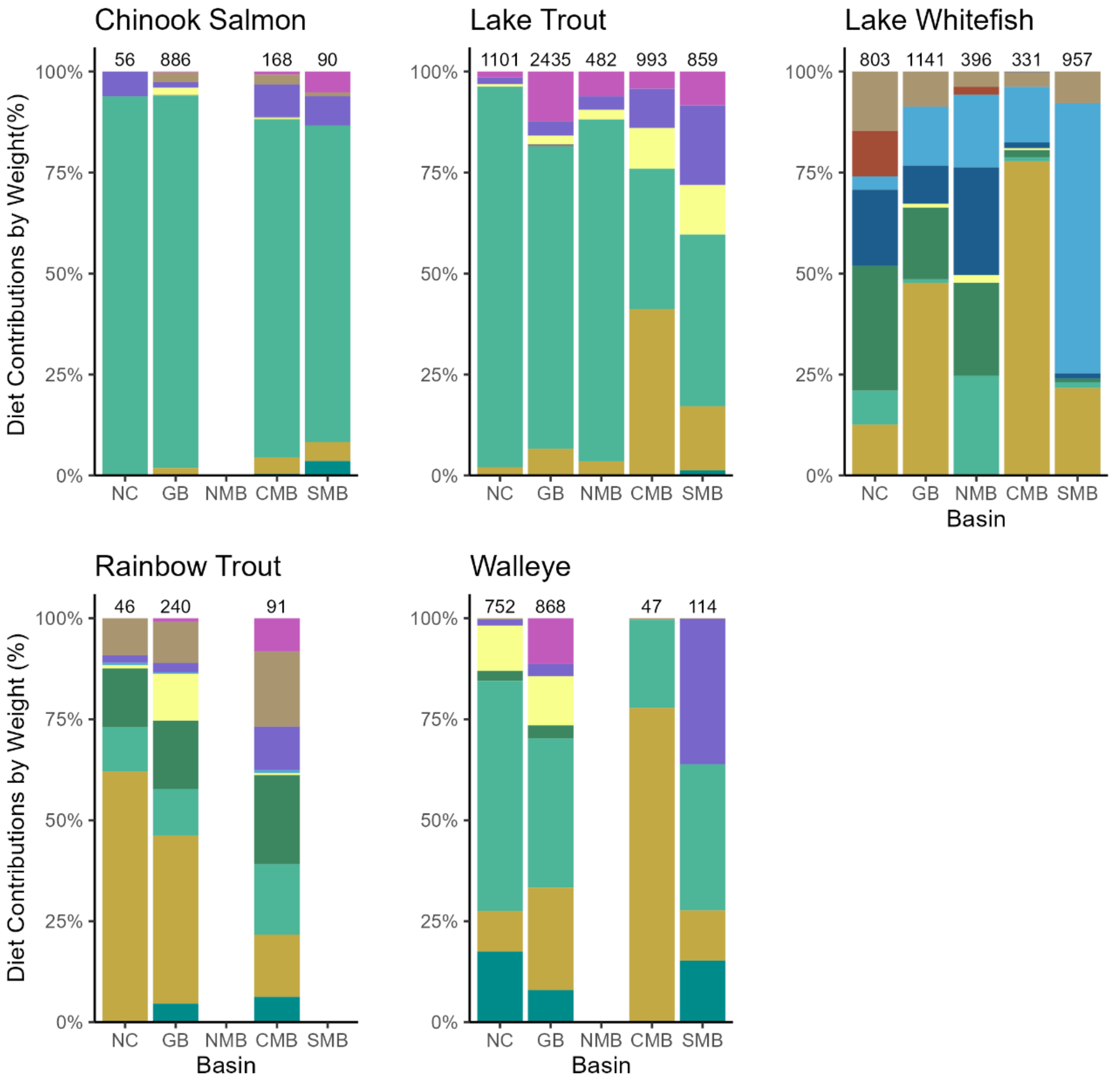

Figure 2.3. Predator diets showing percent contribution by mass of different prey groups from Lake Huron between 2004-2019 (samples pooled within species and region). Different regions are depicted including NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.

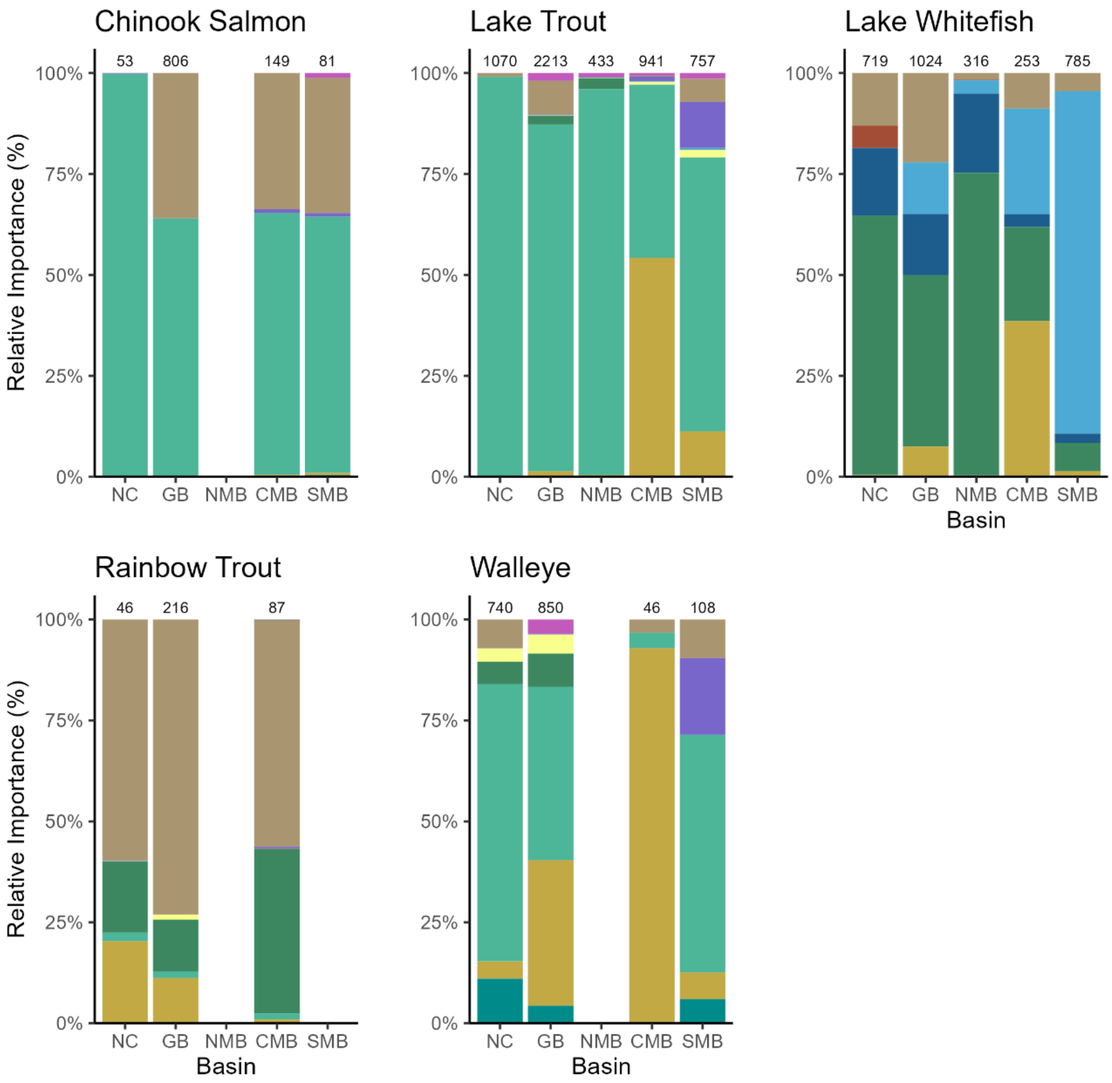

Figure 2.4. Predator diets showing percent contribution of relative importance (IRI %) of different prey types. Different regions are depicted including NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.

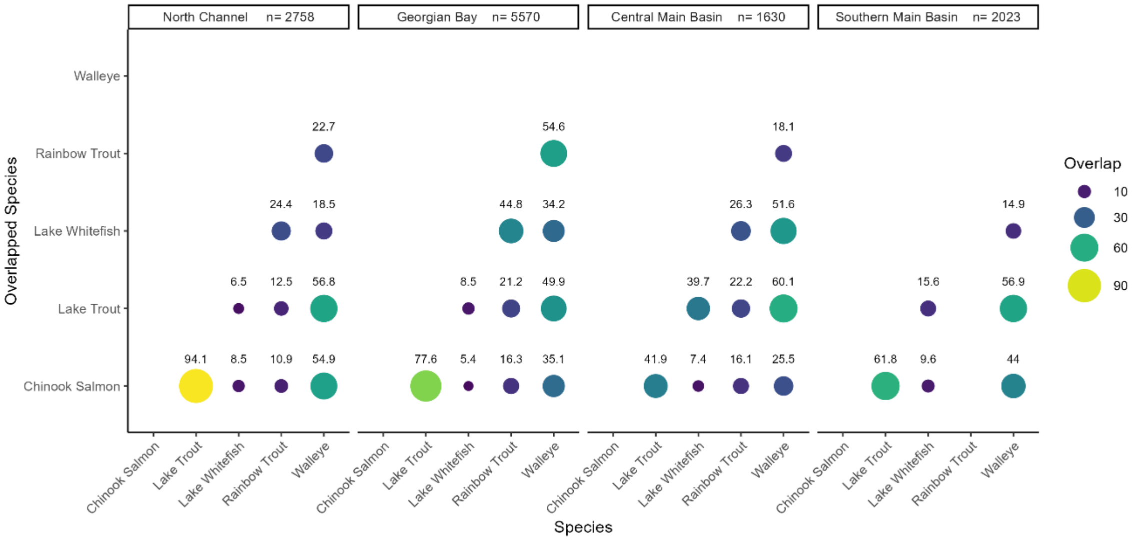

Figure 2.5. Schoener overlap indices by region. Each node between “Species” and “Overlapped Species” indicates the % overlap calculated between the diets. Values >60% are considered significant.

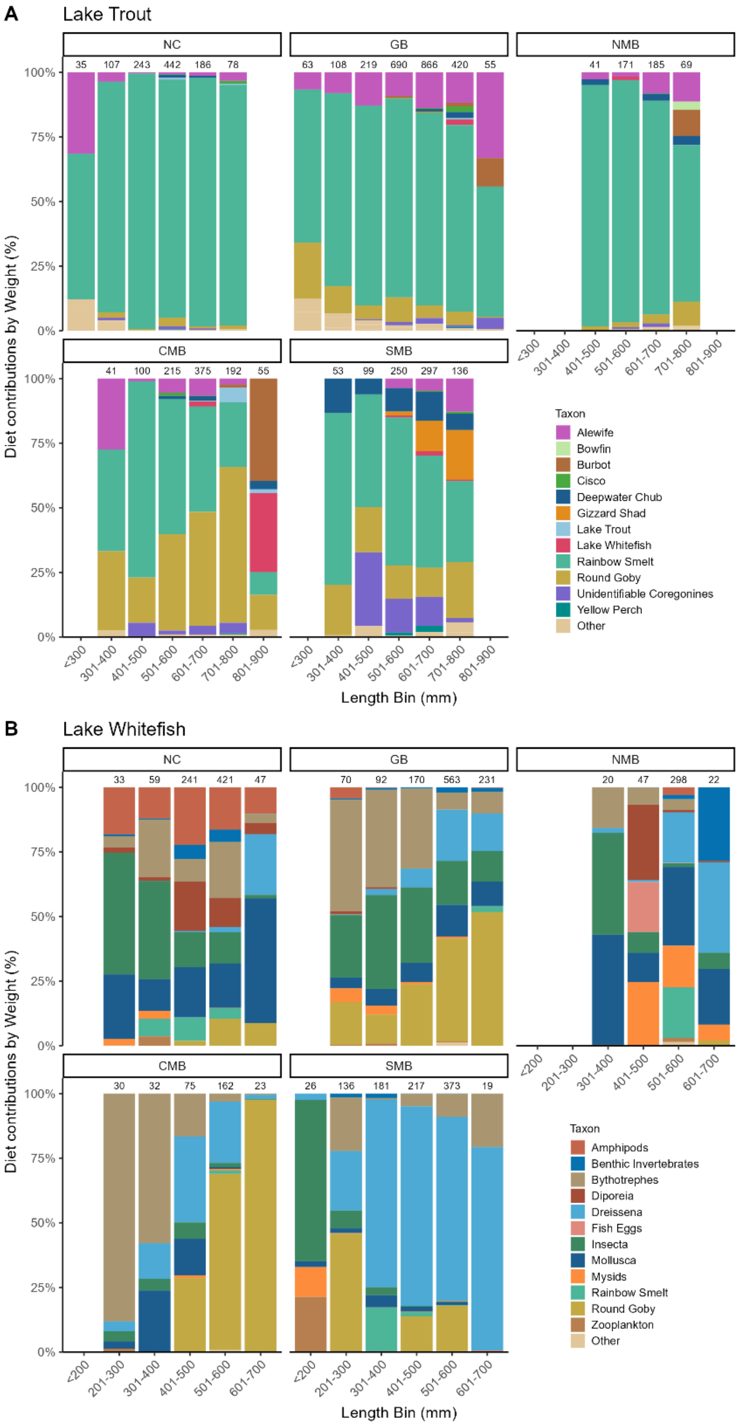

Figure 2.6. Percent contribution of prey mass by total length to diets of lake trout (panel A) and lake whitefish (panel B). Different regions are depicted including NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.

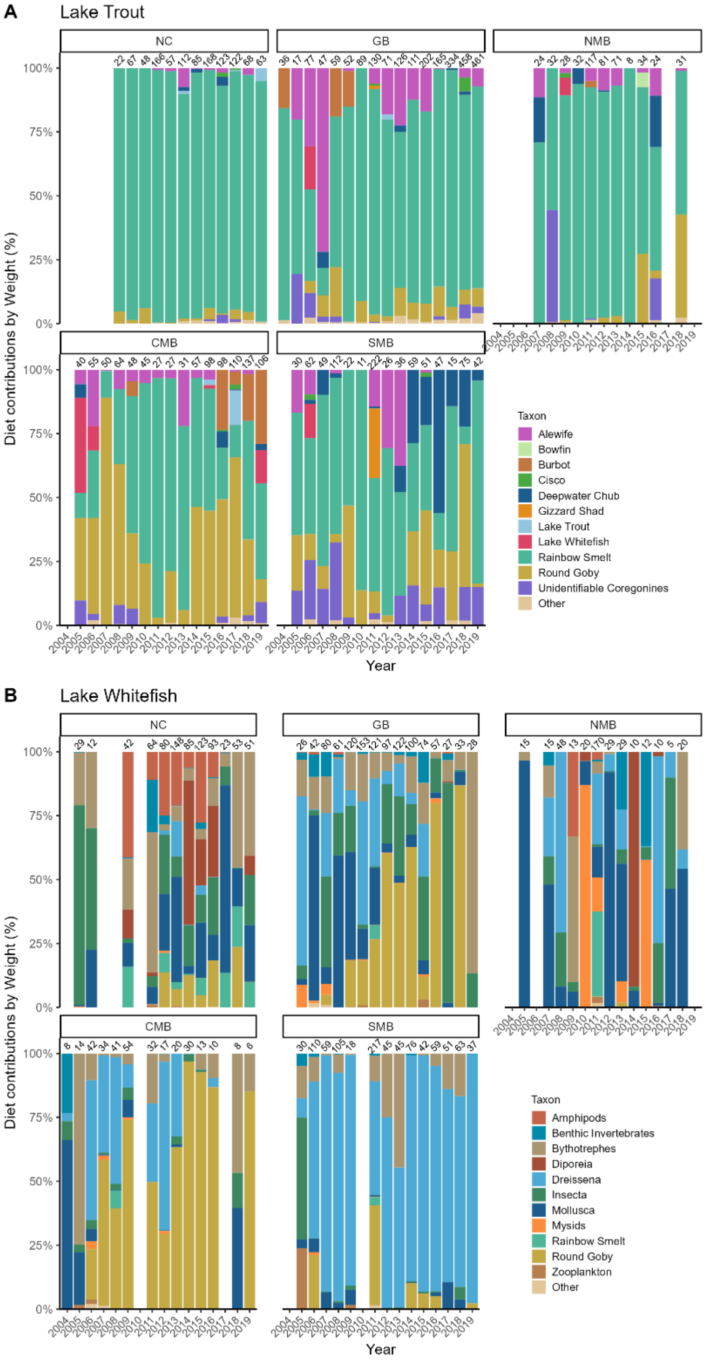

Figure 2.7. Percent contribution of prey mass by year to diets of lake trout (panel A) and lake whitefish (panel B). Different regions are depicted including NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.

