School of Graduate Studies
Bemidji State University
1500 Birchmont Dr NE, #48
Bemidji, MN 56601-2699
218-755-2027

FEEDING PATTERNS AND DIET OVERLAP OF MUSKELLUNGE AND CO-OCCURRING PISCIVORES IN MINNESOTA LAKES

by

Kamden Glade

A Thesis Submitted to the Faculty of the
DEPARTMENT OF BIOLOGY

In Partial Fulfillment of the Requirements
For the Degree of

Master of Science in Biology

BEMIDJI STATE UNIVERSITY
Bemidji, Minnesota, USA

December 2021

STATEMENT BY THE AUTHOR

This thesis has been submitted in partial fulfillment of requirements for an advanced degree at Bemidji State University and is deposited in the University Library to be made available to borrowers under the rules of the library.

Brief quotations from this thesis are allowable without special permission, provided accurate acknowledgement of the source is indicated. Requests for permission to use extended quotations or to reproduce the manuscript in whole or in part may be granted by the Department of Biology or the Dean, College of Business, Mathematics & Sciences when the proposed purpose is in the interest of scholarship. In all other instances, however, permission must be obtained from the author.

Signed:

APPROVAL BY THESIS ADVISOR

THIS THESIS HAS BEEN APPROVED ON THE DATE SHOWN BELOW:

Andrew W. Hafs, Ph.D.
Committee Chair
Professor of Biology

6 Dec 2021
Date

Marilyn D Yoder
Dean, College of Business, Mathematics & Sciences

12/16/21
Date

FEEDING PATTERNS AND DIET OVERLAP OF MUSKELLUNGE AND CO-OCCURRING PISCIVORES IN MINNESOTA LAKES

Kamden Glade

Muskellunge *Esox masquinongy* are the largest member of the family Esocidae found in Minnesota and are managed for trophy angling opportunities with large minimum size requirements, limited harvest, and stocking to support existing populations or expand angling opportunities. While Muskellunge impacts at the community level appear minimal based on available literature, relatively little is known about Muskellunge diets, particularly in Minnesota. In this study, we used gastric lavage to examine gut contents of Muskellunge, Northern Pike *Esox lucius*, Walleye *Sander vitreus*, and Largemouth Bass *Micropterus salmoides*. Diets were quantified using an index of relative importance (IRI) and diet overlap among species was determined using Pianka's index of niche overlap and non-parametric multi-dimensional scaling (NMDS) ordinations. Our experimental design focuses on how the presence or absence of Cisco *Coregonus artedi* impacts diet and overlap, while lakes without Muskellunge were also sampled to compare diets of other piscivores in their presence or absence. Yellow Perch *Perca flavescens* and various centrarchids were important prey items across all lakes for Muskellunge, Northern Pike, and Walleye, while crayfish *Faxonius* spp. and other aquatic invertebrates were critical for Largemouth Bass. Pianka's index of niche overlap indicates that Muskellunge had low levels of dietary overlap with other predators, while Northern Pike and Walleye had relatively high levels of dietary overlap. Additionally, diet overlap tended to be lower among all species when Cisco were present, even though direct predation on Cisco was rarely observed. These results corroborate existing research on diets of Muskellunge, Northern Pike, Walleye, and Largemouth Bass in their native range.

Approved by:

Committee Chair

6 Dec 2021
Date

Committee Member

Committee Member

Graduate Faculty Representative

ACKNOWLEDGMENTS

I would like to thank Andrew Hafs, Brian Herwig, and Tyler Ahrenstorff for providing mentoring and project guidance; Kendra Fink, Erin Haws, Jay Holland, Madison Irons, and Marissa Pribyl for their assistance in the field and lab; the other members of the Hafs lab for their help and support; Jeff Reed, Kyle Zimmer, and students in the Zimmer lab for additional insight and assistance in the field; Loren Miller for his genetic sleuthing; and my family and friends for encouraging my passion for fish long before I studied them. A special thanks to my wife, Alison, for encouraging me to always pursue my passions and for undying love and support when stresses mount. Funding for this project was provided by Bemidji State University and the Federal Aid in Sport Fish Restoration Fund.

