THE CONTRIBUTIONS OF MAYFLIES (EPHEMEROPTERA: *HEXAGENIA* SPP.) AND OTHER INVERTEBRATES TO THE SEASONAL DIET OF WALLEYE (PERCIDAE: *SANDER VITREUS*)

A Thesis Submitted to the Committee on Graduate Studies
in Partial Fulfillment of the Requirements for the Degree of Master of
Science in the Faculty of Arts and Science

TRENT UNIVERSITY

Peterborough. Ontario, Canada

Environmental and Life Sciences M.Sc. Graduate Program

May 2022

ABSTRACT

The contributions of mayflies (Ephemeroptera: *Hexagenia*) and other invertebrates to the seasonal diet of Walleye (Percidae: *Sander vitreus*)

Ayden Ricker-Held

Walleye (*Sander vitreus*) are an ecologically and economically significant fish harvested by recreational and commercial fisheries across Ontario. Adult Walleye are piscivores, but anecdotal evidence from anglers suggests that Walleye often target aquatic insects such as mayfly larvae (Ephemeroptera). My research examined the diet of Walleye caught from May to September in Lake St. Joseph in northern Ontario. I examined the stomach contents of angle harvested Walleye to identify the prey over two summers. Through morphological analysis of stomach contents, mayflies were found to be a significant prey source for Walleye, during larval emergence events in early summer, and to a lesser extent throughout the rest of the summer season. These findings are important for long term management of Walleye populations and associated resources. I also assess the potential and problems of Walleye management and research from my experiences of having worked with industry, government, and university partners on this project.

KEYWORDS: Food web interactions, predator prey, piscivore, invertebrate, alternative prey

ACKNOWLEDGMENTS

The first person I would like to thank is my supervisor David Beresford, my entomology and data analysis expert. Without his guidance and support I never would have assembled my team and acquired the funds to carry out the project. Throughout the entire process Dave has been there to answer questions and lend his advice to produce the quality product expected from this project. Dave not only influenced my academic life, but through his actions and dedication made me a better person.

Thank you to my involved committee member Dak de Kerckhove our fisheries, data collection and Walleye expert. Without your expertise and time I would not have produced a complete study. Unfortunately, many of the fisheries experiments encountered issues and was not the quality of data expected, but I learned so much from working together.

Thank you to my involved committee member Chris Wilson my project design, genetics and fisheries expert. Your knowledge and guidance alleviated many stressors and taught me much about the scientific process and addressing unanswered questions. Hopefully the Walleye stomachs will turn into a DNA metabarcoding project in the near future.

Mitacs was absolutely instrumental in making this project a possibility. The majority of our funding was through 2 years of a Mitacs Accelerate Internship program. Without your expertise and financial support my project would have functioned differently. Additionally, thank you for all of the media attention, support and opportunities to promote the project. Through Mitacs small business month I was able to share my research on television, radio, magazines, newspapers, online bulletins and was featured at the 20th anniversary of Mitacs hosted by the Lieutenant Governor of Canada. The experience from those opportunities will benefit me for a lifetime. Thank you to John Knight and his assistance in securing the Mitacs Accelerate and helping me navigate the first steps of the Accelerate program.

The Old Post Lodge has been instrumental to the success of this project. Thank you to Jonathan Grace, John Grace and Wendy Grace. Without the three of you as working together as a family we would not have planned and funded the project effectively. Thank you for permitting a research project to exist alongside your regular activities and the use of your infrastructure. Lake St. Joseph is an amazing waterbody in large part to the help and dedication of the Grace family. I extend a special thank you to all the patrons of the Old Post Lodge who helped me collect my data and were interested in the scientific process.

Trent University was where I completed my lab work and attended classes for the completion of the Environmental Life Sciences M.Sc. program. I would like to extend a huge thank you to Linda Cardwell who answered all of my questions and help me assemble the team to tackle this project. Your smiling face was always a welcome sight.

Thank you to Kaitlyn Fleming, Katherine Vezsenyi, Kayla Vizza, Erika Galvez and all of my lab mates in the Beresford Lab for all the laughs, positive encouragement, advice and knowledge.

Thank you to all of the volunteers I had the pleasure to work on this project with. Thank you to my friends and fellow outdoors enthusiasts Matt Shrum, Neil Leduc and Carl Evans for collecting some of the data I could not. Thank you to Brenda Forde, Katie Volpe, Jacey Moore, Cathy Yuen for their hours of volunteer work helping me dissect my wonderfully scented Walleye stomachs. Than you to Bronwyn Gauly and Ashley Clarkin-Summers for their identification skills to learn what mayflies and insects we found in Lake St. Joseph.

Finally thank you to my friends and family who’s support for this project made it possible from the start. My dad, Todd Held, thank you for all of your support of this project and always believing in me.

PREFACE: MY STORY

This project began in 2016, when I was hired as a fishing guide by the Old Post Lodge, operating on Lake St. Joseph. For all of my life I spent as much time on water as possible, and dedicated the rest of my time to researching and learning about the ecosystems that were so close to my heart. After a few short days on Lake St. Joseph I learned that theory was no substitute for being immersed in natural systems. The fishing was incredible in quality and quantity, but the most surprising part came when we were catching Walleye in a meter of water cast after cast. When I voiced my surprise it was met with “just wait till the mayfly hatch.”

Growing up in rural southern Ontario, most of my childhood fishing stories were about driving north to fish. The goal was to harvest enough for a fish fry, and Walleye were the most sought-after table fare. We learned from experience that whenever mayflies were hatching our trip north was futile. The story was always the same, the fish were not eating in their usual spots, and the few we caught were stuffed with insects.

When I saw my first St. Joe mayfly hatch it was overwhelming: exoskeletons from the metamorphosis – what we called shucks – covered the surface of the water, and adults made a living and decomposing carpet along the shoreline. These events occurred in late June and Walleye were drawn to the shallows, often crowded into water less than one metre deep. Watching Walleye regurgitate mayflies as they were dragged, by my line, toward the boat left no doubt in my mind as to why those fish were in the shallows.

When I began my undergraduate degree in 2016, I tried to find out about the phenomenon I had experienced, researching the relationship between Walleye and mayflies, but little was written on the subject. What began as a simple search for papers on the topic, has ended up being the focus of my M.Sc. research.

Early in the 2017 fall I proposed a graduate research project exploring the interactions of Walleyes and mayflies. This simple pursuit became a reality with a collaboration that includes David Beresford, an entomologist in Trent's ENLS graduate studies program, Dak de Kerckhove and Chris Wilson from the Ontario Ministry of Natural Resources and Forestry, and project funding from both industry and the federal government through a Mitacs grant in association with the Old Post Lodge.

The experiences and lessons from this project will shape my life forever and I hope our findings will lead to healthier and more resilient ecosystems. This work is presented for you to read.

TABLE OF CONTENTS

List of Tables and Figures

CHAPTER 1: WALLEYE PREY AND LIFE HISTORY LITERATURE REVIEW

> *"Young walleye feed mostly on small plankton organisms. With increasing size, aquatic insects and their larvae and numerous other invertebrates are eaten. With further growth, fish such as yellow perch, minnows, suckers and ciscoes are important food items."* *MacKay 1963.*

> *"In summer large numbers of mayflies are eaten." Scott 1954.*

Adult Walleye (*Sander vitreus* (Mitchill, 1818)) are found over much of central and eastern North America, ranging from Nunavut to Florida, but are most abundant in the mid-latitudes (Colby et al. 1979). A voracious predator of smaller fish (Chipps and Graeb, 2011), Walleye prefer large water bodies, rivers and lakes, including the Great Lakes (Colby et al. 1979). Historically, Walleye have been an important food sources for humans in North America, likely first harvested over 5,000 years ago (Schalz et al. 2011), and continue to be harvested by individuals and commercially (Schalz et al. 2011). Their importance has resulted in this species being one of the most sought after, studied, managed, and consumed fish in North America, with evidence that this has been the case since humans first appeared on this continent (Berkes et al. 1994, Berkes 1998, Islam and Berkes 2016).

As a result, our knowledge of Walleye life history and ecology is extensive, but not complete however, with some important knowledge gaps associated with their response to changing habitats. Walleye numbers have declined in polluted systems, especially in the industrialized regions where they were once plentiful (Schneider and Leach 1977, Rypel et al. 2018, Hansen et al. 2019). Comparing Walleye predatory and feeding behaviour in polluted and unpolluted and still intact systems has revealed that Walleye consume different prey in these systems, which might be an important part of maintaining healthy Walleye populations (see for example Stasko et al. 2015, Edmunds et al. 2019). For example, much is known about how immature Walleye predation on invertebrates changes with growth and development, however the importance of invertebrate prey for adult Walleye is not known. While adult Walleye in some systems are known to consume invertebrates, in particular mayflies, life history studies focus almost exclusively on the importance of fish prey (e.g. Graeb et al. 2005). Similarly, management strategies of Walleye populations, while generally recognising the importance of managing habitat, rarely, if ever, directly address the role of invertebrate prey for adult Walleye (Haas and Schaeffer 1992, Slipke and Duffy 1997). This is not so much of an oversight as reflecting the evidence from lab studies (Graeb et al. 2005) and studies of systems where mayflies populations are no longer abundant such as Lake Erie (see for example Ma et al. 2021). Yet anecdotally, Walleye are perceived by anglers in some systems and watersheds to feed almost exclusively upon mayflies during periods when adult mayflies are emerging.

Walleye life history

Walleye spawn in spring when lakes are ice free in shallow water, upstream in tributaries and on rock and gravel bars (Bozek et al. 2011a). Eggs are broadcast over the spawning substrate and then fertilized by males (Hartman 2009). Immature Walleye suffer high mortality during their first year of growth, with less than 1% surviving due to suitable habitat, competition and predation (Bozek et al. 2011b). Walleye mature across a range of ages, sizes, depending on latitude, and the glacial refugia of founding populations (Zhao et al. 2008). Adults reach sexual maturity from 35 – 45 cm long (Bozek et al. 2011b). In Ontario, this takes about eight years for females (Colby et al. 1979), but females can mature between 3 and 11 years; males reach maturity earlier, from two to nine years (Bozek et al. 2011b). Physiological growth and development is temperature dependent, with Walleye growing more slowly in colder northern waters, living about 20 years, with some able to live up to 30 years or more, growing to be over 1 meter long (Venturelli et al. 2010).

Due to their large, light sensitive eyes, adult Walleye thrive in turbid waterways with low visibility, large littoral zones and deep oxygen rich water (Zhao et al. 2008, Hartman 2009). Walleye move horizontally and vertically in the water column daily and seasonally following available forage (Hartman 2009).

Feeding

"Successful management of Walleye and Sauger populations often requires a detailed knowledge of prey resources." Chipps and Graeb 2011.

As a general rule predators target prey that is the most energetically efficient for the predator to capture and consume which commonly means the larger the better (Mihalitsis and Bellwood 2017), and as Walleye get older and larger they generally prefer larger prey and are less likely to target smaller prey items (Kaufman et al. 2009, Bozek et al. 2011b, Giacomi et al. 2013). However, this preference for larger prey means that there are proportionately fewer prey (Giacomi et al. 2013). Consequently, where Walleye density is higher, their average size is typically smaller, generally attributed to increased intraspecific competition for prey (Bozek et al. 2011b).

The main diet of adult Walleye consists of those smaller fish commonly categorized as baitfish (Rose et al. 1999, Quist et al. 2002, Frey et al. 2003, Mosindy 1980). Depending on the time of year, walleye may feed multiple times a day to once every couple days, depending on water temperature and the size of their last meal (Kaufman et al. 2009, Bozek et al. 2011b). Not all prey have the same net benefit to Walleye, with different species of baitfish affecting Walleye growth and development rates Swenson 1977, Little et al. 1998, Bozek et al. 2011b, Sheppard et al. 2015). For example, Walleye that can prey upon large deep bodied fish such as Cisco and smelt have relatively rapid growth rates (Kaufman et al. 2009, Bozek et al. 2011b). Feeding on a larger more energy rich prey is energetically profitable, allowing mature fish to be larger (Kaufman et al. 2009, Bozek et al. 2011b). Yet of the various baitfish and other prey species consumed by Walleye, Yellow Perch are perhaps the most significant across the entire Walleye range, being both abundant and widespread in littoral and pelagic zones of most waterbodies (Haas and Schaeffer 1992, Swenson 1977, Colby et al. 1979).