Chapter 3: Regional isotopic niches of lake trout and lake whitefish following a regime shift in Lake Huron

3.1 Abstract

The trophic niches occupied by fish are expected to reflect food web characteristics and will vary based on stressors and ecosystem conditions. I investigated the trophic niches of two species of management importance, lake trout (*Salvelinus namaycush*) and lake whitefish (*Coregonus clupeaformis*), in Lake Huron where profound shifts in ecosystem productivity have occurred over the past 20 years. Lake trout populations, once largely extirpated from Lake Huron, have shown signs of recovery in some areas of the lake but not in others. Lake whitefish populations increased in abundance through the 1990's but have since undergone substantial declines in recruitment, condition, growth, abundance, and commercial yield. Saugeen Ojibway Nation knowledge holders identified interactions with lake trout as a possible factor contributing to the declines of lake whitefish. I compared the patterns in size and shape of the isotopic niches between lake trout and lake whitefish. I also describe the trophic positions of lake trout and lake whitefish across five regions of Lake Huron and used these findings to describe the potential for competition between the two species, and of predation of lake whitefish by lake trout. Lake whitefish had significantly broader niche sizes than lake trout, largely owing to a greater range of $\delta^{13}C$ in lake whitefish. Overlap values were generally considered low between the two species, ranging from 0.5- 32.8% of the lake whitefish niche falling within that of lake trout. Overlap was highest in Georgian Bay, indicating the greatest potential for competition among regions. Predation potential was the highest in the central and southern main basins, where lake trout have enrichment of

the $\delta^{15}N$ isotope consistent with one trophic level above lake whitefish. Lake whitefish had broader niches and energetic sources in the northern areas of the lake than lake whitefish from the southern areas of the lake, supported by diet data showing more diverse diets than in the southern areas where diets are dominated by invasive species. Lake trout niches indicate feeding significantly further nearshore in Georgian Bay than other regions, consistent with data showing the importance of round goby to the diets. While lake trout and lake whitefish do interact, I concluded that the amount of predation and competition overall was not of a strong enough magnitude to have greatly contributed to lake-wide declines of lake whitefish.

3.2 Introduction

Over the past two decades, the Lake Huron food web has experienced drastic changes across multiple trophic levels in response to anthropogenic stressors, such as climate change and invasive species. Broadly, these changes include declines in offshore productivity (Hecky and DePinto, 2020), changes to nutrient cycling (Hecky et al. 2004; Rennie et al. 2009a), and disruptions to lower food webs (Barbiero et al. 2018). These changes are suggestive of a “regime shift” (Barbiero et al. 2018; Rudstam et al. 2020), where the ecosystem transitions from one state to another, often associated with disturbance (Scheffer and Carpenter, 2003). Invasive dreissenid mussels acting as ecosystem engineers have been implicated in many of the recent changes in Lake

Huron; their ability to intercept and shunt nutrients towards the nearshore alters the resources available to species at broad spatial scales (Hecky et al. 2004).

Stable isotope analysis can be used to better understand food web structure and determine the assimilation of energy sources used by an animal (Hecky and Hesslein, 1995). This use of energetic sources as well as distribution of a species within an ecosystem can be conceptualized as a “trophic niche” or a “hypervolume” that is occupied by a population (Hutchingson, 1957). Using stable isotopes is useful for describing patterns in food webs, as an organism’s tissues can reflect an integrated signature of energy sources over longer time frames than are possible by using stomach contents for dietary studies (Vander Zanden et al. 2015). Additionally, dietary studies of fish populations from the Great Lakes tend to be biased towards catches from the open-water months of April- November because those are the months when agency monitoring programs that collect the data are typically conducted. Two common isotopes used to study the feeding ecology of freshwater fish are stable forms of Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$; Peterson and Fry, 1987; Vander Zanden and Rasmussen, 1999). Changes in the $\delta^{13}C$ and $\delta^{15}N$ ratio relative to an isotopic baseline can indicate resource use or trophic position of consumers (Post, 2002). From prey to predator, enrichment of the $\delta^{15}N$ to $\delta^{14}N$ ratio, compared to that of atmospheric nitrogen, can often be predicted (Canseco et al. 2022), and in aquatic systems, a 3‰-4‰ enrichment has been found consistent with one trophic level (Bearhop et al. 2004). There is also an increase in $\delta^{15}N$ with transition from shallower to deeper benthic regions (Vander Zanden and Rasmussen, 1999). Ratios of $\delta^{13}C$ to $\delta^{12}C$ relative to those found in the standard Pee Dee belemnite limestone remain relatively unchanged in the food chain, but can provide information about the energy pathways, for example from benthic or pelagic sources (Schmidt et al. 2007). As such, using stable isotopes provides an opportunity to detect shifts in trophic position, trophic niche size, overlap between species, and changes in food web structure (Wang et al. 2018).

Changes in isotopic values of fish have been documented in Lake Huron, including that of lake whitefish (Rennie et al. 2009a; Fera et al. 2017), a commercially fished species that are of significant cultural and economic importance to Indigenous communities in the Great Lakes region (Ebener et al. 2021; Almack et al. 2023). Lake whitefish populations have experienced decreases in abundance, growth, condition, and recruitment associated with the invasion of dreissenid mussels (Rennie et al. 2015; Gobin et al. 2016; Fera et al. 2017; Ebener et al. 2021). Associated with these declines are reported changes in the diet, depth distribution, and occupied isotopic niche of lake whitefish (Rennie et al. 2009b; Fera et al. 2017; Trumpickas et al. 2022). Lake-wide shifts of the lake whitefish niche towards the nearshore occurred within five years of dreissenid mussel invasion (Fera et al. 2017) and were accompanied by a shift in the mean capture depth towards shallower areas (Rennie et al. 2009b). In a multi-species study using samples collected over 70 years, lake whitefish niches in South Bay shifted further towards the nearshore than other species in the most recent time period (Trumpickas et al. 2022). Similar trends in isotopic niches and growth rates of lake whitefish have occurred across the Great Lakes except for Lake Superior where dreissenid mussels have not become well established (Fera et al. 2015, 2017).

Several shifts to the diet of lake whitefish in Lake Huron have been reported since 2003 when the regime shift occurred. A historically important prey item of juvenile and adult lake whitefish, *Diporeia*, experienced significant declines in distribution and density with increased abundance of dreissenid mussels (Pothoven and Nalepa, 2006). Consumption of the nutritionally poorer dreissenid mussels were associated with diminished condition, growth, and altered maturation schedules when compared with a diet high in *Diporeia* (Pothoven and Madenjian, 2013; Rennie et al. 2009). Regional consumption of *Diporeia* was recently documented in the North Channel and northern main basins of Lake Huron, totalling over 12% and 2% of the diet biomasses of lake whitefish respectively (Chapter 2; note also that this research is in press at the Journal of Great Lakes Research). In Georgian Bay and the central and southern main basins, *Diporeia* were not found in lake whitefish diets, but instead invasive species including round goby, dreissenid mussels and *Bythotrephes* were dominant (Chapter 2). The increased consumption of round goby by lake whitefish (Pothoven and Madenjian, 2013) may further influence the shift in the occupied niche of lake whitefish. Round goby has been identified as a driver of a shift towards a more nearshore diet in lake trout (Rush et al. 2012), but this has not been specifically examined in lake whitefish.

Concerns about the declines in lake whitefish are shared by management agencies and by Indigenous communities around lakes Huron and Michigan where the changes have been the most profound. On the Saugeen (Bruce) Peninsula, the Saugeen Ojibway Nation (SON), comprising two sister First Nations (the Chippewas of Nawash

Unceded First Nation and the Chippewas of Saugeen First Nation), have lived and fished throughout their traditional territory since time immemorial (Gobin and Lauzon, 2019). Lake whitefish are an essential part of the culture, diet, identity, and sovereignty of the SON (Gobin et al. 2023, Almack et al. 2023). To better understand fisheries concerns among community members, interviews and community meetings were held within SON, with the findings outlined in a publication by Gobin et al. (2023). One of the topics of concern brought forward was the stocking of lake trout, and the potential interactions between lake trout and lake whitefish that could be contributing to declines of lake whitefish. SON brought forward two hypotheses, (i) that lake trout were predating on lake whitefish; (ii) that there was competition for resources (e.g., food, habitat) between lake trout and lake whitefish (Almack et al. 2023). SON fish harvesters were reporting higher catches of lake trout, and a higher frequency of lake whitefish in the stomach contents of lake trout. Lake trout have been stocked into Lake Huron since the 1970's for rehabilitation following population declines and collapses in the 1940's (Eshenroder et al. 1995). SON community members expressed their concerns regarding ecosystem impacts of stocking predators into a lake with decreased productivity and less prey fish availability (Gobin et al. 2023). These concerns led to the creation of a collaborative two-eyed seeing project between SON, the Ontario Ministry of Natural Resources and Forestry and academic partners to use both western science and Indigenous ecological knowledge to explore the interactions between lake trout and lake whitefish. In using the two-eyed seeing approach, results obtained through the western science and the Indigenous Ecological lenses may differ. However, validating the results of one eye with the other or coming to conclusions about which perspective is correct is not part of the two-eyed seeing process. Instead, the goal is to co-produce knowledge, gain a broader understanding of the changing Lake Huron ecosystem, and to build and foster relationships between team members, MNRF, and SON. It is my hope that the collective knowledge will be used to inform fisheries management and conservation actions for lake whitefish in Lake Huron and to inform SON's and MNRF's fishery assessment programs.

Lake trout populations have shown signs of recovery in some parts of Lake Huron since 2004, but to varying degree (Lenart et al. 2020; Roseman et al. 2020). Improved natural reproduction may be partially due to the lack of alewife in the lake, as previously high consumption of these non-native planktivores created a thiamine deficiency in lake trout and resulted in poor egg quality (Riley et al. 2011). Alewife collapsed in Lake Huron in 2003 (Riley et al. 2008) and haven't recovered since. Wild recruitment of lake trout is highest in the western end of the North Channel and the northern and central areas of the main basin (Lenart et al. 2020). Natural reproduction of lake trout in the main basin made up 40-70% of the fishery in 2017, up from 12-52% during the 2005-2010 period (Lenart et al. 2020). Stocking from the main basin was then reallocated to prioritize rehabilitation zones in Georgian Bay and the North Channel (Lenart et al. 2020). However, populations of lake trout are still well below the fisheries management objectives for the lake (Lenart et al. 2020). In addition to lake trout, non-native chinook salmon are also stocked in lakes Huron and Michigan. An abundance of both native and stocked predators has led to concerns about the ability of the diminished prey base to support these predator populations (Paterson et al. 2008; Roseman et al. 2014). Populations of the once-dominant prey fish alewife decreased by up to 99% in 2003 (Bence et al. 2008; Riley et al. 2008) and was followed by massive reductions in offshore prey fish abundance, now at just 20% of the mean abundance reported between 1976 and 1996 (Riley et al. 2020). The native prey community has been largely absent from the diets of top predators (Roseman et al. 2014; Chapter 2), and the impacts to the niches of lake trout and lake whitefish are largely unexplored in Lake Huron outside of South Bay (Trumpickas et al. 2022).

In this study, I used several metrics to describe the isotopic niches of lake trout and lake whitefish across five regions of Lake Huron: the North Channel, Georgian Bay, and the main basin divided into northern, central, and southern areas (Figure 3.1). I used archived scale samples from over 950 fish collected between 2014-2022 as part of agency monitoring programs and from SON fish harvesters. With these samples I conducted stable isotope analyses (using $\delta^{13}C$ and $\delta^{15}N$) to calculate the niche size, an indicator of the breadth of resources used and the trophic position of fish in each region. As the diets of lake trout and lake whitefish vary regionally in Lake Huron (Chapter 2), their isotopic signatures may also differ. Environmental gradients and physiological processes including geology and temperature will influence the stable isotope ratios in an organism's tissue (Peterson and Fry, 1987). Isotopic gradients in the lake have been reported for carbon and nitrogen isotopic values, where both are increased with increasing latitude (Eberts et al. 2017).

I calculated the overlap between the niches of lake trout and lake whitefish in each region, which is a relative measure of the degree to which two species are obtaining their energy from similar sources and could be used to understand whether there is potential for competition (Hutchinson, 1957; Alley, 1982). I calculated the enrichment of lake trout $\delta^{15}N$ compared to lake whitefish to consider whether there is potential for lake trout to predate on lake whitefish, as one trophic level between prey and predator is often identified as a 3-4‰ increase in $\delta^{15}N$ (Peterson and Fry, 1987). These isotope metrics will provide an assessment of the degree of regional variation in isotopic niches and provide an evaluation of the potential for competition or predation between two important native fish species during an unprecedented time of ecosystem change.

3.3 Methods

Sample Collection

Scales were collected from lake trout and lake whitefish between 2014 and 2022 by the Upper Great Lakes Management Unit of the Ontario Ministry of Natural Resources and Forestry as part of their annual monitoring programs including sport fish (angler), commercial fisheries, and nearshore and offshore index netting surveys. Gill nets are the primary capture techniques used by nearshore, offshore, and commercial fishing programs. Fish associated with the sport fish programs are primarily caught by angling. Additional samples were collected by Saugeen Ojibway Nation commercial fishers between 2019 and 2022 using gill and trap nets. Scale samples were collected in all statistical districts in the Ontario waters of Lake Huron including the North Channel, Georgian Bay, and the main basin (Figure 3.1). Within each of the five regions, samples from all years were grouped. Sampling events and sample sizes vary by region based on survey schedules and relative abundances of fish. Scale samples were processed for isotopes for the same individual fish that I analyzed stomach content data for in Chapter 2.

Scale processing for stable isotope analysis

Scales were processed from one hundred (fewer if unavailable) randomly selected lake trout and lake whitefish per region. As fish scales grow throughout the lifetime of the fish, their use for isotopic analysis reflects the entire lifetime of diet sources of the fish, compared to using muscle or liver tissue used in other studies that reflects the diet consumed over the past few months (Weidel et al. 2011; Vander Zanden et al. 2015). Only scales from fish between the ages of 2 and 10 years were processed, a similar approach to Trumpickas et al. (2022), to reduce the impacts of ontogenetic diet shifts. Fish younger than 2 years old at the time of capture would not have undergone the ontogenetic shifts associated with adult feeding, and fish older than 10 could have experienced the pre-regime shift ecosystem if they were captured in 2014. The number of scales available per region reflect changes in netting effort, agency priorities, and changes to the fish community. In total, 951 scales were processed and underwent stable isotope analysis (Table 3.1). Scales were prepared for stable isotope analysis following Rennie et al. (2013). Scales were retrieved from storage scale envelopes, soaked in distilled water overnight, cleaned of residual soft tissue and dried for >4 hours at 60°C. The first two scale annuli were removed (using a modified 21G syringe for lake trout and a 2.5mm biopsy punch for lake whitefish), as both species undergo ontogenetic shifts (ie. from planktivore to either piscivore or benthivore). Remaining scale tissues were measured to weigh between 0.25-0.45mg and placed in a 5x3.5mm tin cup. Lake trout samples required one to eleven scales to achieve this weight, but lake whitefish samples were almost always cut from a single scale, or infrequently from two scales. Samples that were cut from a large lake whitefish scale were cut in a narrow wedge-shaped slice including representation from all annuli. Samples were sent to the Environmental Isotope Laboratory at University of Waterloo in Ontario. The analysis of solid materials for ^{13}C and ^{15}N isotope measurements was determined using a 4010 Elemental Analyzer (Costech Instruments, Italy) to combust the sample material and convert to gas, then sent through a coupled Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer (CFIRMS). Standard delta notation (δ) was used to report the per mil (parts per thousand, ‰) difference, against the primary reference scale of Vienna Pee Dee Belemnite (VPDB) for δ^{13}C and Atmospheric Air for δ^{15}N as follows:

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

Quality control checks reported an error of 0.2‰ δ^{13}C and 0.3‰ δ^{15}N.

