# A COMPREHENSIVE STUDY OF PREDATOR DIETS IN LAKE HURON

By

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## A THESIS

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#### ABSTRACT

Lake Huron has a history of overfishing, habitat degradation, and introductions of nonnative species that have resulted in a dynamic ecosystem with a prey base of primarily nonnative species. In the mid-2000s, a massive shift in the ecosystem occurred when Alewife and Chinook Salmon populations collapsed. This led to an increase in native Lake Trout and Walleye populations, despite the continued low prey biomass. Alternative prey such as non-native Round Goby and Rainbow Smelt have supported predator foraging, but it is unclear if current prey biomass levels can support the continued expansion of Lake Trout and Walleye populations. I conducted a comprehensive diet study of angler-caught predators in 2017 and 2018 to evaluate current spatial and temporal trends in the diets of the major predators of Lake Huron within the context of historical foraging conditions. I observed several prominent spatiotemporal trends for the majority of Lake Huron predator diets, including a shift in consumption from Round Goby to Rainbow Smelt between spring and summer, and an overall reduced consumption of Round Goby in Saginaw Bay compared to the main basin. I also found an increased reliance on Round Goby by native Walleye and Lake Trout compared to previous studies while Chinook Salmon continued to rely upon Rainbow Smelt and Alewife. Evidence from gut fullness indices and size distributions of consumed prey indicate that forage conditions in Lake Huron continue to decline. Overall, the predator community continues to be reliant on non-native prey, and forage conditions may be indicative of prey limitation for the foreseeable future.

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#### CHAPTER I: A HISTORY OF ECOLOGICAL CHANGES IN LAKE HURON

Fish of the Great Lakes have been an important resource for humans for millennia. Evidence of tools used to catch fish have been found from as early as 3000 B.C., and since then, fishing equipment has increased in sophistication and effectiveness (Cleland 1982). However, a combination of the increased gear efficiency (Cleland 1982) and high levels of fishing effort spurred by increased demand for fish (Berst and Spangler 1973) contributed to large decreases in the population of many native fish species, including Lake Sturgeon *Acipenser fulvescens*, Cisco *Coregonus artedi*, Lake Whitefish *C. clupeaformis*, and deepwater ciscoes *Coregonus* spp. in the early 1900s (Smith 1968). While these early changes were detrimental to the fishery, many fish populations in the Great Lakes remained productive and stable through the 1940s (Smith 1968).

Between the 1940s and 1960s, a suite of anthropogenic changes led to the collapse of most commercially important fisheries. An increase in pollution caused by urbanization, agricultural runoff, and runoff from oil fields likely contributed to eutrophication and lowered water quality in Lake Huron (Beeton 1965; Beeton 1969). Along with an increased sediment load, logging also destroyed habitat for both river and reef spawning fishes (Fielder and Baker 2019; Kelso et al. 1996). The construction and dredging of shipping canals also decreased spawning habitat for native fish and decreased upper lakes water levels (Bennion and Manny 2011). To compound the environmental impacts on fish populations, many non-native species began to invade the Great Lakes due in part to the construction of numerous shipping canals that connected the Atlantic seaboard to Lake Erie and the Upper Great Lakes from the 1830s onward (Mills et al. 1993). The reconstruction of the Welland Canal that allowed ships to bypass Niagara Falls in 1932 allowed Alewife *Alosa pseudoharengus* and Sea Lamprey *Petromyzon marinus* to

invade Lake Huron (by 1933 (MacKay 1934) and 1937 (Applegate 1950), respectively). Other invasive species such as Rainbow Smelt *Osmerus mordax* were purposely released into Crystal Lake, Michigan, in 1912 (Creaser 1925) and subsequently spread into the Great Lakes in the 1920s (Van Oosten 1937).

The establishment of several invasive species, including Sea Lamprey, Alewife, and Rainbow Smelt, caused substantive and catastrophic changes to the Great Lakes ecosystem. Combined with overfishing, Sea Lamprey predation led the Lake Trout Salvelinus namaycush commercial catch in Lake Huron to decrease from 2268 t in 1938 to 76 t in 1954, and effectively collapsed the population (Smith and Tibbles 1980). Sea Lamprey also reduced populations of Burbot Lota lota, Lake Whitefish, catostomids, Walleye Stizostedion vitreus, Rainbow Trout Oncorhynchus mykiss, and deepwater ciscoes (including C. johannae, C. nigripinnis, C. zenithicus, C. alpenae, C. reighardi, and C. kiyi) throughout the Great Lakes (Berst and Spangler 1973; Christie 1974; Smith and Tibbles 1980; Smith 1964). As fish populations declined, commercial fisheries continued to catch fish to meet market demand (Brenden et al. 2012; Smith 1968). Following the decline of Lake Trout and subsequent reduction in the population of large prey fish, the Alewife population quickly increased to nuisance levels in lakes Michigan and Huron (Tanner and Tody 2002). Fishery productivity declined in lakes Ontario, Huron, and Michigan following Alewife establishment due to a decline in abundant shallow-water planktivores, minor piscivores, and deepwater planktivores (Smith 1970). While some native species, such as Yellow Perch *Perca flavescens*, were physically displaced to offshore areas, others, including C. kiyi, Bloater C. hoyi, Cisco, and Emerald Shiner Notropis atherinoides, decreased as a result of negative interactions with seasonal migration of dense shoals of Alewife (Smith 1968). Alewife and Rainbow Smelt also consumed newly hatched fry of other native

fishes such as Lake Trout, Burbot, Deepwater Sculpin *Myoxocephalus thompsonii*, Walleye, and Yellow Perch (Brandt et al. 1987; Brooking et al. 1998; Crowder 1980; Evans and Loftus 1987; Kohler and Ney 1980; Krueger et al. 1995; Loftus and Hulsman 1986; Madenjian et al. 2008). Lake Trout that consumed abundant Alewife suffered from thiamine deficiency that led to decreased recruitment due to Early Mortality Syndrome (Brown et al. 2005; Fisher et al. 1996; Fitzsimons et al. 2007). As a result of the impacts to fish populations caused by overfishing, pollution, habitat degradation, and invasive species, Lake Huron was dominated by Sea Lamprey, Alewife, and Bloater in the late 1950s (Smith 1968). With few large fish available, the commercial fishery declined sharply in the late 1950s and early 1960s (Brenden et al. 2012; Smith 1968).

In response to the low Lake Trout abundance and high Sea Lamprey abundance, the Great Lakes Fishery Commission (GLFC) began Sea Lamprey control efforts in 1955 to increase the productivity of fish stocks shared between the United States and Canada (Fetterolf 1980). While Sea Lamprey control was observed to be effective by 1967 (Smith 1968), the continued lack of predators was problematic as Alewife continued to reach nuisance levels and had negative impacts on tourism and anglers (Tanner and Tody 2002). Fisheries managers found unmet demand for fishing opportunities from recreational anglers, while commercial fishers reduced effort in response to low populations of desired species (Tanner and Tody 2002). The timing of the loss of predator fishes, the decline in commercial fishing, and new emphasis on natural resource management initiated a shift of priorities from a commercial fishery to a sport fishery (Tanner and Tody 2002). In 1966, lakes Michigan and Superior received 818,000 Coho Salmon *O. kisutch* smolts from Oregon (Tanner and Tody 2002). Following the successful return of jack Coho Salmon to rivers and the establishment of a viable recreational fishery, Chinook

Salmon *O. tshawytscha* were stocked in 1967 in Lake Michigan, and thereafter both Chinook and Coho salmon were stocked throughout the Great Lakes (Tanner and Tody 2002). The recreational fishery soon became economically more valuable than the commercial fishery, with an estimated \$1 and \$2 billion brought each year to Great Lakes economies during the 1970s and 80s (Fetterolf Jr 1980; Talhelm 1988) compared to an estimated \$200 million regional economic impact of commercial fisheries (Brown et al. 1999). As the salmon population increased, mean age and size of Alewife and Rainbow Smelt decreased in Lake Huron (Dobiesz et al. 2005) and concerns were raised that stocking levels were too high for the forage fish available in the lakes (Stewart et al. 1981). Therefore, managers began to reduce stocking levels in some locations in 1985 (Keller et al. 1990).

Despite the success of Pacific salmon stocking, managers also had goals to protect and restore Lake Huron's native fish community (Francis et al. 1979). In 1977, the GLFC assessed the prospect of rehabilitating the Great Lakes and in 1981, formulated a goal to "secure fish communities, based on foundations of stable self-sustaining stocks, supplemented by judicious plantings of hatchery-reared fish, and provide from these communities an optimum contribution of fish, fishing opportunities and associated benefits to meet needs identified by society for: wholesome food, recreation, employment and income, and a healthy human environment," (GLFC 1981). In particular, Lake Trout were targeted for restoration efforts with substantial stocking efforts throughout the Great Lakes. Lake Trout were sustained entirely by stocking in lakes Michigan and Huron from the 1970s through the 1990s as little measurable recruitment of wild-born Lake Trout occurred in these lakes (Eshenroder et al. 1995).

In the late 1980s and early 1990s, a new wave of invasive species from the Ponto-Caspian region entered Lake Huron via ballast water (Jude et al. 1992; Ricciardi and Rasmussen

1998). These included *Bythotrephes longimanus* (Bythotrephes) (1984), Round Goby *Neogobius* melanostomus (1990), and Dreissenid mussels (1988 for Zebra Mussels Dreissena polymorpha and 1997 Quagga Mussels D. bugensis (Dreissenids)) (Jude et al. 1992; Mills et al. 1993; Vanderploeg et al. 2002). While the predatory cladoceran spiny water flea (*Bythotrephes*) had an impact on the Lake Huron food web as predators (on zooplankton) and competitors (with larval fish) (Vanderploeg et al. 2002), Dreissenids and Round Goby are more relevant to the current study. Dreissenids filter mass quantities of seston (phytoplankton, detritus, and suspended sediment) and microzooplankton from the water column. In some locations such as Lake Erie, Dreissenids can clear 99.4% of the water column per day (Vanderploeg et al. 2002). Compared to native Great Lakes primary consumers such as zooplankton and unionid mussels, Dreissenids are far more efficient consumers and competitors of zooplankton (Vanderploeg et al. 2002). Their high filtering rate allows them to affect nutrient availability, particularly in nearshore areas where Zebra Mussels initially colonized at high densities (Hecky et al. 2004). As they take up nitrogen, phosphorus, and silicon, the unassimilated portion of these nutrients is released as pseudofeces into the benthos where it is inaccessible to the pelagic community (Hecky et al. 2004; Vanderploeg et al. 2002). For example, Barbiero et al. (2011) found evidence for decreased spring primary production throughout Lake Huron based on declines in both phytoplankton volumes and chlorophyll-a that likely led to observed decreases in zooplankton biomass. Scientists also observed decreases in offshore production and zooplankton, which are hypothesized to be caused at least in part by sequestration of nutrients by nearshore Dreissenids (Barbiero et al. 2018; Hecky et al. 2004; Vanderploeg et al. 2010).

There are few potential mechanisms that could deliver nutrients sequestered by Dreissenid mussels to the pelagic zone. Round Goby are a natural predator of *Dreissena* spp. and

represent a potential benthic-pelagic link in the Great Lakes (He et al. 2015) as they are consumed by Walleye, Lake Trout, Smallmouth Bass *Micropterus dolomieu*, Lake Whitefish, and Rainbow Trout (Johnson et al. 2005; Pothoven and Madenjian 2013; Roseman et al. 2014). However, Round Goby are also detrimental to native fish populations. They consume eggs at spawning sites (Chotkowski and Marsden 1999), use aggression to displace other benthic species (Dubs and Corkum 1996), and compete with other benthic fish species, such as Mottled Sculpin *Cottus bairdii*, for spawning habitat (Janssen and Jude 2001). There is currently a paucity of data to quantify energy transfer between Round Goby and the pelagia in Lake Huron, yet there is a need to understand the implications of the dreissenid/Round Goby trophic linkage on upper trophic levels.

Many prey species (including Mottled Sculpin, Deepwater Sculpin, Logperch *Percina caprodes*, Johnny Darter *Etheostoma nigrum*, Rainbow Smelt, Bloater, Spottail Shiner *N. hudsonius*, and Yellow Perch) in Lake Huron decreased in abundance in the mid-1990s (Riley et al. 2008). For example, Alewife declined by 99.9% between 1994 and 2006, with the largest proportional decline (82%) in 2003 (He et al. 2016; Riley et al. 2008). While the exact cause of the decline in total prey abundances is still unknown, there are many hypotheses involving both top-down and bottom-up effects. Bence et al. (2008) and Dettmers et al. (2012) posit that Alewives collapsed due to a combination of increased predation by Chinook Salmon and Double-crested Cormorants *Nannopterum auritum* (hereafter cormorants). However, Riley et al. (2008) hypothesized that if predation was an important cause of prey declines, predatory fish were primarily responsible since cormorants increased prior to prey fish declines, while increases in the predatory fish population were synchronous with prey fish declines (Dobiesz et al. 2005). Barbiero et al. (2012) raise the possibility that declines in Lake Huron productivity led to

Alewife declines, whereas Nalepa et al. (2007) connect the Alewife collapse to the coinciding loss of their *Diporeia* prey and the expansion of Dreissenids, specifically Quagga Mussels, into the profundal zone. Both He et al. (2015) and Kao et al. (2016) hypothesized that both top-down effects from predatory fish and bottom-up effects were responsible for the Alewife collapse, whereas Dunlop and Riley (2013) posit that a cold winter initiated the collapse, followed by lack of food for Alewife being the primary suppressor of recovery. Riley and Dunlop (2016) argued against the conclusions of He et al. (2015), and reinforced the argument for the role of winter severity. Bence et al. (2016) rebutted criticisms of He et al. (2015) by Riley and Dunlop (2016), maintaining that the evidence supported a role for predation in the collapse, and argued that evidence of cold temperatures or winter severity in causing declines in Alewife abundance was weak. While the exact cause of the Alewife collapse remains unclear, impacts of the collapse remain relevant for the Lake Huron food web because Alewife biomass remains low (O'Brien et al. 2019).

The Alewife collapse led to additional changes to the Lake Huron community. The catch of Chinook Salmon, one of the most valuable recreational fisheries, declined by over 50% in 2004 due to the loss of their preferred prey (Bence et al. 2008). As the Alewife population remained low, the body condition of Chinook Salmon decreased (He et al. 2008) even though total Chinook Salmon abundance remained low (Clark et al. 2016). The lack of compensatory growth indicates a continued lack of prey availability (He et al. 2015; Roseman et al. 2014).

The loss of Alewife had the opposite impact on native predators. Buoyed for years by extensive stocking, populations of wild-spawned Walleye and Lake Trout expanded, particularly in Saginaw Bay and Northern Lake Huron, respectively (Fielder et al. 2007; Fielder and Thomas 2006; Riley et al. 2007). The Walleye population achieved management recovery goals in 2005

and the 33-year stocking program was halted in 2006 (Fielder and Baker 2019). While Lake Trout have yet to attain full recovery, wild recruitment has increased due in part to increased thiamine levels in eggs that resulted from decreased reliance on thiaminase-abundant Alewife prey (Fitzsimons et al. 2010; He et al. 2012). Current management plans seek to reduce Lake Trout stocking with the hope that the population will soon be recovered (Lake Huron Technical Committee 2016).

In addition to Chinook Salmon, other prey fish populations in Lake Huron decreased during and immediately following Alewife collapse. In particular, sculpins, Ninespine Stickleback Pungitius pungitius, Troutperch Percopsis omiscomaycus, and non-native Rainbow Smelt remained low after Alewife collapsed, although Bloater and Emerald Shiner increased in abundance (Roseman and Riley 2009; Schaeffer et al. 2008). Despite the loss of Alewife as a predator, the Yellow Perch population continued to decrease as Walleye switched predation on Alewife to Yellow Perch (Ivan et al. 2011). Overall prey biomass has increased slowly over the decade following Alewife collapse but remains low compared to historical levels (O'Brien et al. 2019). Despite an initial increase in abundance (Schaeffer et al. 2008), Emerald Shiner biomass has remained low in recent years (O'Brien et al. 2019). In contrast to many species that decreased in abundance, Bloater and Cisco have increased. Bloater currently comprise the majority of the pelagic prey fish biomass (O'Brien et al. 2019). Round Goby biomass has been variable in Lake Huron and has decreased since 2012, with future population equilibrium uncertain (Gorman 2019). Total population biomass of Round Goby is unknown, and is certainly much higher than swept area values calculated from the USGS bottom-trawl survey (He et al. 2015) most likely due to low catchability stemming from low occupancy of trawlable habitat by Round Gobies in the fall when the survey is done.