Invertebrate prey

Walleye begin life as predators of invertebrates, consuming larger prey as they grow (Chipps and Graeb 2011). In lab studies, immature Walleye switch to preying upon fish at about 20 mm long (Graeb et al. 2005), a shift that does not occur until Walleye are 50 mm long under field conditions (Chipps and Graeb 2011). This change in diet from benthivory to piscivory is so pronounced that it is described as a shift (see for example the literature review on p 304 in Chipps and Graeb 2011) with Walleye over 100 mm choosing to feed exclusively on fish when these are present (Galarowicz et al. 2006). The reasons for this shift is simple enough, fish prey are a better food source than invertebrate prey, both due to the larger size of fish prey, and the more rapid growth of Walleye fed fish compared to Walleye fed invertebrates (Galarowicz et al. 2006). Why this is so is likely due to much of the carbon in invertebrate prey, largely consisting of chitin, being indigestible by fish compared to the carbon content of fish prey (Sterner and George 2000, Sullivan et al. 2014).

As a result what is known about invertebrates as prey is largely restricted to studies of immature Walleye. Walleye are known to prey upon invertebrates which can reduce pressure on the primary fish prey species (Haas and Schaeffer 1992, Colby and Baccante 1996, Rose et al. 1999, Sheppard et al. 2015). In addition, invertebrate prey are necessary for the long-term success of Walleye populations (Ritchie and Colby 1988, Slipke and Duffy 1997, Rose et al. 1999, Mosindy 1980), attributed to invertebrates being the main food source of Yellow Perch (Haas and Schaeffer 1979, Rose et al. 1999). During the earliest juvenile stages Walleye feed on zooplankton, shifting to large invertebrates as they grow (Rose et al. 1999, Bozek et al. 2011b). Nevertheless, there are some studies that directly address invertebrates as prey for adult Walleye. More commonly, the larger invertebrate prey are immature aquatic insects: mayflies, dragonflies and damselflies, caddisflies, and midges (orders Ephemeroptera, Odonata, Plecoptera, Trichoptera, Chironomidae), as well as crustaceans (Amphipoda, Decapoda), worms (Oligochaeta), and leeches (Hirundinea) (Colby et al. 1979, Ritchie and Colby 1988, Slipke and Duffy 1997, Quist et al. 2002). In the Glen Elder Reservoir, Kansas, chironomids (midges) were the most abundant invertebrate prey item for small immature Walleye during spring and early summer (Rose et al. 1999, Quist et al. 2002, Sheppard et al. 2015), after which gizzard shad became the forage of choice for the larger summer Walleye (Quist et al. 2002).

Mayflies as prey

Among the few studies that mention invertebrate prey of Walleye, there is a general consensus that mayflies are the most important for immature Walleye less than 35 cm (Swenson 1977, Colby et al. 1979, Slipke and Duffy 1997, Little et al. 1998, Sheppard et al. 2015). In Lake Oneida, New York, mayflies were targeted by smaller Walleye when Yellow Perch were not readily available, and in years when mayflies were abundant, young of the year Walleye recruitment increased due to lower mortality over the entire summer (Rose et al. 1999).

Generally, mayflies tend to be more important for Walleye north of the Great Lakes region (Ritchie and Colby 1988, Colby and Baccante 1996, Sheppard et al. 2015, Mosindy 1980), with this being a lake-dependent phenomenon (Swenson 1977, Colby et al. 1979, Frey et al. 2003). This is likely due to low mayfly numbers in the more industrially developed regions due to associated changes in lake characteristics. Historically, mayflies were reported to be an important food source for Walleye in Oneida Lake during the 1950s and 1960s, a period when mayflies were abundant (Kolar et al. 1998, Rose et al. 1999). As mayflies disappeared from Oneida Lake, small Walleye lost this prey food source, and shifted their diet to smaller fish, and other invertebrates such as midge larvae (Price 1963, cited by Kolar et al. 1977). This same shift in diet away from mayflies by small Walleye was seen in Lake Erie (among others) as mayflies numbers rapidly declined. These declines were most likely due to eutrophication and increased water pollution throughout the 1950s and 1960s (Kolar et al. 1977). In Lake Erie, small Walleye also compensated by shifting to midge larvae (Price 1963, cited by Kolar et al. 1977).

For both Walleye and Yellow Perch, having access to abundant mayfly prey could possibly reduce cannibalism in young of both species based on the following arguments. For example, low Yellow Perch numbers can cause young of the year Walleye to increase cannibalism (Forney 1974). For Yellow Perch, cannibalism increases when invertebrate prey numbers are low (Tarby 1974). From this, it is a reasonable inference that abundant and accessible mayfly prey could act to mitigate cannibalism in both species either directly or indirectly (Rose et al. (1999).

The availability of mayflies for Walleye changes throughout the season, and is highest during the mayfly hatch in mid-June to July, when mayflies are swimming upwards in the water column to the surface to emerge as adults. At this time, mayflies are large, exposed in the water column, aggregated, and abundant. From an energetic point of view, it is reasonable to suggest that mayflies would offer the highest net nutritional gain for adult Walleye at this time, offsetting their smaller size relative to fish prey by their abundance and ease of capture. Indeed, adult Walleye have been found to prey upon mayflies (Little et al. 1998, Slipke and Duffy 1997), particularly during the mayfly hatching period, with a study north of Lake Superior finding 8.3% of adult Walleye (45-50 cm long) with mayflies in their stomachs (Mosindy 1980). The mayfly hatch occurs shortly after Walleye spawn in late spring and can continue into early summer, depending on the latitude of the waterbody (Riklik and Momot 1982, Colby and Baccante 1996, Frey et al. 2003, Bozek et al. 2011b). While smaller fish are abundant in northern lakes, it is possible that where mayflies are abundant in northern lakes they provide a much needed nutritional benefit for Walleye at this time, being a nutrient rich easy to catch food source.

Management

From the above, it is not surprising that the main emphasis of published management plans and recommendations that refer to mayflies do so as food for Yellow Perch (Rose et al. 1999). For example, Wisconsin's state management plan for Walleye does not have the word mayflies in it (Hewett and Simonson 1998); Iowa's management plan mentions mayflies but does not incorporate invertebrates into any adaptive management strategies (Gelwicks et al. 2019). One could argue that this is not necessary in regions where mayflies are no longer present in the same abundance as in northern lakes, especially if management includes Walleye stocking. In addition, this lack of specific mention can be misleading; almost all jurisdictions have policies in place for protecting habitat and water quality, evidenced by the renewal of Lake Eire water quality and habitat, including retuning mayflies (Koonce et al. 1996, Schloesser et al. 2000). Nevertheless, this complete exclusion of mayflies from management plans that purport to improve water quality is curious.

Knowledge gaps on Walleye life history

As far as I can tell, there exist knowledge gaps on Walleye life history regarding the role of invertebrates, and mayflies in particular. At this time, we do not know: do Walleye older than young of year also exploit invertebrates as a significant food source as opposed to an occasional easy prey item? If so, do mature adult Walleye benefit from preying upon mayflies after spawning as a source of high quality and easily obtained nutrition? What affect will a reduction of mayfly numbers have on Walleye in northern lakes if mayflies are not only a common prey but an important prey? Should management plans actively include managing for mayflies, which could mean having to incorporate terrestrial considerations regarding maintaining healthy adult mayfly populations?

This is a long list of questions. It is the scope of rest of this thesis to try and answer the first of these, a necessary precursor to being able to answer the rest.

REFERENCES

Berkes, F., George, P. J., Preston, R. J., Hughes, A., Turner, J., and Cummins, B. D. 1994. Wildlife harvesting and sustainable regional native economy in the Hudson and James Bay Lowland, Ontario. *Arctic* 47: 350-360.

Berkes, F. 1998. Chapter 5: Indigenous knowledge and resource management systems in the Canadian subarctic. In Berkes, F., Folke, C., and Colding, J. (Eds), *Linking social and ecological systems: Management practices and social mechanisms for building resilience* (pp. 98-128). Cambridge University Press.

Bozek, M., Haxton, T., Raabe, J. 2011a. Chapter 5: Walleye and Sauger Habitat. In B. Barton (Ed), *Biology, Management and Culture of Walleye and Sauger* (pp. 133-197). American Fisheries Society.

Bozek, M., Baccante, D., Lester, N. 2011b. Chapter 7: Walleye and Sauger Life History. In B. Barton (Ed), *Biology, Management and Culture of Walleye and Sauger* (pp. 233-301). American Fisheries Society.

Chipps, S. and Graeb, B. 2011. Chapter 8: Feeding Ecology and Energetics. In B. Barton (Ed), *Biology, Management and Culture of Walleye and Sauger* (pp. 303-319). American Fisheries Society.

Colby, P. J., and Baccante, D. A. 1996. Dynamics of an experimentally exploited walleye population: sustainable yield estimate. *Annales Zoologici Fennici* 33: 589-599.

Colby, P. J., McNicol, R. E., and Ryder, R. A. 1979. Synopsis of biological data on the walleye *Stizostedion v. vitreum* (Mitchill 1818*). FAO Fisheries Synopses (FAO)*. no. 119.

Fisheries and Oceans Canada. 2021. Survey of Recreational Fishing in Canada, 2015. *Fisheries and Oceans Canada*. https://waves-vagues.dfo-mpo.gc.ca/Library/40753220.pdf.

Frey, A., Bozek, A., Edwards, C., Newman, S. 2003. Diet overlap and predation between smallmouth bass and walleye in a north temperate lake. *Journal of Freshwater Ecology* 18: 43-54.

Gelwicks, G., Flammang, M., Meerbeek, J., and Bowler, M. 2019. *Walleye Management Plan*. Iowa Department of Natural Resources. https://www.researchgate.net/profile/Jonathan-Meerbeek/publication/339882580_Iowa_Department_of_Natural_Resources_Walleye_Management_Plan/links/5e6a3abd299bf1b9f7cec2f1/Iowa-Department-of-Natural-Resources-Walleye-Management-Plan.pdf.

Galarowicz, T. L., Adams, J. A., and Wahl, D. H. 2006. The influence of prey availability on ontogenetic diet shifts of a juvenile piscivore. *Canadian Journal of Fisheries and Aquatic Sciences* 63: 1722-1733.

Graeb, B. D., Galarowicz, T., Wahl, D. H., Dettmers, J. M., and Simpson, M. J. 2005. Foraging behavior, morphology, and life history variation determine the ontogeny of piscivory in two closely related predators. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2010-2020.

Haas, R. and Schaeffer, J. 1992. Predator-Prey and Competitive interaction Among Walleye, Yellow Perch, and Other Forage Fishes in Saginaw Bay, Lake Huron. Michigan *Department of Natural Resources Fisheries Division Research Report*. No. 1984.

Hansen, G. J., Winslow, L. A., Read, J. S., Treml, M., Schmalz, P. J., and Carpenter, S. R. 2019. Water clarity and temperature effects on walleye safe harvest: an empirical test of the safe operating space concept. *Ecosphere* 10: 1-12, e02737.

Hartman, G. F. 2009. A biological synopsis of walleye *(Sander vitreus).* Fisheries and Oceans Canada. *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, 2888: 48 pp.

Hewett, S. W., and Simonson, T. D. 1998. Wisconsin's Walleye management plan: moving management into the 21st century No. 43. *Bureau of Fisheries Management and Habitat Protection,* Wisconsin Department of Natural Resources.

Islam, D., and Berkes, F. 2016. Indigenous peoples' fisheries and food security: a case from northern Canada. *Food Security* 8: 815-826.

Kaufman, S. D., Morgan, G. E., and Gunn, J. M. 2009. The role of ciscoes as prey in the trophy growth potential of walleyes. *North American Journal of Fisheries Management* 29: 468-477.

Kolar, C. S., Hudson, P. L., and Savino, J. F. 1997. Conditions for the return and simulation of the recovery of burrowing mayflies in western Lake Erie. *Ecological Applications* 7: 665-676.

Koonce, J. F., Busch, W. N., and Czapla, T. 1996. Restoration of Lake Erie: contribution of water quality and natural resource management. *Canadian Journal of Fisheries and Aquatic Sciences* 53: 105-112.

Little, A. S., Tonn, W. M., Tallman, R. F., and Reist, J. D. 1998. Seasonal variation in diet and trophic relationships within the fish communities of the lower Slave River, Northwest Territories, Canada. *Environmental Biology of Fishes* 53: 429-445.