Duplicate samples were processed for 86 randomly selected fish from both species and all regions to assess analytical precision. There were no significant differences for either $\delta^{13}C$ or $\delta^{15}N$ between duplicates (paired *t*-test across both species; $\delta^{13}C$: t = 0.424, p = 0.37. To avoid pseudoreplication, only one of these two duplicates was randomly selected for inclusion in the analyses outlined below. Isotopic values were not corrected to baseline values because samples of primary consumers (such as unionid mussels) were not available from the broad temporal and spatial range necessary to be informative. Lake trout and lake whitefish move broadly across Lake Huron, including among different basins and regions (Adlerstein et al. 2007; Eberts et al. 2017; Binder et al. 2017), and thus, applying regional baseline corrections would not have been appropriate or possible.

Statistical Analyses

All data collected for this project were entered and maintained in a Microsoft Access database and subsequently analyzed using the statistical software program R version 4.2.3 (R Core Team, 2023). The stable isotope dataset is available in the Supplementary Material Table S1. Potential outlier values were assessed using a one-sided Grubb's tests for both species within each region at a $p < .05$ significance level using the R package 'outliers' (Komsta, 2011). Outliers were removed, and the Grubb's test was re-run until no further outliers were identified. In total, 19 fish were removed as outliers (2%). Subsequent analyses were run including and excluding the outliers to assess the impacts to the overall conclusions.

To better understand the resource use and trophic ecology of the lake trout and lake whitefish across Lake Huron, I calculated the mean, standard deviation, and ranges of the $\delta^{13}C$ and $\delta^{15}N$ signatures. $\delta^{13}C$ becomes enriched (closer to 0, as $\delta^{13}C$ signatures are negative) when moving from offshore/pelagic to nearshore/benthic areas (Vander Zanden and Rasmussen, 1999). Comparing the mean $\delta^{13}C$ values of lake trout and lake whitefish provides an indication of which regions fish are deriving their energy (i.e., where in the environment they are feeding). $\delta^{15}N$ becomes enriched from prey to predator, so determining the population mean indicates from which trophic level the population is obtaining their energy from. Comparisons of $\delta^{15}N$ and $\delta^{13}C$ values were made between species, bin sizes and regions using three-factor Analysis of Variance (ANOVA) calculated in R. The criterion for significance was $p < 0.05$ (the significance level used for all statistical tests in my study). I performed a subsequent Tukey test if $\delta^{13}C$ or $\delta^{15}N$ values differed significantly by any factor or interaction (Table A2.1). Length bins for lake whitefish were < 450 mm in total length for small fish, and > 450 mm for large fish. For lake trout, the fish were in the small bin if < 550 mm in total length, and large if > 550 mm. Lengths of fish in each region varied, and the lengths of lake whitefish from the central main basin were not evenly distributed (Shapiro-Wilks, $W=0.96$, $p<0.05$), and had fewer fish <400mm ($n=23$). This lack of smaller fish is likely due to the widespread recruitment failures of lake whitefish over the past 20 years (Ebener et al. 2021), making it difficult to obtain smaller fish for samples. The lengths of lake whitefish in the other regions as well as lake trout from all regions were normally distributed, determined using Shapiro Wilks tests (W=0.996, p=0.45) for lake trout and (W=0.983, p=0.15) for lake whitefish.

Bivariate plots were also used to analyze enrichment relationships between lake trout and lake whitefish. The centroid of the bivariate plot provided the carbon and nitrogen means of each regional population of lake trout and lake whitefish. The enrichment values were the calculated differences between lake trout and lake whitefish for both carbon and nitrogen centroids from the bivariate plots (Table 3.2).

Carbon range and nitrogen range are defined as the spread of $\delta^{13}C$ and $\delta^{15}N$ values covered by the data points (Table 3.1). The carbon range can represent the breadth of the dietary carbon sources that a population uses, and the nitrogen ranges indicates the trophic levels that the population occupies (Layman et al. 2007). I used a paired t-test to compare the carbon and nitrogen ranges of lake trout and lake whitefish, using region as the paired variable.

Stable isotope Bayesian Ellipses in R (SIBER) in R version 4.2.3 (R Core Team, 2023) was used to estimate the regional isotopic niche areas for lake trout and lake whitefish (Jackson et al. 2011). I described niche size as a Bayesian standard ellipse area (SEA_B), and the Bayesian approach runs 10,000 iterations which allows for statistical comparison and calculates credible interval of niche sizes (Table 3.1). The SEA_B is a measure of niche size and increases with the use of isotopically diverse energy sources (Jackson et al. 2011). Bayesian statistics were used to calculate the likelihood (%) that the niche of one species would be smaller than the other. Within species, I also used the

Bayesian estimations to determine the likelihood that large fish have larger niches than smaller fish, and the likelihood that fish from one region have larger niches than in each of the other regions.

I described overlap between the niches of lake trout and lake whitefish using the fraction overlap between the niche sizes. The R package SIBER (Jackson et al. 2011) calculates the areas of niches for populations 1 and 2 as well as the area shared between the two niches; the shared area is then used as a proportion of either niche that is overlapping. This method produces two values; the proportion of the standard ellipse area (representing 95% of the data) of each population that overlaps with the other.

3.4 Results

Carbon and nitrogen means

Lake Huron lake trout and lake whitefish occupied broad ranges in the stable carbon and nitrogen isotope biplot, using the two standard deviation bivariate ellipse: lake trout $\delta^{13}C$ ranged from -23.9‰ to - 17.1‰ and -23‰ to -14.4‰ for lake whitefish while $\delta^{15}N$ ranged from 10.5‰-15.7‰ for lake trout and 7.9‰-13.7‰ for lake whitefish (Figure 3.2a).

I ran a three-way ANOVA on a sample of 951 stable isotope samples to examine the effect of species, fish length and region on both the $\delta^{13}C$ and $\delta^{15}N$ values. There was a significant three-way interaction for $\delta^{13}C$, $F(4, 924) = 3.647$, $p < .0059$ and all of the two-way interactions were significant. With species grouped, Georgian Bay $\delta^{13}C$ values were significantly higher than in the other four regions (Tukey, all $p < 0.01$; Table A2.1). There were no other significant differences in the $\delta^{13}C$ values between any of the other regions for lake trout or lake whitefish ($p > 0.05$). Within region and species pairings, lake whitefish $\delta^{13}C$ values were significantly greater than lake trout in the North Channel and Georgian Bay ($p < .01$) and ($p < .05$), respectively.

There was not a significant three-way interaction for $\delta^{15}N$, $F(4, 924) = 1.9$, $p = 0.453$ between species, region and length bin. However, there were significant interactions between species and region $F(4, 924) = 55.8$, $p < .001$, and between length bin and region $F(4,924) = 19.6$, $p < .001$. Mean $\delta^{15}N$ was higher for lake trout than lake whitefish in all 5 regions (Tukey, all $p < .001$). For lake whitefish, the $\delta^{15}N$ means differed significantly from each other among all regions. North Channel mean $\delta^{15}N$ values for both lake trout and lake whitefish were higher than in all other areas (Tukey all $p < .05$).

Size bin comparisons revealed that larger (>550 mm) lake trout in all five regions had higher nitrogen values than smaller (<550 mm) lake trout (Figure 3.2b), though only significantly higher in the southern main basin ($p < .05$). There were no differences in the carbon means for small and large lake trout in any region. Lake whitefish $\delta^{13}C$ values were significantly higher for large fish than small fish in Georgian Bay ($p < .05$), but in the southern main basin, small lake whitefish had higher $\delta^{13}C$ values than large lake whitefish ($p < .001$)). There were no differences in the nitrogen means for small and large lake whitefish in any of the regions.

Carbon and nitrogen ranges

The paired t-test indicated that lake whitefish overall had significantly wider carbon ranges than lake trout ($t(4) = 5.7$, $p < .01$), but there were no significant differences in the nitrogen ranges between lake trout and lake whitefish overall. Within species, lake whitefish carbon ranges were the widest in the North Channel, and narrowest in the central main basin (Table 3.1, Figure A2.1). For lake trout, carbon ranges in the North Channel and Georgian Bay were very similar, and larger than those from the main basin. Nitrogen ranges were more consistent both between species and between regions than the carbon ranges.

Niche size

Niche size varied among regions (Figure 3.3), with lake whitefish having consistently larger niche sizes than lake trout across and within regions. Of the Bayesian niche size iterations, 0% of the lake whitefish niches were smaller than the lake trout niche in 4 regions: North Channel, Georgian Bay, northern main basin, and the southern main basin. In the central main basin, 0.05% of the lake whitefish niches were smaller than those of lake trout niches.

Within species, lake whitefish niches were the largest in Georgian Bay and the North Channel (3.58 and 4.56 SEA_B respectively) and the smallest in the southern main basin (2.42 SEA_B; Table 3.1). The niche of lake whitefish from the North Channel was larger than the niche sizes from Georgian Bay in 96% of the iterations, larger than the northern main basin niches 96.4% of the time, and larger than the central and southern main basins 100 % of the iterations (SIBER results). Niche sizes were similar between lake whitefish from Georgian Bay and the northern main basin, where Georgian Bay niches were larger than those of the northern main basin in just 62.58% of the iterations.

Lake trout niche size varied little across regions (0.77 – 1.81 SEA_B). The largest lake trout niche sizes were in the central main basin and Georgian Bay (1.77 and 1.81 SEA_B respectively). Northern main basin niche size for lake trout was smaller than that of the other regions between 99.2-100% of the iterations. This may be partially due to the smaller sample size of 71 individuals instead of 100 from the other regions, though ellipse size was corrected for in the analysis. Georgian Bay and central main basin niches were the largest, and were larger than the niche sizes of the other three regions in over 99.5% of the iterations.

Lake trout and lake whitefish body length influenced niche size. For lake whitefish, smaller fish (<450 mm) had larger niches than the longer (>450 mm) lake whitefish between 80 and 97.5% of the time, except for in the central main basin, where small lake whitefish niches were always smaller than those of larger fish (Bayesian SIBER ellipses). For lake trout, the niches of small fish (<550 mm) were smaller than niches of larger fish between 57.5-95% of the time, and only in Georgian Bay were the niches of small lake trout larger than those of larger lake trout (Bayesian SIBER ellipse).

Niche overlap

Using the proportion of the niche area shared by the two species, a greater proportion of lake trout niches were overlapped by lake whitefish niches than vice versa (Table 3.2). The niches of lake whitefish in the central and southern main basins are smaller than in the North Channel and Georgian Bay, and the overlap amounts of one species niche into the other were closer values. For example, in the central main basin, 17.0 % of the lake trout niche was shared with lake whitefish and 11.1 % of the lake whitefish niche was shared by lake trout. In the North Channel, the amount of overlap of lake whitefish into lake trout was over 4x higher than lake trout into lake whitefish niches (41.6 % compared to 10.2 %).

The percentage of the lake trout and lake whitefish standard ellipse that overlapped was the highest in Georgian Bay and lowest in the northern main basin. Two values were produced, and for all regions, the amount of lake trout niche overlapped by lake whitefish is higher than the alternative. Georgian Bay had the highest percentages of niche space overlap (23.1- 45.9%). For all three main basin regions, area of overlap values did not exceed 17% in either direction.

Overlap values varied regionally with bin sizes of lake trout and lake whitefish (Table A2.2). The region with the least overlap is the northern main basin, where the highest proportion of shared niche space was just 17.9% of small lake trout niche overlapping with small lake whitefish. In the central main basins, small lake whitefish had 0% overlap of the niche space with both small and large lake trout. However, my dataset was relatively limited in the quantity of small lake whitefish I was able to obtain for the central main basin (n= 23).

Carbon and nitrogen enrichment

The carbon signature taken from the centroid of the bivariate plots were minimally enriched in lake trout relative to lake whitefish in the central main basin (+ 0.06 ‰). In the other four areas, lake trout had on average lower carbon values than lake whitefish, indicating higher reliance on offshore energy sources. The greatest difference was in the North Channel, where lake trout had carbon signatures 0.73 ‰ lower than lake whitefish. The $\delta^{15}N$ values of the lake trout niches in all regions were enriched compared to lake whitefish by 1.9 – 2.9 ‰, lowest in the North Channel and highest in the central main basin (Table 3.3).

3.5 Discussion

I observed significant regional variation in trophic position, niche size and degree of niche overlap between lake trout and lake whitefish, thus highlighting the importance of considering regional patterns when identifying the scope of competition and predation between the two species. The niches of lake whitefish had more regional variation and were larger than the niches of lake trout which were much more consistent in size across the lake. Niche overlap between lake trout and lake whitefish also varied regionally, indicating differences in the likelihood of resource competition between the species. Lake trout nitrogen signatures were enriched relative to lake whitefish, although they only approached levels consistent with significant predation in two of the five study regions. Finally, lake trout carbon signatures were lower than lake whitefish for all but one region (central main basin), indicating that lake trout are deriving more of their energy from offshore habitats than lake whitefish. Overall, post-regime shift lake whitefish in Lake Huron derive their energy from lower trophic levels in more nearshore waters and appear to have a broader and more variable niche than lake trout. Below, I describe these patterns in more detail and discuss the implications of these findings for evaluating the scope for competition and predation between lake trout and lake whitefish.

Niche overlap values between lake trout and lake whitefish were low overall, indicating that the potential for competition between the two species is not likely to be substantial. I considered significant overlap to be >60%, the same value used in the Schoener diet overlap index (Schoener, 1970), and the same threshold used in other studies (Guzzo et al. 2013; Ogloff et al. 2019). In every region, lake whitefish had larger niches than lake trout, contributing to i) higher proportions of the lake trout niche overlapped by lake whitefish and ii) higher proportions of lake whitefish niches extending past the lake trout niche within bivariate space, indicating lake whitefish use of energetic sources not used by lake trout. Isotopic space used by one species and not the other could identify prey resources which are not being competed for (Vander Zanden et al. 1999; Johnston et al. 2018). If there is a low overlap of lake trout niche into the niche of lake whitefish, this means that lake whitefish have a broader range of prey on which they can rely on, thus making it less likely for overlap with lake trout. Both lake trout and eat fish and invertebrate prey, explaining why lake trout are within the lake whitefish niche, but since the lake trout diet is much more focused on fish, the subset of common prey to be impacting lake whitefish is small.

Low levels of niche overlap occurred in central and southern main basins (Table 3.2), which differed from overlap indices measured from a detailed diet study (Chapter 2) which made use of the same fish samples from my stable isotope analysis. An index of diet overlap (the Schoener index) was higher in the central main basin than other regions, which was attributed to the common consumption by both consumers of round goby (41% of lake trout and 67% of lake whitefish diet biomass). Conversely, the highest isotopic niche overlap values were in Georgian Bay where the diet overlap values were very low (8.5%), though both species also consumed round goby (6.5% of diet biomass for lake trout and 41% for lake whitefish; Chapter 2). Along with diet, isotopic niches have been found to vary regionally; Eberts et al. (2017) found regionally distinct isotopic clusters of lake whitefish in Lake Huron, primarily distinguished by $\delta^{13}C$ values, which may relate to differences in diet diversity, though were likely also related to lake-wide isotopic gradients. Isotopic concentrations of both $\delta^{13}C$ and $\delta^{15}N$ were also found to be enriched with increasing latitude, and $\delta^{15}N$ enrichment was concentrated in the North Channel and northern main basin (Eberts et al. 2017), areas in my study that also had enriched $\delta^{15}N$ values compared with more southern sites. Both stable isotope and diet analyses have limitations that may contribute to the differences observed between the overlap metrics. Stable isotopes provide a more integrated examination of energetic sources over a lifetime than stomach contents, thus the tissue does not immediately reflect the isotopic composition of its diet (Vander Zanden et al. 2015). Additionally, the time required for diet composition to be reflected in tissues varies, and the isotopic composition of tissue is not always in equilibrium with diet (Vander Zanden et al. 2015).

The potential for lake trout predation on lake whitefish based on isotopic differences in $\delta^{15}N$ is somewhat mixed among regions. In the central and southern main basins, the enrichment of the nitrogen of lake trout above lake whitefish are 2.9‰ and 2.81‰ respectively (Table 3.3). Enrichment levels 3-4 ‰ is the range researchers generally consider to be one trophic level (Peterson and Fry, 1987), and a specific value of 3.4‰ is commonly used in fisheries studies as one trophic level and thus could indicate that one species is feeding predominately on the other (Vander Zanden and Rasmussen, 2001; Post, 2002). Along with nitrogen enrichment, however, an overlap in carbon is important when considering likelihood of interactions since carbon is indicative of resource use and habitat; overlap or enrichment in carbon values may reveal competition or predation, respectively (Layman et al. 2007; Ogloff et al. 2019). Levels of carbon overlap between lake trout and lake whitefish do indicate that these species share some of the same habitats, and lake trout carbon ranges fit within those of lake whitefish in all five regions. Carbon enrichment that occurs with predation is less pronounced than nitrogen enrichment; and has been reported as a 0.47‰ increase in $\delta^{13}C$ from prey to predator (Vander Zanden and Rasmussen, 2001). In my study, only the lake trout from the central main basin were carbon enriched compared to lake whitefish, and by only 0.06 ‰., and lake trout in the other four areas had lower carbon signatures than lake whitefish, which could indicate inconsistency with a predation relationship. While there is greater potential of predation in the central main basin, based on the nitrogen and carbon enrichment values, it does not likely indicate significant predation pressure on lake whitefish by lake trout. A diet study of these same fish supports this finding, where lake trout were found to consume more lake whitefish in the central main basin than elsewhere. However, the contribution of lake whitefish to the total biomass consumed by lake trout was overall very small (<5% total biomass; Chapter 2).Thus, the isotopic results combined with the diet study indicate low levels overall of predation by lake trout on lake whitefish.