There are still concerns that the current prey biomass is insufficient to fulfill predator community demand (Roseman et al. 2014). The increase of native predator populations together with expanded Atlantic Salmon *Salmo salar* stocking program (Johnson 2017; Tucker et al. 2014) continues the recent history of a top-heavy food web where prey could be limiting. Future changes to the ecosystem are also uncertain. With a bottom-up regulated system that is apparently controlled by Dreissenids (Bunnell et al. 2014) and self-regulated predator populations (Fielder et al. In press; Johnson et al. 2010), stocking is no longer an effective tool to manipulate the ecosystem (Stewart et al. 1981).

More information on the relationships between trophic levels is necessary to further understand how recent changes to the ecosystem could affect the future sustainability of the Lake Huron food web. Diet studies are one way to quantify the interactions between trophic levels (Chipps and Garvey 2007; DeBruyne et al. 2013). Many studies in Lake Huron have quantified predator-prey relationships and identified key prey resources that sustain predator populations (Diana 1990; Haas and Schaeffer 1992; Happel et al. 2017; He et al. 2015; Pothoven et al. 2017; Roseman et al. 2014). Historically, salmonines and Walleye relied upon Alewife and Rainbow Smelt as their main prey (Diana 1990; Haas and Schaeffer 1992), but since the Alewife collapse, Round Goby have increased in dietary importance for Lake Trout and Walleye (Happel et al. 2017; He et al. 2015; Pothoven et al. 2017; Roseman et al. 2014). Updated information is necessary to clarify our understanding of interactions between trophic levels as both predator and prey populations continue to change. Spatial variation in wild recruitment of Lake Trout (He 2019) has also created the need to better understand spatiotemporal variation in diets as a means to inform lakewide recovery targets.

In the next chapter, I describe a comprehensive diet study of Lake Huron piscine predators conducted between 2017 and 2018 that incorporates the spatiotemporal variation across multiple predator species. In particular, I identify the current role of non-native prey fish (especially Round Goby) as prey to salmonines and Walleye in Lake Huron. This study provides a more complete picture of the trophic relationships within Lake Huron and is intended to support ongoing efforts to quantify predator demand in Lake Huron. Further, this study provides baseline information that could be used as changes in the Lake Huron food web are tracked in the future.

#### WORKS CITED

- Applegate, V. C. 1950. Natural history of the Sea Lamprey, *Petromyzon marinus*, in Michigan. Dissertation. University of Michigan.
- Barbiero, R. P., B. M. Lesht, and G. J. Warren. 2011. Evidence for bottom–up control of recent shifts in the pelagic food web of Lake Huron. Journal of Great Lakes Research 37(1):78-85.
- Barbiero, R. P., B. M. Lesht, and G. J. Warren. 2012. Convergence of trophic state and the lower food web in Lakes Huron, Michigan and Superior. Journal of Great Lakes Research 38(2):368-380.
- Barbiero, R. P., B. M. Lesht, G. J. Warren, L. G. Rudstam, J. M. Watkins, E. D. Reavie, K. E. Kovalenko, and A. Y. Karatayev. 2018. A comparative examination of recent changes in nutrients and lower food web structure in Lake Michigan and Lake Huron. Journal of Great Lakes Research 44(4):573-589.
- Beeton, A. M. 1965. Eutrophication of the St. Lawrence Great Lakes. Limnology and Oceanography 10(2):240-254.
- Beeton, A. M. 1969. Changes in the environment and biota of the Great Lakes. Pages 150-187 in N. A. o. Sciences, editor. Eutrophication: Causes, consequences, correctives; proceedings of a symposium, Washington, D.C.
- Bence, J. R., J. E. Johnson, J. He, J. S. Schaeffer, S. Riley, R. J. Young, M. Ebener, D. Reid, L. C. Mohr, and D. Gonder. 2008. Offshore predators and their fish community. Pages 11-36 *in* J. R. Bence, and L. Mohr, editors. The state of Lake Huron in 2004, Ann Arbor, Michigan.
- Bence, J. R., C. P. Madenjian, J. X. He, S. A. Pothoven, N. E. Dobiesz, D. G. Fielder, J. E. Johnson, M. P. Ebener, A. R. Cottrill, L. C. Mohr, and S. Koproski. 2016. Reply to comments by Riley and Dunlop on He et al. (2015). Canadian Journal of Fisheries and Aquatic Sciences 73:865-868.
- Bennion, D. H., and B. A. Manny. 2011. Construction of shipping channels in the Detroit River: History and environmental consequences. U.S. Geological Survey.
- Berst, A. H., and G. R. Spangler. 1973. Lake Huron: The ecology of the fish community and man's effects on it. Great Lakes Fishery Commission, 21.
- Brandt, S. B., D. M. Mason, D. B. Macneill, T. Coates, and J. E. Gannon. 1987. Predation by Alewives on larvae of Yellow Perch in Lake Ontario. Transactions of the American Fisheries Society 116(4):641-645.
- Brenden, T. O., R. W. Brown, M. P. Ebener, K. Reid, and T. J. Newcomb. 2012. Great Lakes commercial fisheries: historical overview and prognoses for the future. Pages 339-397 *in* W. W. Taylor, A. Lynch, and N. Leonard, editors. Great Lakes fisheries policy and management: a binational perspective, 2<sup>nd</sup> edition. Michigan State University Press, East Lansing, Michigan.

- Brooking, T. E., L. G. Rudstam, M. H. Olson, and A. J. VanDeValk. 1998. Size-dependent Alewife predation on larval Walleyes in laboratory experiments. North American Journal of Fisheries Management 18(4):960-965.
- Brown, R. W., M. Ebener, and T. Gorenflo. 1999. Great Lakes commercial fisheries: Historical overview and prognosis for the future. Pages 307-354 *in* W. W. Taylor, and C. P. Ferreri, editors. Great Lakes fisheries policy and management: A binational perspective, 1st edition. Michigan State University Press, East Lansing, MI.
- Brown, S. B., J. D. Fitzsimons, D. C. Honeyfield, and D. E. Tillitt. 2005. Implications of thiamine deficiency in Great Lakes salmonines. Journal of Aquatic Animal Health 17(1):113-124.
- Bunnell, D. B., R. P. Barbiero, S. A. Ludsin, C. P. Madenjian, G. J. Warren, D. M. Dolan, T. O. Brenden, R. Briland, O. T. Gorman, J. X. He, T. H. Johengen, B. F. Lantry, B. M. Lesht, T. F. Nalepa, S. C. Riley, C. M. Riseng, T. J. Treska, I. Tsehaye, M. G. Walsh, D. M. Warner, and B. C. Weidel. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. BioScience 64(1):26-39.
- Chipps, S., and J. E. Garvey. 2007. Assessment of diets and feeding patterns. C. S. Guy, and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society.
- Chotkowski, M. A., and E. J. Marsden. 1999. Round Goby and Mottled Sculpin predation on Lake Trout eggs and fry: Field predictions from laboratory experiments. Journal of Great Lakes Research 25(1):26-35.
- Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. Journal of the Fisheries Research Board 31(5):827-854.
- Clark, R. D., J. R. Bence, R. M. Claramunt, J. E. Johnson, D. Gonder, N. D. Legler, S. R. Robillard, and B. D. Dickinson. 2016. A spatially explicit assessment of changes in Chinook Salmon fisheries in Lakes Michigan and Huron from 1986 to 2011. North American Journal of Fisheries Management 36(5):1068-1083.
- Cleland, C. E. 1982. The inland shore fishery of the Northern Great Lakes: Its development and importance in prehistory. American Antiquity 47(4):761-784.
- Creaser, C. W. 1925. The establishment of the Atlantic smelt in the upper waters of the Great Lakes. Papers of the Michigan Academy of Science, Arts, and Letters 5:405-424.
- Crowder, L. B. 1980. Alewife, Rainbow Smelt and native fishes in Lake Michigan: competition or predation? Environmental Biology of Fishes 5(3):225-233.
- DeBruyne, R. L., J. T. H. Coleman, J. R. Jackson, L. G. Rudstam, and A. J. VanDeValk. 2013. Analysis of prey selection by double-crested cormorants: A 15-year diet study in Oneida Lake, New York. Transactions of the American Fisheries Society 142(2):430-446.
- Dettmers, J. M., C. I. Goddard, and K. D. Smith. 2012. Management of alewife using Pacific salmon in the Great Lakes: Whether to manage for economics or the ecosystem. Fisheries 37(11):495-501.

- Diana, J. S. 1990. Food habits of angler-caught salmonines in western Lake Huron. Journal of Great Lakes Research 16(2):271-278.
- Dobiesz, N. E., D. A. McLeish, R. L. Eshenroder, J. R. Bence, L. C. Mohr, M. P. Ebener, T. F. Nalepa, A. P. Woldt, J. E. Johnson, R. L. Argyle, and J. C. Makarewicz. 2005. Ecology of the Lake Huron fish community, 1970-1999. Canadian Journal of Fisheries and Aquatic Sciences 62(6):1432-1451.
- Dubs, D. O., and L. D. Corkum. 1996. Behavioral interactions between Round Gobies (*Neogobius melanostomus*) and Mottled Sculpins (*Cottus bairdii*). Journal of Great Lakes Research 22(4):838-844.
- Dunlop, E. S., and S. C. Riley. 2013. The contribution of cold winter temperatures to the 2003 Alewife population collapse in Lake Huron. Journal of Great Lakes Research 39(4):682-689.
- Eshenroder, R. L., N. Robert Payne, J. E. Johnson, C. Bowen, and M. P. Ebener. 1995. Lake Trout rehabilitation in Lake Huron. Journal of Great Lakes Research 21:108-127.
- Evans, D. O., and D. H. Loftus. 1987. Colonization of inland lakes in the Great Lakes region by Rainbow Smelt, *Osmerus mordax*: Their freshwater niche and effects on indigenous fishes. Canadian Journal of Fisheries and Aquatic Sciences 44(S2):249-266.
- Fetterolf Jr, C. M. 1980. Why a Great Lakes Fishery Commission and why a Sea Lamprey International Symposium. Canadian Journal of Fisheries and Aquatic Sciences 37(11):1588-1593.
- Fielder, D. G., and J. P. Baker. 2019. Recovery of Saginaw Bay Walleye, Lake Huron. Pages 411-430 in C. C. Krueger, W. W. Taylor, and S.-J. Youn, editors. From catastrophe to recovery: Stories of fishery management success. American Fisheries Society, Bethesda, Maryland.
- Fielder, D. G., A. S. Briggs, and M. V. Thomas. In press. Status and trends of the fish community of Saginaw Bay, Lake Huron 2012-2017. Michigan Department of Natural Resources, Fisheries Report.
- Fielder, D. G., J. S. Schaeffer, and M. V. Thomas. 2007. Environmental and ecological conditions surrounding the production of large year classes of Walleye (*Sander vitreus*) in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 33(sp1):118-132.
- Fielder, D. G., and M. V. Thomas. 2006. Fish population dynamics of Saginaw Bay, Lake Huron 1998-2004. State of Michigan, 2083.
- Fisher, J. P., J. D. Fitzsimons, G. F. Combs, and J. M. Spitsbergen. 1996. Naturally occurring thiamine deficiency causing reproductive failure in Finger Lakes Atlantic Salmon and Great Lakes Lake Trout. Transactions of the American Fisheries Society 125(2):167-178.
- Fitzsimons, J. D., S. Brown, L. Brown, D. Honeyfield, J. He, and J. E. Johnson. 2010. Increase in Lake Trout reproduction in Lake Huron following the collapse of Alewife: Relief from thiamine deficiency or larval predation? Aquatic Ecosystem Health & Management 13(1):73-84.

- Fitzsimons, J. D., B. Williston, G. Williston, L. Brown, A. El-Shaarawi, L. Vandenbyllaardt, D. Honeyfeld, D. Tillitt, M. Wolgamood, and S. B. Brown. 2007. Egg thiamine status of Lake Ontario salmonines 1995–2004 with emphasis on Lake Trout. Journal of Great Lakes Research 33(1):93-103.
- Francis, G. R., J. J. Magnuson, H. A. Regier, and D. R. Talhelm. 1979. Rehabilitating Great Lakes ecosystems. Great Lakes Fishery Commission, Ann Arbor, Michigan.
- GLFC. 1981. A joint strategic plan for management of Great Lakes Fisheries, Ann Arbor, MI.
- Gorman, O. T. 2019. Prey fish communities of the Laurentian Great Lakes: A cross-basin overview of status and trends based on bottom trawl surveys, 1978-2016. Aquatic Ecosystem Health & Management 22(3):263-279.
- Haas, R. C., and J. S. Schaeffer. 1992. Predator-prey and competitive interactions among Walleye, Yellow Perch, and other forage fishes in Saginaw Bay, Lake Huron. Michigan Department of Natural Resources, Fisheries Research Report 1984.
- Happel, A., J. L. Jonas, P. R. McKenna, J. Rinchard, J. X. He, and S. J. Czesny. 2017. Spatial variability of Lake Trout diets in Lakes Huron and Michigan revealed by stomach content and fatty acid profiles. Canadian Journal of Fisheries and Aquatic Sciences 75:95-105.
- He, J. X. 2019. Regions and sub-regions of Lake Trout in the main basin of Lake Huron. Journal of Aquatic Research and Marine Sciences 2(1):97-105.
- He, J. X., J. R. Bence, J. E. Johnson, D. F. Clapp, and M. P. Ebener. 2008. Modeling variation in mass-length relations and condition indices of Lake Trout and Chinook Salmon in Lake Huron: A hierarchical Bayesian approach. Transactions of the American Fisheries Society 137(3):801-817.
- He, J. X., J. R. Bence, C. P. Madenjian, S. A. Pothoven, N. E. Dobiesz, D. G. Fielder, J. E. Johnson, M. P. Ebener, R. A. Cottrill, L. C. Mohr, and S. R. Koproski. 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. Canadian Journal of Fisheries and Aquatic Sciences 72(1):7-23.
- He, J. X., J. R. Bence, E. F. Roseman, D. G. Fielder, and M. P. Ebener. 2016. Using timevarying asymptotic length and body condition of top piscivores to indicate ecosystem regime shift in the main basin of Lake Huron: a Bayesian hierarchical modeling approach. Canadian Journal of Fisheries and Aquatic Sciences 73(7):1092-1103.
- He, J. X., M. P. Ebener, S. C. Riley, A. Cottrill, A. Kowalski, S. Koproski, L. Mohr, and J. E. Johnson. 2012. Lake Trout status in the main basin of Lake Huron, 1973–2010. North American Journal of Fisheries Management 32(2):402-412.
- Hecky, R. E., R. E. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 61(7):1285-1293.

- Ivan, L. N., T. O. Höök, M. V. Thomas, and D. G. Fielder. 2011. Long-term and interannual dynamics of Walleye and Yellow Perch in Saginaw Bay, Lake Huron. Transactions of the American Fisheries Society 140(4):1078-1092.
- Janssen, J., and D. J. Jude. 2001. Recruitment failure of Mottled Sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, induced by the newly introduced Round Goby *Neogobius melanostomus*. Journal of Great Lakes Research 27(3):319-328.
- Johnson, J. E. 2017. Review of attributes of landlocked Atlantic Salmon in relation to their management in Lake Huron, Fisheries Report 17, Lansing, MI.
- Johnson, J. E., S. P. DeWitt, and D. J. A. Gonder. 2010. Mass-marking reveals emerging self regulation of the Chinook Salmon population in Lake Huron. North American Journal of Fisheries Management 30(2):518-529.
- Johnson, T. B., D. B. Bunnell, and C. T. Knight. 2005. A potential new energy pathway in central Lake Erie: The Round Goby connection. Journal of Great Lakes Research 31:238-251.
- Jude, D., R. Reider, and G. Smith. 1992. Establishment of Gobiidae in the Great Lakes Basin. Canadian Journal of Fisheries and Aquatic Sciences 49(2):416-421.
- Kao, Y.-C., S. A. Adlerstein, and E. S. Rutherford. 2016. Assessment of top-down and bottomup controls on the collapse of Alewives (*Alosa pseudoharengus*) in Lake Huron. Ecosystems 19(5):803-831.
- Keller, M., K. D. Smith, and R. W. Rybicki. 1990. Review of salmon and trout management in Lake Michigan, 14.
- Kelso, J. R. M., R. J. Steedman, and S. Stoddart. 1996. Historical causes of change in Great Lakes fish stocks and the implications for ecosystem rehabilitation. Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1):10-19.
- Kohler, C. C., and J. Ney, J. 1980. Piscivority in a land-locked Alewife (*Alosa pseudoharengus*) population. Canadian Journal of Fisheries and Aquatic Sciences 37(8):1314-1317.
- Krueger, C. C., D. L. Perkins, E. L. Mills, and J. Ellen Marsden. 1995. Predation by Alewives on Lake Trout fry in Lake Ontario: Role of an exotic species in preventing restoration of a native species. Journal of Great Lakes Research 21:458-469.
- Lake Huron Technical Committee. 2016. Strategy for reducing Lake Trout stocking in Lake Huron. Great Lakes Fishery Commission.
- Loftus, D. H., and P. F. Hulsman. 1986. Predation on larval Lake Whitefish (*Coregonus clupeaformis*) and Lake Herring (*C. artedii*) by adult Rainbow Smelt (*Osmerus mordax*). Canadian Journal of Fisheries and Aquatic Sciences 43(4):812-818.
- MacKay, H. H. 1934. Record of the Alewife from Lake Huron. Copeia 1934(2):97-97.
- Madenjian, C. P., R. O'Gorman, D. B. Bunnell, R. L. Argyle, E. F. Roseman, D. M. Warner, J. D. Stockwell, and M. A. Stapanian. 2008. Adverse effects of Alewives on Laurentian

Great Lakes fish communities. North American Journal of Fisheries Management 28(1):263-282.

- Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19(1):1-54.
- Nalepa, T. F., D. L. Fanslow, S. A. Pothoven, A. J. Foley, and G. A. Lang. 2007. Long-term trends in benthic macroinvertebrate populations in Lake Huron over the past four decades. Journal of Great Lakes Research 33(2):421-436.
- O'Brien, T. P., S. A. Farha, D. M. Warner, P. C. Esselman, K. Phillips, S. Lenart, and C. Olds. 2019. Status and trends of pelagic prey fish in Lake Huron, 2018.
- Pothoven, S. A., and C. P. Madenjian. 2013. Increased Piscivory by Lake Whitefish in Lake Huron. North American Journal of Fisheries Management 33(6):1194-1202.
- Pothoven, S. A., C. P. Madenjian, and T. O. Höök. 2017. Feeding ecology of the Walleye (Percidae, *Sander vitreus*), a resurgent piscivore in Lake Huron (Laurentian Great Lakes) after shifts in the prey community. Ecology of Freshwater Fish 26(4):676-685.
- Ricciardi, A., and J. B. Rasmussen. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences 55(7):1759-1765.
- Riley, S. C., and E. S. Dunlop. 2016. Misapplied survey data and model uncertainty result in incorrect conclusions about the role of predation on Alewife population dynamics in Lake Huron: a comment on He et al. (2015). Canadian Journal of Fisheries and Aquatic Sciences 73:860-864.
- Riley, S. C., J. X. He, J. E. Johnson, T. P. O'Brien, and J. S. Schaeffer. 2007. Evidence of widespread natural reproduction by Lake Trout *Salvelinus namaycush* in the Michigan waters of Lake Huron. Journal of Great Lakes Research 33(4):917-921.
- Riley, S. C., E. F. Roseman, S. J. Nichols, T. P. O'Brien, C. S. Kiley, and J. S. Schaeffer. 2008. Deepwater demersal fish community collapse in Lake Huron. Transactions of the American Fisheries Society 137(6):1879-1890.
- Roseman, E. F., and S. C. Riley. 2009. Biomass of deepwater demersal forage fishes in Lake Huron, 1994–2007: Implications for offshore predators. Aquatic Ecosystem Health & Management 12(1):29-36.
- Roseman, E. F., J. S. Schaeffer, E. Bright, and D. G. Fielder. 2014. Angler-caught piscivore diets reflect fish community changes in Lake Huron. Transactions of the American Fisheries Society 143(6):1419-1433.
- Schaeffer, J. S., D. M. Warner, and T. P. O'Brien. 2008. Resurgence of Emerald Shiners *Notropis atherinoides* in Lake Huron's main basin. Journal of Great Lakes Research 34(3):395-403.

- Smith, B. R., and J. J. Tibbles. 1980. Sea Lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: History of invasion and control, 1936–78. Canadian Journal of Fisheries and Aquatic Sciences 37(11):1780-1801.
- Smith, S. H. 1964. Status of the deepwater cisco population of Lake Michigan. Transactions of the American Fisheries Society 93(2):155-163.
- Smith, S. H. 1968. Species succession and fisheries exploitation in the Great Lakes. Journal of the Fisheries Research Board of Canada 25(4):667-693.
- Smith, S. H. 1970. Species interactions of the Alewife in the Great Lakes. Transactions of the American Fisheries Society 99(4):754-765.
- Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society 110(6):751-763.
- Talhelm, D. R. 1988. The international Great Lakes sport fishery of 1980. Great Lakes Fishery Commission.
- Tanner, H. A., and W. H. Tody. 2002. History of the Great Lakes salmon fishery: A Michigan perspective. Pages 139-153 in K. D. Lynch, M. L. Jones, and W. W. Taylor, editors. Sustaining North American Salmon: Perspectives Across Regions and Disciplines. American Fisheries Society, Bethesda, Maryland.
- Tucker, S., A. Moerke, G. Steinhart, and R. Greil. 2014. First record of natural reproduction by Atlantic salmon (*Salmo salar*) in the St. Marys River, Michigan. Journal of Great Lakes Research 40(4):1022-1026.
- Van Oosten, J. 1937. The dispersal of smelt, *Osmerus mordax* (Mitchill), in the Great Lakes Region. Transactions of the American Fisheries Society 66(1):160-171.
- Vanderploeg, H. A., J. R. Liebig, T. F. Nalepa, G. L. Fahnenstiel, and S. A. Pothoven. 2010. Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan. Journal of Great Lakes Research 36:50-59.
- Vanderploeg, H. A., T. F. Nalepa, D. J. Jude, E. L. Mills, K. T. Holeck, J. R. Liebig, I. A. Grigorovich, and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 59(7):1209-1228.

#### CHAPTER II: A COMPREHENSIVE STUDY OF PREDATOR DIETS IN LAKE HURON

## INTRODUCTION

Recent changes in the Lake Huron food web have led to concerns regarding the sustainability of the current predator community. A combination of factors including overfishing, pollution, and invasion of Sea Lamprey *Petromyzon marinus* led to the collapse (e.g., Walleye *Stizostedion vitreum*, Yellow Perch *Perca flavescens*), and in some cases extirpation (e.g., Lake Trout *Salvelinus namaycush*, Cisco *Coregonus artedi*), of several native species populations (Berst and Spangler 1973; Smith 1968). The collapse of native predators allowed the population of invasive Alewife *Alosa pseudoharengus* to expand to nuisance levels (Smith 1970). In response, Lake Huron managers introduced two Pacific salmon species, Coho Salmon *Oncorhynchus kisutch* and Chinook Salmon *O. tshawytscha*, to provide angling opportunities and control populations of Alewife (Tanner and Tody 2002). The introduction of Pacific salmon was successful, and by the late 1980s, the Lake Huron piscivore community was dominated by non-native Pacific salmon and Alewife. However, changes to the ecosystem were forthcoming as a new suite of invasions from the Ponto-Caspian region began.

Species from the Ponto-Caspian region unintentionally introduced in the late 1980s and early 1990s led to dramatic changes in the Lake Huron food web. Zebra Mussels *Dreissena polymorpha*, Quagga Mussels *D. bugensis*, and Round Goby *Neogobius melanostomus* led to wholesale ecosystem changes that reconfigured the Lake Huron ecosystem (Vanderploeg et al. 2002). Dreissenids (*Dreissena* spp.) can filter upwards of 10 times the amount of seston (phytoplankton, detritus, and suspended sediment) and microzooplankton compared to native unionids (Vanderploeg et al. 2002). This has in part decreased the overall productivity of the Lake Huron pelagic zone and led to the benthification of energy pathways (Barbiero et al. 2009; Hecky et al. 2004; Mayer et al. 2014). Alewife abundances declined substantially during 1994-1996 and then by 99.9% of this lower level between 1994 and 2006, with the largest decline in 2003 ("collapse"; Riley et al. 2008, He et al. 2016). There is disagreement regarding the cause of the collapse, (see Chapter 1), but there is general agreement that lower pelagic productivity has contributed to the failure of Alewife to recover after their collapse (Bence et al. 2016, Riley and Dunlop 2016). As Alewife were the primary prey of Chinook Salmon (Diana 1990), their collapse led to a dramatic decrease in Chinook Salmon abundance in 2004 (Dettmers et al. 2012), with at least part of the decline in Chinook Salmon abundance in Lake Huron now hypothesized to be due to migration to Lake Michigan during the fishing season (Clark et al. 2016). Since the mid-2000s, overall prey biomass has remained low despite modest increases in native prey populations including Bloater C. hoyi, Cisco, and Emerald Shiner Notropis atherinoides (O'Brien et al. 2019). The notable exception is invasive Round Goby, which have been consistently captured in routine surveys since their introduction in the early 1990s (Gorman 2019). However, current survey methods are unable to accurately quantify their abundances (He et al. 2015; Johnson et al. 2005a), leading to questions regarding their role in the Lake Huron ecosystem and influence on management-specific benchmarks including the size-at-age and condition of top predators (He et al. 2016). The net result of these changes is that there is substantial uncertainty regarding the stability of the Lake Huron food web, particularly given recent increases in native predator species.

Increases in wild populations of native predators such as Lake Trout and Walleye occurred concomitantly with declines in Alewife abundance. Walleye have reached desired recovery benchmarks while wild Lake Trout natural reproduction has increased (Fielder et al.

2014; Fielder et al. 2007; Riley et al. 2007). Recent increases in the stocking of Atlantic Salmon *Salmo salar* (Johnson 2017) have also increased angling opportunities vacated by Chinook Salmon. The persistent low prey abundances combined with increased biomass of native predators have led to concerns that current prey abundances may be insufficient to satisfy demands of the predator community (Kraus et al. 2014; Roseman et al. 2014), which could threaten the continued recovery of native predators. Quantification of predator-prey relationships are needed to identify critical prey resources that sustain continued recovery of native fish communities in Lake Huron.

Diet studies are one way to detect how ecosystem changes affect predator-prey relationships (Chipps and Garvey 2007). For example, prior to Alewife collapse and Round Goby invasion, Diana (1990) and Haas and Schaeffer (1992) found that Clupeids (predominantly Alewife) and Rainbow Smelt Osmerus mordax formed nearly 100% of the diets of all Lake Huron salmonines and Walleye. After the Alewife collapse and Round Goby invasion, Roseman et al. (2014) found that Round Goby were heavily incorporated into diets of Lake Trout and Walleye, seemingly in place of Alewife; only Chinook Salmon diets continued to be dominated by Alewife. These results from 2009-2011 were echoed by more recent studies of Lake Trout (Happel et al. 2017) and Walleye (Pothoven et al. 2017), although these studies had a more limited sampling design compared to Diana (1990) and Roseman et al. (2014) in terms of the species, time periods, or locations they evaluated. While these studies are informative of foraging conditions within specific time periods and locations, a new comprehensive study is needed to update diet information and clarify spatiotemporal variation in prey consumption across predators. Lake Huron has continued to change since 2011, therefore data from Roseman et al. (2014) may not represent current conditions and there is a need to identify the importance of

non-native prey fish (specifically Round Goby) in the Lake Huron food web. Comprehensive diet studies of top predators are particularly valuable because the results are useful to identify community-wide and spatiotemporal trends in prey utilization critical to predator sustainability.

Herein, I describe the results of a comprehensive diet study of angler-caught piscine predators in Lake Huron. The objectives of this study were to determine the degree of spatiotemporal variation in predator diets and to provide a perspective on current foraging conditions for predators in Lake Huron within the context of previous studies (Roseman et al. 2014). I investigated whether predator diets varied by month, catch location, and year, both within the current study and between the current study and Roseman et al. (2014). I report the overall composition of predator diets, ration size, and the size of prey consumed to describe forage conditions available for Lake Huron predators.

#### METHODS

#### Field Methods

I analyzed diets from angler-caught predators Walleye, Lake Trout, Chinook Salmon, Coho Salmon, Pink Salmon *O. gorbuscha*, Rainbow Trout *O. mykiss* (lake form is often referred to as steelhead), Brown Trout *Salmo trutta*, and Atlantic Salmon from Lake Huron in 2017 and 2018. Predator stomachs were collected through a multi-agency effort between April and October of both years. Michigan Department of Natural Resources (MDNR) creel clerks and U.S. Fish and Wildlife (USFWS) biotechnicians collected predator stomachs from anglers in the course of their regular surveys. U.S. Geological Survey Great Lakes Science Center (USGS) biologists and technicians removed approximately 30 angler-caught Walleye carcasses from the freezer at Linwood Beach Marina in Linwood, MI, every two weeks. In addition to agency collections, Lake Huron anglers were asked to volunteer stomachs to the study and were supplied

with pre-printed tags for predator and catch information. All partner agencies and volunteer anglers recorded the species, date caught, location, and total length of the predator before removing the stomach from the fish. Port locations were grouped by Great Lakes Fishery Commission statistical districts (Smith et al. 1961) to simplify locations provided by anglers (Figure 1). In 2017, USGS biologists attended fishing tournaments and collected approximately 30 fish per species when possible. In 2018, a more concerted effort was made to ensure an appropriate sample size was achieved for each species, particularly as it relates to predator length. To ensure a wide distribution of sizes, I divided each predator species into four size categories: 200-399 mm, 400-599 mm, 600-799 mm, and >800 mm (Elliott et al. 1996). I attempted to collect a maximum of 15 stomachs/size class/species/statistical district every two weeks. All stomach samples from fresh fish were immediately preserved on ice and placed in a -20 °C freezer upon arrival at Michigan State University (MSU) or at an MDNR field office. All samples were brought to MSU for analysis.

## Lab Methods

Predator stomachs were removed from freezers and thawed in cool water before processing. Prey were identified to the lowest taxonomic group possible. Fish prey were identified to species and invertebrate prey to order. Identification of prey was based on external features unless the item was in a state of advanced digestion. Heavily digested prey fish were identified to species by bony structures such as otoliths and cleithra (Traynor et al. 2010). Initially, the prey in each taxon were counted and the first 30 prey fish were measured to either total length, standard length, or backbone length, depending on the state of digestion. If vertebral columns were not complete, I counted the number of vertebrae and related the partial vertebral length to total length using methods of Anderson et al. (2019). Examination of preliminary data



Figure 1: Map of Lake Huron statistical districts (from Smith et al. 1961). This study only included fish landed in the State of Michigan (United States).

determined that I could reduce the number of prey fish measured to 15 to reduce processing time yet retain valuable prey length data. Therefore, all 2018 samples and 16% of 2017 samples were based on processing only 15 prey fish to determine length. Invertebrates and non-fish prey items were blotted dry and weighed to the nearest 0.1 mg (wet weight). A correction factor of 5 mg (0.005 g) was added to all prey weights to account for scale error on prey that weighed <1 mg. Mass-at-capture was estimated for all partially digested prey fish from published length-weight relationships derived from the length of bony structures (cleithra, partial and full vertebrate), or standard lengths (Anderson et al. 2019; Knight et al. 1984). Unidentifiable prey fish were removed from further analysis. Prey were grouped into eight categories based on proportion by mass in diets to increase interpretability: Yellow Perch, Alewife, Round Goby, Rainbow Smelt, Coregonids, other fish, invertebrates, and other (a full list of prey can be found in Table 5 of the Appendix). Earthworms were removed from analysis due to their prevalence as bait (Roseman et al. 2014).

## Data Analysis

Data from predator stomachs were analyzed to assess current spatiotemporal patterns in predator diets, understand the integration of invasive prey species into the upper food web, and compare current foraging patterns to the most recent comprehensive diet study in Lake Huron (data from Roseman et al. 2014). I provide data summaries of predator diets (by species) by frequency of occurrence and average proportion prey by weight. Frequency of occurrence was used to provide evidence of commonness of individual prey species in predator diets. Average diet proportions were used to provide evidence for the overall contribution of prey biomass to the diet (across statistical district, calendar year, month, and predator size). I summarized diets across strata for a given factor, so for example monthly diets are summarized across all statistical districts. This provides a more holistic perspective to identify spatial and temporal trends that emerged from the data (see Appendix for summaries across strata within each factor for data specific to each statistical district). I used a zero-one inflated beta model in R (Rigby and Stasinopoulos 2005; R Core Team 2019) to compare average diet proportions of the most common prey species between seasons (spring (April-June) and summer (July-September)) within the predator species and statistical districts for the predators within statistical districts that contained the most samples.