TABLE OF CONTENTS

Contents

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

Chapter 1: FEEDING PATTERNS AND DIET OVERLAP OF MUSKELLUNGE AND CO-OCCURRING PISCIVORES IN MINNESOTA LAKES

Abstract.- Muskellunge *Esox masquinongy* are the largest member of the family Esocidae found in Minnesota and are managed for trophy angling opportunities with large minimum size requirements, limited harvest, and stocking to support existing populations or expand angling opportunities. While Muskellunge impacts at the community level appear minimal based on available literature, relatively little is known about Muskellunge diets, particularly in Minnesota. In this study, we used gastric lavage to examine gut contents of Muskellunge, Northern Pike *E. lucius*, Walleye *Sander vitreus*, and Largemouth Bass *Micropterus salmoides*. Diets were quantified using an index of relative importance (IRI) and diet overlap among species was determined using Pianka's index of niche overlap and non-parametric multi-dimensional scaling (NMDS) ordinations. Our experimental design focuses on how the presence or absence of Cisco *Coregonus artedi* impacts diet and overlap, while lakes without Muskellunge were also sampled to compare diets of other piscivores in their presence or absence. Yellow Perch *Perca flavescens* and various Centrarchids were important prey items across all lakes for Muskellunge, Northern Pike, and Walleye, while crayfish *Faxonius* spp. and other aquatic invertebrates were critical for Largemouth Bass. Pianka's index of niche overlap indicates that Muskellunge had low levels of dietary overlap with other predators, while Northern Pike and Walleye had relatively high levels of dietary overlap. Additionally, diet overlap tended to be lower among all species when Cisco were present, even though direct predation on Cisco was rarely observed. These results corroborate existing research on diets of Muskellunge, Northern Pike, Walleye, and Largemouth Bass in their native range.

Introduction

Muskellunge *Esox masquinongy* are the largest member of the family Esocidae found in Minnesota and are managed for trophy angling opportunities with large minimum size requirements and low bag limits. Additional management strategies include supplemental stocking in native Muskellunge waters, as well as new introductions to expand angling opportunities and disperse angling pressure throughout the state (MN DNR 2008; MN DNR 2016). However, anglers and biologists have expressed concern over how new introductions might impact resident sport and prey fish communities (Kerr 2016). While Muskellunge impacts at the community level appear to be minimal (Knapp et al. 2012, 2020), relatively little is known about Muskellunge feeding behavior in Minnesota.

Muskellunge are a popular sport fish throughout their range with around 100 waters containing native or stocked Muskellunge (including hybrids) in Minnesota alone (MN DNR 2016). However, relatively little research has been done on their diets, and a large percentage of fish sampled in diet studies are captured with empty stomachs (Bozek et al. 1999; Kerr 2016). While a variety of aquatic and terrestrial organisms have been found in Muskellunge diets, fish comprise the largest portion (Anderson 1948; Scott and Crossman 1973; Bozek et al. 1999). Young Muskellunge primarily feed on invertebrates, cyprinids, and young-of-the-year sunfish (Krska and Applegate 1982; Kapuscinski et al. 2012). As Muskellunge reach adulthood, larger prey items such as catastomids become increasingly important (Brenden et al. 2004; Woomer et al. 2012). In northern Wisconsin, Yellow Perch *Perca flavescens* and White Sucker *Catostomus commersonii* were the most important prey items in Muskellunge diets in 34 lakes over a three year study (Bozek et al. 1999). However, soft-rayed prey were shown to be preferred by Muskellunge in a lab setting (Wahl and Stein 1988). These findings were supported by a high proportion of Gizzard Shad *Dorosoma cepedianum* present in diets from Illinois and Ohio reservoirs (Wahl and Stein 1991; Wolter et al. 2012), and an apparent selection for catostomids and cyprinids in Lake St. Clair (Spooner 2016). While various studies show Muskellunge will consume Cisco *Coregonus artedi* when present (Oehmcke et al. 1958; Bozek et al. 1999; Kerr and Grant 2000) and Cisco presence positively impacts Muskellunge size structure (VanderBloemen et al. 2020), few studies have specifically examined Muskellunge predation on Cisco (Kerr 2016).