Along with regional differences in the likelihood of predation, body length of lake trout is likely to influence the predation risk to lake whitefish. Large lake trout had significantly higher $\delta^{15}N$ signatures than the small lake trout in the central ($p< 0.05$) and southern main basins ($p<0.001$), likely related to the increased consumption of higher trophic level fish like burbot, lake whitefish, and gizzard shad with increased body length (Chapter 2). Lake whitefish that are vulnerable to predation by lake trout (all sampled lake trout were <1000 mm) are likely smaller than 250mm, as an optimum prey to predator length ratios is cited as 0.25, with declining preference for prey either smaller or larger than that (Jones et al. 1993). Of the eight lake whitefish that were consumed by lake trout, seven were between 135- 230mm, and the other individual was 380mm total length. Lake whitefish totalled 19% of the total biomass in the diet of central main basin lake trout > 800 mm in total length although sample size was very low (Chapter 2). In the other regions, biomass proportions of lake whitefish range between 0.4 and 1.1% of the diet of lake trout and were more commonly consumed by larger lake trout. Conversely, lake trout from the North Channel and the northern main basin consume mostly rainbow smelt, which doesn't change with length. So, while widespread predation of lake whitefish by lake trout was not supported by the current isotope data, having isotopic samples from a greater proportion of large-sized lake trout may reveal different trends.

There are limitations to what stable isotope analysis can reveal about predator-prey relationships, and in this study, the stable isotope results may be better used to compare the degree to which lake trout and lake whitefish are taking in energy from diverse sources. For example, the carbon enrichment of lake trout over lake whitefish in the central main basin may be indicative of lake trout consuming other prey items with carbon-enriched signatures in this area, more than evidence of predation of lake whitefish. Lake trout feeding from nearshore, carbon-enriched sources is supported by the diet data finding that 41% of the central main basin biomass of lake trout diets were comprised of round goby, a prey item that has been used as a representative of the nearshore carbon signature (Rush et al. 2012). However, round goby captured from sites 8-10m in depth were more carbon-depleted than those from <5m (Barton et al. 2005). Similar trends were reported by Rennie et al. for many benthic invertebrate taxa including dreissenid mussels (2009), which introduces some uncertainty relating diet items to isotopic signatures, as other than the capture location of the fish, we do not know where that fish was primarily feeding.

Lake whitefish had significantly larger isotopic niches than lake trout in all five regions, largely driven by their significantly wider carbon ranges, which indicate a more varied diet (Peterson and Fry, 1987). Broad use of carbon sources is commonly found in generalist populations (Fagan et al. 2012). Eberts et al. (2017) also found wide carbon ranges of Lake Huron lake whitefish and niche size values consistent with other freshwater generalists, and found that lake whitefish niches were larger than niches of salmonids and gobies. My findings of a broad niche are supported by diet data (Chapter 2); a Shannon diversity index calculated from diet data found more diverse diets for lake whitefish than lake trout in all regions (Table A1.2). Lake whitefish are known to be flexible feeders and their diets vary widely by region and size classes (Pothoven and Nalepa, 2006; Rennie et al. 2009b; Pothoven and Madenjian, 2013; Chapter 2). Species that can obtain energy from a variety of sources are more likely to be resilient in the event of ecosystem shifts and potential prey loss (Skúlason and Smith, 1995). There was a significant positive correlation between lake whitefish niche size and Fulton's condition factor (R^2= 0.969, df= 3, p< .01; Figure 3.4). Lake whitefish from the North Channel have a significantly higher mean Fulton's condition factor than lake whitefish from all other regions, and the southern main basin fish have the lowest condition factor (Figure A2.2). Growth rates and condition of lake whitefish from the southern main basin were reduced by up to 50% since the late 1980's, attributable to density-dependent feeding (Fera et al. 2015; Gobin et al. 2015). Additionally, resource availability has been cited as a potential driver in body condition of lake whitefish; condition factor of adult lake whitefish in South Bay was positively correlated with the abundance of *Diporeia*; a historically important prey item for lake whitefish (Rennie and Verdon, 2008). Additionally, consumption of dreissenid mussels by lake whitefish is also associated with decreased condition factor (Pothoven and Madenjian, 2013; Rennie et al. 2009b) as well as shifting of their niche towards the nearshore in South Bay, Lake Huron (Trumpickas et al. 2022). Further research has been proposed into determining if there is a threshold of adult body condition where the larval or juvenile condition of their offspring is reduced (Ebener et al. 2021). Though lake whitefish niche sizes are significantly larger than lake trout niches, the niche size of predators has reportedly become increasingly similar as the richness of prey declines (Stasko et al. 2015), and as Lake Huron has undergone declines of prey diversity (Riley et al. 2020), lake trout and lake whitefish niches may be impacted or become more similar in size over time.

Further, there are regional differences in the niche size within the lake whitefish populations in Lake Huron, being larger in the North Channel and Georgian Bay than in the central and southern main basins. This indicates that the energy obtained by fish in the northern areas are potentially from more diverse sources (Fagan et al. 2012). These results are also supported by diet data (Chapter 2), within the Ontario waters of Lake Huron, the most diverse lake whitefish diets were in the North Channel (Chapter 2), with a Shannon diversity index of 2.50 compared to the central and southern main basin; 1.93 and 1.79 respectively (Table A1.2). Eberts et al. (2017) also reported regional variation in lake whitefish niche size, with an over four-fold increase in niche size between Sydney Bay (Georgian Bay) and Scougall Bank (central main basin), primarily driven by the variation in carbon values (niche width; Eberts et al. 2017). In addition to diet diversity, prey specialization by individuals can also drive the niche width of predators (Vander Zanden et al. 2010; Bolnick et al. 2011), and research suggests that many generalist populations are composed of specialized individuals with niches as a subset of the population (Araújo et al. 2011). Lake whitefish diets from lakes Huron and Superior have shown moderate to high levels of specialization on prey items including quagga mussels, *Mysis relicta* and fish, among others (Pothoven and Nalepa, 2006; Woodard et al. 2021). There is substantial support that niche sizes of lake whitefish are regionally variable, whether due to levels of individual specialization, learned behaviours, resource density, or other ecological factors (Bolnick et al. 2011; Eberts et al. 2017).

Lake trout from Georgian Bay had significantly higher carbon signatures than lake trout from all other regions. This could, at least, in part be caused by δ^{13}C gradients in the lake, Eberts et al. found that δ^{13}C enrichment occurred in a southwestern to northeastern direction across the lake, with the highest values in Georgian Bay (2017), potentially due to enriched baselines or a particularly nearshore diet. Higher carbon could also indicate more nearshore/benthic feeding, however, the diet data I have for Georgian Bay does not support this. The diet of lake trout in Georgian Bay is dominated by pelagic species including rainbow smelt (74%) and alewife (12% by biomass; Chapter 2) which are expected to have a lower carbon signature than more nearshore or benthic species like round goby (Rush et al. 2012). While lake trout in Georgian Bay do consume nearshore-associated round goby (6.5% of the total biomass), the diet proportion of round goby is similar to the other four regions, and much lower than in the central main basin (41% diet biomass). The biomass proportion of round goby in lake trout diets was relatively unchanged in the diet study period (2004-2019), though as round goby was reported to be widespread as of 2002 (Schaeffer et al. 2005), the initial rate of uptake by lake trout was not documented by the study. Roseman et al. found an increased reliance on round goby by lake trout in Lake Huron after the collapse of alewife (2014). This diet switch from alewife to round goby may improve recruitment as lake trout are known to experience thiamine deficiency complex (early mortality syndrome) when consuming thiamine-rich alewife (Fitzsimmons et al. 1999, 2005; Johnson et al. 2015). Round goby in particular has been associated with the shift towards more nearshore δ^{13}C signatures for lake trout in Lake Ontario following round goby invasion in the 1990's (Rush et al. 2012). Round goby may be acting as ecosystem engineers through redistributing carbon to predatory fish that has been bound to dreissenid mussels (Vanderploeg et al. 2002; Johnson et al. 2005).

Round goby consumption may have also affected lake whitefish trophic niches; I found that large lake whitefish from Georgian Bay had significantly higher carbon signatures than smaller fish, consistent with increased consumption of round goby and decreased consumption of *Bythotrephes* by lake whitefish with increased body length (Chapter 2). Another major lake whitefish diet shift from *Diporeia* towards dreissenid mussels is well-documented, and influenced the isotopic niche of lake whitefish towards the nearshore (Rennie et al. 2009b; Fera et al. 2017). Trumpickas et al. found that lake whitefish niches shifted more towards the nearshore than all other species studied in their South Bay study (2022). Along with this increased consumption of dreissenid mussels, consumption of round goby by lake whitefish in South Bay was also proposed by Trumpickas et al. (2022) as a potential contributor to the nearshore drift of lake whitefish. The consumption of round goby by lake whitefish before 2007 was uncommon, and now over 20% of individuals in the main basin consumed round goby (Pothoven and Madenjian, 2013; Chapter 2). The central main basin was where lake whitefish were found to eat the largest proportion of round goby by volume, followed by Georgian Bay (Chapter 2). The regional shift to round goby consumption away from dreissenid mussels could positively impact growth rates (Pothoven and Madenjian, 2013). However, the potential benefits to lake whitefish will depend on the relative energy expenditure of prey capture and the assimilation of different prey types to the diet (Pothoven and Madenjian, 2013), research areas which are yet largely unexplored. With these differences in isotopic niches and associated feeding regimes across Lake Huron, we could expect regional variation in lake whitefish growth rates, recruitment, and sustainable harvest.

A potential future direction for research is to create a mixing model using isotopically distinct energy sources of potential prey to better understand the energetic contributions to lake trout and lake whitefish over their lifetimes. I was limited in this study to describing the general energetic sources used and the range of $\delta^{15}N$ values associated with trophic levels of these populations of lake trout and lake whitefish. With the inclusion of known prey, we can create better models to quantify the relative contributions of different prey types (Vander Zanden and Rasmussen, 2001), and assess the risk of predation to lake whitefish by lake trout. Another future option for research would be to use muscle tissue instead of scales to allow us to examine the diet seasonally – the use of muscle tissue collected throughout the year may reveal seasonal diet patterns as it reflects the energetic sources over the past few months instead of most of a lifetime revealed using scales (Vander Zanden et al. 2015). Additionally, the study of very large lake trout (>800 mm) captured from index or commercial programs could provide context into the predation risk to lake whitefish, as from the diet study, the largest lake trout are more likely to include lake whitefish in their diets as well as other large-bodied species like gizzard shad, bowfin and burbot (Chapter 2). Also underrepresented in my study are small lake whitefish, particularly from the central main basin as many of the samples are from commercial netting which targets larger body sizes. Additionally, recruitment declines in Lake Huron since 2001 have resulted in lower catches of young individuals (Cottrill et al. 2020).

This study provided information on the interactive potential between lake trout and lake whitefish using stable isotope analysis and comparing with diet information. Given the overall low overlap in niches, and the low rates of predation of lake trout on lake whitefish, it seems unlikely that lake trout competition or predation have caused the broadscale declines in lake whitefish across the lake. Lake trout and lake whitefish were found to interact through predation or competition at low rates, and perhaps regional difference in diets contribute to some of the regional variation seen in population dynamics. Though, the interactions do not appear to be on the scale required to have suppressed lake whitefish populations. Further study of the energetic contributions to lake whitefish diets and their trophic niches throughout various life stages is warranted, as widespread juvenile recruitment failures have been associated with low larval production and growth (Cunningham and Dunlop, 2023; Ebener et al. 2021). Considering the dire circumstances facing lake whitefish in Lake Huron, monitoring the isotopic niches and prey use by lake whitefish may assist in determining fishery management actions to protect and support the fishery. Ultimately our knowledge of the regional energetic sources and niche characteristics can be used to better understand the response of lake trout and lake whitefish populations to broad ecological change.

3.6 Acknowledgements

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Table 3.1. Sample sizes, fish total length (mm; mean ± 1 SE), stable isotope ratios (mean ± 1 SE), niche sizes and credible intervals of lake trout (LT) and lake whitefish (LWF) collected between 2014 and 2019 in five regions of Lake Huron. The credible interval is a range of possible niche sizes for the population and will contain the true niche size 95% of the time. Carbon and nitrogen ranges were calculated using two standard deviations on the δ ^{13} C and δ ^{15} N points in bivariate space, respectively. Regions are abbreviated as follows: NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.

Region	Species	n	Total Length	δ^{13}C (‰)	δ^{15}N (‰)	Mode Niche Size (SEA$_B$)	Credible Interval (95%)	Carbon range	Nitrogen range
NC	LT	101	550 ± 8.3	-20.03 ± 0.85	13.37 ± 0.52	1.12	0.71 - 1.18	1.67 ± 0.86	1.04 ± 0.05
	LWF	100	463 ± 7.8	-19.33 ± 2.00	11.39 ± 0.81	4.56	3.47-5.27	4.01 ± 0.201	1.62 ± 0.08
GB	LT	108	566 ± 9.5	-19.00 ± 0.84	12.31 ± 0.85	1.81	1.34-2.02	1.68 ± 0.08	1.70 ± 0.08
	LWF	114	492 ± 8.3	-18.33 ± 1.76	10.58 ± 0.69	3.58	2.66-4.13	3.53 ± 0.17	1.38 ± 0.06
NMB	LT	71	609 ± 8.6	-20.07 ± 0.47	13.30 ± 0.52	0.77	0.54-0.97	0.95 ± 0.06	1.03 ± 0.06
	LWF	61	521 ± 7.3	-19.43 ± 1.42	10.50 ± 0.78	3.42	2.24-4.19	2.84 ± 0.19	1.56 ± 0.10
CMB	LT	103	559 ± 9.6	-19.66 ± 0.72	12.75 ± 0.80	1.77	1.41-2.12	1.45 ± 0.07	1.60 ± 0.08
	LWF	109	535 ± 7.7	-19.82 ± 1.09	9.88 ± 0.79	2.72	2.31-3.44	2.19 ± 0.11	1.57 ± 0.07
SMB	LT	100	543 ± 9.0	-19.88 ± 0.53	12.29 ± 0.73	1.18	0.88-1.36	1.05 ± 0.05	1.46 ± 0.06
	LWF	101	442 ± 9.6	-19.77 ± 1.11	9.55 ± 0.69	2.42	1.86-2.93	2.22 ± 0.11	1.38 ± 0.07

Table 3.2. Overlap metrics for lake trout and lake whitefish by region.

		North Channel	**Georgian Bay**	**Northern main basin**	**Central main basin**	**Southern main basin**
Standard ellipse area overlap	% of LT niche space shared by LWF	41.6	45.9	5.3	17.0	14.1
	% of LWF niche space shared by LT	10.2	23.1	1.2	11.1	6.8

Table 3.3. Stable isotope enrichment values of lake trout relative to lake whitefish. The distance between centroids is the Euclidean distance between centroids on the bivariate plot (Figure 3.2a).