Ma, Q., Jiao, Y., Zhou, C., and Ren, Y. 2021. Sexual and spatio-temporal variation of Lake Erie Walleye growth and maturity: A consequence of multiple impacting factors. *Aquaculture and Fisheries* 6: 400-413.

Mackay, H. 1963. *Fishes of Ontario*. Ontario Department of Land and Forest.

Mosindy, T. 1980. The ecology of northern pike, Esox lucius Linnaeus, in Savanne Lake, Ontario [Doctoral dissertation, Lakehead University]. Lakehead University. https://knowledgecommons.lakeheadu.ca/handle/2453/2390.

Quist, M. C., Guy, C. S., Bernot, R. J., and Stephen, J. L. 2002. Seasonal variation in condition, growth and food habits of walleye in a Great Plains reservoir and simulated effects of an altered thermal regime. *Journal of Fish Biology* 61: 1329-1344.

Riklik, L., and Momot, W. T. 1982. Production ecology of *Hexagenia limbata* in Savanne Lake, Ontario. *Canadian Journal of Zoology* 60: 2317-2323.

Ritchie, B. J., and Colby, P. J. 1988. Even-odd year differences in walleye year-class strength related to mayfly production. *North American Journal of Fisheries Management* 8: 210-215.

Rose, K. A., Rutherford, E. S., McDermot, D. S., Forney, J. L., and Mills, E. L. 1999. Individual-based model of yellow perch and walleye populations in Oneida Lake. *Ecological Monographs* 69: 127-154.

Rypel, A. L., Goto, D., Sass, G. G., and Vander Zanden, M. J. 2018. Eroding productivity of walleye populations in northern Wisconsin lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 75: 2291-2301.

Schloesser, D. W., Krieger, K. A., Ciborowski, J. J., and Corkum, L. D. 2000. Recolonization and possible recovery of burrowing mayflies (Ephemeroptera: Ephemeridae: *Hexagenia* spp.) in Lake Erie of the Laurentian Great Lakes. *Journal of Aquatic Ecosystem Stress and Recovery* 8: 125-141.

Schneider, J. C., and Leach, J. H. 1977. Walleye (*Stizostedion vitreum vitreum*) fluctuations in the Great Lakes and possible causes, 1800–1975. *Journal of the Fisheries Board of Canada* 34: 1878-1889.

Scott, W. B. 1954. Freshwater fishes of Eastern Canada. *University of Toronto Press*, Toronto. 137 pp.

Sheppard, K. T., Davoren, G. K., and Hann, B. J. 2015. Diet of walleye and sauger and morphological characteristics of their prey in Lake Winnipeg. *Journal of Great Lakes Research* 41: 907-915.

Slipke, J. W., and Duffy, W. G. 1997. Food habits of walleye in Shadehill Reservoir, South Dakota. *Journal of Freshwater Ecology* 12: 11-17.

Sterner, R. W., and George, N. B. 2000. Carbon, nitrogen, and phosphorus stoichiometry of cyprinid fishes. *Ecology* 81: 127-140.

Sullivan, M. L., Zhang, Y., and Bonner, T. H. 2014. Carbon and nitrogen ratios of aquatic and terrestrial prey for freshwater fishes. *Journal of Freshwater Ecology* 29: 259-266.

Swenson, W. A. (1977). Food consumption of walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*) in relation to food availability and physical conditions in Lake of the Woods, Minnesota, Shagawa Lake, and western Lake Superior. *Journal of the Fisheries Board of Canada* 34: 1643-1654.

Venturelli, P. A., Lester, N. P., Marshall, T. R., and Shuter, B. J. 2010. Consistent patterns of maturity and density-dependent growth among populations of walleye (*Sander vitreus*): application of the growing degree-day metric. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 1057-1067.

Zhao, Y., Shuter, B. J., and Jackson, D. A. 2008. Life history variation parallels phylogeographical patterns in North American walleye (*Sander vitreus*) populations. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 198-211.

CHAPTER 2: The contribution of invertebrates, in particular mayflies, to the seasonal diet of Walleye on Lake St. Joseph

ABSTRACT

Walleye (*Sander vitreus*) are ecologically and economically significant fish harvested by recreational and commercial fisheries across Ontario. Mainly piscivores, less is known about how important invertebrate prey are for adult Walleye. Angler anecdotal evidence suggests that Walleye extensively prey upon mayfly larvae (Ephemeroptera) as larvae swim toward the surface to emerge into adults. I examined the stomach contents of Walleye caught from May to September in Lake St. Joseph in northern Ontario. Mayflies were a significant prey of Walleye during larval emergence events in early summer, and to a lesser extent the rest of the summer season. I discuss management implications of these results.

KEYWORDS: Food web interactions, predator prey, piscivore, invertebrate, alternative prey

INTRODUCTION

Walleye are an important piscivorous species harvested both commercially and recreationally (Rose et al. 1999, Quist et al. 2002, Frey et al. 2003, Mosindy 1980). While it is known that invertebrates can be important prey for immature Walleye, evidence of this possible food source for adult Walleye is largely absent from published accounts of Walleye life history. Curiously, angler anecdotal evidence from northern Ontario lakes suggests there are times of the year when adult Walleye appear to feed almost entirely on mayflies.

In this paper, I report on the stomach contents of angler-harvested Walleye obtained in Lake St. Joseph, Ontario, to determine the importance of mayflies and other invertebrates as prey of adult Walleye. I tested the hypothesis that mayflies are actively sought by adult Walleye, and as such are an important part of the Walleye diet, especially during mayfly emergence periods when immature mayflies move up though the water column to emerge as adults. Based on this hypothesis I should find abundant mayflies in most, if not all, stomachs of adult Walleye harvested during the mayfly emergence period. Finding only few sporadic or occasional mayflies throughout the season, or not coinciding with adult emergence periods, while interesting in itself, would not provide evidence for the hypothesis, and indicate that adult Walleye predation on mayflies is more opportunistic, the result of *ad hoc* encounters, and not actively preyed upon, meaning that mayflies are not important as prey species. Further adult Walleye should be evident in those parts of the lake where and when mayflies are abundant.

Mayflies (Ephemeroptera) are a species-rich invertebrate group that spends the majority of their life as an aquatic larvae (Schloesser and Hiltunen, 1984). Mayflies, in particular *Hexagenia*, are known to be bioindicators of good water quality (Vander Zanden and Vadeboncoeur, 2002). Ephemeropterans are known to be sensitive to disturbance in their environment, making them a point of potential concern in our changing climate and increasing human footprint (Vadeboncoeur et al. 2002, Elbrecht et al. 2016, Tiwari and Rachlin, 2018). In the spring and early summer mayflies emerge *en masse* from the substrate of water-ways to emerge into their adult stage (Elbrecht et al. 2016, Tiwari and Rachlin, 2018). During this emergence they are an important food source for aquatic and terrestrial organisms and transfer energy sequestered in the substrate to the surface ecosystems (Jones and Mackereth 2016).

One of the largest, and most abundant of these mayflies is *Hexagenia limbata*, a mud burrowing species with nymphs that can be as much as 5cm long (Heise et al. 1987). *Hexagenia* larvae inhabit the benthic zone of freshwater ecosystems (Vadeboncoeur et al. 2002), burrowing into the soft substrate for shelter (Horst 1976). After one to two years in this substrate, mature larvae swim up the water column to emerge at the surface as adults. After about three days during which mating occurs, females oviposit eggs on the water's surface, which are then distributed by wind and wave action (Heise et al. 1987).

As poikilotherms, mayfly development is temperature dependent (Giberson and Rosenberg 1992). Development starts at 8℃, and is optimal from 15-20℃ (Giberson and Rosenberg 1992). The emergence of larvae as adults, or hatch, appears to coincide with the stabilization of water temperature across the main water basin, when surface temperatures reach approximately 18℃ (Giberson and Rosenberg, 1992). Under these conditions, fish species that require cooler oxygenated water move toward deeper water to take advantage of increased pelagic productivity stimulated by the rising water temperature (McQueen et al. 1986). The mayfly hatch draws the food web and productivity back into the littoral zone, with fish predators such as yellow perch (Clady and Hutchinson 1976, Schaeffer et al. 2000) and small mouth bass (Corkum et al. 2006) feeding on the hatching mayflies. Sixty years ago, specifically in

Minnesota and other areas across Canada and the upper Midwest, mayflies during emergences were so abundant that driving was dangerous due to cars slipping on roads covered in mayflies (Fremling 1968), although even at that time these events were becoming rare as *Hexagenia* disappeared from polluted lakes (Fremling 1968). During these emergence events the mayflies are at their nutritional peak (Cavaletto et al. 2003) and most vulnerable to predation (Corkum et al. 2006).

This study reports on the stomach contents of adult Walleye collected by anglers from Lake St. Joseph, Ontario, Canada, in the summers of 2018 and 2019.

MATERIALS AND METHODS

Study Site

Lake St. Joseph is a freshwater reservoir spanning 148 km and occupying 493 km^2. The predominant bedrock is a granite from the Canadian Shield. It is a unique water body that empties into two directions, historically northward as the head waters for the Albany River, and currently emptying southward through Root Bay connecting to Lac Seul. By the Lake St. Joseph Diversion agreement, both the Ontario and Manitoba governments divert and store water for the purpose of generating power (RSM 1990). The lake is a large mesotrophic reservoir, with a low to moderate nutrient levels influencing aquatic productivity. The water is stained brown due to the large numbers of wetlands in the catchment and subsequent inputs of dissolved carbon, with 1 to 2 m Secchi depth visibility (Keddy, 2010). It has a maximum depth of ~30 m, but most of the main basin is ~12 to 15 m, with sand, mud, dense macrophyte communities, islands, and rock piles, both exposed and subsurface.

The lake is subject to unpredictable water fluctuations. During the 2018 field season the water level was 2 m lower than 2017. Normally water levels fluctuate 1 m throughout the summer and fall, with the highest water level mid July, lowest in spring and fall. The surrounding area is typical of the boreal forest with woody vegetative communities composed primarily of: trembling aspen (*Populus tremuloides*); balsam poplar (*Populus balsamfera*); paper birch (*Betula papyrifera*); black spruce (*Picea mariana*); jack pine (*Pinus banksiana*); white spruce (*Picea glauca*); balsam fir (*Abies balsamea*) and wild raspberry (*Rubus occidentalis*). There is a diverse mix of forested areas, small plains and wetlands strewn across the landscape (Adams and Olver 1977).

Adult female Walleye in Lake St. Joseph reach maturity between 25 and 45 cm at about 3.5 years, with some observed to live up to 22 years, and reach over 70 cm long (Honsey et al. 2017). From 1923 to 1974, commercially there were about 0.42 kg per hectare harvested each year from Lake St. Joseph, 21,600 kg/year (Adams and Olver 1977). By 2005, this had dropped to around 18,000 kg, but still the largest commercial harvest of Walleye in the province (Browne 2007). Commercial fishing is no longer permitted on Lake St. Joseph.

The Lake St. Joseph Accords

Lake St. Joseph is located within the traditional territory of the Mishkeegogamang First Nation community. It has lake specific fishing and accessibility regulations designed to preserve the lake's fishery and surrounding habitat called the Lake St. Joseph Accords. These accords were agreed upon by the Ontario Ministry of Natural Resources and Forestry and lodge operators located on the lake. Under the MNRF regulations on typical waterbodies, each angler with an Ontario sport fishing license is allowed to harvest 4 Walleye, with only one over 18.1 inches (46 cm) with lures outfitted with up to 4 hooks per line (https://ontarionature.org/wp-content/uploads/2017/10/remoteness_sells.pdf). However, under the accord, tackle is limited to one barbless hook, a unique restriction in Ontario. Non-Canadians require special license, and non-residents are not permitted to camp on the shore. Revenue from the non-resident fishing tags are intended for conservation efforts and research on Lake St. Joseph (https://www.ontario.ca/document/ontario-fishing-regulations-summary/fisheries-management-zone-2#section-0).

Field Data Collection

All field work was based out of the Old Post Lodge (51° 8' 18" N, 90° 15' 57" W), located at the east end of the lake, using their infrastructure and resources. The Old Post is a fishing resort built on the historical site of Osnaburgh House, a former Hudson's Bay Company outpost (Del Vecchio 2007).