I used two metrics to describe foraging patterns experienced by predators: ration size and prey total length. To compare ration sizes, I used a stomach fullness metric that is calculated by dividing the mass-at-capture of prey in stomachs by the estimated predator weight (Hyslop

1980). Predator weight was predicted from length-weight relationships in 2017-18 MDNR creel survey data of available predator species (Chinook Salmon, Lake Trout, Walleye, Atlantic Salmon, and Rainbow Trout). I conducted statistical tests in R (Hyslop 1980; R Core Team 2019) on ration sizes of non-empty stomachs to determine if overall feeding conditions for predators in Lake Huron have changed through time. I log-transformed ration data for Chinook Salmon, Lake Trout, and Walleye to better approximate normality, given that the untransformed values were skewed due to the large number of low-decimal values (i.e., below 0.01). Although data still did not adhere to normality standards (Shapiro test, p-value <0.05), a Box-Cox normality plot indicated lambda values between 0 and 0.5 for all species. A value of 0 indicates a log transformation, and the post-transformation ration data began to generally approximate normality. Following transformation, I analyzed the data by ANOVA including factors of individual study years (2009-2011 (Roseman et al. 2014) and 2017-2018 (current study)), predator species, and their interaction. I conducted a Tukey's HSD post-hoc test to further evaluate significant ANOVA results.

I compared the total length of the prey fish most commonly consumed (i.e., with the highest sample sizes): Round Goby consumed by Lake Trout and Walleye, Rainbow Smelt and Alewife consumed by Lake Trout and Chinook Salmon, and Yellow Perch consumed by Walleye. I used non-parametric methods in R (Pohlert 2014) to determine statistical differences in prey size distributions within several study strata given *a priori* assumptions of normality violations for prey fish that could have multiple age classes represented in predator stomachs. Data from multiple individual predators were pooled for each stratum used in an analysis to form the stratum size distributions, treating each consumed prey item as an independent sample within each stratum. I used a Kruskal-Wallis test to determine if there were significant yearly

differences in prey lengths consumed by all predators for each prey species I analyzed. I followed significant findings with a Nemenyi post-hoc test (Pohlert 2014) to evaluate differences between individual pairs of years for all predator species. I used Dunn's test for multiple comparisons (Dunn 1964) to test whether prey sizes consumed by individual predator species differ in particular years. I used the Wilcoxon Rank-Sum test to determine if individual predator species consumed different sizes of a given prey species. I also performed Wilcoxon Rank-Sum tests to determine whether size distributions of a given prey species differed between the periods of 2009-2011 (Roseman et al. 2014) and this study.

I attempted to formally test for differences between proportion by weight at capture of the prey categories identified above for all predators across statistical districts (six levels), length (4 levels), month (seven levels), and year (two levels) with a 4-factor permutational multivariate analysis of variance (PERMANOVA) in PRIMER-E (Anderson 2001). PERMANOVA compares multivariate data sets using a pseudo-F value created by running permutations of the data, eliminating the need for some of the more restrictive assumptions that limit the use of the more traditional MANOVA. I used the redistributed proportion prey by wet weight to create the Bray-Curtis similarity matrix used to run PERMANOVA. However, the model did not consistently converge on PERMANOVA results due to sample size constraints. Samples for certain months and length groups were unavailable, particularly for the three southernmost statistical districts. This created holes in my sample design that did not allow me to include interaction terms. When I ran the analysis using Type III sum of squares (SS) and included interactions, the main effects of the model were inestimable. Therefore, I halted attempts at statistical tests on this specific topic and kept diet composition comparisons descriptive.

## RESULTS

I collected a total of 3,256 stomachs from anglers in 2017 and 2018. Of those, 3,136 had complete information and were used in analysis (Figure 2, Table 1). The majority of the samples were Lake Trout (48%) and Walleye (33%), followed by Chinook Salmon (10%), Atlantic Salmon (3%), Coho Salmon (3%), Rainbow Trout (2.5%), Pink Salmon (<1%), and Brown Trout (<1%). Angling regulations restricted the size and seasonal availability of some predator species (MDNR 2016; MDNR 2018). Lake Trout were required to have a minimum length of 381 mm and to be harvested between January 1 and September 30 in all statistical districts in 2017 and in MH-1 and MH-2 in 2018. Harvest was permitted year-round in statistical districts MH-3 – MH-6 in 2018. All other salmon species harvest was permitted year-round with a minimum size of 254 mm. Walleye had a minimum size limit of 381 mm in all statistical districts except for MH-4 where the minimum size limit was 330 mm.

The proportion of empty stomachs varied among species. Overall, 32% of all collected stomachs were empty, but fewer were empty in 2018 (29%) than 2017 (37%). Pink Salmon had the lowest proportion of empty stomachs at 0%, whereas Walleye had the highest proportion at 44% (Table 2). In total, predator species consumed 75 taxa of fish and invertebrates. 451 stomachs contained unidentified prey fish.

Species	Minimum Length (mm)	Maximum length (mm)	Mean length (mm)	Standard Deviation
Lake Trout	394	953	649	79
Walleye	318	775	471	92
Chinook Salmon	432	1029	719	115
Atlantic Salmon	445	767	602	79
Coho Salmon	381	889	506	73
Rainbow Trout	394	775	632	79
Pink Salmon	318	483	402	45
Brown Trout	401	629	527	88

Table 1: Minimum, maximum, mean, and standard deviation of predator length.

	Year					
_	2017		2018		—	
Species	F	Ε	F	Ε	% Empty	Total
Lake Trout	456	228	631	181	27%	1496
Walleye	325	252	256	206	44%	1039
Chinook Salmon	44	39	154	82	38%	319
Atlantic Salmon	23	1	65	2	3%	91
Coho Salmon	34	2	43	11	14%	90
Rainbow Trout	24	4	41	10	18%	79
Pink Salmon	6	0	11	0	0%	17
Brown Trout	2	1	2	0	20%	5
Annual Percent	63%	37%	71%	29%		
Total	914	527	1203	492	32%	3136

Table 2: Sample sizes for angler-caught predators in 2017 and 2018. Species are listed in order of abundance. F = fed (contained prey), E = empty stomach.



Figure 2: Length-Frequency distributions of predators used in this study (stacked area plot, bin width = 30 mm)

## Frequency of Occurrence

Fishes were the most commonly observed prey for most predator species. For Lake Trout, 54% of non-empty stomachs contained Round Goby and 34% contained Rainbow Smelt, while only 28% contained invertebrates. Walleye commonly consumed invertebrates (37%), but 24% consumed Round Goby and 16% consumed Yellow Perch. The vast majority (>70%) of Chinook Salmon stomachs contained fish, dominated by Rainbow Smelt (45%) and Alewife (22%). However, invertebrates were more common than Alewife in Chinook Salmon stomachs (35%). The majority of Atlantic Salmon also consumed Rainbow Smelt (56%), but invertebrates and Other Fish were also frequently consumed (55% and 40%, respectively). The Other Fish category for Atlantic Salmon included salmonids (42% of Other Fish), Emerald Shiner (16% of Other Fish), Ninespine Stickleback Pungitius pungitius (20% of Other Fish), Threespine Stickleback Gasterosteus aculeatus (18% of Other Fish), and Morone spp. (3% of Other Fish). Coho Salmon stomachs most often contained Other Fish (41%), which included primarily Emerald Shiner (76% of Other Fish consumed by Coho Salmon), although Spottail Shiner *Notropis hudsonius*, salmonids, *Morone* spp, and Threespine Stickleback were also consumed (see Appendix Table 3 for details). Invertebrates (37%) and Rainbow Smelt (17%) were also frequently observed in Coho Salmon diets. Rainbow Trout diets contained invertebrates most often (83%), while Rainbow Smelt were the most common prey fish (28%). The majority of Pink Salmon diets contained invertebrates (88%), whereas the majority of Brown Trout stomachs contained Round Goby (75%). Unidentified prey fish were found in all predator species, including Coho Salmon (36% of stomachs), Walleye (30%), Atlantic Salmon (29%), Brown Trout (25%), Pink Salmon (24%), Chinook Salmon (22%), Rainbow Trout (17%), and Lake Trout (16%).

#### Diet Proportions by Wet Mass

#### Lake Trout

Lake Trout diets were dominated by Round Goby in 2017, whereas Rainbow Smelt were more common in 2018 (Figure 3A). In both years, Lake Trout captured in spring (April – June) typically consumed mostly Round Goby, while in summer (July – September) they consumed more Rainbow Smelt (Figures 4A and 4B, Appendix Figures 12-13). For both MH-1 and MH-2 I found a significant difference between spring and summer in the average proportion of Round Goby and Rainbow Smelt consumed (zero-one inflated beta model, MH-1: Round Goby p-value <0.001, Rainbow Smelt p-value <0.001; MH-2: Round Goby p-value =0.003, Rainbow Smelt pvalue =0.005). There was also a significant difference between 2017 and 2018 Round Goby consumption in MH-1 (zero-one inflated beta model, p-value <0.05), but no interaction between year and season (p-value >0.05). Spatial patterns were less distinct. Round Goby comprised between 50%-80% of Lake Trout diets in all statistical districts in 2017, except MH-3 and MH-5. In these statistical districts, Roundy Goby comprised 14% and 37% of Lake Trout diets, respectively (Figure 4C). In 2018, Round Goby continued to be an important prey item in most locations except MH-4. Rainbow Smelt were an important prey species in more statistical districts in 2018 compared to



*Figure 3: Average proportion of prey based on wet weight for each predator species for 2009-2011 (from Roseman et al. 2014) and 2017-2018. The numbers above the stacked bars* 

Figure 3 (cont'd): represents the number of stomachs that contained prey. A: Lake Trout, B: Walleye, C: Chinook Salmon, D: Atlantic Salmon, E: Coho Salmon, F: Rainbow Trout, G: Pink Salmon, H: Brown Trout.

2017, comprising >19% in one statistical district in 2017 compared to five in 2018 (Figure 4C and 4D, Appendix Figures 12-13). Lake Trout size had no obvious influence on observed diets, although Rainbow Smelt were slightly less common in larger fish (Figures 4E and 4F).

Walleye

Patterns in Walleye diets were generally similar to those in Lake Trout diets with the exception of the contribution of Yellow Perch. Like Lake Trout, Walleye consumed a high proportion of Round Goby throughout 2017 and 2018 and had an increase in Rainbow Smelt in 2018. Unlike Lake Trout, Yellow Perch made up a significant portion of Walleye diets (Figure 3B). Following the seasonal consumption pattern observed in Lake Trout, Walleye consumed Round Goby in spring, with Yellow Perch and Rainbow Smelt combined comprising upwards of 40% of Walleye diets in summer (Figures 5A and 5B, Appendix Figures 14-15). However, comparisons of average prey consumption between spring and summer were not significantly different (zero-one inflated beta model, Round Goby in MH-2: p-value = 0.47; Yellow Perch in MH-4: p-value = 0.20). Walleye diets varied substantially across statistical districts, although low sample sizes in some areas weaken this inference. Round Goby were consumed in all statistical districts, but Walleye consumption of this species was much lower in MH-4 compared to others. Yellow Perch, however, were consumed exclusively in MH-4 (Figures 5C and 5D, Appendix Figures 14-15). In contrast to Lake Trout, as Walleye increased in size, the proportion of Round Goby increased and the proportion of invertebrates and Yellow Perch decreased (Figures 5E and 5F).


Figure 4: Lake Trout average proportion of prey based on wet weight across months (A and B), statistical districts (C and D), and predator size (E and F) for 2017 (A, C, and E) and 2018 (B, D, and F). The numbers above the stacked bars represents the number of stomachs that contained prey.



Figure 5: Walleye average proportion of prey based on wet weight across months (A and B), statistical districts (C and D), and predator size (E and F) for 2017 (A, C, and E) and 2018 (B, D, and F). The numbers above the stacked bars represents the number of stomachs that contained prey. Statistical districts without stacked bars are representative of stomachs removed from analysis due to unidentifiable prey that could not be redistributed.

## Chinook Salmon

Chinook Salmon primarily consumed Rainbow Smelt and Alewife throughout both 2017 and 2018 (Figure 3C). Although my observations of Chinook Salmon diets are limited to specific statistical districts (primarily MH-1), Chinook Salmon appear to follow the same pattern as Lake Trout in that they consume Rainbow Smelt primarily in July-September. In contrast to both Lake Trout and Walleye, Chinook Salmon consumed a higher proportion of Rainbow Smelt in 2017 than in 2018 (Figures 6A and 6B, Appendix Figures 16-17). Chinook Salmon also consumed Alewife in summer months, although Alewife were both more abundant in the diet and consumed for a longer period in 2018 compared to 2017 (Figures 6A and 6B). The relatively few Chinook Salmon diet samples from outside MH-1 did not include any Alewife for either 2017 and 2018 (Figures 6C and 6D, Appendix Figures 16-17). Chinook Salmon size appeared to have little influence on diet composition (Figures 6E and 6F).

## Atlantic Salmon

Atlantic Salmon diets were more diverse than those of Chinook Salmon and Walleye. Other fish (including salmonids, Emerald Shiner, Ninespine Stickleback, Threespine Stickleback, and *Morone* spp.) made up the majority of prey biomass consumed in 2017, but Rainbow Smelt was the primary prey in 2018 (Figure 3D). Similar to Lake Trout and Chinook Salmon, Atlantic Salmon also consumed Rainbow Smelt in MH-1 only in 2017, but this prey was found in diets in five statistical districts in 2018 (Figures 7C and 7D, Appendix Figures 18-19). Alewife were only consumed in MH-1 and MH-2.



Figure 6: Chinook Salmon average proportion of prey based on wet weight across months (A and B), statistical districts (C and D), and predator size (E and F) for 2017 (A, C, and E) and 2018 (B, D, and F). The numbers above the stacked bars represents the number of stomachs that contained prey. Statistical districts without stacked bars are representative of stomachs removed from analysis due to unidentifiable prey that could not be redistributed.



Figure 7: Atlantic Salmon average proportion of prey based on wet weight across months (A and B) and statistical districts (C and D) for 2017 (A and C) and 2018 (B and D). The numbers above the stacked bars represents the number of stomachs that contained prey.

# Coho Salmon

Other fish (primarily Emerald Shiner) made up the majority of Coho Salmon diet composition in 2017, but Rainbow Smelt comprised the highest proportion of diets in 2018, a pattern similar to that seen for other predators (Figure 3E). Sample sizes were too low to compare diets across time and space, but I again observed an increase in the number of locations with Rainbow Smelt present in diets in 2018 (Figure 8D, Appendix Figures 20-21).



Figure 8: Coho Salmon average proportion of prey based on wet weight across months (A and B) and statistical districts (C and D) for 2017 (A and C) and 2018 (B and D). The numbers above the stacked bars represents the number of stomachs that contained prey fish. Statistical districts without stacked bars are representative of stomachs removed from analysis due to unidentifiable prey that could not be redistributed.

# Rainbow Trout

For Rainbow Trout, approximately 80% of diet wet mass was invertebrates, and the remainder was fish. The prey fish portion of the diet was dominated by Round Goby in 2017 and Rainbow Smelt in 2018 (Figure 3F). Although sample sizes were low, I did observe some temporal and spatial patterns, similar to the previous species described. When Round Goby were consumed, they were primarily consumed in spring (Figure 9A), whereas Rainbow Smelt were

primarily consumed in summer (Figure 9B). Similar to Chinook Salmon and Atlantic Salmon diets, Alewife were only consumed in MH-1 and the number of statistical districts with Rainbow Trout that consumed Rainbow Smelt increased from 2017 to 2018 (Figure 9C and 9D, Appendix Figures 22-23).

#### Pink Salmon and Brown Trout

Pink Salmon primarily consumed invertebrates in both 2017 and 2018, although Rainbow Smelt comprised a 4% higher proportion of diet wet mass in 2018 (Figure 3G, Appendix Figures 24-25). Brown Trout primarily consumed Round Goby in 2017 and 2018 (Figure 3H). Due to extremely low sample sizes, I did not compare the diets across time or space for either of these species (Appendix Figures 26-27).