Region	Distance Between Centroids	Nitrogen Enrichment	Carbon Enrichment
North Channel	2.03	1.89	-0.729
Georgian Bay	2.06	1.95	-0.659
Northern main basin	2.85	2.77	-0.656
Central main basin	2.93	2.93	0.057
Southern main basin	2.81	2.81	-0.083

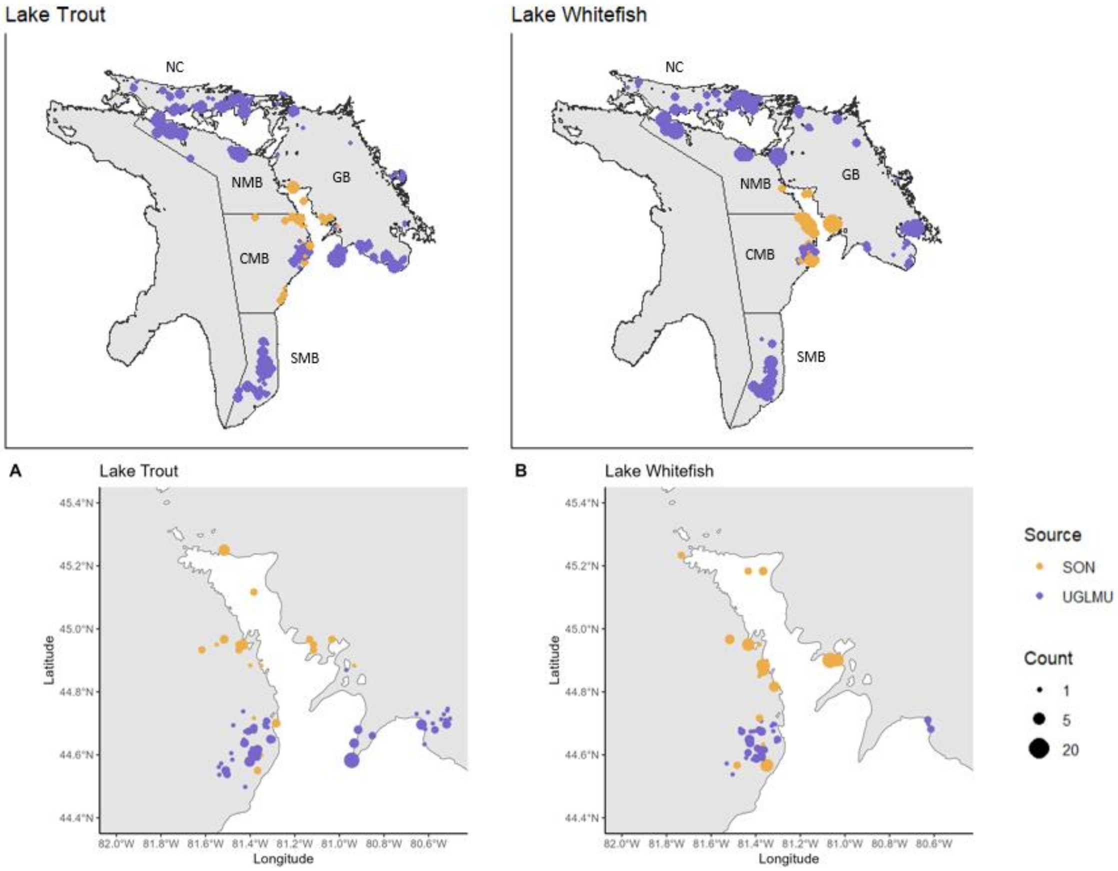

Figure 3.1. Map of Lake Huron with statistical districts used to categorize sample origins. Capture locations of fish analyzed in this study for stable isotope analysis. Samples were obtained from Saugeen Ojibway Nation (SON) harvesters and monitoring programs conducted by the Upper Great Lakes Management Unit (UGLMU). Regional acronyms are as follows: NC= North Channel, GB= Georgian Bay, NMB= Northern main basin, CMB= central main basin, SMB= Southern main basin. Inset shows the Saugeen (Bruce) Peninsula.

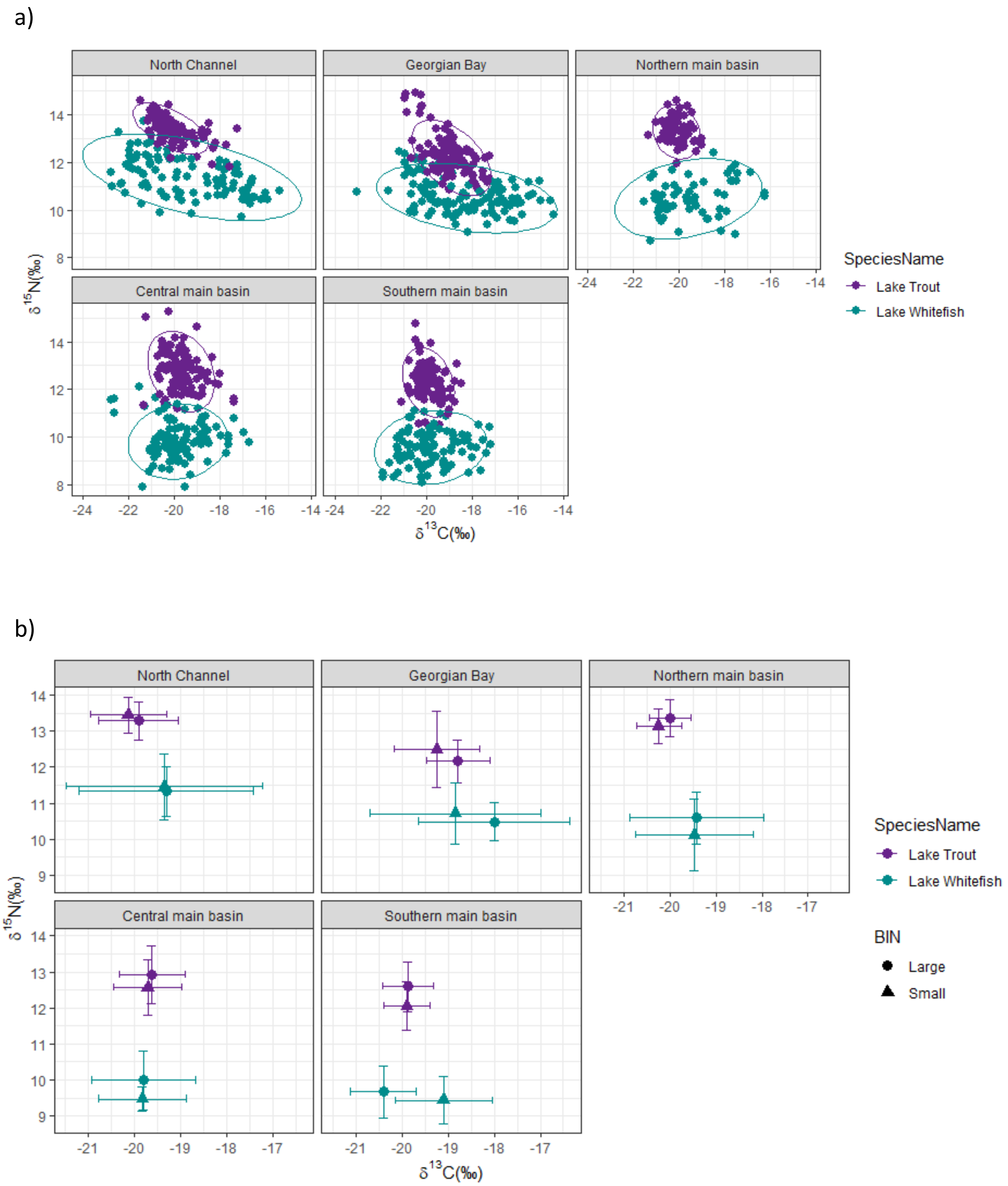

Figure 3.2. Isotopic niches of lake trout and lake whitefish for different regions of Lake Huron. a) The median 95% $\delta^{13}C$ and $\delta^{15}N$ isotopic niche for Lake Huron lake trout and lake whitefish from 2014 – 2019 are indicated by coloured ellipses. b). the centroid position and standard deviation (indicated by cross bars) for Lake Huron lake trout and lake whitefish of two size bins from 2014 – 2019. Circles indicate the large individuals and triangles indicate the small individuals.

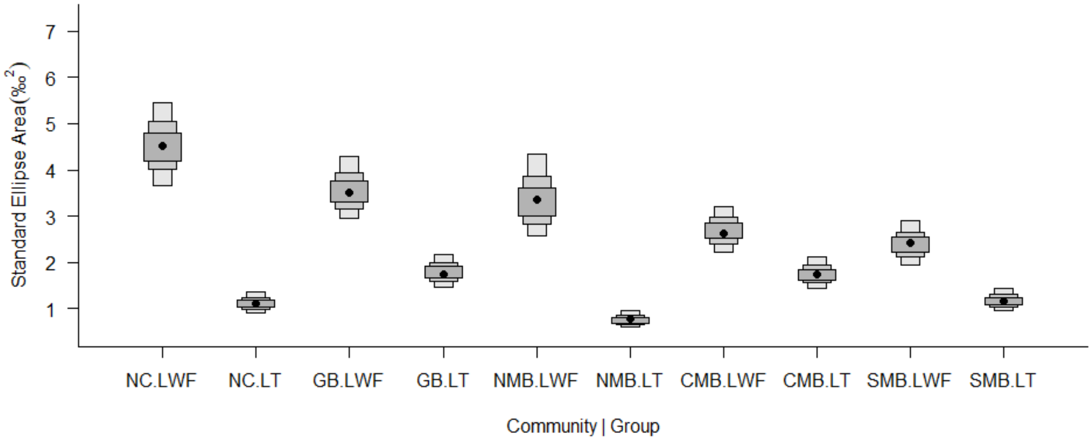

Figure 3.3. Regional niche size of lake trout (LT) and lake whitefish (LWF) in Lake Huron using SIBER (stable isotope Bayesian ellipses in R), containing 50%, 95% and 99% of the credible niche sizes. Regional acronyms are as follows: NC= North Channel, GB= Georgian Bay, NMB= Northern main basin, CMB= central main basin, SMB= Southern main basin.

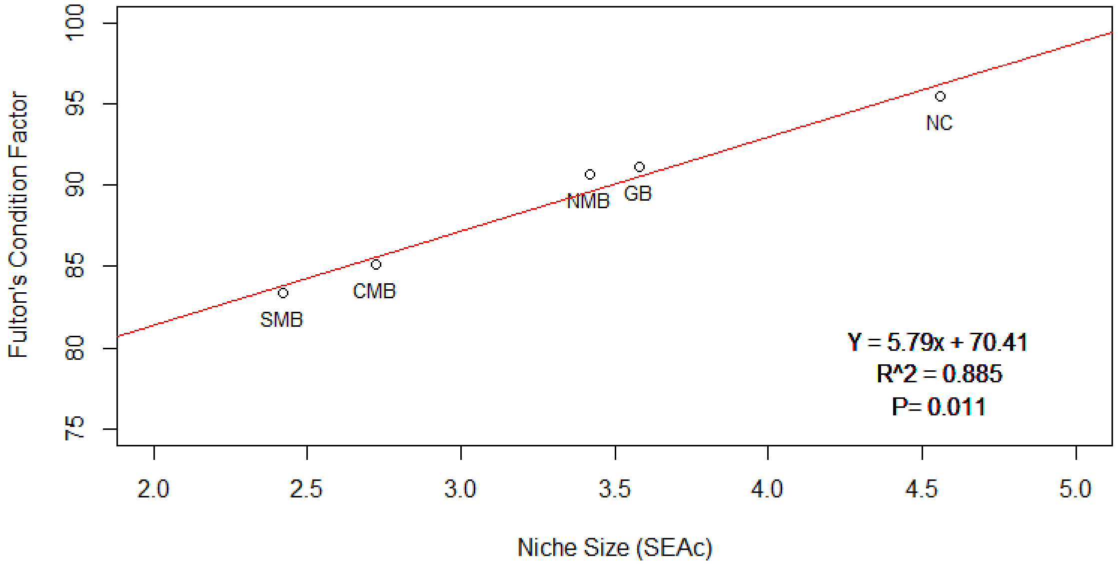

Figure 3.4. Lake whitefish Fulton's condition factor by niche size (SEA_B) and region of Lake Huron, 2014-2019. Regional acronyms are as follows: NC= North Channel, GB= Georgian Bay, NMB= Northern main basin, CMB= central main basin, SMB= Southern main basin.

Chapter 4: General Discussion

My study represented the Western science component of a collaborative two-eyed seeing project with the Saugeen Ojibway Nation and agency partners to better understand the interactions between lake trout and lake whitefish. The overall objective of this thesis was to examine the regional energetic and trophic dynamics of lake trout and lake whitefish considering recent abundance declines of lake whitefish in Lake Huron. Specifically, I aimed to determine whether lake trout were consuming lake whitefish and if lake trout and lake whitefish were competing for energetic resources in Lake Huron. To answer these questions, I used two main exploratory methods: 1) stomach content analysis and 2) stable isotope analysis. In chapter 2 I described the diets of lake trout and lake whitefish by examining fish stomach contents and examined relative consumption of lake whitefish by lake trout considering regional, temporal and prey/predator length factors (now in press at the Journal of Great Lakes Research). Though I did not find evidence of meaningful contributions of lake whitefish to lake trout diet, I did find higher rates of consumption in the central main basin, and lake whitefish were more commonly consumed by larger lake trout (>800mm). My diet study also revealed an overall low potential for competition based on diet overlap, although there was regional variation. The central main basin, due to the common consumption of round goby, had the highest diet overlap between lake trout and lake whitefish. In chapter 3 I described and compared the isotopic niches of lake trout and lake whitefish to identify potential interactions between the two species. Across regions, lake trout had smaller niche sizes, ate at consistently higher trophic levels and further offshore than lake whitefish. I found little overlap between the isotopic niches of lake trout and lake whitefish overall, but these values were the highest in Georgian Bay. While the niches of lake trout did not appear to be consistent with substantial lake whitefish predation, the nitrogen enrichment observed in the central and southern main basins is within the scope of predation. The nitrogen enrichment between lake whitefish and lake trout indicates the potential for predation of lake trout on lake whitefish, however the isotopic niche (which factors in both N and C) suggests the level of predation overall is low. This low predation overall is consistent with the stomach content analysis which found very few lake whitefish in lake trout stomachs.

To my knowledge, dietary analyses had not been completed for lake trout and lake whitefish in all three basins of the Ontario waters of Lake Huron before, so the broad regional component of this diet study was very informative. While both species had regional and temporal diet variability, this was especially pronounced for lake whitefish. The widespread loss of the important prey item *Diporeia* spp. was meaningful for lake whitefish, as it represented a massive shift in the caloric densities of prey available and a disruption to historic energetic pathways between the pelagic and benthic environments (McNickle et al. 2006; Pothoven and Nalepa, 2006). New linkages in the pelagic-benthic energetic transfer include round goby and dreissenid mussels (Rush et al. 2012; Pothoven et al. 2001), both consumed by lake whitefish. My study found a high level of relative importance and consistent reliance on dreissenid mussels between 2004 and 2019 in the southern main basin, also reported by Pothoven and

Madenjian (2013). Dreissenid mussel consumption has been found to negatively impact body condition and growth in lake whitefish (Rennie et al. 2009; Pothoven and Madenjian, 2013). Also reported by Pothoven and Madenjian was the increase in round goby consumed by lake whitefish (2013); my study found a significant increase in the proportion of round goby in the central main basin diet over the 16 year study period. This increased consumption was noteworthy, as prior to the 1980's consumption of any fish was considered incidental (Ihssen, 1981). Round goby consumption is also meaningful from the perspective of overlap between lake trout and lake whitefish in the central main basin, as historically, lake trout and lake whitefish would not likely have had much shared prey, thus this dietary overlap is presumably novel.

Round goby and dreissenid mussels have been implicated in the isotopic niche shifts of predatory fish towards the nearshore in the Great Lakes (Hecky et al. 2004; Rush et al. 2012). In a study covering 70 years of food web change in South Bay, all species of fish examined shifted towards nearshore from the 1980-1999 time period to the 2000-2017 time period, but none so much as the lake whitefish (Trumpickas et al. 2022). Trumpickas et al. hypothesized the isotopic shifts for lake whitefish towards the nearshore could be associated with diet changes along with the increased benthic and nearshore productivity (2022). While my study didn't look at trophic niche changes over time, I found that the niches of lake whitefish from the central and southern main basin with diets high in round goby and dreissenid mussels respectively, were significantly smaller than the other regions, and the condition factors of these lake whitefish were also significantly lower. Lake whitefish from the North Channel had the most diverse diets, and still included *Diporeia* spp., an important, high calorie diet component before the early 2000's (Pothoven et al. 2001; Pothoven and Nalepa, 2006). The diverse diet of the North Channel lake whitefish is reflected by the largest isotopic niches among regions and a wide range of carbon sources utilized. As diverse diets are associated with resilience in a variable environment (Skúlason and Smith, 1995), the consumption of a less diverse diet of invasive species and the presumed associated niche size decrease may prove to be detrimental to lake whitefish in a continually changing ecosystem.