Walleye stomachs and data were collected each day when possible, from Walleye harvested using rod and reel, by patrons staying at the lodge. I accompanied patrons acting in the capacity of a fishing guide which allowed me to collect harvest data: catch date, location, time of day, water depth. The length of each harvested Walleye was recorded post mortem. All Walleye data, data on angling activities, and supporting macroinvertebrate data were collected between May 24th and September 1st 2018, and between June 12th and August 8th, 2019. Only those Walleye that were harvested by patrons were used for this study, and all Walleye sampled were over 350 mm and therefore considered sexually mature (Hartman 2009).

Upon capture, Walleye that were being kept for harvest were affixed with a numbered brass tag attached by a metal clip inserted through the bottom jaw. The tag number was recorded in a notebook along with location, date, time of day, depth of water and Walleye length. At the end of each day, after processing (filleted), stomachs were removed and placed in a Whirlpack bag with the corresponding identification tag. Samples were stored in a -20℃ chest freezer until analysis. In 2018, when possible the catch per unit effort (CPUE) was recorded each day, calculated as the number of fish caught, number of rods in the water and time with lines in the water.

Macroinvertebrate collection

Macroinvertebrates were sampled during the summer of 2018 at two sites, known to hold walleye throughout the season and that experiences a mayfly hatch, using rock bag traps. One site was in 2.5 metres deep amongst rocks along a sand flat (onshore site: 51°08'07"N 90°16'24"W), and the second at 6 m deep on an offshore rock reef within a bay (the offshore site: 51°07'36"N 90°17'07"W). These were used to assess what immature species were present and in what proportional abundance. The sites were chosen to allow me to access sample bags without being disturbed by boat traffic. My sampling methods were designed to create an artificial habitat of rocks in a bag and allow a variety of insects to colonize these rock bag traps. Rock bag traps were made using 25 lb onion bags, filled with ~10 kg of hand-sized rocks from the shoreline. The filled bag was then put into a second bag, tied to rope outfitted with an identification buoy, and deployed. Traps remained in place for a minimum of one week, from June 10 to 17, June 24 to July 1, July 29 to August 5, and August 25 to September 1, 2018.

On retrieval, bags were placed in a large container for processing. Both rocks and bags were washed to remove organisms attached to the mesh, and then redeployed. Collected specimens were stored in glass vials containing 80% ethanol for later identification to order, and to family for mayflies. The nearshore location was a rocky outcropping close to shore in a sheltered bay, a mix of boulders, cobble, and gravel. The offshore location was 6 m deep and 50m from the shoreline.

During the 2019 field collection season adult mayflies were collected via aerial sweep net methods, during emergence events on July 4 and July 9 for identification to family level, and where possible species (Needham 1996).

Stomach content analysis

The contents of the frozen Walleye stomachs were counted, and then identified to class, order, and family where possible using OBBN protocols and morphological keys (Needham 1996), after stomachs were thawed. Stomach contents were sorted and invertebrates placed in vials with 95% ethanol for identification and counting. Any remaining stomach and contents were placed in separate vials with 80% ethanol for long term storage. All identifications were confirmed by Dr. Armin Namayandeh (Trent University).

Statistical analysis

Empty stomachs were not included in diet analyses, but were included in any analyses having to do with fish behaviour or activity. Several relationships were tested to determine if prey changed based on Walleye size, depth of capture and date of capture. These were tested using either linear or quadratic regressions (PAST 4.10, Hammer et al. 2001). Specific linear regressions were number of invertebrates in each stomach vs Walleye length, the depth caught vs the date, the length of Walleye caught vs date. In all analyses using date or time of year, this was given as the numeric day of year, where 1 represents Jan 1 and 365 represents Dec 31.

First I tested the hypothesis, mayflies makeup an important part of the walleye diet during mayfly emergence periods, when immature mayflies move up though the water column to emerge as adults, directly by fitting the numeric date to an invertebrate/fish index (consumption of invertebrates vs. prey type). I used a quadratic regression for this because the hatch occurred about midsummer. Because these data were not normal, this index was transformed into natural logarithms (ln). The index was calculated for both 2018 and 2019 as:

$$\text{invertebrate/fish index} = ln\,(\text{no. inverts/stomach} + 1) - ln\,(\text{no. fish/stomach}+1) \quad (1)$$

where no. inverts./stomach is the number of invertebrates per Walleye stomach, and no. fish/stomach is the number of fish per Walleye stomach. The use of logarithms also enabled me to essentially test how the proportion by number of each prey type changed over the entire season. One was added so that any stomachs with zero counts of either type of prey could be included as a zero score, e.g. $ln(1) = 0$. While it was expected that mayflies would outnumber fish prey when present, this method allowed me to assess the relative change in the abundance of prey type per stomach over the season. For example, if on June 10 one Walleye had 100 mayflies and only 2 fish prey, the index value would be $ln(100+1) – ln(2+1) = 4.615 – 1.099 = 3.517$. The model used was:

$$\text{invertebrate/fish index} = a * (\text{date})^2 + b * (\text{date}) + c \quad (2)$$

The hypothesis would be supported the number of Walleye with mayflies in their stomachs peaked during the hatch period.

I further tested the hypothesis to see if only the smaller Walleye tended to prey upon invertebrates. The test used was a linear regression of Walleye length vs number of invertebrates per stomach. This was a more indirect test of the hypothesis, which would be supported if there was no significant effect of length on the number of invertebrates per stomach. For this test data from 2018 and 2019 were pooled.

Three other tests were run to identify Walleye predatory behaviour patterns. Two of these were simple linear regressions of date vs depth of capture, and date vs Walleye length. The third test was to correlate CPUE against the number of invertebrates and the number of fish in each harvested stomach. Because these data were not normal, these tests were done as non-parametric tests on the ranks using Spearman's r (Sokal and Rohlf 1995).

Because I tested several tests from the same data set, the p values were corrected using the sequential Bonferroni method, where the corrected significance cut-off level for $\alpha = 0.05$, was determined as $[1 - (1 - \alpha)]/k$, where k is the number of tests performed, with tests ranked from smallest to largest *p* (Sokal and Rohlf 1995).

RESULTS

Walleye were sampled from the eastern half of the main body of Lake St. Joseph at 58 locations (Fig. 1). I collected a total of 178 stomachs, 130 in 2018 and 47 in 2019. Of these, 63 and 15 stomachs were empty in 2018 and 2019 respectively, resulting in a total of 67 and 32 stomachs with prey items in 2018 and 2019 respectively (Fig. 2). Mayflies and fish prey were the most commonly found prey items (Fig. 2). In stomachs collected in 2018 there were 620 mayflies, 103 minnows, and 75 yellow perch; in 2019 there were 262 mayflies, 13 minnows, and 8 yellow perch. All mayflies in stomachs that could be identified to genus (approximately one quarter) belonged to the genus *Hexagenia*. Caddisflies, beetles, dragonflies and crayfish were also present to a lesser extent in some stomachs (Fig. 2).

I caught 156 adult mayflies (2019) by netting, 115 (73.7%) of which belonged to the genus *Hexagenia:* 89 *H. limbata* (16.7%), and 26 *H. rigida* (26.3%). The rock bag catches showed a smaller percentage of *Hexagenia*, 68.4% of the mayflies caught in shallow water but only 31.4% of the mayflies caught in deep water (Table 1). Mayflies were the most abundant insect capture in the rock bags, 43.8% of 203 insects. The second largest group of invertebrates captured were amphipods, 159 (Table 1).

Across the two sampling seasons, foraging over time showed that invertebrates were consumed more than fish early in the season during both years, with the quadratic model maxima occurring during the mayfly hatching period, most noticeably in 2019 (Fig. 3, Table 2). From the fitted quadratic models, the peak dates Walleye preyed on invertebrates were June 21 (numeric date 173) and June 1 (numeric date 153) in 2018 and 2019 respectively. In 2018, over the 2 weeks before and after June 21, of 23 Walleye sampled, 20 (87%) had invertebrates in them but only 10 (43%) had fish prey, compared to the 45 other Walleye stomach sampled outside this period of which 23 (51%) contained invertebrates and 31 (69%) contained fish prey. This was similar to 2019; all 5 Walleye stomachs harvested from May 18 to June 15 contained invertebrates but only one had fish prey, whereas of the 27 stomachs harvested the rest of the year, 24 (89%) contained invertebrate prey and 10 (37%) contained fish prey.

Walleye of all harvested lengths captured consumed invertebrate prey at about the same level (Fig. 4, Walleye length vs invert prey/stomach $y = -1.24x + 62.43$, $R^2 = 0.025$ p = n.s.).

Walleye tended to go to deeper water over the course of the summer, from less than 2 metres on May 19 (numeric date 140) to almost 10 metres by August 17 (numeric date 230) (Fig. 5, date vs Walleye capture depth $y = -0.028x + 2.62$, $R^2 = 0.26$, $p < 0.001$). The length of harvested Walleye changed slightly over the summer, with Walleye tending to be about one to two cm longer by the end of the season (Fig. 6, date vs Walleye length $y = 0.018x + 40.7$, R^2 0.064, $p = 0.001$).

CPUE (2018 data) was not correlated with either the number of invertebrates or the number of fish per stomach (invertebrate prey Spearman's $r = 0.255$, $p = 0.056$, $n = 57$; fish prey Spearman's $r = -0.0047$, $p = 0.97$, $n = 57$).

DISCUSSION

The hypothesis, that adult Walleye consume mayflies, particularly during the hatching period was supported by the results, most Walleye captured during the hatching period had mayflies in their stomachs, some exclusively so. One reason could be simply that mayflies are easy to capture at this time as they leave the benthos, and swim upward in the water column to emerge as adults. There was no evidence that this is affected by the size of adult Walleye (Figure 4, Figure 6). From these results Walleye prey upon mayflies as a main food source during the emergence period when mayflies are abundant, switching to almost exclusively fish prey in the latter half of the summer, yet still consuming a variety of invertebrates prey to some minor extent (Figure 2, Figure 3). This could explain why Walleye seemed to move from the shallower water in the first part of summer into deeper water as the summer progressed (Figure 5).

It would be instructive to study at wider range of fish lengths in early and late summer, to gain a better appreciation of whether mayflies are equally important for all age classes. My results allow the interpretation that outside of the main hatching period, Walleye opportunistically prey upon invertebrates when encountered.

These results are counter to the general understanding Walleye switch to fish prey at an early age and size (Chipps and Graeb 2011). For example, Chipps and Graeb (2011) summarize Walleye diets for major Walleye populations across North America (their Table 8.1), with the only invertebrates mentioned by name being Diptera. One possible explanation is that Walleye prey upon mayflies within a narrow time period, with most targeting mayflies during the mayfly hatch. From an annual perspective, mayflies would not appear to be important prey. However, considering preying upon mayflies occurs shortly after Walleye spawn, when Walleye metabolic demands are likely at their greatest and reserves the lowest, particularly the case for males (Henderson et al. 2003).

This reliance on mayflies may be particularly important for Walleye in northern, cold water lakes. Walleye in southern warmer lake tend to have much higher metabolic rates, growing faster, and having access to a larger variety of fish prey (Baccante and Colby 1996, Medenjian et al. 2018).

In the absence of mayflies, Walleye in Lake St. Joseph would have to find a suitable replacement for that energy source, most likely smaller fish. It is reasonable that if fish prey were a better nutritional source, in terms of hunting costs and nutritional benefit, then Walleye would focus on the best prey. Mayflies move more slowly than minnows, in spring and early summer minnows tend to be smaller than mayflies. In the absence of mayflies, smaller fish prey could be overharvested by Walleye, affecting Yellow Perch or minnow recruitment.

Do we see any evidence of this? In areas where the invertebrate abundance and diversity has already decreased it is difficult to assign this to a lack of mayflies *per se*. However, this has not been examined since the role of mayflies for adult Walleye has not been systematically studied. It is known that mayflies are important prey of juvenile Walleye (Rose et al. 1999). Low mayfly abundance has been associated both directly and indirectly with lower Walleye recruitment and more extreme population fluctuations on an annual basis (Rose et al. 1999). For example, in the 1950s, when the benthic community composition changed from predominately mayflies to mainly midge larvae (*Chironomidae*) in Saginaw Bay, Lake Huron, the mean size of yellow perch fell, which also coincided with a decline in harvested Walleye (Haas and Schaeffer, 1992, their figures 1 and 41).