## **Ration Size**

Predator ration size varied significantly across individual years and across study periods for Chinook Salmon and Lake Trout, but did not vary significantly for Walleye (Figure 10). I found significant pairwise interannual differences between years for Lake Trout between 2009 and 2011, and between 2009 and 2018 (Tukey's HSD, both p <0.025). For Chinook Salmon, a significant interannual difference emerged between 2009 and 2018 (Tukey's HSD, p-value = 0.003), with marginal significance between 2009 and 2011, and 2010 and 2018 (Tukey's HSD, 0.07>p>0.06). For Chinook Salmon, the mean ration was substantially lower in 2009 and 2010 than in all other years, with both years exhibiting mean rations <1.5% of body mass. In contrast, 2011 represented a high-bar mark for ration (Figure 10). Overall, Chinook Salmon rations were significantly higher in the current study as compared to 2009-2011 (ANOVA, p= 0.008), where the back-calculated ration in 2009-2011 averaged 2.1% of body mass, and 2.7% in 2017-2018. Ration size was similar in the current study compared to 2009-2011 for Lake Trout (ANOVA, pvalue >0.3). The similarity across studies was primarily driven by Lake Trout rations in 2011, where the mean ration approached 5% of body mass, which exceeded rations observed in either 2017 or 2018 (4.2% and 4.3%, respectively) (Figure 10). These values were at least 1.8% higher than either 2009 or 2010. As a consequence, I found significant interannual differences in Lake Trout diets (ANOVA, p = 0.004), where Lake Trout rations in 2009 were significantly lower than both 2011 and 2018 (Tukey's HSD, both p<0.025). All other years were similar to one another (all other p>0.13). For Walleye, I found no significant variation among years or between study periods (ANOVA, both p>0.13). Although the mean back-calculated ration for walleye more than doubled from 1.57% in 2009-2011 to 3.24% in 2017-2018, the substantial variation that existed among years prevented inferring that there was a consistent difference in ration between the study periods (Figure 10).

## Prey Size

## Alewife

The sizes of Alewife consumed by Lake Trout and Chinook Salmon changed through time. I found year (Kruskal-Wallis test,  $\chi^2$ =265.53, p-value <0.0001) and study period (Wilcoxon Rank-Sum test, p-value <0.001) to be significant factors influencing the size of Alewife consumed for both predator species. Among years, 2010 represented a unique year where the lengths of consumed Alewife were drastically smaller than all other years (Figure 11, Nemenyi post-hoc test, all pairwise p-values <0.0001). Alewife consumed by predators in 2010 possessed a mean length of 34.3 mm TL, whereas in all other years Alewife mean length was >119.2 mm TL (Figure 11). Alewife lengths in all other years were similar (Nemenyi post-hoc test, all p >0.19). Chinook Salmon and Lake Trout also appeared to consume different sizes of Alewife



Figure 9: Rainbow Trout average proportion of prey based on wet weight across months (A and B) and statistical districts (C and D) for 2017 (A and C) and 2018 (B and D). The numbers above the stacked bars represents the number of stomachs that contained prey and were not removed due to unidentifiable prey fish.



Figure 10: Boxplots comparing log-transformed ration sizes from the current study (2017-2018; blue) to Roseman et al. (2014) (2009-2011; green) by year (left), and by study period (right). Letters in left panel indicate significance groupings for results from Tukey's HSD post-hoc test for pairwise differences among years. Significance is denoted with an asterisk in right panel. Boxplot line corresponds to the median, the lower and upper box edges (hinge) represent the 25<sup>th</sup> and 75<sup>th</sup> percentiles, and the whiskers represent the largest and smallest values at most 1.5 of the inter-quartile range from the hinge (Wickham 2016).

combined across all years (Wilcoxon Rank-Sum test, p-value = 0.001), where Lake Trout

consumed smaller Alewife (mean = 87.7 mm TL, median = 112.0 mm TL) than Chinook Salmon

(mean = 104.9 mm, median = 118 mm). The lower mean value of Alewife lengths consumed by

Lake Trout was driven primarily by the large number of small Alewife consumed in 2010, which

averaged 30.9 mm. As a result, a Dunn's test for pairwise comparisons revealed no significant

differences between Lake Trout and Chinook Salmon within each year (all p>0.5) (Figure 11).

Spatial differences in the size of Alewife consumed were apparent across years within a given statistical district, but not across species within any year/statistical district combination. I limited interspecies comparisons to statistical district/year combinations where both species were sampled. Chinook Salmon only consumed Alewife in MH-1 in every study year and MH-2 in 2011 and 2018, limiting potential comparisons across species. Nonetheless, I found no differences in Alewife sizes consumed by Lake Trout and Chinook in every year/statistical district combination I evaluated (Dunn's test, all p >0.5). For Lake Trout, I found that the size distribution consumed in MH-1 in 2010 was similar to that consumed in MH-6 in 2010, but differed from the size distribution found in MH-1 in all other study years (Dunn's test, all p <0.003). All other year/statistical district combinations were statistically similar (Dunn's test, all p >0.5). Similarly, the size distribution of Alewife consumed by Chinook Salmon in MH-1 in 2010 differed from that consumed in MH-1 in all other years (Dunn's test, all p >0.05), but there was no difference in Alewife size between any other year/statistical district combination (Dunn's test, all p > 0.5). These results are echoed somewhat when analyzed by study period. I found a significant difference in the size of Alewife consumed by Lake Trout and Chinook in MH-1 during 2009-2011 (Dunn's test, p<0.0001), but not for any other study/statistical district combination. For Lake Trout, I found a significant difference in the size of Alewife consumed in MH-1 between surveys (Dunn's test, p < 0.001), and a difference between MH-1 and MH-2 during 2009-2011 (Dunn's test, p < 0.001), but no difference between these two statistical districts in 2017-2018.



*Figure 11: Box plot of Alewife lengths (mm) found in Chinook Salmon and Lake Trout stomachs in 2009-2011 (Roseman et al. 2014) and during the current study.* 

#### Rainbow Smelt

The size of Rainbow Smelt consumed by Lake Trout and Chinook Salmon (combined) appears to vary annually. I found that the size of Rainbow Smelt consumed by these predator species differed significantly between every pair of years (Figure 12, Kruskal-Wallis test,  $\chi^2$ =2309.4, p-value <0.0001; Nemenyi post-hoc test, all pairwise p-values <0.0001), and across study periods (Wilcoxon Rank-Sum test, p-value <0.001). Rainbow Smelt consumed by both Lake Trout and Chinook Salmon were smaller in 2017-2018 (mean 71.6 mm TL, median = 74.5 mm TL) as compared to 2009-2011 (mean = 81.8 mm TL, median = 86.0 mm TL). The size of Rainbow Smelt also differed between Lake Trout and Chinook Salmon (Wilcoxon Rank-Sum

test, p-value <0.001), with Lake Trout generally consuming larger Rainbow Smelt (Figure 12, mean = 77.8 mm TL, median = 79.7 mm TL) than Chinook Salmon (Figure 11D, mean = 66.2 mm TL, median = 57.0 mm TL). In contrast to Alewife, I found significant pairwise differences between Rainbow Smelt lengths consumed by Chinook Salmon and Lake Trout in all years except 2017 (Dunn's test, all p-values <0.03 except 2017 where p = 0.52) (Figure 12).

Spatial differences in the size of Rainbow Smelt consumed were apparent across years within a given statistical district and within a year/statistical district combination across predator species. Pairwise comparisons yielded complex patterns that were not easy to generalize, and indicate context-specific consumption across statistical districts, years, and predator species. In general, Rainbow Smelt consumed by Lake Trout in MH-4, MH-5, and MH-6 differed from at least one northern statistical district depending on the year. In 2009, MH-5 significantly differed from MH-1, but no other statistical districts differed from one another. In 2010, MH-4 differed from all other districts, whereas no other districts differed from one another. In 2011, all statistical districts were similar. In 2017, I found that MH-6 differed from both MH-1 and MH-2, whereas in 2018 MH-5 differed from all other statistical districts. For Chinook Salmon, most differences in Rainbow Smelt size distributions arose from comparisons between MH-1 and all other statistical districts. MH-1 differed from at least one other statistical district in 2010, 2011, and 2018. In 2009 and 2017, all statistical districts were similar except for MH-2, where 2017 represented an anomalous year relative to all other years besides 2009. The comparison of Lake Trout to Chinook Salmon revealed that both species consumed similar-sized Rainbow Smelt in almost all locations besides MH-1. I found significant differences in Rainbow Smelt size consumed by Lake Trout and Chinook Salmon in MH-1 in every year besides 2017, but not in any other year/statistical district combination besides MH-4 in 2018.



*Figure 12: Box plot comparison of Rainbow Smelt lengths (mm) found in Chinook Salmon and Lake Trout stomachs in 2009-2011 (Roseman et al. 2014) and during the current study (2017-2018).* 

## Round Goby

Round Goby size distributions found in predator diets exhibited substantial annual variation. I found a significant effect of year on the sizes of Round Goby consumed by combined Lake Trout and Walleye (Kruskal-Wallis test,  $\chi^2$ =121.87, p-value <0.0001). Post-hoc tests revealed significant differences among most years, with 2010 an exception where this year was similar to 2017 (Figures 13 Nemenyi post-hoc test, p-value= 0.8 for 2010 vs 2017). Sizes of Round Goby did differ among study periods (Wilcoxon Rank-Sum test, p-value <0.0001), with predators within the current study period consuming smaller Round Goby (mean = 70.0 mm TL, median = 67.13 mm TL) as compared to 2009-2011 (mean = 74.2 mm TL, median = 70.8 mm

TL). Overall, Walleye appeared to consume larger Round Goby compared to Lake Trout (Wilcoxon Rank-Sum test, p-value <0.0001), although there is some indication that this relationship may have changed through time. I found that from 2009-2011, Lake Trout (Figure 11A) consumed similar-sized or slightly larger Round Gobies compared to Walleye (Dunn's test, all p-values >0.35), whereas in 2017-2018 the mean size of Round Goby consumed by Walleye (Figure 13) was 8-10 mm larger than Lake Trout (Dunn's test, both p-values <0.001) (Figure 13).



*Figure 13: Box plot comparison of Round Goby lengths (mm) found in Lake Trout and Walleye stomachs in 2009-2011 (Roseman et al. 2014) and during the current study (2017-2018).* 

Spatial patterns of Round Goby consumption appeared to be more context-dependent for Lake Trout than Walleye. Whereas the size distribution of Round Goby consumed by Lake Trout remained similar across years in MH-1, MH-3, and MH-6, size distributions varied nearly annually in MH-2 and MH-5. In MH-4, Round Goby consumed by Lake Trout differed significantly only between 2009 and 2017 (Dunn's test, p=0.014). The year 2009 represented a unique year in that the size distribution of Round Goby consumed by Lake Trout were similar across statistical districts (Dunn's test, all pairwise p-values >0.5). In 2010, MH-3 significantly differed from all other statistical districts (Dunn's test, all pairwise p-values >0.5). In 2010, MH-3 significantly others were similar to each other (all p>0.1). MH-1 represented a unique statistical district relative to both MH-2 and MH-5, but all other statistical district comparisons were not significantly different. In 2017, MH-5 and MH-6 both differed from MH-4, and MH-6 differed from MH-2 (Dunn's tests, all p-values <0.01). MH-5 represented a unique statistical district in 2018, where I found pairwise differences between this statistical district and MH-1, MH-2, and MH-3 (Dunn's test, all p-values <0.001). All other comparisons were not significant in this year.

For Walleye, I found few differences in pairwise comparisons of Round Goby size distributions among statistical districts. The size distribution of Walleye diets was not statistically distinguishable across years within a given statistical district, and across statistical districts within a given year. One exception to this is MH-2, where walleye consumed significantly different Round Goby sizes between 2010 and 2017. All other pairwise comparisons were not significant (all p>0.19).

#### Yellow Perch

Yellow Perch size distributions varied among years (Figure 14E, Kruskal-Wallis test,  $\chi^2$ =56.4, p-value <0.0001). No Yellow Perch lengths from Walleye were available for analysis in2010. Pairwise comparisons revealed that 2009 was not distinguishable from any other year (Nemenyi post-hoc test, p-values all >0.05), although there was a marginal difference between



Figure 14: Prey length-frequency plots of kernel density estimates for prey length (mm) from the current study and Roseman et al. (2014) for Round Goby consumed by Lake Trout (A), Round Goby consumed by Walleye (B), Rainbow Smelt consumed by Lake Trout (C), Rainbow Smelt consumed by Chinook Salmon (D), Yellow Perch consumed by Walleye (E), and Alewife consumed by Lake Trout (F).

2009 and 2017 (Nemenyi post-hoc test, p-value = 0.056). Yellow Perch lengths in 2011 were significantly different from 2017, which in turn differed from 2018 (Nemenyi post-hoc test, p-

values all <.0001). Sizes of Yellow Perch varied between study periods as well (Wilcoxon Rank-

Sum test, p-value <0.0001) with Walleye consuming much smaller Yellow Perch in the current study (mean = 69.5 mm TL, median = 63. 9 mm TL) than in 2009-2011 (mean = 96.2 mm TL, median = 90.45 mm TL).

#### DISCUSSION

This study represents the first comprehensive diet study of angler-caught predators in Lake Huron in nearly a decade (Roseman et al. 2014). Diet studies conducted since Roseman et al. (2014) are generally limited by species or particular locations (Happel et al. 2017; Pothoven et al. 2017). Comprehensive diet studies provide important comparisons to single-species studies and can highlight overall ecosystem-wide foraging trends. Additionally, comprehensive diet studies that utilize spatial and temporal stratification schemes can help illuminate variation in prey selection across species in space and time that ultimately provide a more complete picture of trophic dynamics within a given ecosystem (e.g., Garvey et al. 1998; Velip and Rivonker 2018; Livernois et al. 2019). For instance, I observed extensive seasonal and spatial diet variation of Lake Huron salmonines and Walleye in 2017 and 2018. Condensing this variation into lakewide averages (i.e., Figures 3-9) does provide a robust overview of predator foraging, however, variation in diet composition and sample sizes would lead to over-representation of diet items found at locations with higher sample sizes (Bettoli and Miranda 2001). For example, the lakewide average diet for Walleye indicates a high proportion of Yellow Perch due to the higher sample sizes from MH-4, even though Walleye from other areas consumed high proportions of Round Goby. This spatial difference is important to consider when assessing Walleye foraging impacts to prey community in different locations. Likewise, several predator species, including Lake Trout, Walleye, and Rainbow Trout consumed Round Goby early in the year and switched to Rainbow Smelt later. Thus, a lakewide and temporally-integrated sample could not detect

these important seasonal dynamics, and potentially would produce a misleading picture of the importance of these prey.

There are inherent issues to working with stomachs collected by anglers. For example, I was unable to control collection dates, locations, and targeted species. As a result, the stomachs I collected from anglers may not reflect what would be seen in a random sample of the Lake Huron fish community or individual categories of predators within the community (Brandt 1986). This is exacerbated by minimum size limits (MDNR 2016; MDNR 2018) that prevent the inclusion of small (sub-legal) fish in the analysis. In addition, Roseman et al. (2014) suggested that salmonids seasonally migrate and the fishery progresses northward from May through the summer. These processes created an unbalanced sampling design that limited interpretation of seasonal and/or spatial trends. For example, the majority of Walleye in this study were captured in Saginaw Bay throughout the year, allowing me to make seasonal comparisons within MH-4. However, it was difficult to make conclusions about seasonal trends in the main basin because sample sizes were lower and there were inadequate samples for each month within some statistical districts. While it is possible to pool the samples throughout the main basin to investigate seasonal trends (Pothoven et al. 2017), in the current study I do not have evidence to support this approach. One way to increase interpretability would be to obtain samples in all months across all statistical districts, which may be possible if more volunteer anglers contributed stomachs to the project, or else if I conducted my own sampling in each area/time strata.

#### **Diet Composition**

Round Goby and Rainbow Smelt were the two most commonly consumed prey species in this study. However, their consumption was highly dependent on season and predator capture

location. In addition, one of the major differences between 2017 and 2018 was a ubiquitous increase in the consumption of Rainbow Smelt across locations and seasons.