This study will contribute learnings from a Western science lens to the broader two-eyed seeing project. The process of bringing Western science and SON ecological knowledge together helps to build an integrated understanding of the issue and provides an opportunity to use insights from one knowledge system to enhance the other (Durie, 2004). My study identified higher rates of dietary overlap between lake trout and lake whitefish as well as higher predation on lake whitefish in the central main basin; one of the areas within the traditional territory of SON. Though overall, my findings do not suggest that lake trout are contributing significantly to the declines in lake whitefish. While the focus of the study was on the interactions between lake trout and lake whitefish, I was also able to use the large datasets to better understand other factors impacting lake whitefish including consumption of sub-optimal prey like dreissenids, or novel prey like round goby and the small niche sizes that may be associated with that consumption. We are reminded of the flexibility in diet that lake whitefish are capable of, and their ability to consume a variety of prey which may have a range of implications for their health.

As Lake Huron's ecosystem changes into the future, the dynamics between lake trout and lake whitefish, both long-lived species, are likely to change as well. Given the substantial regional differences in the diets and niches of lake trout and lake whitefish, the nature of their interactions is not likely to change consistently across the lake. Predator-prey relationships in Lake Huron have also undergone substantial change, including the collapse of alewife populations, prey fish biomass reductions, and the presumed prey limitation for lake trout and other top predators such as chinook salmon and walleye (Roseman and Riley, 2009; Roseman et al. 2014). My study found high levels of overlap (>94%) between chinook salmon and lake trout in the North Channel due to the near-complete reliance on rainbow smelt, and significant diet overlap values were also found in Georgian Bay and the southern main basin. The high reliance on rainbow smelt could negatively impact lake trout and chinook salmon if the biomass of adult rainbow smelt continues to decline like it has since the 1990's (Riley et al. 2020) and if no other prey increases to fill this niche. The demand for prey fish by changing predator populations further contributes to uncertainties about the stability of Lake Huron's food web.

Future studies will include the genetic identification of dietary prey items, as the unknown items within the diet represent a significant amount of uncertainty for this and other diet studies. Regionally, 15-30% of lake trout diets were unidentified fish remains, which are likely proportional to the known makeup of consumed fish if fish species have an equal probability of being difficult to identify. However, there is some uncertainty and it is certainly possible for more lake whitefish to be present in the stomachs than I was able to identify. Additionally, species that were only identifiable to family (Coregonus spp.) made up 1-6% of regional lake trout diets, and may also contain lake whitefish. Another future direction may be to use muscle tissue for stable isotope analysis, which will reveal shorter-term energetic sources than scales, providing insight into fall and winter trophic relationships that are relatively lacking in this diet dataset.

With the regional variation in the diets and isotopic niches across Lake Huron, we might expect varying levels of interactions between lake trout and lake whitefish with potential implications for recruitment and sustainable harvest rates. Moreover, wild lake trout in the main basin is on an upward trend (Lenart et al. 2020), and lake whitefish spawning stock biomass has declined since 2006 (Ebener et al. 2021), further challenging the ability to recruit new individuals to the population (Cunningham and Dunlop, 2022). The results of my MSc thesis research suggest that assessments of predatory fish diets and isotopic niches through long-term monitoring programs can be used to describe the important food web linkages between predators and prey types and helps to quantify some system-level responses to broad ecological change in Lake Huron.

As my thesis focuses only on the western science component of a broader two-eyed seeing study, it is important that the research I present in this document is not considered in isolation. I encourage readers of my thesis to seek out future products produced by our broader interdisciplinary team, including the outcomes of the interviews with SON knowledge holders. The two-eyed seeing approach reminds me that there are multiple ways of knowing, and our ability to co-learn leads to a more holistic understanding, which is particularly important when conducting research on complex socio-ecological issues such as changes to fish populations in Lake Huron. It is so valuable to me that we have opportunities to learn from each other, and better understand the complex fisheries interactions and relationships within Lake Huron. The next steps for this project are to share learnings from both knowledge systems at a structured workshop and to collaboratively make recommendations that inform fisheries management actions and future research priorities.

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Appendix 1. Supplemental material for stomach content analyses

Table A1.1. Categories assigned to each taxon type for the general diet comparison figures (Figures 2.3 and 2.4) and for the detailed diet analysis of lake trout (Figures 2.6a and 2.7a) and lake whitefish (Figures 2.6b and 2.7b).

TAXON LABEL	All Predators: Figures 2.3 and 2.4	Lake Trout: Figures 2.6a and 2.7a	Lake Whitefish: Figures 2.6b and 2.7b
Alderflies, Dobsonflies, Fishflies	Other Invertebrates	Insecta	Insecta
Alewife	Alewife	Alewife	Alewife
Amphipods	Other Invertebrates	Invertebrates	Amphipods
Amphipods (Deep Water)	Other Invertebrates	Invertebrates	Diporeia
Aquatic Oligochaete Worms	Other Invertebrates	Benthic Invertebrates	Benthic Invertebrates
Beetles	Other Invertebrates	Insecta	Insecta
Bivalves, Clams	Mollusca	Mollusca	Mollusca
Blackchin Shiner	Other Fish	Fish	Fish
Bluntnose Minnow	Other Fish	Fish	Fish
Bowfin	Other Fish	Bowfin	Fish
Brook Stickleback	Other Fish	Sticklebacks	Fish
Brown Bullhead	Other Fish	Fish	Fish
Burbot	Other Fish	Burbot	Fish
Bythotrephes longimanus	Bythotrephes	Bythotrephes	Bythotrephes
Caddisflies	Other Invertebrates	Insecta	Insecta
Carps and Minnows	Other Fish	Fish	Fish
Cisco	Coregonus spp.	Cisco	Fish
Common Sunfishes, Eared Sunfishes	Other Fish	Fish	Fish

Copepods	Zooplankton	Zooplankton	Zooplankton
Coregonus spp.	Unknown Coregonines	Unknown Coregonines	Fish
Crayfishes	Other Invertebrates	Benthic Invertebrates	Benthic Invertebrates
Creek Chub	Other Fish	Fish	Fish
Crustaceans	Other Invertebrates	Benthic Invertebrates	Benthic Invertebrates
Damselflies, Dragonflies	Other Invertebrates	Insecta	Insecta
Deepwater Chub	Coregonus spp.	Deepwater Chub	Fish
Deepwater Sculpin	Other Fish	Deepwater Sculpin	Fish
Fish Eggs	Fish Eggs	Fish Eggs	Fish Eggs
Gastropods, Slugs, Snails	Mollusca	Mollusca	Mollusca
Gizzard Shad	Other Fish	Gizzard Shad	Fish
Hornyhead Chub	Other Fish	Fish	Fish
Inorganic	Inorganic	Inorganic	Inorganic
Insects	Other Invertebrates	Insecta	Insecta
Isopods, Pillbugs, Sowbugs	Other Invertebrates	Benthic Invertebrates	Benthic Invertebrates
Johnny Darter	Other Fish	Fish	Fish
Juvenile Cisco or Bloater	Unknown Coregonines	Coregonus spp.	Coregonus spp.
Lake Trout	Other Fish	Lake Trout	Fish
Lake Whitefish	Coregonus spp.	Lake Whitefish	Lake Whitefish
Largemouth Bass	Other Fish	Fish	Fish
Leeches	Other Invertebrates	Benthic Invertebrates	Benthic Invertebrates
Longnose Sucker	Other Fish	Fish	Fish
Mayflies	Other Invertebrates	Insecta	Insecta
Midges	Other Invertebrates	Insecta	Insecta
Mites, Ticks	Other Invertebrates	Benthic Invertebrates	Benthic Invertebrates
Molluscs	Mollusca	Mollusca	Mollusca

Mosquitoes, Gnats, True Flies	Other Invertebrates	Insecta	Insecta
Nematodes	Other Invertebrates	Benthic Invertebrates	Benthic Invertebrates
Ninespine and Tenspine Stickleback	Other Fish	Fish	Fish
Northern Pike	Other Fish	Fish	Fish
Opossum Shrimp	Other Invertebrates	Mysids	Mysids
Ostracods	Other Invertebrates	Zooplankton	Zooplankton
Plant Matter	Plant Matter	Plant Matter	Plant Matter
Pumpkinseed	Other Fish	Fish	Fish
Quagga Mussels	Dreissena	Dreissena	Dreissena
Rainbow Smelt	Rainbow Smelt	Rainbow Smelt	Rainbow Smelt
Rainbow Trout	Other Fish	Fish	Fish
Rock Bass	Other Fish	Fish	Fish
Round Goby	Round Goby	Round Goby	Round Goby
Round Whitefish	Other Fish	Fish	Fish
Salmonids	Other Fish	Salmonids	Fish
Sculpin	Other Fish	Sculpin	Fish
Sea Lamprey	Other Fish	Fish	Fish
Sticklebacks	Other Fish	Fish	Fish
Stoneflies	Other Invertebrates	Insecta	Insecta
Suckers	Other Fish	Fish	Fish
Sunfishes	Other Fish	Fish	Fish
Threespine Stickleback	Other Fish	Fish	Fish
Trout-Perch	Other Fish	Fish	Fish
True Bugs	Other Invertebrates	Insecta	Insecta

Unidentifiable Organic Matter	Unidentifiable Organic Matter	Unidentifiable Organic Matter	Unidentifiable Organic Matter
Unidentified Fish	Unidentified Fish	Unidentified Fish	Unidentified Fish
Unidentified Invertebrate	Unidentified Invertebrate	Unidentified Invertebrate	Unidentified Invertebrate
Walleye	Other Fish	Fish	Fish
Water Fleas	Bythotrephes	Bythotrephes	Bythotrephes
Yellow Perch	Yellow Perch	Yellow Perch	Yellow Perch
Zebra Mussels	Dreissena	Dreissena	Dreissena

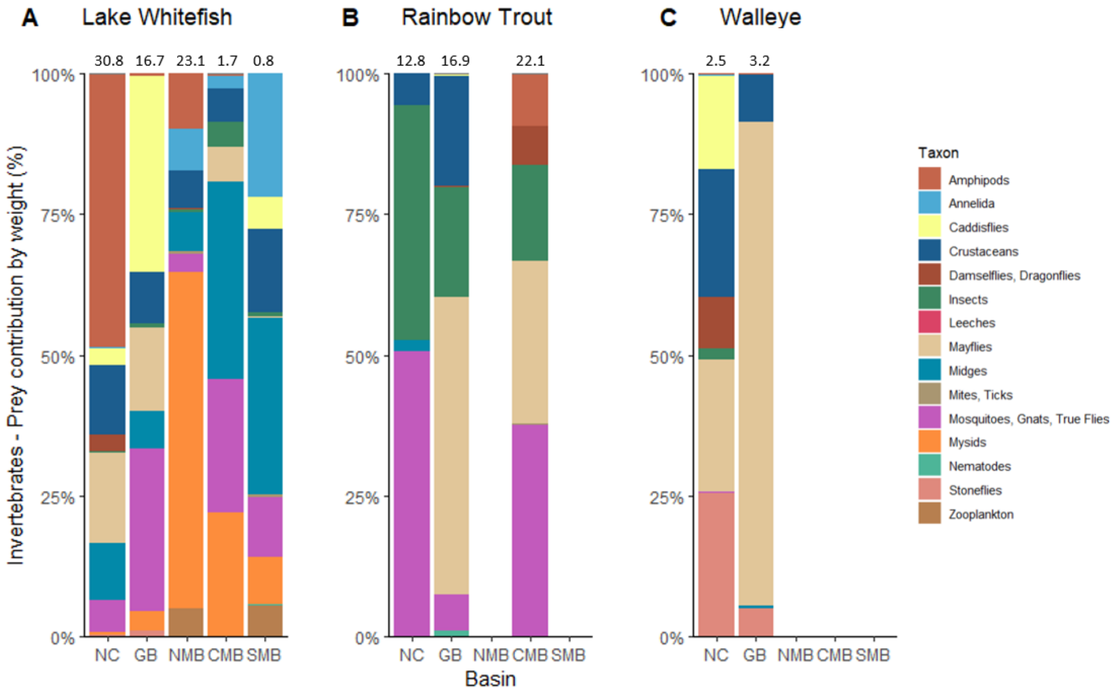


Figure A1.1. The proportion of various invertebrates in the diets of lake whitefish, rainbow trout and walleye within the “Other Invertebrate” category used in Figures 3-4. The values at the top of each column indicate the proportion of that regional diet comprised by the “Other Invertebrates” category. NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, SMB= southern main basin.

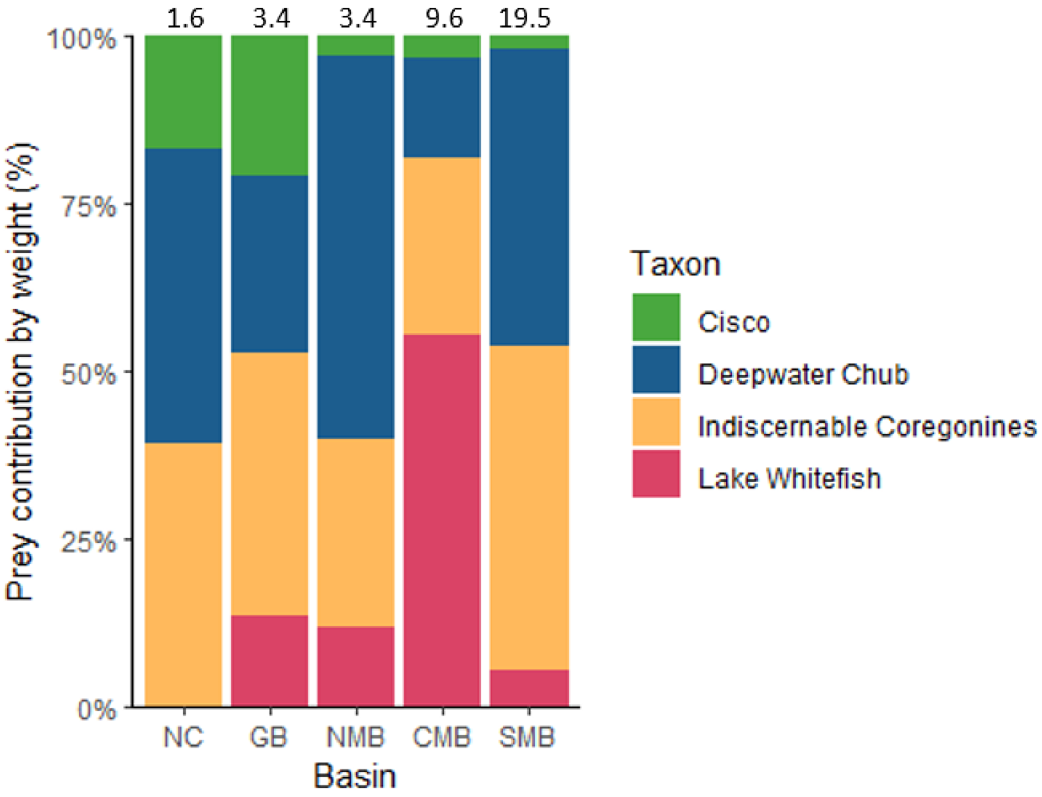


Figure A1.2. The proportion of various coregonines in the lake trout diet within the *Coregonus* spp. category used in Figures 3-4. There were low sample sizes for the other predatory species with Coregonus spp. as stomach contents and did not require plots. Coregonus spp. were any species of coregonines that could not be identified as cisco, deepwater chub, or lake whitefish. The values at the top of each column indicate the proportion of that regional diet comprised by the "Coregonus spp." category. NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, SMB= southern main basin.