Management implications

Mayflies, in particular *Hexagenia,* are known to be bioindicators of good water quality (Vander Zanden and Vadeboncoeur, 2002). Even though the importance of invertebrates is known, invertebrate management and regular monitoring has been regularly bypassed in the final stages of management plans (Sheppard et al. 2015). My results suggest that the energetic benefit of preying upon mayflies need to be better understood in northern systems where *Hexagenia* are still abundant. Current knowledge gaps include how important *Hexagenia* are in other lakes, if this is similar in all Walleye fisheries, or if this varies depending the ecosystem itself. Potential areas to explore include the growing season, cumulative degree days, habitat size and biogeography of the waterbody themselves. This approach will also create an awareness of the condition of the surrounding watershed being as an important part of Walleye conservation – mayflies cannot flourish if pesticides flow into these systems. (Elbrecht et al. 2016, Tiwari and Rachlin, 2018). A developed monitoring plan would be an invaluable tool for managers looking to bolster the ecosystem as a whole to improve fish populations.

Table 1. Numbers of invertebrates captured in macroinvertebrate traps (rock bag traps) in 2018, sorted by taxonomic group. Macroinvertebrate traps were placed in 0.6 on shore and in 2.5 m on an offshore reef. Numbers in parentheses under Ephemeroptera are the number of mayflies from the genus *Heptagenia*.

Date	Depth	Insects						Crustaceans	
		Coleoptera	Diptera	Ephemeroptera	Hemiptera	Odonata	Trichoptera	amphipods	crayfish
June 10-17	0.6 m	2	11	51 (12)	0	0	4	115	7
June 24-July 1	0.6 m	2	1	7 (2)	1	1	6	25	1
Aug 25-Sept 1	0.6 m	23	34	12 (8)	0	0	0	14	1
June 10-17	2.5 m	0	2	1	0	0	1	1	0
June 24-July 1	2.5 m	0	1	11 (6)	0	0	8	3	0
July 29-Aug 5	2.5 m	0	1	0	0	0	2	0	0
Aug 25-Sept 1	2.5 m	0	2	7 (7)	0	0	1	1	0
total	0.6 m	27	46	70 (22)	1	1	10	154	9
total	2.5 m	0	6	19 (13)	0	0	12	5	0
total	both	27	52	89 (35)	1	1	22	159	9

Table 2. Sequential Bonferroni test results. The corrected significance cutoff level is for α = 0.05, determined as [1 - (1 – α)]/k, where k is the number of tests performed, with tests ranked from smallest to largest *p* (Sokal and Rohlf 1995).

test	n	R^2	p	k	corrected p value [1-(1-a)]/k
date vs Walleye capture depth	177	0.255	7.63E-13	4	0.0127
date vs Walleye length	177	0.064	0.0007	3	0.017
Polynomial regression 2018	67	0.1898	0.001188	2	0.025
Polynomial regression 2019	32	0.3637	0.001423	1	0.05
Walleye length vs invert prey/stomach	99	0.0246	0.12074		

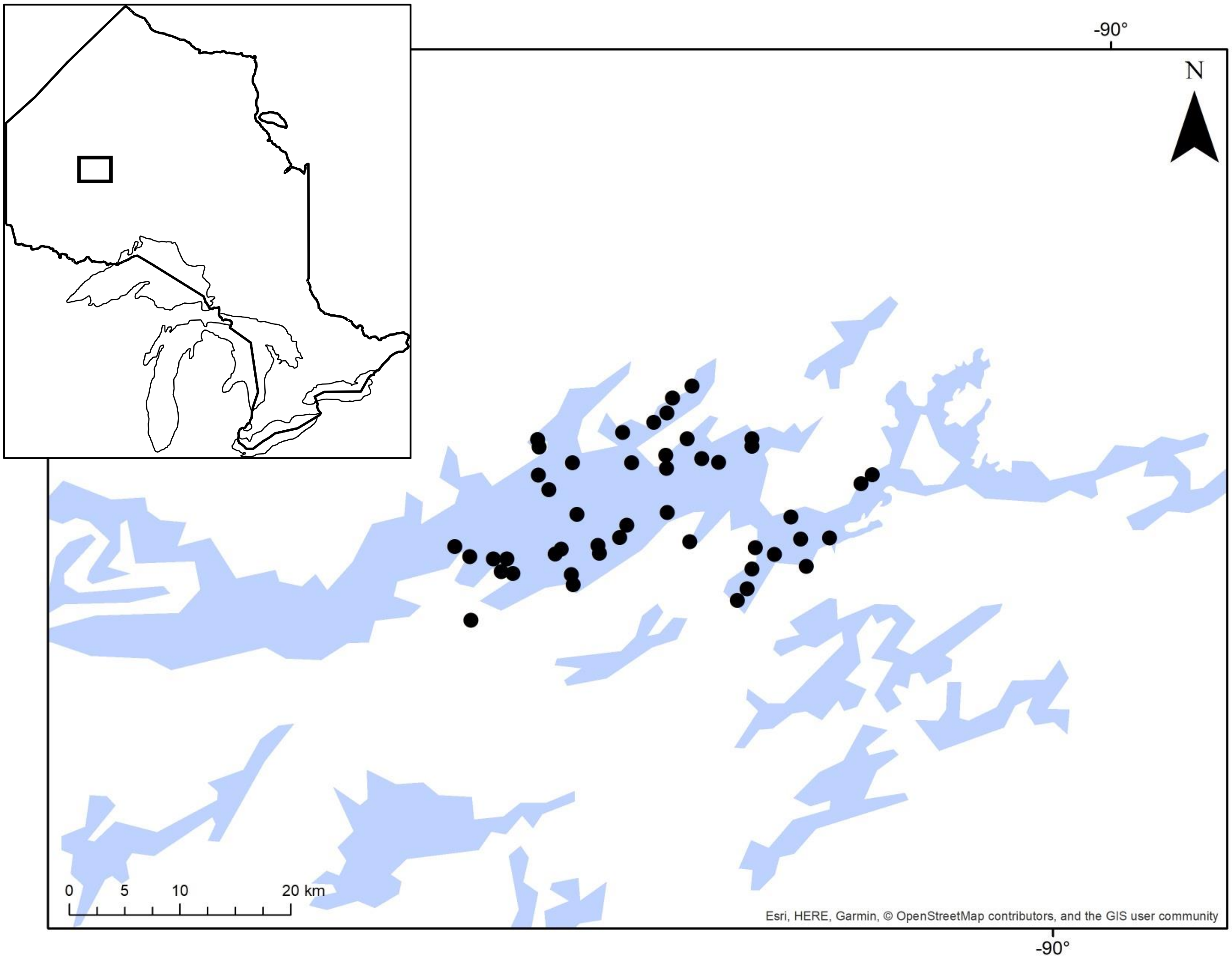

Figure 1. Map of Lake St. Joseph in northern Ontario showing the sites Walleye data were collected during the 2018 and 2019 collection seasons (dots). Inset shows the location of the map area in Ontario.

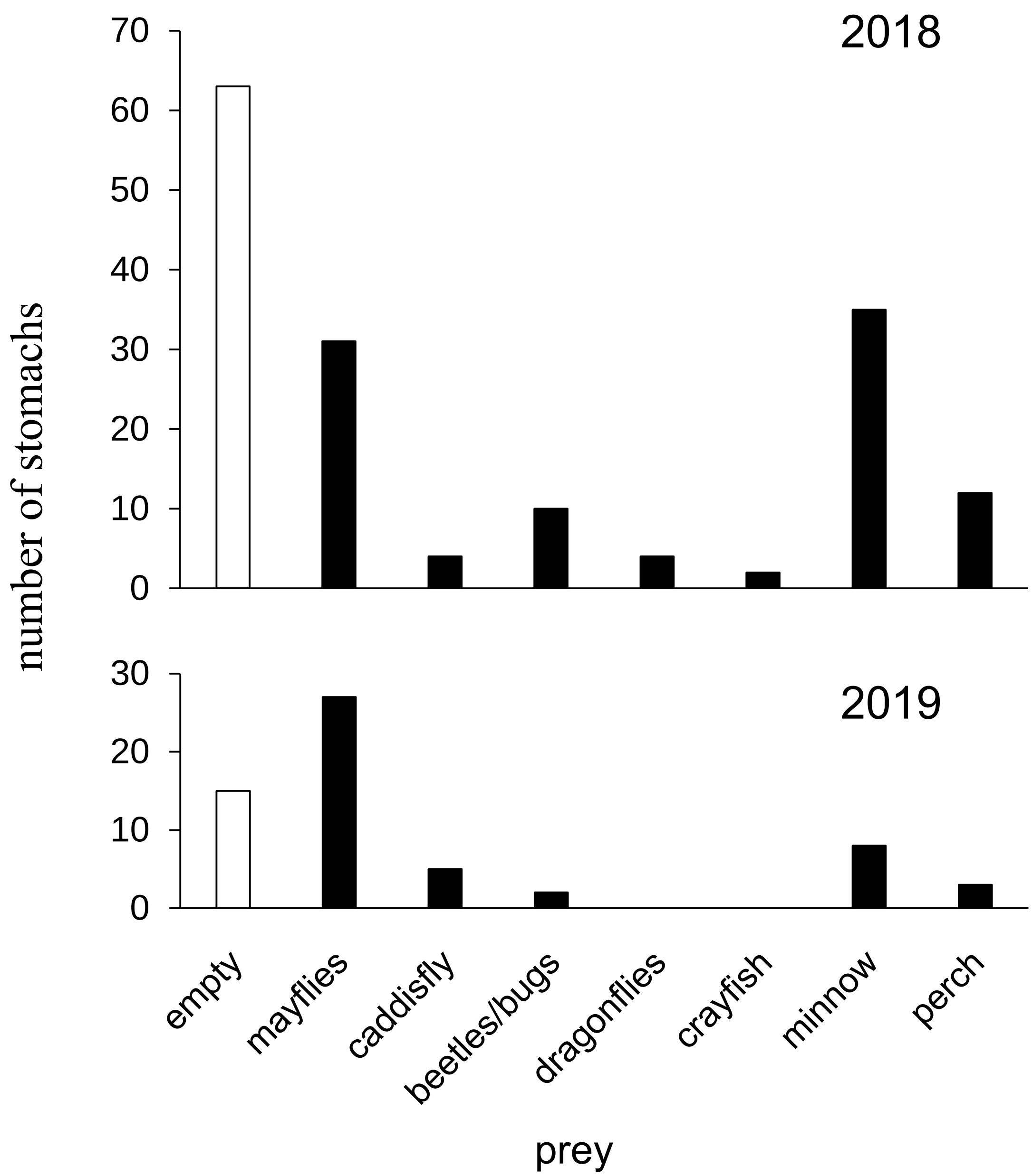

Figure 2. Abundance of different prey items found in Walleye stomachs in 2018 and 2019, ordered by abundance (most to least) for invertebrates on the left side, and the two fish groups on the right.