The proportion of Round Goby consumed by Lake Trout, Walleye, and Atlantic Salmon has increased since 2009 and 2010 (Roseman et al. 2014). Lakewide, Round Goby attained 50% consumption by Lake Trout and 25% by Walleye during our study. Pothoven et al. (2017) reported that Round Goby comprised 58% of Walleye diets in the main basin, and while I observed similar proportions (57% of Walleye diets in the main basin), MH-2 (74%) and MH-5 (73%) were even higher. Round Goby consumption in Lake Huron appears to exceed consumption in other locations including Lake Michigan (Jacobs et al. 2010), Lake Ontario (Dietrich et al. 2006; Rush et al. 2012; Hoyle et al. 2017; Mumby et al. 2018), Lake Erie (Johnson et al. 2005b), and some invaded inland lakes (Herbst et al. 2016), but is similar to levels observed in the St. Lawrence River (Reyjol et al. 2010). The frequency of Round Goby in predator diets and the resulting high diet proportion of this prey species lends evidence to the assertion that predators are dependent upon Round Goby in Lake Huron. Despite some interannual variation, Round Goby have likely replaced Alewife as the dominant prey for many Lake Huron salmonines and Walleye (Diana 1990; He et al. 2015). However, one must be cautious in this assertion because Round Goby are not prevalent in predator diets in all locations and seasons.

Seasonal trends were apparent for most species in Lake Huron. In particular, Lake Trout and Walleye consumed Round Goby primarily in spring, and shifted towards other fishes (Rainbow Smelt for Lake Trout, Yellow Perch for Walleye) later in summer and early fall. Seasonal progressions of prey are common for both species (Forney 1974; Diana 1990; Elrod and O'Gorman 1991; Haas and Schaeffer 1992; Herbst et al. 2016; Pothoven et al. 2017).

However, my data indicates that seasonal progressions are highly dependent on location. I observed Walleye in Saginaw Bay undergo a progression of prey items that differed from individuals in the main basin, similar to the progression observed by Pothoven et al. (2017). Walleye inside Saginaw Bay consumed Yellow Perch later in summer, whereas those outside continued to consume Round Goby or consumed Rainbow Smelt. The difference in seasonal progression of Walleye diets inside and outside Saginaw Bay likely has implications for overall seasonal growth patterns (Rand et al. 1994; Dobiesz 2003; Madenjian et al. 2006; Kao et al. 2015; Dai et al. 2019), although the dominant influence of preferred prey availability could swamp effects of even major differences in prey species composition across Lake Huron locales (Madenjian et al. 2018). Nonetheless, continued monitoring of Lake Huron predator diets needs to consider seasonal progressions with the understanding that local prey fish community composition will affect our interpretation of seasonal trends.

I found substantial evidence for spatial variation in predator diets for most predator species. My data suggest three general spatial regions of Lake Huron: Saginaw Bay (MH-4), northern Lake Huron (MH-1 and MH-2), and central-southern Lake Huron (MH-3, MH-5, and MH-6). The proportion of Round Goby consumed by Lake Trout and Walleye in Saginaw Bay was half of that in the rest of Lake Huron. Alewife and Rainbow Smelt were predominantly consumed by Lake Trout and Chinook Salmon in MH-1 and MH-2, while outside of these statistical districts, Chinook Salmon consumed far higher proportions of invertebrates as compared to their more northern counterparts, similar to findings by Happel et al. (2017) and Roseman et al. (2014). Happel et al. (2017) similarly indicated that Lake Trout consumed Alewife only in MH-1 and MH-2, and while Roseman et al. (2014) did not report spatiallyexplicit prey consumption, Chinook Salmon diets contained over 20% Alewife and were predominantly captured in MH-1 and MH-2. The spatial trends of prey consumption observed are likely a reflection of both prey availability and predator selection. Alewife abundances are higher in northern statistical districts, whereas Yellow Perch are more abundant in MH-4 (Fielder et al. In press; O'Brien et al. 2019). While spatial overlap with prey could lead to the presumption that predators in Lake Huron are opportunistic samplers of their environment, other data I present contradicts this assertion. For instance, Walleye (in 2017 and 2018) and Lake Trout (in 2018) consumed far fewer Round Goby in MH-4 compared to other statistical districts, despite their availability there (Fielder et al. In press). Walleye in Saginaw Bay achieved similar levels of Round Goby consumption as the Bay of Quinte (Hoyle et al. 2017) and Lake Erie (Madenjian et al. 2018), systems more similar to Saginaw Bay in terms of productivity and fish assemblage (Collingsworth et al. 2017). Predators may focus on other prey than Round Goby when alternatives are abundant due to the lower energy density of Round Goby (Johnson et al. 2005b). Clearly predators can be selective about which prey they consume and change their selectivity in response to prey conditions (Werner and Mittelbach 1981; Mittelbach 1983; Schmitt and Holbrook 1984; Elrod and O'Gorman 1991; Morato et al. 2000), and this is evidenced in my study by differences in diets among species when sampled at concomitant times and locations. However, the net outcome of the interaction between predator selectivity and local prey abundances on diets remain unresolved in Lake Huron.

Additional evidence for predator selectivity may be present in the distribution of predator samples, which was uneven across the lake. In Lake Huron, predators may congregate in locations where preferred prey are more abundant. Abundant preferred prey can act to concentrate predators in proximal locations (Nachman 1981; Sih 1984; Rose and Leggett 1990; Kitchell et al. 1994; Bax 1998). For instance, the presence of Atlantic Cod (*Gadus morhua*) was

associated with a spawning aggregation of their main prey, Capelin (*Mallotus villosus*) in areas of Atlantic Canada (Rose and Leggett 1990). However, the assertion that preferred prey can act to concentrate predators in proximal locations in Lake Huron is obscured by the dependence of my samples on angler-caught fish and a lack of information related to both predator and prey fish seasonal movement patterns (Landsman et al. 2011). Thus, spatially uneven angler effort may obscure true predator distributions. Further data on the movement and distribution of Lake Huron predators and prey would inform this discussion and help clarify the relative influence of preferred prey abundance, predator distributions, and predator selectivity on diet composition.

## Foraging Conditions in Lake Huron

The combination of prey size distribution, ration size, and proportion of fish with empty stomachs can be used to improve our understanding of the forage conditions available to predators. My study complements previous documentation of predator diets (Roseman et al. 2014), both of which are likely necessary to identify the difference between nominal interannual variation and wholesale ecosystem paradigm shifts. Low ration size could be indicative of future decreases in growth rates (Brett and Shelbourn 1975; Elliott 1975). I observed higher ration size in the current study compared to Roseman et al. (2014), indicating better foraging conditions. This idea is supported by a lower proportion of empty stomachs in the current period compared to Roseman et al. (2014). Nonetheless, spatially-integrated estimates of prey abundance in Lake Huron indicate that prey abundance remains low. One hypothesis that could explain this discrepancy is an increase in prey heterogeneity that concentrates predators near dense patches of prey (Sih 1984; Hassell and May 1988; Shurin and Allen 2001). Thus, spatially-integrated survey estimates of prey abundance remain low, but predators are able to forage successfully on remaining patches.

Pelagic prey size distributions in predator diets may be symptomatic of continued low prey abundance. Lake Trout and Chinook Salmon in Roseman et al. (2014) and Diana (1990) demonstrated evidence of niche partitioning with larger Rainbow Smelt consumed by Lake Trout and smaller Rainbow Smelt consumed by Chinook Salmon. However, in the current study, both Lake Trout and Chinook Salmon consumed similarly sized Rainbow Smelt, likely from the 2017 age class (O'Brien et al. 2018; O'Brien et al. 2019). The switch from a broader range of age classes consumed in periods of high prey abundance (Diana 1990) to a single year class could be a symptom of a declining Rainbow Smelt population with a narrower range of available sizes (O'Brien et al. 2019). Similar trends were observed prior to the Alewife collapse when multiple year classes failed (Bence et al. 2008). Alewife continue to be a limited portion of predator diets. Although there are differences between Alewife size distributions consumed by predators across years, consumption in this study and in Roseman et al. (2014) focuses on a single, centralized peak that corresponds with abundant year-classes (O'Brien et al. 2019). Historically, predators consumed a broad range of Alewife sizes (with bimodal peaks at 100 mm and 175 mm mean TL (see Diana 1990)). The constriction of the Alewife size distribution found in diets is likely due to continued trends of low Alewife abundance in the lake and the more constricted size distribution of Alewife that is available (O'Brien et al. 2019)

Walleye and Lake Trout potentially demonstrated niche partitioning in their consumption of Round Goby based on size. However, recent differences in Round Goby size distributions consumed by Walleye and Lake Trout are not consistent with those observed by Roseman et al. (2014). From 2009-2011, Lake Trout consumed similar-sized or larger Round Goby than Walleye, while in the current study period Walleye consumed larger Round Goby than Lake Trout. Reasons for this difference are unclear, but could be a symptom of a shift in depth

distributions or a change in seasonal migration patterns of Round Goby, predators, or both. Round Goby are demonstrated to move towards shallower depths in spring (Walsh et al. 2007), when they are likely to be encountered by Lake Trout and Walleye (Bergstedt et al. 2012). However, interactions between Round Goby size and encounter rates with Lake Trout and Walleye are unknown and highlights the importance of emerging work on Round Goby distributions, densities, and seasonal movements.

Yellow Perch consumed by Walleye were smaller in the current study compared to Roseman et al. (2014). The mean length of Yellow Perch length in this study (mean TL = 72.3 mm) corresponds to the mean length of age-0 Yellow Perch in Saginaw Bay from trawls (mean Age-0 TL = 74.4 mm in 2017 (Fielder et al. In press), 78.2 mm in 2018 (T. Wills, Michigan Department of Natural Resources, Fisheries Division, unpublished data). I observed few Yellow Perch >120 mm, indicating Walleye consumption is focused almost exclusively on age-0 fish. Roseman et al. (2014) also observed age-0 Yellow Perch in predator diets, but these age-0 fish were in addition to larger Yellow Perch that corresponded to older ages (Fielder and Thomas 2014). Thus, Walleye consumption may provide an important mechanism for the continued low survival of age-0 Yellow Perch currently observed in Saginaw Bay (Fielder et al. In press). Given the lack of alternative abundant pelagic prey species (such as Cisco and Alewife) and continued successful Walleye year class recruitment, high mortality of age-0 Yellow Perch in Saginaw Bay is likely to continue (Ivan et al. 2011; Fielder and Thomas 2014; Fielder et al. In press).

#### Management Implications

Predators in Lake Huron continue to be reliant upon non-native prey. Round Goby, Rainbow Smelt, and Alewife still dominate the diets of most Lake Huron piscine predator

species. Round Goby appear to be more important compared to previous studies, and predators appear to be prey-limited based on evidence from ration data and historically low prey fish abundances. Continued reliance upon Round Goby is likely unless predators exploit growing populations of Cisco and Bloater. Nonetheless, some concern is warranted regarding the continued reliability of Round Goby as an abundant prey resource. Their prevalence in diets has increased, but their average size has decreased. The mechanisms behind this decrease in size are unclear, but could be informed by in-depth studies of Round Goby population sizes, demographics, and growth. Currently, Round Goby populations are difficult to assess at broad spatial scales (Johnson et al. 2005a), and more work needs to occur to establish clear life history and growth patterns across regions of Lake Huron (but see French and Black 2009; Duan et al. 2016)).

This study provides data that are particularly valuable for modeling efforts. In Lake Huron, statistical-catch-at-age models are often used to track predator populations (Fielder and Bence 2014). However, more recent modeling efforts explicitly incorporate predator-prey interactions through bioenergetics (He et al. 2015). A key input to this modeling effort is updated diets for the diversity of predators that exist in Lake Huron. Thus, an updated model will aid fisheries managers in their effort to restore a self-sustaining ecologically balance fish community (DesJardine et al. 1995). In a constantly changing ecosystem, managers must identify critical predator-prey linkages that support sustainable food webs. Diet studies provide direct evidence of those predator-prey linkages and should be performed at regular intervals. As my study demonstrates, spatiotemporal variation is an important factor in prey consumption. Future studies should incorporate and attempt to prioritize sampling times and locations that minimize effort while maximizing utility.

#### WORKS CITED

- Anderson, M., B. A. Turschak, S. Czesny, and J. L. Jonas. 2019. Quantitative methods to reconstruct length and weight of Great Lakes prey fishes from dietary observations of bony structures. Journal of Great Lakes Research.
- Anderson, M. J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences 58(3):626-639.
- Barbiero, R. P., R. Vinebrooke, M. Balcer, D. C. Rockwell, and M. L. Tuchman. 2009. Recent shifts in the crustacean zooplankton community of Lake Huron. Canadian Journal of Fisheries and Aquatic Sciences 66(5):816-828.
- Bax, N. J. 1998. The significance and prediction of predation in marine fisheries. ICES Journal of Marine Science 55:997-1030.
- Bence, J. R., J. E. Johnson, J. He, J. S. Schaeffer, S. Riley, R. J. Young, M. Ebener, D. Reid, L. C. Mohr, and D. Gonder. 2008. Offshore predators and their fish community. Pages 11-36 in J. R. Bence, and L. Mohr, editors. The state of Lake Huron in 2004, Ann Arbor, Michigan.
- Bergstedt, R. A., R. L. Argyle, C. C. Krueger, and W. W. Taylor. 2012. Bathythermal habitat use by strains of Great Lakes- and Finger Lakes-origin Lake Trout in Lake Huron after a change in prey fish abundance and composition. Transactions of the American Fisheries Society 141(2):263-274.
- Berst, A. H., and G. R. Spangler. 1973. Lake Huron: The ecology of the fish community and man's effects on it. Great Lakes Fishery Commission, 21.
- Bettoli, P. W., and L. E. Miranda. 2001. Cautionary note about estimating mean length at age with subsampled data. North American Journal of Fisheries Management 21(2):425-428.
- Brandt, S. B. 1986. Food of trout and salmon in Lake Ontario. Journal of Great Lakes Research 12(3):200-205.
- Brett, J. R., and J. E. Shelbourn. 1975. Growth rate of young Sockeye Salmon, Oncorhynchus nerka, in relation to fish size and ration level. Journal of the Fisheries Research Board of Canada 32(11):2103-2110.
- Bunnell, D. B., R. P. Barbiero, S. A. Ludsin, C. P. Madenjian, G. J. Warren, D. M. Dolan, T. O. Brenden, R. Briland, O. T. Gorman, J. X. He, T. H. Johengen, B. F. Lantry, B. M. Lesht, T. F. Nalepa, S. C. Riley, C. M. Riseng, T. J. Treska, I. Tsehaye, M. G. Walsh, D. M. Warner, and B. C. Weidel. 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: Bottom-up and top-down regulation. BioScience 64(1):26-39.
- Chipps, S., and J. E. Garvey. 2007. Assessment of diets and feeding patterns. C. S. Guy, and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society.

- Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. Journal of the Fisheries Research Board 31(5):827-854.
- Clark, R. D., J. R. Bence, R. M. Claramunt, J. E. Johnson, D. Gonder, N. D. Legler, S. R. Robillard, and B. D. Dickinson. 2016. A spatially explicit assessment of changes in Chinook Salmon fisheries in Lakes Michigan and Huron from 1986 to 2011. North American Journal of Fisheries Management 36(5):1068-1083.
- Collingsworth, P. D., D. B. Bunnell, M. W. Murray, Y.-C. Kao, Z. S. Feiner, R. M. Claramunt, B. M. Lofgren, T. O. Höök, and S. A. Ludsin. 2017. Climate change as a long-term stressor for the fisheries of the Laurentian Great Lakes of North America. Reviews in Fish Biology and Fisheries 27(2):363-391.
- Dai, Q., D. B. Bunnell, J. S. Diana, S. A. Pothoven, L. Eaton, T. P. O'Brien, and R. T. Kraus. 2019. Spatial patterns of rainbow smelt energetic condition in Lakes Huron and Erie in 2017: Evidence for Lake Huron resource limitation. Journal of Great Lakes Research 45(4):830-839.
- DesJardine, R. L., T. K. Gorenflo, R. N. Payne, and J. D. Schrouder. 1995. Fish-community objectives for Lake Huron, Great Lakes Fisheries Commission Special Publication 95-1.
- Dettmers, J. M., C. I. Goddard, and K. D. Smith. 2012. Management of alewife using Pacific salmon in the Great Lakes: Whether to manage for economics or the ecosystem. Fisheries 37(11):495-501.
- Diana, J. S. 1990. Food habits of angler-caught salmonines in western Lake Huron. Journal of Great Lakes Research 16(2):271-278.
- Dietrich, J. P., B. J. Morrison, and J. A. Hoyle. 2006. Alternative ecological pathways in the Eastern Lake Ontario food web—Round Goby in the diet of Lake Trout. Journal of Great Lakes Research 32(2):395-400.
- Dobiesz, N. E. 2003. An evaluation of the role of top piscivores in the fish community of the main basin of Lake Huron. M. S. University. Dissertation. Ann Arbor, MI.
- Duan, Y. J., C. P. Madenjian, C. X. Xie, J. S. Diana, T. P. O'Brien, Y. M. Zhao, J. X. He, S. A. Farha, and B. Huo. 2016. Age and growth of Round Gobies in Lake Huron: Implications for food web dynamics. Journal of Great Lakes Research 42(6):1443-1451.
- Dunn, O. J. 1964. Multiple comparisons using rank sums. Technometrics 6(3):241–252.
- Elliott, J. M. 1975. The growth rate of Brown Trout (*Salmo trutta* L.) fed on reduced rations. Journal of Animal Ecology 44(3):823-842.
- Elliott, R. F., P. J. Peeters, M. P. Ebener, R. W. Rybicki, P. J. Schneeberger, R. J. Hess, J. T. Francis, G. W. Eck, and C. P. Madenjian. 1996. Conducting diet studies of Lake Michigan piscivores A protocol.