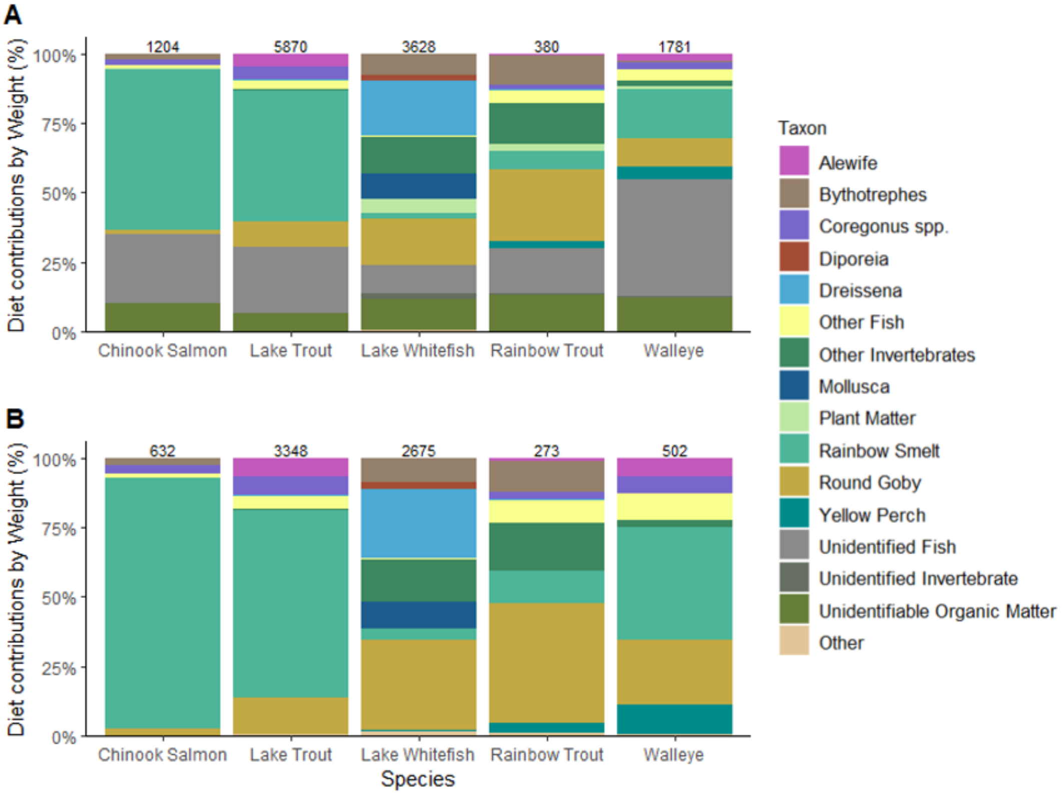
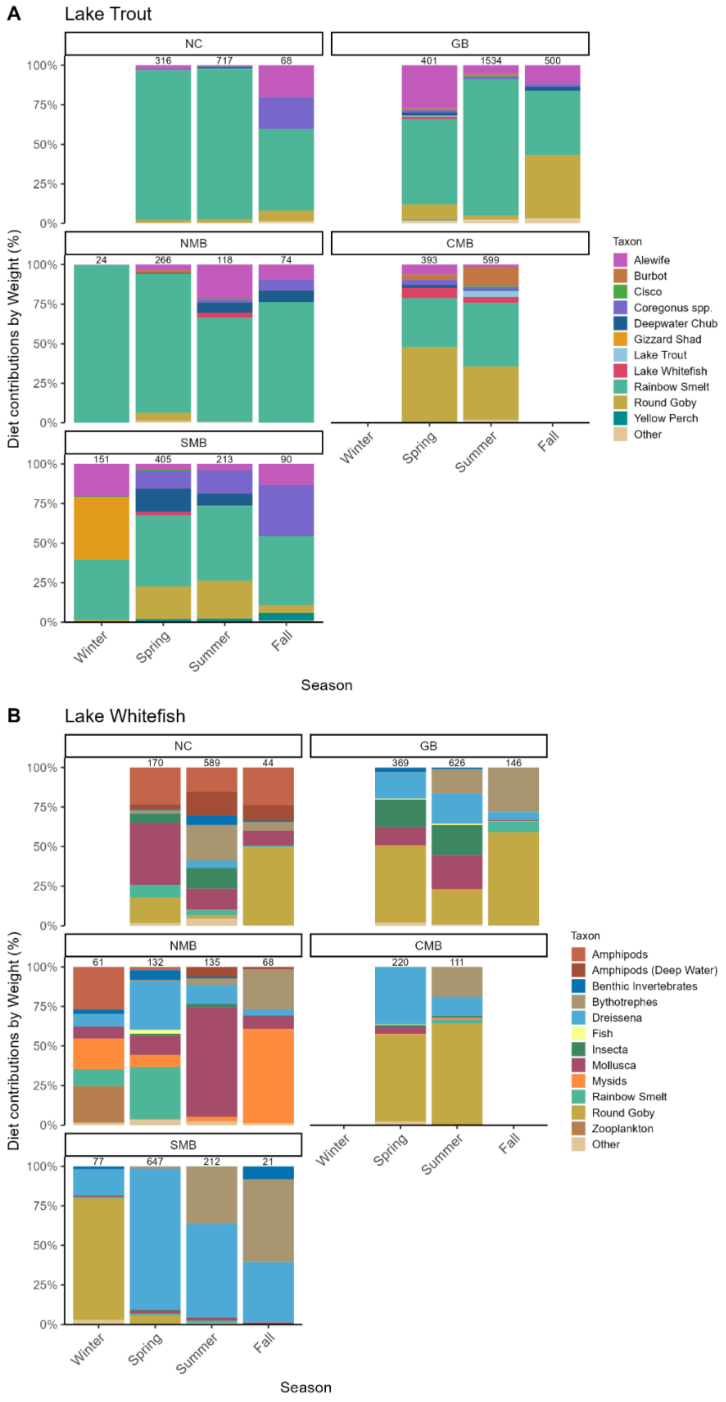


Figure A1.3. Predator diet items by weight (A: including unknown items, B: known diet items only). The category labelled 'other' is composed of prey species that composed at most 2% of any predators' diet and were minimal or absent in the diet of other species, so were grouped into one legend entry. The categories "Other Fish" and "Other Invertebrates" are composed of identifiable species, but that totalled less than 2% of any one predator diet and were thus grouped with others to maintain a more condensed legend. Unknown fish and invertebrates were proportionally reallocated to known fish and invertebrate species. Different regions are depicted including NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.

Table A1.2. Results from the Shannon Diversity Index using the % weight of prey items consumed in each region by predator.

Shannon's Diversity Index (% Weight)	**NC**	**GB**	**NMB**	**CMB**	**SMB**
Chinook salmon	0.3	0.86	n/a	1.09	0.93
Lake trout	0.49	1.36	0.78	1.75	1.99
Lake whitefish	2.42	2.32	2.31	1.85	1.66
Rainbow trout	1.75	2.35	n/a	2.4	n/a
Walleye	1.8	2.07	n/a	0.9	1.6

Figure A1.4. Percent contribution of prey mass by season to diets of lake trout (panel A) and lake whitefish (panel B). Different regions are depicted including NC= North Channel, GB= Georgian Bay, NMB= northern main basin, CMB= central main basin, and SMB= southern main basin.



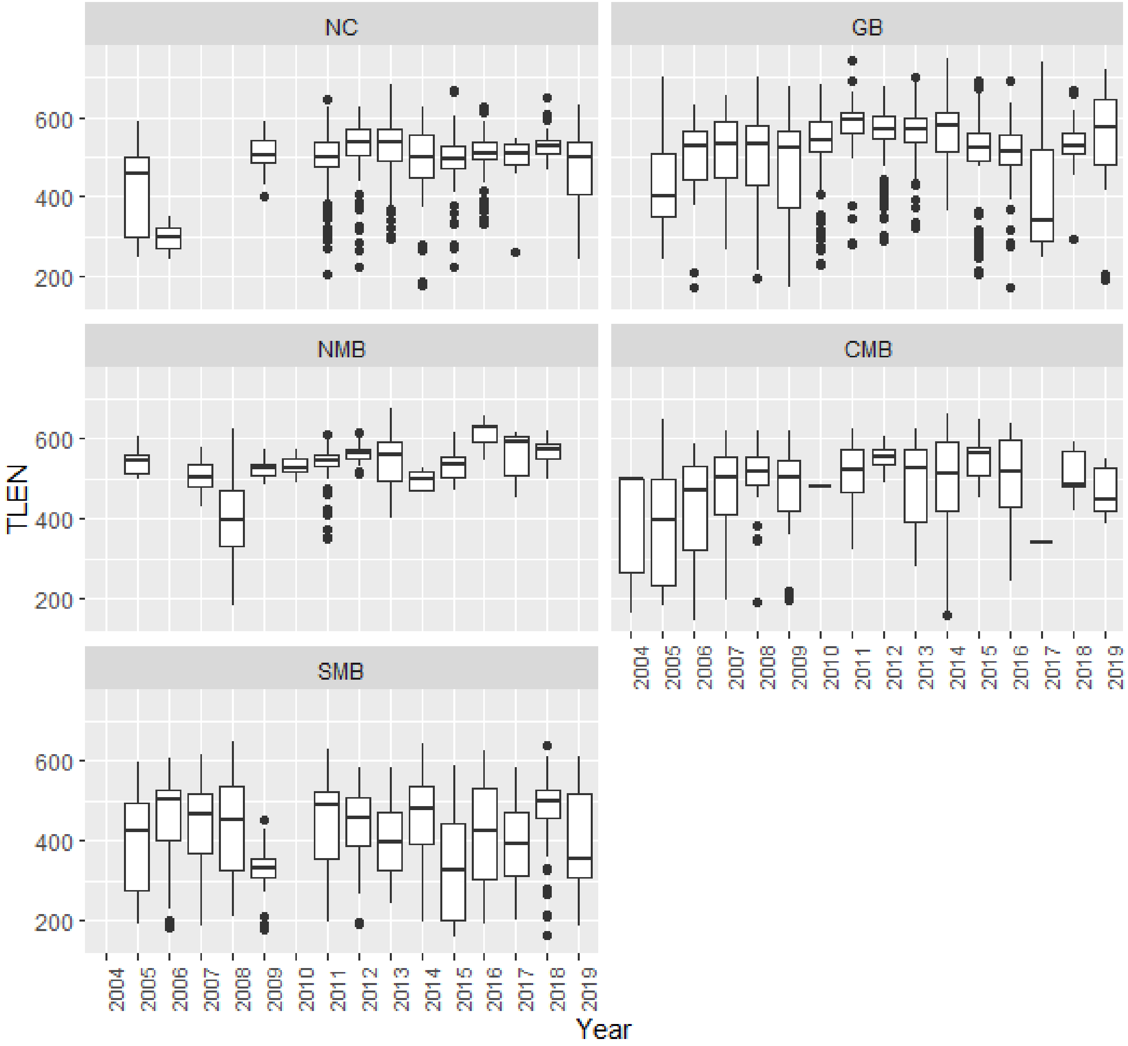


Figure A1.5. Total lengths of lake whitefish included in this study. In Georgian Bay, the northern and central main basin, more recent years had slightly larger fish on average than earlier years, and thus could bias the proportions of fish prey in the diets of lake whitefish.

Appendix 2. Supplemental material for isotope analyses

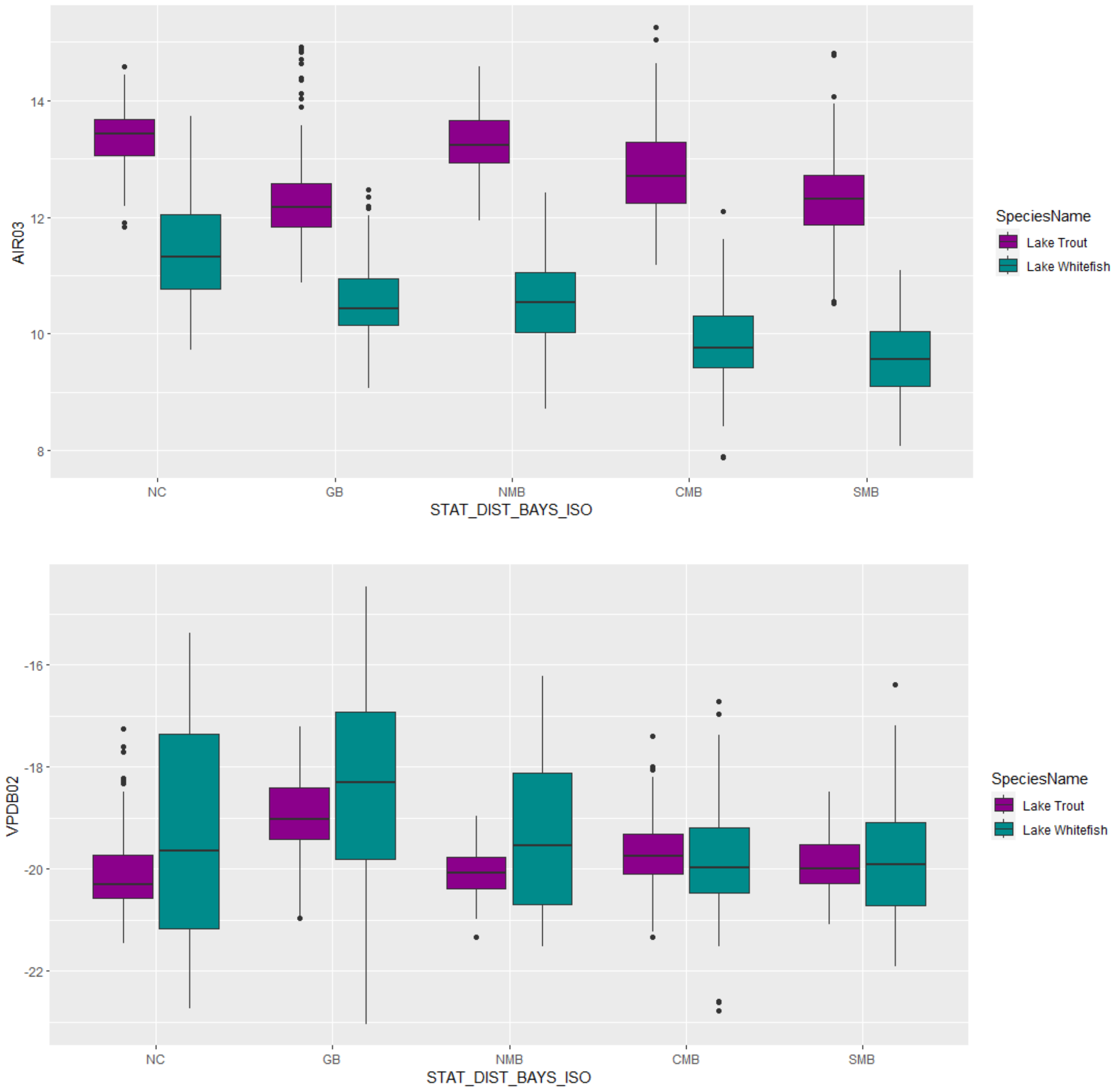


Figure A2.1. Regional Nitrogen (AIR03) and Carbon (VPDB02) ranges of lake trout and lake whitefish stable isotopes from Lake Huron, 2014-2019. Regional acronyms are as follows: NC= North Channel, GB= Georgian Bay, NMB= Northern main basin, CMB= central main basin, SMB= Southern main basin.