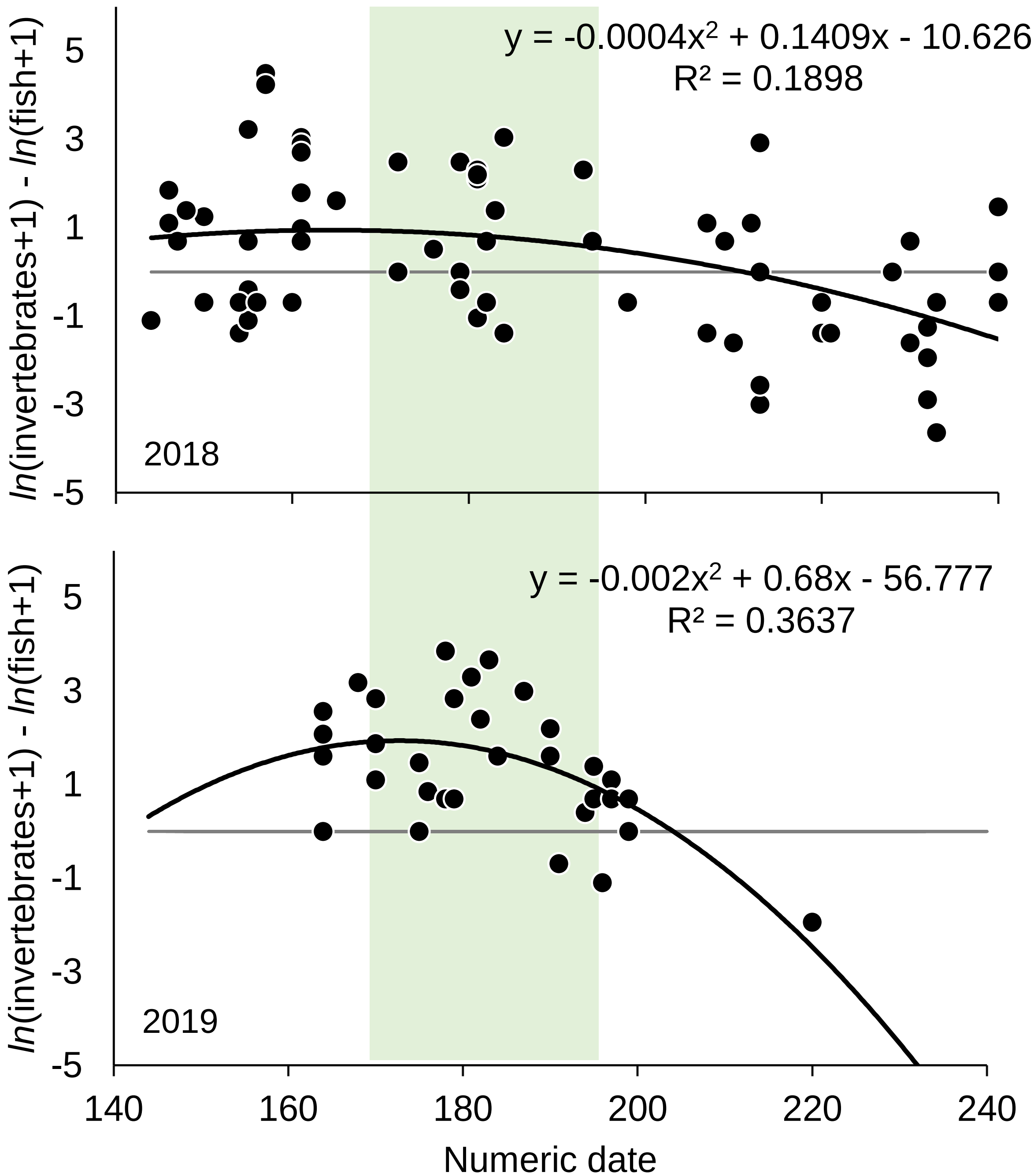

Figure 3. Consumption of invertebrates vs. fish numbers across the 2018 and 2019 season. The green bar in the 2019 season indicates visual evidence of mayfly emergence.

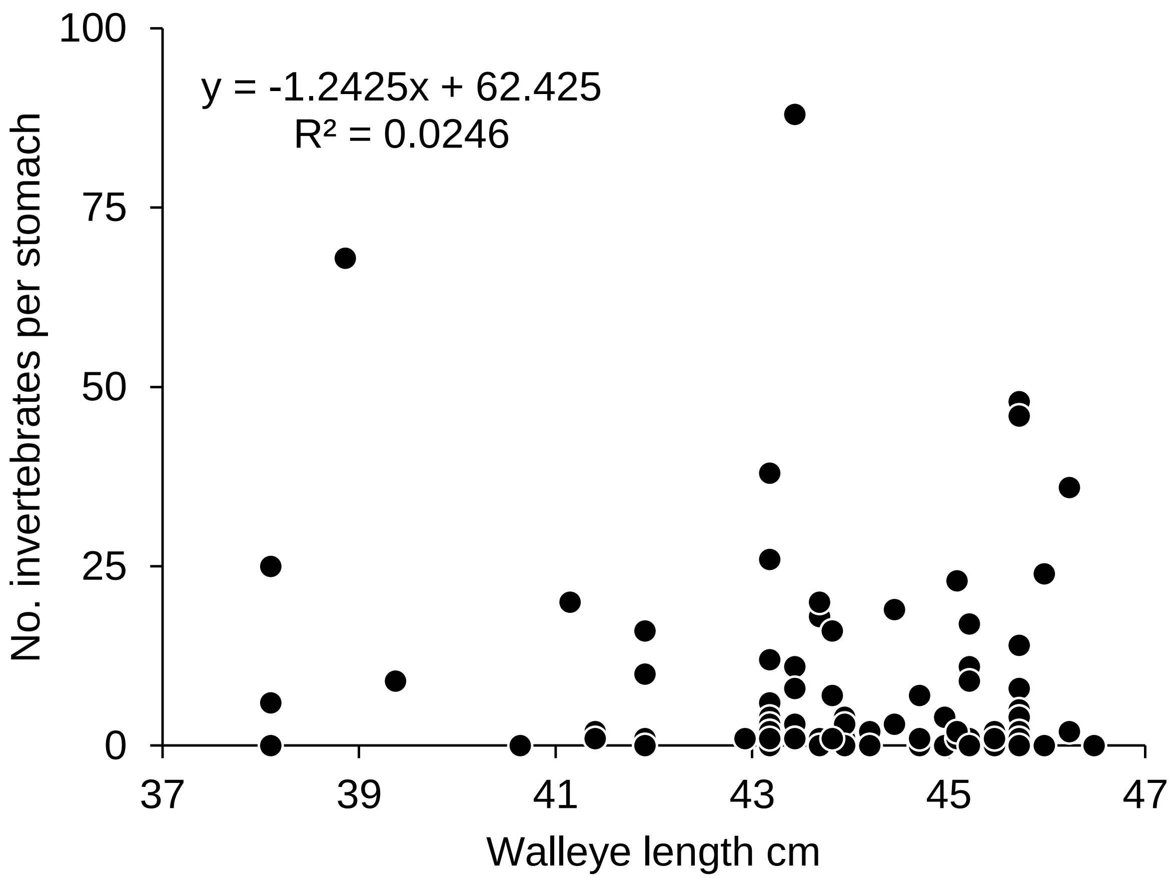

Figure 4. Number of invertebrate prey items in Walleye stomachs compared to the length of harvested walleye.

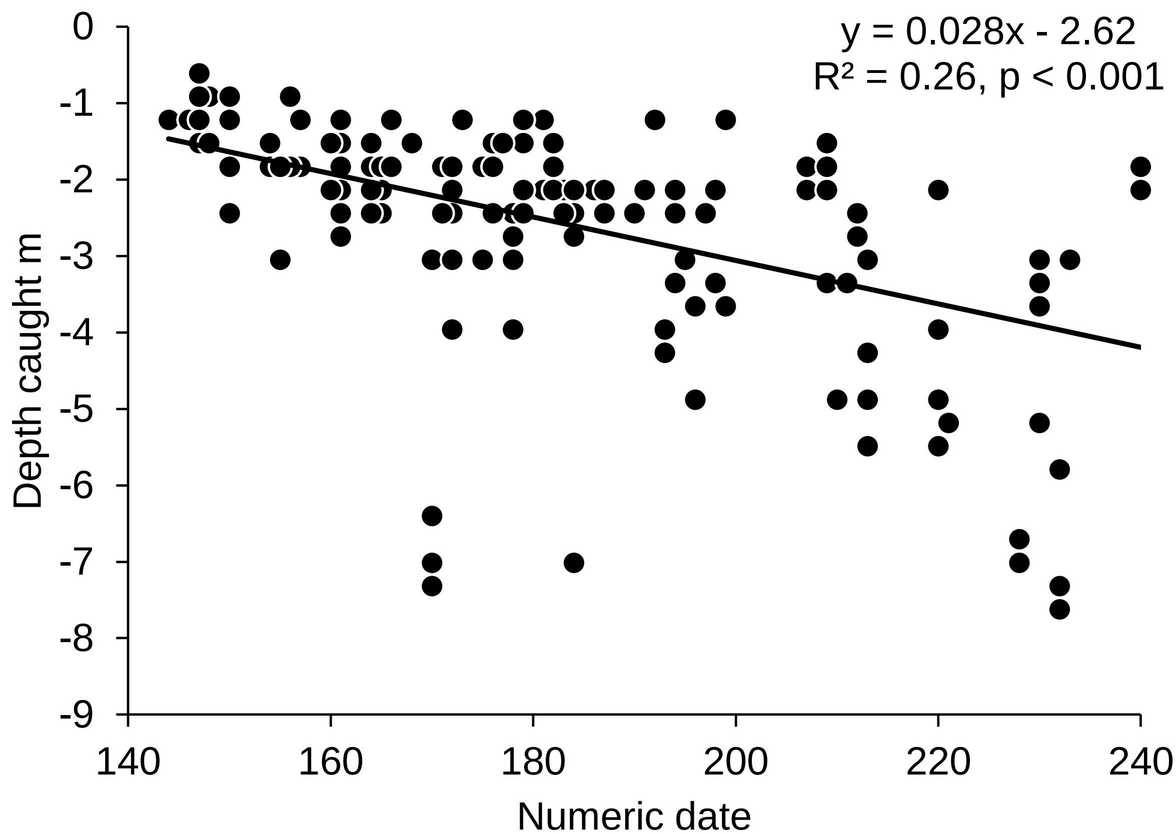

Figure 5. Depth of water each fish was caught from compared to numerical day of the year (Numeric date). Pooled data from 2018 and 2019.

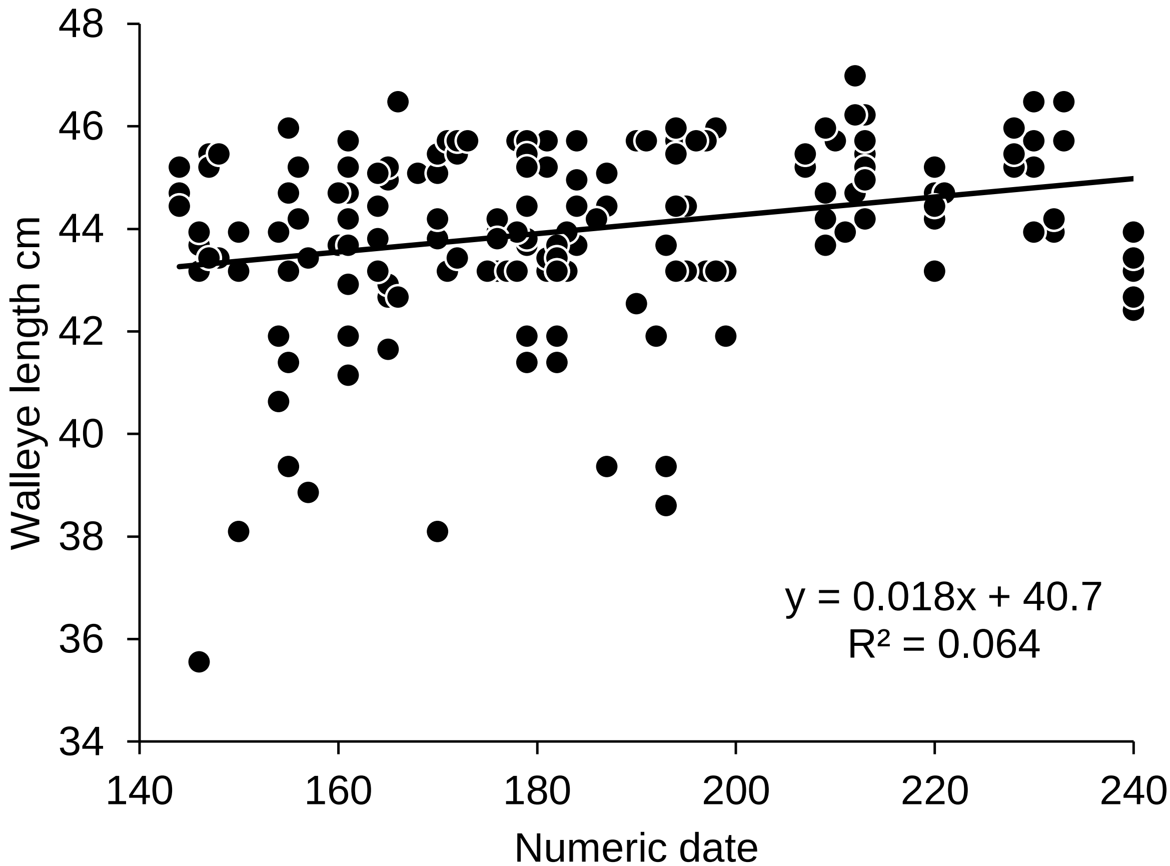

Figure 6. Length of Walleye harvested across the sampling season, 2018 and 2019 data combined.