- Elrod, J. H., and R. O'Gorman. 1991. Diet of juvenile Lake Trout in Southern Lake Ontario in relation to abundance and size of prey fishes, 1979–1987. Transactions of the American Fisheries Society 120(3):290-302.
- Fielder, D. G., and J. R. Bence. 2014. Integration of auxiliary information in statistical catch-atage (SCA) analysis of the Saginaw Bay stock of Walleye in Lake Huron. North American Journal of Fisheries Management 34(5):970-987.
- Fielder, D. G., A. S. Briggs, and M. V. Thomas. In press. Status and trends of the fish community of Saginaw Bay, Lake Huron 2012-2017. Michigan Department of Natural Resources, Fisheries Report.
- Fielder, D. G., T. L. Kolb, T. M. Goniea, D. L. Wesander, and K. S. Schrouder. 2014. Fisheries of Saginaw Bay, Lake Huron 1986-2010. State of Michigan, 02.
- Fielder, D. G., J. S. Schaeffer, and M. V. Thomas. 2007. Environmental and ecological conditions surrounding the production of large year classes of Walleye (*Sander vitreus*) in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 33(sp1):118-132.
- Fielder, D. G., and M. V. Thomas. 2014. Status and trends of the fish community of Saginaw Bay, Lake Huron 2005-2011. State of Michigan, 03.
- Forney, J. L. 1974. Interactions between Yellow Perch abundance, Walleye predation, and survival of alternate prey in Oneida Lake, New York. Transactions of the American Fisheries Society 103(1):15-24.
- French, J. R. P., and M. G. Black. 2009. Maximum length and age of Round Gobies (*Apollonia melanostomus*) in Lake Huron. Journal of Freshwater Ecology 24(1):173-175.
- Garvey, J. E., N. A. Dingledine, N. S. Donovan, and R. A. Stein. 1998. Exploring spatial and temporal variation within reservoir food webs: Predictions for fish assemblages. Ecological Applications 8(1):104-120.
- Gorman, O. T. 2019. Prey fish communities of the Laurentian Great Lakes: A cross-basin overview of status and trends based on bottom trawl surveys, 1978-2016. Aquatic Ecosystem Health & Management 22(3):263-279.
- Haas, R. C., and J. S. Schaeffer. 1992. Predator-prey and competitive interactions among Walleye, Yellow Perch, and other forage fishes in Saginaw Bay, Lake Huron, 1984.
- Happel, A., J. L. Jonas, P. R. McKenna, J. Rinchard, J. X. He, and S. J. Czesny. 2017. Spatial variability of Lake Trout diets in Lakes Huron and Michigan revealed by stomach content and fatty acid profiles. Canadian Journal of Fisheries and Aquatic Sciences 75:95-105.
- Hassell, M. P., and R. M. May. 1988. Spatial heterogeneity and the dynamics of parasitoid-host systems. Annales Zoologici Fennici 25(1):55-61.

- He, J. X., J. R. Bence, C. P. Madenjian, S. A. Pothoven, N. E. Dobiesz, D. G. Fielder, J. E. Johnson, M. P. Ebener, R. A. Cottrill, L. C. Mohr, and S. R. Koproski. 2015. Coupling age-structured stock assessment and fish bioenergetics models: a system of time-varying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. Canadian Journal of Fisheries and Aquatic Sciences 72(1):7-23.
- He, J. X., J. R. Bence, E. F. Roseman, D. G. Fielder, and M. P. Ebener. 2016. Using timevarying asymptotic length and body condition of top piscivores to indicate ecosystem regime shift in the main basin of Lake Huron: a Bayesian hierarchical modeling approach. Canadian Journal of Fisheries and Aquatic Sciences 73(7):1092-1103.
- Hecky, R. E., R. E. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. N. Charlton, and T. Howell. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 61(7):1285-1293.
- Herbst, S. J., B. M. Roth, D. B. Hayes, and J. D. Stockwell. 2016. Walleye foraging ecology in an interconnected chain of lakes influenced by nonnative species. Transactions of the American Fisheries Society 145(2):319-333.
- Hoyle, J. A., J. P. Holden, and M. J. Yuille. 2017. Diet and relative weight in migratory Walleye (*Sander vitreus*) of the Bay of Quinte and eastern Lake Ontario, 1992–2015. Journal of Great Lakes Research 43(5):846-853.
- Hyslop, E. J. 1980. Stomach contents analysis -- a review of methods and their application. Journal of Fisheries Biology 17:411-429.
- Ivan, L. N., T. O. Höök, M. V. Thomas, and D. G. Fielder. 2011. Long-term and interannual dynamics of Walleye and Yellow Perch in Saginaw Bay, Lake Huron. Transactions of the American Fisheries Society 140(4):1078-1092.
- Jacobs, G. R., C. P. Madenjian, D. B. Bunnell, and J. D. Holuszko. 2010. Diet of Lake Trout and Burbot in Northern Lake Michigan during spring: Evidence of ecological interaction. Journal of Great Lakes Research 36(2):312-317.
- Johnson, J. E. 2017. Review of attributes of landlocked Atlantic Salmon in relation to their management in Lake Huron, Fisheries Report 17, Lansing, MI.
- Johnson, T. B., M. Allen, L. D. Corkum, and V. A. Lee. 2005a. Comparison of methods needed to estimate population size of Round Gobies (*Neogobius melanostomus*) in Western Lake Erie. Journal of Great Lakes Research 31:78-86.
- Johnson, T. B., D. B. Bunnell, and C. T. Knight. 2005b. A potential new energy pathway in central Lake Erie: The Round Goby connection. Journal of Great Lakes Research 31:238-251.

- Kao, Y.-C., C. P. Madenjian, D. B. Bunnell, B. M. Lofgren, and M. Perroud. 2015. Temperature effects induced by climate change on the growth and consumption by salmonines in Lakes Michigan and Huron. Environmental Biology of Fishes 98(4):1089-1104.
- Kitchell, J. F., L. A. Eby, X. He, D. E. Schindler, and R. A. Wright. 1994. Predator-prey dynamics in an ecosystem context. Journal of Fish Biology 45(sA):209-226.
- Knight, R. L., F. J. Margraf, and R. F. Carline. 1984. Piscivory by Walleyes and Yellow Perch in Western Lake Erie. Transactions of the American Fisheries Society 113(6):677-693.
- Kraus, R., M. Rogers, P. M. Kocovsky, W. H. Edwards, B. Bodamer-Scarbo, K. Keretz, S. Berkman, C. P. Madenjian, D. B. Bunnell, T. J. Desorcie, M. J. Kostich, P. M. Armenio, J. V. Adams, D. M. Warner, S. A. Farha, T. P. O'Brien, L. Ogilvie, R. M. Claramunt, D. Hanson, D. W. Hondorp, L. Kaulfersch, N. Watson, S. C. Riley, E. F. Roseman, M. A. Chriscinske, T. R. Tucker, J. E. Ross, P. M. Armenio, W. Woelmer, M. R. Vinson, L. M. Evrard, O. T. Gorman, D. L. Yule, and B. C. Weidel. 2014. Compiled reports to the Great Lakes Fishery Commission of the annual bottom trawl and acoustics surveys, 2013.
- Landsman, S. J., V. M. Nguyen, L. F. G. Gutowsky, J. Gobin, K. V. Cook, T. R. Binder, N. Lower, R. L. McLaughlin, and S. J. Cooke. 2011. Fish movement and migration studies in the Laurentian Great Lakes: Research trends and knowledge gaps. Journal of Great Lakes Research 37(2):365-379.
- Livernois, M. C., F. J. Fodrie, K. L. Heck, and S. P. Powers. 2019. Emergent intraspecific multiple predator effects shape estuarine trophic dynamics across a gradient of habitat complexity. Journal of Experimental Marine Biology and Ecology 511:120-128.
- Madenjian, C. P., T. A. Hayden, T. B. Peat, C. S. Vandergoot, D. G. Fielder, A. M. Gorman, S. A. Pothoven, J. M. Dettmers, S. J. Cooke, Y. Zhao, and C. C. Krueger. 2018.
  Temperature regimes, growth, and food consumption for female and male adult walleye in Lake Huron and Lake Erie: a bioenergetics analysis. Canadian Journal of Fisheries and Aquatic Sciences 75(10):1573-1586.
- Madenjian, C. P., S. A. Pothoven, J. M. Dettmers, and J. D. Holuszko. 2006. Changes in seasonal energy dynamics of Alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. Canadian Journal of Fisheries and Aquatic Sciences 63(4):891-902.
- Mayer, C. M., L. E. Burlakova, P. Eklöv, D. Fitzgerald, A. Y. Karatayev, S. A. Ludsin, S.
  Millard, E. L. Mills, A. P. Ostapenya, L. G. Rudstam, B. Zhu, and T. V. Zhukova. 2014.
  Benthification of freshwater lakes: Exotic mussels turning ecosystems upside down.
  Pages 575-585 in T. F. Nalepa, and D. W. Schloesser, editors. Quagga and Zebra
  Mussels: Biology, Impacts, and Control, 2nd edition. CRC Press, Boca Raton, FL.

MDNR. 2016. 2016-2017 Michigan Fishing Guide. M. D. o. N. Resources, editor.

MDNR. 2018. 2018 Michigan Fishing Guide. M. D. o. N. Resources, editor.

Mittelbach, G. G. 1983. Optimal foraging and growth in bluegills. Oecologia 59(2):157-162.

- Morato, T., R. S. Santos, and J. P. Andrade. 2000. Feeding habits, seasonal and ontogenetic diet shift of blacktail comber, *Serranus atricauda* (Pisces: Serranidae), from the Azores, north-eastern Atlantic. Fisheries Research 49(1):51-59.
- Mumby, J. A., S. M. Larocque, T. B. Johnson, T. J. Stewart, J. D. Fitzsimons, B. C. Weidel, M. G. Walsh, J. R. Lantry, M. J. Yuille, and A. T. Fisk. 2018. Diet and trophic niche space and overlap of Lake Ontario salmonid species using stable isotopes and stomach contents. Journal of Great Lakes Research 44(6):1383-1392.
- Nachman, G. 1981. Temporal and spatial dynamics of an acarine predator-prey system. Journal of Animal Ecology 50(2):435-451.
- O'Brien, T. P., S. A. Farha, D. M. Warner, P. C. Esselman, K. Phillips, S. Lenart, and C. Olds. 2019. Status and trends of pelagic prey fish in Lake Huron, 2018.
- O'Brien, T. P., D. M. Warner, P. C. Esselman, S. A. Farha, S. Lenart, C. Olds, and K. Phillips. 2018. Status and trends of pelagic prey fish in Lake Huron, 2017.
- Pohlert, T. 2014. The Pairwise Multiple Comparison of Mean Ranks Package (PMCMR).
- Pothoven, S. A., C. P. Madenjian, and T. O. Höök. 2017. Feeding ecology of the Walleye (Percidae, *Sander vitreus*), a resurgent piscivore in Lake Huron (Laurentian Great Lakes) after shifts in the prey community. Ecology of Freshwater Fish 26(4):676-685.
- R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rand, P. S., B. F. Lantry, R. O'Gorman, R. W. Owens, and D. J. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario, 1978–1990: Implications for salmonine energetics. Transactions of the American Fisheries Society 123(4):519-534.
- Reyjol, Y., P. Brodeur, Y. Mailhot, M. Mingelbier, and P. Dumont. 2010. Do native predators feed on non-native prey? The case of Round Goby in a fluvial piscivorous fish assemblage. Journal of Great Lakes Research 36(4):618-624.
- Rigby, R. A., and D. M. Stasinopoulos. 2005. Generalized additive models for location, scale and shape, (with discussion). Applied Statistics 54:507-554.
- Riley, S. C., J. X. He, J. E. Johnson, T. P. O'Brien, and J. S. Schaeffer. 2007. Evidence of widespread natural reproduction by Lake Trout Salvelinus namaycush in the Michigan waters of Lake Huron. Journal of Great Lakes Research 33(4):917-921.
- Riley, S. C., E. F. Roseman, S. J. Nichols, T. P. O'Brien, C. S. Kiley, and J. S. Schaeffer. 2008. Deepwater demersal fish community collapse in Lake Huron. Transactions of the American Fisheries Society 137(6):1879-1890.
- Rose, G. A., and W. C. Leggett. 1990. The importance of scale to predator-prey spatial correlations: An example of Atlantic fishes. Ecology 71(1):33-43.

- Roseman, E. F., J. S. Schaeffer, E. Bright, and D. G. Fielder. 2014. Angler-caught piscivore diets reflect fish community changes in Lake Huron. Transactions of the American Fisheries Society 143(6):1419-1433.
- Rush, S. A., G. Paterson, T. B. Johnson, K. G. Drouillard, G. D. Haffner, C. Hebert, E., M. T. Arts, D. J. McGoldrick, S. M. Backus, B. F. Lantry, J. R. Lantry, T. Schaner, and A. T. Fisk. 2012. Long-term impacts of invasive species on a native top predator in a large lake system. Freshwater Biology 27:2342-2355.
- Schmitt, R. J., and S. J. Holbrook. 1984. Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. Oecologia 63(1):6-12.
- Shurin, J. B., and E. G. Allen. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. The American Naturalist 158(6):624-637.
- Sih, A. 1984. The behavioral response race between predator and prey. The American Naturalist 123(1):143-150.
- Smith, S. H. 1968. Species succession and fisheries exploitation in the Great Lakes. Journal of the Fisheries Research Board of Canada 25(4):667-693.
- Smith, S. H. 1970. Species interactions of the Alewife in the Great Lakes. Transactions of the American Fisheries Society 99(4):754-765.
- Smith, S. H., H. J. Buettner, and R. Hile. 1961. Fishery statistical districts of the Great Lakes. Great Lakes Fishery Commission, Technical Report No. 2, Ann Arbor, MI.
- Tanner, H. A., and W. H. Tody. 2002. History of the Great Lakes salmon fishery: A Michigan perspective. Pages 139-153 in K. D. Lynch, M. L. Jones, and W. W. Taylor, editors. Sustaining North American Salmon: Perspectives Across Regions and Disciplines. American Fisheries Society, Bethesda, Maryland.
- Traynor, D., A. Moerke, and R. Greil. 2010. Identification of Michigan fishes using cleithra. G. L. F. Commission. Miscellaneous Publication 2010-02. Ann Arbor, MI.
- Vanderploeg, H. A., T. F. Nalepa, D. J. Jude, E. L. Mills, K. T. Holeck, J. R. Liebig, I. A. Grigorovich, and H. Ojaveer. 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 59(7):1209-1228.
- Velip, D. T., and C. U. Rivonker. 2018. Trophic dynamics of few selected nearshore coastal finfishes with emphasis on prawns as prey item. Journal of Sea Research 136:28-36.
- Walsh, M. G., D. E. Dittman, and R. O'Gorman. 2007. Occurrence and food habits of the Round Goby in the profundal zone of southwestern Lake Ontario. Journal of Great Lakes Research 33(1):83-92, 10.

- Werner, E. E., and D. J. Hall. 1974. Optimal foraging and the size selection of prey by the Bluegill Sunfish (*Lepomis macrochirus*). Ecology 55(5):1042-1052.
- Werner, E. E., and G. G. Mittelbach. 1981. Optimal foraging: Field tests of diet choice and habitat switching. Integrative and Comparative Biology 21(4):813-829.

Wickham, H. 2016. ggplot2: Elegant graphics for data analysis. Springer-Verlag New York.