Table A2.1. Tukey results between regions for lake trout and lake whitefish a) Carbon signatures, and b) Nitrogen signatures

a)

Group1	Group2	estimate	conf.low	conf.high	p.adj	p.adj.signif
Lake Trout:North Channel	Lake Whitefish:North Channel	0.695716	0.151732	1.239701	2.19E-03	**
Lake Trout:North Channel	Lake Trout:Georgian Bay	1.033168	0.496931	1.569405	6.54E-08	****
Lake Trout:North Channel	Lake Whitefish:Georgian Bay	1.699625	1.173651	2.2256	1.60E-13	****
Lake Trout:North Channel	Lake Trout:Northern main basin	-0.04298	-0.64265	0.556676	1.00E+00	ns
Lake Trout:North Channel	Lake Whitefish:Northern main basin	0.599635	-0.03238	1.231651	7.98E-02	ns
Lake Trout:North Channel	Lake Trout:Central main basin	0.363402	-0.17661	0.903413	5.04E-01	ns
Lake Trout:North Channel	Lake Whitefish:Central main basin	0.212822	-0.321	0.746647	9.61E-01	ns
Lake Trout:North Channel	Lake Trout:Southern main basin	0.141607	-0.41099	0.694207	9.98E-01	ns
Lake Trout:North Channel	Lake Whitefish:Southern main basin	0.257457	-0.28518	0.800093	8.90E-01	ns
Lake Whitefish:North Channel	Lake Trout:Georgian Bay	0.337452	-0.19596	0.870866	5.95E-01	ns
Lake Whitefish:North Channel	Lake Whitefish:Georgian Bay	1.003909	0.480813	1.527006	7.55E-08	****
Lake Whitefish:North Channel	Lake Trout:Northern main basin	-0.7387	-1.33584	-0.14156	3.71E-03	**
Lake Whitefish:North Channel	Lake Whitefish:Northern main basin	-0.09608	-0.7257	0.533541	1.00E+00	ns
Lake Whitefish:North Channel	Lake Trout:Central main basin	-0.33231	-0.86952	0.204893	6.26E-01	ns

Lake Whitefish:North Channel	Lake Whitefish:Central main basin	-0.48289	-1.01388	0.048095	1.11E-01	ns
Lake Whitefish:North Channel	Lake Trout:Southern main basin	-0.55411	-1.10397	-0.00425	4.65E-02	*
Lake Whitefish:North Channel	Lake Whitefish:Southern main basin	-0.43826	-0.97811	0.101588	2.31E-01	ns
Lake Trout:Georgian Bay	Lake Whitefish:Georgian Bay	0.666457	0.151422	1.181493	1.80E-03	**
Lake Trout:Georgian Bay	Lake Trout:Northern main basin	-1.07615	-1.66624	-0.48606	4.46E-07	****
Lake Trout:Georgian Bay	Lake Whitefish:Northern main basin	-0.43353	-1.05647	0.189408	4.53E-01	ns
Lake Trout:Georgian Bay	Lake Trout:Central main basin	-0.66977	-1.19913	-0.1404	2.61E-03	**
Lake Trout:Georgian Bay	Lake Whitefish:Central main basin	-0.82035	-1.3434	-0.2973	3.42E-05	****
Lake Trout:Georgian Bay	Lake Trout:Southern main basin	-0.89156	-1.43376	-0.34936	1.00E-05	****
Lake Trout:Georgian Bay	Lake Whitefish:Southern main basin	-0.77571	-1.30775	-0.24367	1.85E-04	***
Lake Whitefish:Georgian Bay	Lake Trout:Northern main basin	-1.74261	-2.32339	-1.16183	1.61E-13	****
Lake Whitefish:Georgian Bay	Lake Whitefish:Northern main basin	-1.09999	-1.71412	-0.48586	8.01E-07	****
Lake Whitefish:Georgian Bay	Lake Trout:Central main basin	-1.33622	-1.85519	-0.81726	2.31E-13	****
Lake Whitefish:Georgian Bay	Lake Whitefish:Central main basin	-1.4868	-1.99933	-0.97428	1.69E-13	****
Lake Whitefish:Georgian Bay	Lake Trout:Southern main basin	-1.55802	-2.09007	-1.02597	1.68E-13	****
Lake Whitefish:Georgian Bay	Lake Whitefish:Southern main basin	-1.44217	-1.96386	-0.92047	1.54E-13	****

Lake Trout:Northern main basin	Lake Whitefish:Northern main basin	0.64262	-0.03569	1.320925	8.08E-02	ns
Lake Trout:Northern main basin	Lake Trout:Central main basin	0.406387	-0.18713	0.999906	4.77E-01	ns
Lake Trout:Northern main basin	Lake Whitefish:Central main basin	0.255807	-0.33209	0.843704	9.33E-01	ns
Lake Trout:Northern main basin	Lake Trout:Southern main basin	0.184591	-0.42041	0.789589	9.94E-01	ns
Lake Trout:Northern main basin	Lake Whitefish:Southern main basin	0.300442	-0.29547	0.896352	8.49E-01	ns
Lake Whitefish:Northern main basin	Lake Trout:Central main basin	-0.23623	-0.86243	0.389959	9.73E-01	ns
Lake Whitefish:Northern main basin	Lake Whitefish:Central main basin	-0.38681	-1.00768	0.234053	6.16E-01	ns
Lake Whitefish:Northern main basin	Lake Trout:Southern main basin	-0.45803	-1.09511	0.179053	4.03E-01	ns
Lake Whitefish:Northern main basin	Lake Whitefish:Southern main basin	-0.34218	-0.97064	0.28628	7.80E-01	ns
Lake Trout:Central main basin	Lake Whitefish:Central main basin	-0.15058	-0.6775	0.376338	9.96E-01	ns
Lake Trout:Central main basin	Lake Trout:Southern main basin	-0.2218	-0.76773	0.324136	9.56E-01	ns
Lake Trout:Central main basin	Lake Whitefish:Southern main basin	-0.10594	-0.64179	0.429898	1.00E+00	ns
Lake Whitefish:Central main basin	Lake Trout:Southern main basin	-0.07122	-0.61103	0.468598	1.00E+00	ns
Lake Whitefish:Central main basin	Lake Whitefish:Southern main basin	0.044635	-0.48497	0.574244	1.00E+00	ns
Lake Trout:Southern main basin	Lake Whitefish:Southern main basin	0.11585	-0.43268	0.664379	1.00E+00	ns

b)

Group1	Group2	estimate	conf.low	conf.high	p.adj	p.adj. signif
Lake Trout:North Channel	Lake Whitefish:North Channel	-1.97813	-2.30912	-1.64714	6.77E-14	****
Lake Trout:North Channel	Lake Trout:Georgian Bay	-1.05652	-1.3828	-0.73024	1.63E-13	****
Lake Trout:North Channel	Lake Whitefish:Georgian Bay	-2.79293	-3.11296	-2.4729	6.77E-14	****
Lake Trout:North Channel	Lake Trout:Northern main basin	-0.07071	-0.43558	0.294155	1	ns
Lake Trout:North Channel	Lake Whitefish:Northern main basin	-2.86141	-3.24596	-2.47685	6.77E-14	****
Lake Trout:North Channel	Lake Trout:Central main basin	-0.60768	-0.93625	-0.27911	2.78E-07	****
Lake Trout:North Channel	Lake Whitefish:Central main basin	-3.48501	-3.80982	-3.1602	6.77E-14	****
Lake Trout:North Channel	Lake Trout:Southern main basin	-1.06795	-1.40418	-0.73172	1.65E-13	****
Lake Trout:North Channel	Lake Whitefish:Southern main basin	-3.81299	-4.14316	-3.48282	6.77E-14	****
Lake Whitefish:North Channel	Lake Trout:Georgian Bay	0.921608	0.597048	1.246167	1.58E-13	****
Lake Whitefish:North Channel	Lake Whitefish:Georgian Bay	-0.8148	-1.13309	-0.49652	2.54E-13	****
Lake Whitefish:North Channel	Lake Trout:Northern main basin	1.907414	1.544082	2.270746	6.77E-14	****
Lake Whitefish:North Channel	Lake Whitefish:Northern main basin	-0.88328	-1.26638	-0.50018	2.56E-11	****
Lake Whitefish:North Channel	Lake Trout:Central main basin	1.370445	1.043577	1.697312	6.77E-14	****
Lake Whitefish:North Channel	Lake Whitefish:Central main basin	-1.50689	-1.82997	-1.1838	6.77E-14	****

Lake Whitefish:North Channel	Lake Trout:Southern main basin	0.910178	0.575611	1.244745	1.57E-13	****
Lake Whitefish:North Channel	Lake Whitefish:Southern main basin	-1.83486	-2.16334	-1.50639	6.77E-14	****
Lake Trout:Georgian Bay	Lake Whitefish:Georgian Bay	-1.73641	-2.04979	-1.42304	6.77E-14	****
Lake Trout:Georgian Bay	Lake Trout:Northern main basin	0.985806	0.626763	1.344849	1.54E-13	****
Lake Trout:Georgian Bay	Lake Whitefish:Northern main basin	-1.80489	-2.18392	-1.42586	6.77E-14	****
Lake Trout:Georgian Bay	Lake Trout:Central main basin	0.448837	0.126743	0.77093	0.000467	***
Lake Trout:Georgian Bay	Lake Whitefish:Central main basin	-2.42849	-2.74675	-2.11024	6.77E-14	****
Lake Trout:Georgian Bay	Lake Trout:Southern main basin	-0.01143	-0.34133	0.318474	1	ns
Lake Trout:Georgian Bay	Lake Whitefish:Southern main basin	-2.75647	-3.08019	-2.43275	6.77E-14	****
Lake Whitefish:Georgian Bay	Lake Trout:Northern main basin	2.722218	2.36884	3.075597	6.77E-14	****
Lake Whitefish:Georgian Bay	Lake Whitefish:Northern main basin	-0.06848	-0.44215	0.305194	1	ns
Lake Whitefish:Georgian Bay	Lake Trout:Central main basin	2.185249	1.869483	2.501015	6.77E-14	****
Lake Whitefish:Georgian Bay	Lake Whitefish:Central main basin	-0.69208	-1.00393	-0.38023	1.70E-10	****
Lake Whitefish:Georgian Bay	Lake Trout:Southern main basin	1.724982	1.401252	2.048712	6.77E-14	****
Lake Whitefish:Georgian Bay	Lake Whitefish:Southern main basin	-1.02006	-1.33749	-0.70263	1.62E-13	****
Lake Trout:Northern main basin	Lake Whitefish:Northern main basin	-2.7907	-3.20341	-2.37798	6.77E-14	****

Lake Trout:Northern main basin	Lake Trout:Central main basin	-0.53697	-0.8981	-0.17584	0.00012	***
Lake Trout:Northern main basin	Lake Whitefish:Central main basin	-3.4143	-3.77201	-3.05659	6.77E-14	****
Lake Trout:Northern main basin	Lake Trout:Southern main basin	-0.99724	-1.36535	-0.62912	1.60E-13	****
Lake Trout:Northern main basin	Lake Whitefish:Southern main basin	-3.74228	-4.10486	-3.37969	6.77E-14	****
Lake Whitefish:Northern main basin	Lake Trout:Central main basin	2.253726	1.872715	2.634737	6.77E-14	****
Lake Whitefish:Northern main basin	Lake Whitefish:Central main basin	-0.62361	-1.00138	-0.24584	9.01E-06	****
Lake Whitefish:Northern main basin	Lake Trout:Southern main basin	1.793459	1.405823	2.181095	6.77E-14	****
Lake Whitefish:Northern main basin	Lake Whitefish:Southern main basin	-0.95158	-1.33397	-0.56919	5.43E-13	****
Lake Trout:Central main basin	Lake Whitefish:Central main basin	-2.87733	-3.19794	-2.55672	6.77E-14	****
Lake Trout:Central main basin	Lake Trout:Southern main basin	-0.46027	-0.79244	-0.12809	0.000522	***
Lake Trout:Central main basin	Lake Whitefish:Southern main basin	-3.20531	-3.53135	-2.87927	6.77E-14	****
Lake Whitefish:Central main basin	Lake Trout:Southern main basin	2.417064	2.088611	2.745517	6.77E-14	****
Lake Whitefish:Central main basin	Lake Whitefish:Southern main basin	-0.32798	-0.65022	-0.00573	0.0422	*
Lake Trout:Southern main basin	Lake Whitefish:Southern main basin	-2.74504	-3.0788	-2.41129	6.77E-14	****

Table A2.2. Overlap values between lake trout (LT) and lake whitefish (LWF) using the proportion of standard ellipse overlap for all combinations of small and large fish in a) North Channel, b) Georgian Bay, c) northern main basin, d) central main basin and e) southern main basin.

a)

		Small LT Small LWF	Small LT Large LWF	Large LT Large LWF	Large LT Small LWF
North Channel	% of LT niche space shared by LWF	46.0	26.9	35.2	52.3
	% of LWF niche space shared by LT	8.9	6.2	11.0	13.6
Georgian Bay	% of LT niche space shared by LWF	49.6	33.1	33.9	59.1
	% of LWF niche space shared by LT	27.0	26.2	14.9	17.9
Northern main basin	% of LT niche space shared by LWF	17.9	4.9	2.4	13.9
	% of LWF niche space shared by LT	3.1	1.2	0.5	2.2
Central main basin	% of LT niche space shared by LWF	0	27.4	18.6	0
	% of LWF niche space shared by LT	0	15.6	11.1	0
Southern main basin	% of LT niche space shared by LWF	7.9	22.0	7.5	0.3
	% of LWF niche space shared by LT	4.0	14.9	5.4	0.1

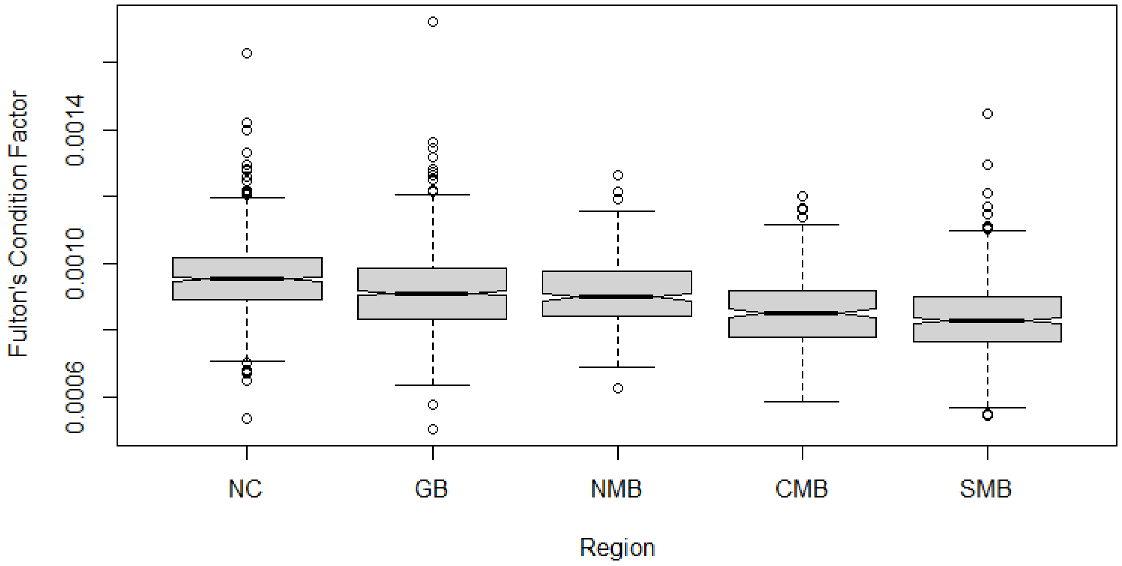


Figure A2.2. Fulton's condition factor of lake whitefish by region of Lake Huron. Regional acronyms are as follows: NC= North Channel, GB= Georgian Bay, NMB= Northern main basin, CMB= central main basin, SMB= Southern main basin.

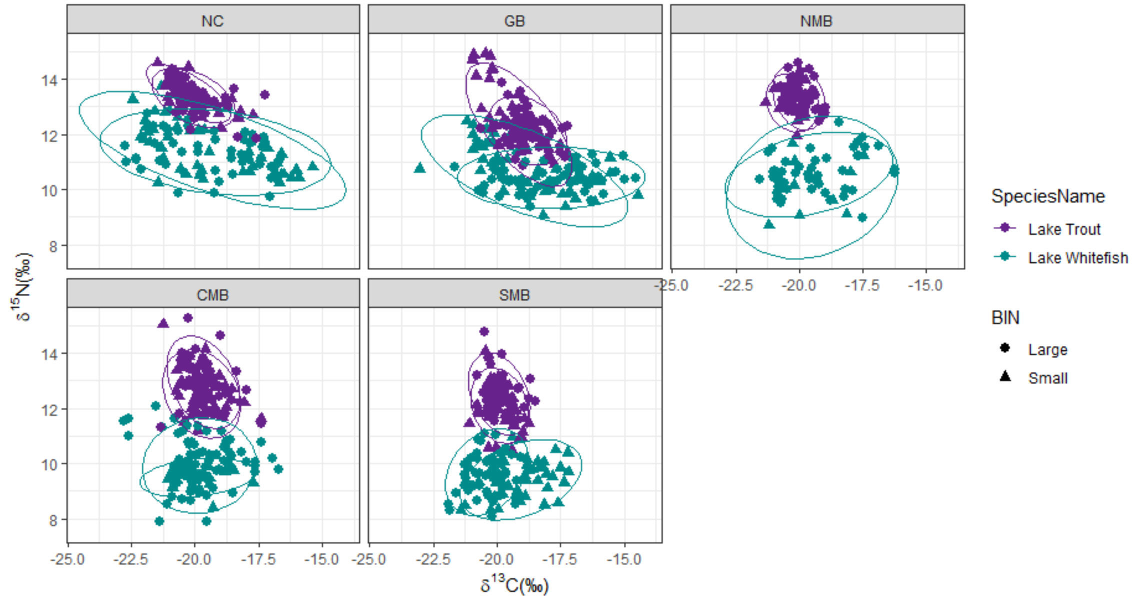


Figure A2.3. Median 95% δ^{13}C and δ^{15}N isotopic niche for Lake Huron lake trout and lake whitefish of two size bins from 2014 – 2019 indicated by ellipses. Size bins for lake trout were <550 mm for small and > 550mm for large. Size bins for lake whitefish were <450mm for small and >450mm for large. Circles indicate the large individuals and triangles indicate the small individuals.