REFERENCES

Adams, G. F., and Olver, C. H. 1977. Yield properties and structure of boreal percid communities in Ontario. *Journal of the Fisheries Board of Canada* 34: 1613-1625.

Baccante, D. A., and Colby, P. J. 1996. Harvest, density and reproductive characteristics of North American walleye populations. *Annales Zoologici Fennici* 33: 601-615.

Browne, D. R. 2007. Freshwater fish in Ontario's boreal: Status, conservation and potential impacts of development. *Wildlife Conservation Society Canada Conservation Report* No. 2. Toronto, Ontario, Canada.

Clady, M., and Hutchinson, B. 1976. Food of the yellow perch, *Perca flavescens*, following a decline of the burrowing mayfly, *Hexagenia limbata*. Ohio Journal of Science 786: 133-138.

Corkum, L. D., Ciborowski, J. J., and Dolan, D. M. 2006. Timing of *Hexagenia* (Ephemeridae: Ephemeroptera) mayfly swarms. *Canadian Journal of Zoology* 84: 1616-1622.

Del Vecchio, M. 2007. Osnaburgh house: a microcosm of Canadian history. https://oldpost.com/assets/oz-house.pdf.

Elbrecht, V., Beermann, A. J., Goessler, G., Neumann, J., Tollrian, R., Wagner, R., Wlecklik, A., Piggott, ,J. J., Matthaei, ,C. D., and Leese, F. 2016. Multiple-stressor effects on stream invertebrates: a mesocosm experiment manipulating nutrients, fine sediment and flow velocity. *Freshwater Biology* 61: 362-375.

Fremling, C. R. 1968. Documentation of a mass emergence of *Hexagenia* mayflies from the Upper Mississippi River. *Transactions of the American Fisheries Society* 97: 278-281.

Frey, A., Bozek, A., Edwards, C., Newman, S. 2003. Diet overlap and predation between smallmouth bass and walleye in a north temperate lake. *Journal of Freshwater Ecology* 18: 43-54.

Hammer, Ø., Harper, D.A.T., and P. D. Ryan, 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4(1): 9pp.

Heise, B. A., Flannagan, J. F., and Galloway, T. D. 1987. Life histories of *Hexagenia limbata* and *Ephemera simulans* (Ephemeroptera) in Dauphin Lake, Manitoba. *Journal of the North American Benthological Society* 6: 230-240.

Honsey, A. E., Staples, D. F., and Venturelli, P. A. 2017. Accurate estimates of age at maturity from the growth trajectories of fishes and other ectotherms. *Ecological Applications* 27: 182-192.

Giberson, D. J., and Rosenberg, D. M. 1992. Effects of temperature, food quantity, and nymphal rearing density on life-history traits of a northern population of *Hexagenia*

(Ephemeroptera: Ephemeridae). *Journal of the North American Benthological Society* 11: 181-193.

Henderson, B. A., Collins, N., Morgan, G. E., and Vaillancourt, A. 2003. Sexual size dimorphism of walleye (Stizostedion vitreum vitreum). *Canadian Journal of Fisheries and Aquatic Sciences* 60: 1345-1352.

Hewett, S. W., and Simonson, T. D. 1998. Wisconsin's Walleye management plan: moving management into the 21st century (No. 43). *Bureau of Fisheries Management and Habitat Protection*, Wisconsin Department of Natural Resources.

Horst, T. J. 1976. Population dynamics of the burrowing mayfly *Hexagenia limbata*. *Ecology* 57: 199-204.

Jones, N. E., and Mackereth, R. W. (2016). Resource subsidies from adfluvial fishes increase stream productivity. *Freshwater Biology* 61: 991-1005.

Keddy, P. A. 2010. Wetland Ecology: Principles and Conservation. *Cambridge University Press.*

Leather, S. 2018. "Ecological Armageddon" – more evidence for the drastic decline in insect numbers. *Annals of Applied Biology* 172: 1-3.

Madenjian, C. P., Hayden, T. A., Peat, T. B., Vandergoot, C. S., Fielder, D. G., Gorman, A. M., ... and Krueger, C. C. 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: 1573-1586.

Mosindy, T. 1980. *The ecology of northern pike, Esox lucius Linnaeus, in Savanne Lake, Ontario* [Doctoral dissertation, Lakehead University]. Lakehead University. https://knowledgecommons.lakeheadu.ca/handle/2453/2390.

McQueen, D. J., Post, J. R., and Mills, E. L. 1986. Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1571-1581.

Needham, K. M. 1996. An identification guide to the nymphal mayflies (Order Ephemeroptera) of British Columbia. *Resource Inventory Committee* Publ. 046:76 pp.

Polhemus, D. 1993. Conservation of aquatic insects: worldwide crisis or localized threats? *American Zoology* 33: 588-598.

Quist, M. C., Guy, C. S., Bernot, R. J., and Stephen, J. L. 2002. Seasonal variation in condition, growth and food habits of walleye in a Great Plains reservoir and simulated effects of an altered thermal regime. *Journal of Fish Biology* 61: 1329-1344.

Rose, K. A., Rutherford, E. S., McDermot, D. S., Forney, J. L., and Mills, E. L. 1999. Individual-based model of yellow perch and walleye populations in Oneida Lake. *Ecological Monographs* 69: 127-154.

Schaeffer, J. S., Diana, J. S., and Haas, R. C. 2000. Effects of long-term changes in the benthic community on yellow perch in Saginaw Bay, Lake Huron. *Journal of Great Lakes Research* 26: 340-351.

Schloesser, D. and Hiltunen, J. 1984. Life cycle of a mayfly *Hexagenia Limbata* in the St. Marys river between lakes Superior and Huron. *Journal of Great Lakes Research* 10: 435-439.

Sheppard, K. T., Davoren, G. K., and Hann, B. J. 2015. Diet of walleye and sauger and morphological characteristics of their prey in Lake Winnipeg. *Journal of Great Lakes Research* 41: 907-915.

Tiwari, A. and Rachlin, J. 2018. Ecological effects of road de-icing salt on Adirondack forests and headwater streams. *Northeastern Naturalist* 25: 460-478.

Vadeboncoeur, Y., Vander Zanden, M. J., and Lodge, D. M. 2002. Putting the lake back together: reintegrating benthic pathways into lake food web models. *Bioscience* 52: 44-54.

CHAPTER 3: GENERAL DISCUSSION, SUMMARY, CONCLUSIONS

The Walleye mayfly story

The results of this study provide evidence that *Hexagenia* mayflies, and other invertebrates, are preyed upon by adult Walleye in Lake St Joseph. It is a reasonable assumption that this might be the case in other lakes as well, in particular those with similar ecology. At present we do not know how important this is for Walleye. It is possible that in the absence of mayflies, adult Walleye would simply lose an easily caught prey species and instead prey upon smaller fish. This has occurred in more southern systems such as Lake Erie, where *Hexagenia* mayflies had been reduced to only a few minor remnant populations from the 1950s to the 1990s (Krieger et al. 2007, Schloesser and Nalepa 2001), and adult Walleye preyed upon smaller fish almost exclusively (Regier et al. 1969).

In Lake Erie, the commercial Walleye harvest peaked in the mid 1950's followed by a sharp collapse of Walleye populations (Regier et al. 1969). Both the rapid increase and subsequent collapse in the lake Erie fishery were symptomatic of a problem in the Lake Erie Walleye stocks (Regier et al. 1969), explained by, "a combination of limnological changes in the Central Basin, the population explosion of smelt (which was possible, we suggest, largely because of system instabilities traceable to the nature of the fishery), and the direct action of the fishery for the walleye," (Regier et al. 1969). Regier et al. (1969) pointed to the extirpation of *Hexagenia* in Lake Erie as symptomatic of habitat loss and not a contributor to the decline of Walleye stocks. What we do not know is how important mayflies are as a source of nutrition for Walleye. The argument that changes in *Hexagenia* abundance and Walleye numbers are correlated does not alter the fact that changes in *Hexagenia* abundance was followed by a collapse in Walleye numbers, whether this was indirectly due to polluted habitat or directly from the loss of *Hexagenia* as prey for adult Walleye, and/or other fish species (Britt 1955). In either case, abundant *Hexagenia* in Lake Erie was associated with abundant Walleye stocks.

It is reasonable to hypothesize that in Lake St. Joseph (and similar systems) if *Hexagenia* numbers drop, adult Walleye might be forced to prey upon smaller fish, causing lower recruitment of small fish prey. The Lake St. Joseph situation differs from more southern lakes, in that there is not vast input of nutrients, such as can occur in lakes surrounded by agriculture. It is likely that Walleye in northern lake such as Lake St Joseph, are more vulnerable to a reduction in mayfly numbers than more southern lakes. This needs to be understood in order to inform management for populations such as those in Lake St Joseph. At the very least *Hexagenia* abundance should be monitored in order to understand natural population fluctuations, in to distinguish whether a change in abundance is associated with an actual decline of *Hexagenia* populations (Stephanian et al. 2020, Winter et al. 1996, Giberson and Rosenberg 1992, and see Koehnke 2021 for a review of causes of *Hexagenia* decline).

While government management plans express concern for protecting habitat quality which would include mayfly populations as I potential indicator group (Hartig et al. 2020) I cannot find any direct inclusion of *Hexagenia*, or any invertebrate prey directly addressed in any management strategies. To incorporate mayflies into management requires including not just protecting the aquatic habitat and water quality, but ensuring that shoreline and adjacent habitats are not degraded in order to protect invertebrate populations. From this thesis, I would recommend that *Hexagenia* be given specific mention in management plans to direct future research efforts. (If they aren’t placing worth on the invertebrate community to feed the fish then legislation is neglecting the root of the issue within the water body that lead to their decline initially)

It is possible that high quality Walleye fisheries such as those in Lake St. Joseph depend on both high quality aquatic *and* adjacent terrestrial habitats, including such seemingly unrelated factors such as light pollution which can cause the premating death of a massive number of adult mayflies (Corkum et al. 2006). Whether this mortality is significant at the *Hexagenia* population level represents a significant knowledge gap.

The Lake St. Joseph Accords appears at this time to have contributed to the high quality ecosystem and Walleye fishery of Lake St Joseph; one able to sustain a continual harvest. This cooperative agreement is an important success story. The paradigm underlying these accords is that management is about aquatic habitat and harvest. In the advent of future terrestrial development and resource extraction in this area, my research suggests that managing for mayflies should be included as well.

REFERENCES

Britt, N. W. 1955. Stratification in western Lake Erie in summer of 1953: effects on the *Hexagenia* (Ephemeroptera) population. *Ecology* 36: 239-244.

Corkum, L., Ciborowski, J., and Dolan, D. M. 2006. Timing of *Hexagenia* (Ephemeridae: Ephemeroptera) mayfly swarms. *Canadian Journal of Zoology* 84: 1616-1622.

Giberson, D. J., and Rosenberg, D. M. 1992. Effects of temperature, food quantity, and nymphal rearing density on life-history traits of a northern population of *Hexagenia* (Ephemeroptera: Ephemeridae). *Journal of the North American Benthological Society* 11: 181-193.

Hartig, J., Francoeur, S., Ciborowski, J., Gannon, J., Sanders, C., Galvao-Ferreira, P., Knauss, C., Gell, G., and Berk, K. 2020. Checkup: Assessing Ecosystem Health of the Detroit River and Western Lake Erie. https://scholar.uwindsor.ca/softs/9

Koehnke, H. 2021. A review of trends and stressors related to *Hexagenia* mayfly populations to determine future research development. UWL Journal of Undergraduate Research 24: 1-7.

Krieger, K. A., Bur, M. T., Ciborowski, J. J., Barton, D. R., and Schloesser, D. W. 2007. Distribution and abundance of burrowing mayflies (*Hexagenia* spp.) in Lake Erie, 1997–2005. *Journal of Great Lakes Research* 33: 20-33.

Nalepa, T. F., Schloesser, D. W., Pothoven, S. A., Hondorp, D. W., Fanslow, D. L., Tuchman, M. L., and Fleischer, G. W. 2001. First finding of the amphipod *Echinogammarus ischnus* and the mussel *Dreissena bugensis* in Lake Michigan. *Journal of Great Lakes Research* 27: 384-391.