# APPENDIX

Table 3: Frequency of occurrence of prey consumed by Lake Huron predators, 2017-2018 (both years pooled). Species abbreviations as follows: LAT = Lake Trout, WAE = Walleye, CHS = Chinook Salmon, COS = Coho Salmon, RBT = Rainbow Trout, ATS = Atlantic Salmon, PNK = Pink Salmon, BNT = Brown Trout.

Prey Spp	LAT	WAE	CHS	COS	RBT	ATS	PNK	BNT
Alewife	0.03	0.01	0.22	0.00	0.05	0.06	0.00	0.00
Gizzard Shad	0.00	0.02	0.01	0.00	0.00	0.00	0.00	0.00
Rainbow Smelt	0.34	0.08	0.45	0.17	0.28	0.56	0.06	0.00
Brown Bullhead	< 0.01	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00
Stonecat	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Burbot	0.01	0.00	0.00	0.00	0.00	0.01	0.06	0.00
Threespine Stickleback	< 0.01	< 0.01	0.00	0.01	0.00	0.05	0.00	0.00
Ninespine Stickleback	0.01	0.00	0.05	0.00	0.06	0.15	0.00	0.25
Troutperch	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Moronidae spp	< 0.01	< 0.01	0.00	0.01	0.02	0.02	0.00	0.00
Coregonid spp	0.04	0.01	0.02	0.08	0.02	0.00	0.06	0.00
Salmonine spp	0.01	0.00	0.01	0.01	0.00	0.11	0.00	0.00
White Sucker	< 0.01	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00
Emerald Shiner	< 0.01	0.01	0.00	0.36	0.00	0.08	0.00	0.00
Spottail Shiner	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Sand Shiner	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bluntnose Minnow	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Unidentified Minnow	0.00	0.02	0.00	0.01	0.00	0.00	0.00	0.00
Rock Bass	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pumpkinseed	0.00	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00
Logperch	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Yellow Perch	< 0.01	0.16	0.01	0.01	0.02	0.05	0.00	0.00
Sculpin spp	0.01	< 0.01	0.00	0.00	0.00	0.00	0.00	0.00
Round Goby	0.54	0.24	0.06	0.01	0.08	0.15	0.00	0.75
Unidentified Fish	0.16	0.30	0.22	0.36	0.17	0.29	0.24	0.25
Invertebrates	0.28	0.37	0.35	0.37	0.83	0.55	0.88	0.00
Other	0.16	0.08	0.02	0.06	0.20	0.09	0.06	0.50

	LAT		WAE		CHS		COS		RBT		ATS		PNK		BNT	
Prey spp	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Alewife	131.4	354.6	0.1	12.8	193.1	1164.9	0.0	0.0	0.0	16.8	8.9	44.2	0.0	0.0	0.0	0.0
Gizzard Shad	0.0	0.0	11.4	2.7	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rainbow Smelt	331.6	4634.7	19.1	81.6	145.4	972.3	34.1	20.3	17.9	39.1	35.2	235.3	0.0	1.4	0.0	0.0
Brown Bullhead	0.0	2.3	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stonecat	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Burbot	251.1	279.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	3.2	0.0	0.0	0.0
Threespine Stickleback	1.9	3.7	0.0	0.0	0.0	0.0	0.0	6.2	0.0	0.0	1.5	34.3	0.0	0.0	0.0	0.0
Ninespine Stickleback	14.8	8.7	0	0	22.1	1.3	0	0	2.0	1.0	10.3	30.0	0.0	0.0	0.8	0.0
Troutperch	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
White Perch	3.7	0.0	2.5	0.0	0.0	0.0	0.0	1.3	0.0	0.0	0.0	3.6	0.0	0.0	0.0	0.0
White Bass	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	21.5	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Morone spp	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.9	0.0	0.0	0.0	0.0
Bloater	131.6	198.5	1.7	0.6	0.0	24.4	42.6	5.6	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Coregonid Spp	4.6	11.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12.7	0.0	0.0	0.0
Chinook Salmon	70.2	41.9	0.0	0.0	0.0	0.0	0.0	4.7	0.0	0.0	6.1	26.8	0.0	0.0	0.0	0.0

Table 4: Total wet mass (g) of prey taxa consumed by each Lake Huron predator species in 2017 and 2018 (prior to mass-at-capture calculations). Species abbreviations as follows: LAT = Lake Trout, WAE = Walleye, CHS = Chinook Salmon, COS = Coho Salmon, RBT = Rainbow Trout, ATS = Atlantic Salmon, PNK = Pink Salmon, BNT = Brown Trout.
*Table 4 (cont'd)* 

	LA	АT	W	AE	Cl	HS	CO	OS	RI	BT	A	ГS	PN	K	BN	T
Prey spp	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Rainbow Trout	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lake Trout	0.4		0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Coho Salmon	0.0	21.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	47.8	0.0	0.0	0.0	0.0
Unidentified salmonine spp	3.6	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.0
White Sucker	37.8	0.0	72.1	5.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Emerald Shiner	8.5	0.0	11.6	0.0	0.0	0.0	164.8	1.1	0.0	0.0	32.1	0.0	0.0	0.0	0.0	0.0
Spottail Shiner	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sand Shiner	0.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bluntnose Minnow	17.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Minnow (Cyprinidae spp)	0.0	0.0	5.0	2.4	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rock Bass	36.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pumpkinseed	0.0	0.0	0.0	30.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Logperch	5.4	15.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Yellow Perch	5.8	1.3	110.5	114.7	0.0	1.4	0.0	2.6	0.0	0.3	0.0	5.9	0.0	0.0	0.0	0.0
Mottled Sculpin	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Deepwater Sculpin	15.9	61.2	4.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Sculpin Spp	0.0	9.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Round Goby	3980.6	4313.3	586.0	826.1	3.0	32.5	0.0	3.8	51.1	1.0	78.1	123.5	0.0	0.0	23.2	1.1

*Table 4 (cont'd)* 

	LA	ΑT	W	WAE		CHS		COS		RBT		ГS	PNK		BNT	
Prey spp	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Unidentified Fish	110.3	58.6	29.3	34.0	5.2	27.1	13.2	18.4	0.3	0.6	6.8	15.6	4.0	0.1	0.0	0.4
Amphipods	0.3	0.0	0.1	1.5	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.3	0.0	0.0
Bythotrephes	12.3	15.9	12.3	2.3	5.4	21.9	2.8	4.2	0.7	12.7	14.2	22.9	0.1	0.9	0.0	0.0
Trichoptera	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.2	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Coleoptera	14.9	3.4	0.2	0.0	0.0	2.6	0.2	0.0	28.6	7.7	3.6	12.1	0.0	0.4	0.0	0.0
Crayfish	0.0	3.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diptera	13.5	12.2	4.5	13.0	0.0	3.1	1.3	10.6	58.5	39.2	3.2	8.1	0.0	29.2	0.0	0.0
Hemiptera	8.8	0.2	0.0	0.1	0.0	0.0	0.0	0.0	30.3	3.0	0.7	0.6	0.7	0.0	0.0	0.0
Hymenoptera	1.3	18.2	0.1	0.0	0.0	0.0	0.0	0.0	4.9	2.0	0.8	6.4	0.0	0.1	0.0	0.0
Neuroptera	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepidoptera	0.0	0.0	0.3	0.0	0.0	0.0	0.7	0.7	1.8	62.1	29.6	2.5	0.0	0.4	0.0	0.0
Ephemeroptera	3.9	0.0	36.0	13.2	20.3	0.1	0.0	2.8	176.5	74.7	0.2	0.5	0.0	0.0	0.0	0.0
Mysid	0.3	0.3	0.0	0.1	23.5	0.3	0.0	0.1	0.0	0.0	0.0	0.4	0.1	0.0	0.0	0.0
Odonata	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	1.9	0.1	0.0	0.0	0.0	0.0
Orthoptera	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.3	0.0	0.0	0.0	0.0	0.0	0.0
Plecoptera	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0
Spider	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Zebra Mussel	0.4	5.1	0.9	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
Quagga Mussel	17.7	28.5	0.1	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Dreissenid	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Zooplankton	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0

*Table 4 (cont'd)* 

	LA	LAT WAE		CHS		COS		RBT		ATS		PNK		BNT		
Prey spp	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Unidentified Invertebrate	13.3	11.6	13.2	13.8	1.2	2.3	0.5	19.5	1.5	22.5	0.0	4.9	1.8	0.4	0.0	0.0
Fish egg	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Feather	0.1	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unidentified Plant	11.4	7.7	6.0	1.1	0.0	0.0	0.0	0.3	0.3	0.1	0.5	0.5	0.0	0.0	0.0	0.1
Rock	63.5	34.4	6.5	0.9	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
Plastic	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Other	5.4	6.1	0.9	0.1	0.0	0.0	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 5: Total count of prey taxa consumed by each Lake Huron predator species. Species abbreviations as follows: LAT = LakeTrout, WAE = Walleye, CHS = Chinook Salmon, COS = Coho Salmon, RBT = Rainbow Trout, ATS = Atlantic Salmon, PNK = PinkSalmon, BNT = Brown Trout.

	LA	ΑT	W	AE	CI	HS	C	DS	RI	BT	A	ГS	PN	IK	BN	JT
Prey spp	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Alewife	19	32	1	6	14	89	0	0	0	3	2	7	0	0	0	0
Gizzard Shad	0	0	17	5	0	1	0	0	0	0	0	0	0	0	0	0
Rainbow Smelt	1248	2787	42	94	292	436	175	25	97	81	106	319	0	11	0	0
Brown Bullhead	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Stonecat	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Burbot	11	10	0	0	0	0	0	0	0	0	0	1	106	0	0	0
Threespine Stickleback	3	3	1	0	0	0	0	6	0	0	2	23	0	0	0	0
Ninespine Stickleback	10	8	0	0	19	2	0	0	5	2	7	50	0	0	1	0
Troutperch	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
White Perch	3	0	1	0	0	0	0	1	0	0	0	3	0	0	0	0
White Bass	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Unidentified Morone spp	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0
Bloater	20	44	3	2	0	9	4	2	0	4	0	0	0	0	0	0
Unidentified Coregonid spp	6	4	0	0	0	0	0	0	0	0	0	0	10	0	0	0
Chinook Salmon	25	9	0	0	0	0	0	1	0	0	1	7	0	0	0	0
Rainbow Trout	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lake Trout	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

*Table 5 (cont'd)* 

	LA	ΔT	W	AE	Cl	HS	C	OS	RI	<b>BT</b>	A	ГS	PN	JK	B	T
Prey spp	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Coho Salmon	0	4	0	0	0	0	0	0	0	0	0	11	0	0	0	0
Unidentified salmonine spp	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
White Sucker	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Emerald Shiner	8	0	15	0	0	0	108	4	0	0	16	0	0	0	0	0
Spottail Shiner	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Sand Shiner	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bluntnose Minnow	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified minnows (Cyprinidae)	0	0	9	2	0	0	0	2	0	0	0	0	0	0	0	0
Rock Bass	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pumpkinseed	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Logperch	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Yellow Perch	1	3	158	61	0	1	0	6	0	1	0	14	0	0	0	0
Mottled Sculpin	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Deepwater Sculpin	9	32	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Sculpin spp	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Round Goby	1982	2066	229	287	1	14	0	3	10	2	42	52	0	0	13	1
Unidentified Fish	75	139	133	102	18	58	677	78	5	13	46	178	166	29	0	1
Amphipods	2	0	7	66	0	0	1	0	0	15	0	0	0	76	0	0

Table 5 (cont'd)

	LA	ΑT	W	AE	CI	HS	CO	DS	RI	<b>BT</b>	A	ГS	PN	ΙK	BN	T
Prey spp	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Bythotrephes	2010	3597	2970	781	2270	5152	1467	1139	176	2066	2973	4034	43	785	0	0
Trichoptera	0	0	0	0	0	0	0	22	4	3	0	0	0	0	0	0
Coleoptera	28	6	14	0	0	21	15	0	126	102	7	43	0	48	0	0
Crayfish	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diptera	945	378	216	404	0	27	123	713	2192	1102	210	907	2	3810	0	0
Hemiptera	82	2	1	1	0	0	0	1	272	19	6	6	5	1	0	0
Water Mites	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Hymenoptera	17	87	3	0	0	0	2	1	41	31	10	44	0	8	0	0
Neuroptera	0	0	0	1	0	0	3	0	0	0	0	0	0	0	0	0
Lepidoptera	0	1	5	0	0	0	6	6	14	512	260	17	0	31	0	0
Ephemeroptera	32	1	304	117	92	1	0	33	3369	1053	6	8	0	1	0	0
Mysid	9	9	2	2	1	4	0	2	2	2	1	10	10	0	0	0
Odonata	0	1	2	0	0	0	0	1	1	6	33	1	0	0	0	0
Orthoptera	1	2	0	0	0	0	0	1	0	4	0	0	0	1	0	0
Plecoptera	0	0	0	1	0	0	0	1	0	9	0	0	0	3	0	0
Spider	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0
Zebra Mussel	3	10	2	3	0	0	0	0	0	0	0	2	0	0	0	0
Quagga Mussel	44	91	1	3	0	0	0	0	0	0	1	0	0	0	0	0
Unidentified Dreissenid	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Zooplankton	2	2	0	2	0	0	0	0	0	0	2	0	0	2104	0	0
Unidentified Invertebrate	56	21	74	138	1	7	15	121	1	12	1	6	1	2	0	0

*Table 5 (cont'd)* 

	L	АT	W	AE	Cl	HS	C	OS	RI	BT	A	ГS	PN	ΙK	Bľ	NT
Prey spp	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018	2017	2018
Fish Egg	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Feather	1	0	0	3	0	0	0	0	0	1	0	0	0	1	0	0
Unidentified Plant	56	72	27	6	1	1	5	1	10	4	5	6	0	0	1	1
Rocks	73	79	3	4	1	0	0	0	0	0	0	6	0	0	0	0
Plastic	4	0	3	0	0	0	0	0	2	3	0	0	0	0	0	0
Other	4	9	15	2	1	0	13	0	47	2	0	0	0	0	0	0



Figure 15: Lake Trout average proportion of prey based on wet weight statistical districts in 2017. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-4, E: MH-5, F: MH-6.



Figure 16: Lake Trout average proportion of prey based on wet weight statistical districts in 2018. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-4, E: MH-5, F: MH-6.



*Figure 17: Walleye average proportion of prey based on wet weight statistical districts in 2017. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-4, E: MH-5, F: MH-6.* 



*Figure 18: Walleye average proportion of prey based on wet weight statistical districts in 2018. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-4, E: MH-5, F: MH-6.* 



Figure 19: Chinook Salmon average proportion of prey based on wet weight statistical districts in 2017. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-5, E: MH-6. There were no data from MH-4.



Figure 20: Chinook Salmon average proportion of prey based on wet weight statistical districts in 2018. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-4, E: MH-5. There were no data for MH-6.



Figure 21: Atlantic Salmon average proportion of prey based on wet weight statistical districts in 2017. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-5, E: MH-6. There were no data from MH-4.



Figure 22: Atlantic Salmon average proportion of prey based on wet weight statistical districts in 2018. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-4, E: MH-5, F: MH-6.



Figure 23: Coho Salmon average proportion of prey based on wet weight statistical districts in 2017. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-5, C: MH-6. There were no data for MH-2, MH-3, or MH-4.



Figure 24: Coho Salmon average proportion of prey based on wet weight statistical districts in 2018. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-4, D: MH-5, E: MH-6. There were no data for MH-3.



Figure 25: Rainbow Trout average proportion of prey based on wet weight statistical districts in 2017. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-5, D: MH-6. There were no data for MH-3 or MH-4.



*Figure 26: Rainbow Trout average proportion of prey based on wet weight statistical districts in 2018. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-4, E: MH-5. There were no data for MH-6.* 



Figure 27: Pink Salmon average proportion of prey based on wet weight statistical districts in 2017. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2, C: MH-3, D: MH-5. There were no data for MH-4 or MH-6.



Figure 28: Pink Salmon average proportion of prey based on wet weight statistical districts in 2018. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-4, C: MH-5. There were no data for MH-2, MH-3, or MH-6.



Figure 29: Brown Trout average proportion of prey based on wet weight statistical districts in 2017. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-1, B: MH-2. There were no data for MH-3, MH-4, MH-5, or MH-6.



Figure 30: Brown Trout average proportion of prey based on wet weight statistical districts in 2018. The numbers above the stacked bars represents the number of stomachs that contained prey. A: MH-2, B: MH-6. There were no data for MH-1, MH-3, MH-4, or MH-5.