Northern Ontario Angling Tourism Plan 2017. Tourism Northern Ontario. https://destinationnorthernontario.ca/wp-content/uploads/2018/09/Angling.pdf

Regier, H. A., Applegate, V. C., and Ryder, R. A. 1969. The ecology and management of the walleye in western Lake Erie. *Great Lakes Fishery Commission. Technical Report*, 15: 1-101.

Stepanian, P. M., Entrekin, S. A., Wainwright, C. E., Mirkovic, D., Tank, J. L., and Kelly, J. F. 2020. Declines in an abundant aquatic insect, the burrowing mayfly, across major North American waterways. *Proceedings of the National Academy of Sciences* 117: 2987-2992.

Winter, A., Ciborowski, J. J., and Reynoldson, T. B. 1996. Effects of chronic hypoxia and reduced temperature on survival and growth of burrowing mayflies, (*Hexagenia limbata*)(Ephemeroptera: Ephemeridae). *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1565-1571.

CHAPTER 4 - CLOSING REMARKS

My stake in this project and future research: a personal perspective

I am a fishing guide; I need these fish to make my living. In addition, I care about these fish. This is how I connect with nature and how so many other people do too. I can see the ease on my guests' faces when we are on the water, the stress of everyday life is left on shore and we have an experience that cannot be had in urban areas. I have presented the results of my research to undergraduate classes (Trent University), and talked about my experiences. In this way, I have been able to share my own understanding about the importance of preserving habitat, seeing ecological systems as both a resource to be used and protected.

Many things were planned for the project did not go as expected. We planned an entire mark-recapture project to tag Walleye in Lake St. Joseph to estimate their population and understand their seasonal movement in more detail. Even though the whole project was planned to be as low maintenance as possible for industry and government, we were not able to secure all our permits in time, in spite of providing sufficient lead time (a year) for these to be approved. The lack of urgency caused by trying to work with several levels of government caused some of these problems – there seems to be a disconnect between provincial government research, which was my main partner and peopled with very cooperative personnel, and local office enforcement where the permits are housed, where enforcement is the main priority and research less so. This led to my missing the Walleye spawning event because I was unable to get permission for volunteers to assist me in tagging.

The Industry partner underestimated how intrusive this research would be for the daily operation of the business in spite of what I thought was clear communication ahead of time. The demands of rigorous data collection were not understood, and I was not able to use some of the stomachs others had collected due to incomplete data, largely due to the industry partner personnel who were to collect stomachs for me not understanding the importance of meticulous data handling and collection.

These problems are nobody's fault, they are a function of people having a detailed knowledge of their own sphere and areas of expertise, and only a general knowledge of other realms (de Wit-de Vries et al. 2019). I am hoping that my experience will help future projects go smoothly, forewarned is forearmed. In spite of these relatively minor problems, the overall experience was positive, and produced important data. I think the inclusion of all three areas, business, government and academia made this project a success.

Part of the industry

My job is to take people to where the Walleye bite and have fun catching them. I need to know the daily and seasonal patterns of fish to find my clients to the best spots everyday. To achieve this I also need to know what the fish are preying on to get them on the end of the line. Lake St Joseph is a catch and release lake with two fish allowed to be harvested, with very narrow size limits requiring barbless hooks; part of my work is to make sure Walleye are released back unharmed, and any harvested fish are humanely dispatched when kept for consumption. Paying close attention to these details was the inspiration of this project in the first place.

The international clientele of northern fishing lodges want to experience not only the fishing, but also to connect with nature, and are willing to pay large fishing licence fees to do so. Our guests expected to catch fish after spending thousands of dollars to get there, and hundreds of dollars for a license for what is essentially a catch and release experience in the wilderness of northern Ontario. This depends on a healthy and sustainable Walleye population. The amount of money that this form of tourism brings into the local economy is over $100 million a year for Northern Ontario (Northern Ontario Angling Tourism Plan 2017). I guided anglers from as far south as Texas. Conservation and proper management of our resources will lead to sustained revenue for local business who depend on the fishing and outdoor industry.

Mitacs, a Canadian federal government funding agency, works with researchers to provide financial backing for collaboration between academia and industry. This project was undertaken by a team that included scientific expertise from the MNRF, Trent University, and an industrial partner the Old Post Lodge. This approach of including industry, academia and government is ambitious, but as stakeholders, each is necessary for achieving a sustainable fishery. However, bringing these stakeholders together was fraught with pitfalls, the largest one being the different specialized languages used within each sector (Alexander et al. 2020, Thomas and Paul 2019), different goals and timelines of organizations that were not always compatible.

Industry goals

I worked for the Old Post Lodge for 2 years until I became their intern, for the purpose of this project in the spring of 2018. They were founders and part of the Lake St. Joseph Accords for over three decades. This is not just for the sake of conservation: it is to protect the long term sustainability of the business. This is a business, and the demands of staying in business require close attention to profit and loss. In order to fund my project and take part in the Mitacs Accelerate I worked more than 80 hours per week for several months, satisfying the needs of the Old Post in order to keep my scholarship and collect my data. When the contracts were signed, with details and deadlines, the industry partner was cooperative and supportive of our research.

Once at work, the daily demands of the job took over, and the project deadlines became secondary to daily work demands, and for a business daily demands are a matter of continued survival.

The tensions that were created were due to misunderstanding the language of each others' domains. For example, from a business standpoint, this was a save-the-Walleye project, whereas from a scientific standpoint, this was about *Hexagenia* mayflies within the Walleye predator-prey relationship. To non-scientists proficient in accounting, marketing, and customer service, examining adult and larval *Hexagenia*, what were called "bugs" seemed disconnected from the project; adult mayflies are not in the water, Walleye eat minnows, not bugs. From a scientific standpoint, losing time and data because it was necessary to fillet fish, cook over an open fire, and cater to wealthy tourists, seemed absurd, this was not as much science as it was taking time from the project. However, from a science communication standpoint, introducing clients to the questions you were asking and actively engaging them was possibly the largest contribution of this thesis.

Trying to bridge the gap of understanding that was based on two different world views was challenging: each was right based on its own premises, but neither was completely able to understand each other except in a general way. Scientific research requires a stable economic base to allow the luxury of focussing on systems level questions and data collection (Levin et al. 2018); business is based on responding rapidly and competently to situations that create instability (Kim et al. 2021), responding daily to customer demands, anticipating the attitude of each customer to ensure they were happy with the experience. The business side of this partnership was more impressed by the media attention that came through Mitacs than the steady progress in achieving the research goals; the business partner was delighted to talk about it to reporters and promote the business (see for example Mitacs newsletter Oct 19 https://www.mitacs.ca/en/impact/research-scaled-support-walleye-population).

Government goals, the Ministry of Natural Resources and Forestry

Working with the MNRF provided me with access to vast resources and excellent scientists in the research side of this ministry. Government is a unique institution with its own language. The timelines of government, academia, and business are different. Government provides economic and social stability, commonly expressed as sustainability (Stephenson et al. 2019), , business' very survival depends on agility (Kim et al. 2021), with academia existing in its own sphere with research commonly ignored in the larger community (see for example, Hart and Silka 2020, "[these scientists] detailed biophysical investigations of issues such as wetland loss or impacts of nonpoint-source pollution, and lamented that their research was not being used to solve the problems). Working with government I discovered that delays can often arise due to policies and departmental structures. Scientific goals were commonly at odds with administrative process, some research was unable to occur due to the number of permits and departments needed to sign off on seemingly simple project ideas. I worked with fantastic government personnel who helped me negotiate these challenges. However, coming from a business background through academia, the slow policy-driven pace was difficult for me to get used to in many instances. Frankly, and it is not the fault of any person, the institutional approach of government appears to be that while everything must be done by academia and business in a partnership according to fixed deadlines within a rigid paperwork framework, this expectation works one way.

Academic demands, Trent University

Working within academia was similar to working with government, only with its own set of institutional deadlines and expectations. The main areas of discord were that any experience of the reality of business is theoretical (Hart and Silka 2020), again, due to the different nature of these enterprises. This often created challenges, mayfly hatches and Walleye spawning does not occur within an academic schedule, government permitting is not tied to academic demands, and daily business demands are disconnected from all of these things.

Yet, it is the differences that make working together so important, for any kind of achievable sustainability for a resource based local economy. Good intentions are not enough, passing the buck by saying "we need more education" does not solve the language problem nor the one way expectations. There needs to be a concerted effort to learn from business what it needs, without condescension, one that is open to hearing about the lived reality of the individuals involved. The inverse is also true and there must be effort from business to understand the specific elements of concern from the academic world. There also needs to be an honest and clear dissemination about the goals of academia and government for sustainability, not a dumbed down message, but one that makes it clear that sustainability requires a systems approach.

This is not a new insight (see for example Barlie and Saviano 2018, Stephenson et al. 2019, Hart and Silka 2020, de Kerckhove et al. 2021), and this is being done to a large extent, but I also think more can be done in this regard, including local stakeholders, and rights holders, the indigenous communities (Salomon et al. 2019). Researchers need to contribute to more popular outlets on these subjects, editors need to be open to such articles, and these need to be given respect as legitimate extensions of the responsibilities of academic and wildlife research in communicating about science to the wider community.

REFERENCES

Alexander, A., Martin, D. P., Manolchev, C., and Miller, K. 2020. University–industry collaboration: using meta-rules to overcome barriers to knowledge transfer. *The Journal of Technology Transfer* 45: 371-392.

Barile, S., and Saviano, M. 2018. Complexity and sustainability in management: insights from a systems perspective. In *Social dynamics in a systems perspective* (pp. 39-63). Springer, Cham.

Corkum, L., J. Ciborowski,, D.M. Dolan. 2006. Timing of *Hexagenia* (Ephemeridae: Ephemeroptera) mayfly swarms. *Canadian Journal of Zoology* 84: 1616-1622.

Lester, N. P., Sandstrom, de Kerckhove, D. T., Armstrong, K., Ball, H., Amos, J., Dunkley, T., Rawson, M., Addison, P., Dextrase, A., Taillon, D., Wasylenko, B., Lennox III, P., Giacomini, H. C., and Chu, C. 2021. Standardized Broad-Scale Management and Monitoring of Inland Lake Recreational Fisheries: An Overview of the Ontario Experience. Fisheries 46: 107-118.

De Wit-de Vries, E., Dolfsma, W. A., van der Windt, H. J., and Gerkema, M. P. 2019. Knowledge transfer in university–industry research partnerships: a review. *The Journal of Technology Transfer* 44: 1236-1255.

Hart, D. D. and Silka L.. 2020. Rebuilding the ivory tower: a bottom-up experiment in aligning research with societal needs. *Issues in science and technology* 36: 64-70.

Kim, K., Ok, C., Kang, S. C., Bae, J., and Kwon, K. 2021. High-performance work systems with internal and external contingencies: The moderating roles of organizational slack and industry instability. *Human Resource Management* 60: 415-433.

Levin, P. S., Essington, T. E., Marshall, K. N., Koehn, L. E., Anderson, L. G., Bundy, A., Carothers, C., Coleman, F., Gerber, L. R., Grabowski, J. H., Houde, E., Jensen, O. P., Möllmann, C., Rose, K., Sanchirico, J. N., and Smith, A. D. 2018. Building effective fishery ecosystem plans. *Marine Policy* 92: 48-57.

Northern Ontario Angling Tourism Plan 2017. Tourism Northern Ontario. https://destinationnorthernontario.ca/wp-content/uploads/2018/09/Angling.pdf

Salomon, A. K., Quinlan, A. E., Pang, G. H., Okamoto, D. K., and Vazquez-Vera, L. 2019. Measuring social-ecological resilience reveals opportunities for transforming environmental governance. *Ecology and Society* 24(3) article 16.

Stephenson, R. L., Wiber, M., Paul, S., Angel, E., Benson, A., Charles, A., Chouinard, O., Edwards, D., Foley, P., Lane, D., McIsaac, J., Neis, B., Parlee, C., Pinkerton, E., Saunders, M., Squires, K., and Sumaila, U. R. 2019. Integrating diverse objectives for sustainable fisheries in Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 76: 480-496.

Thomas, A., and Paul, J. 2019. Knowledge transfer and innovation through university-industry partnership: An integrated theoretical view. *Knowledge Management Research and Practice* 17: 436-448.