Northern Pike *Esox lucius* are opportunistic predators, feeding on a wide variety of organisms depending on prey availability (Lawler 1965; Mann 1982; Sammons et al. 1994). Diet composition varies widely based on geographic location reflecting differences in dominant regional prey faunas, and consumption of invertebrates is not uncommon (Chapman et al. 1989; Beaudoin et al. 1999; Venturelli and Tonn 2006). In western lakes and reservoirs, various salmonid species compose a large portion of nonnative Northern Pike diets (Walrath et al. 2015; Scheibel et al. 2016). Centrarchids can also be an important diet item in lakes where they are abundant, although evidence suggests Northern Pike are not able to reduce high population densities of stunted sunfishes (*Lepomis* spp.; Beyerle 1971; Margenau et al. 1998). Additionally, lab and field research has shown Northern Pike will selectively feed on soft-rayed fish, such as Gizzard Shad, even when centrarchids are present (Wahl and Stein 1988; Wahl and Stein 1999). In large Minnesota lakes with clear water, Cisco may also be an important prey item, especially for large Northern Pike (Jacobson 1992; Kennedy et al. 2018). However, studies across the Northern Pike range in North America indicate Yellow Perch tend to be the dominant prey item whenever present (Diana 1979; Pierce et al. 2003; Liao et al. 2002, 2004).

Although stomach samples from adult Walleye *Sander vitreus* frequently contain invertebrates (Liao et al. 2002, 2004; Frey et al. 2003), a shift to a piscivorous diet can occur within months, if not weeks, of hatching (Ward et al. 2008). Common prey fishes vary greatly across the Walleye's range depending on dominant prey fish communities in the area. In western rivers and reservoirs, Walleye feed heavily on a variety of salmonid, cyprinid, and sculpin species (Zimmerman 1999). In lakes where they are abundant, soft-rayed fishes such as Gizzard Shad and Alewife *Alosa pseudoharengus* are much more common in Walleye diets (Hartman and Margraf 1992; Knight and Vondracek 1993; Porath and Peters 1997; Olson 2004). In the prairie pothole region of western Minnesota, stocked Walleye primarily fed on invertebrates and Fathead Minnow *Pimephales promelas*, consuming enough minnows to improve the water quality of shallow wetlands (Herwig et al. 2004). In many Minnesota lakes, Walleye primarily prey upon Yellow Perch, with the two species often experiencing fluctuations in abundance and size structure due to the predator-prey relationship (Pierce and Tomcko 2003; Pierce et al. 2006). Additionally, Cisco appear to be an important prey item in lakes where they are present and may increase the overall growth potential of Walleye that consume them (Jacobson 1994; Kaufman et al. 2009).

Largemouth Bass *Micropterus salmoides* are known to be highly opportunistic generalist predators, consuming a wide variety of fish, aquatic invertebrates, and terrestrial organisms (Hodgson and Kitchell 1987; Ahrenstorff et al. 2009). Although relatively rare in occurrence, terrestrial vertebrates have been shown to comprise a large portion of the overall biomass consumed (Hodgson and Hansen 2005, Sass et al. 2011). Similarly, crayfish contribute a relatively large portion of biomass consumed in lakes where this group of crustaceans are common (Kelling 2014; Kelling et al. 2016). Sunfishes (Dibble and Harrel 1997; Pothoven et al. 1999), Yellow Perch (Reed and Parsons 1996), and shads (Miranda and Pugh 1997) are common prey fish throughout the Midwest. Less common prey fish include Fathead Minnow (Dibble and Harrel 1997), White Sucker, and Black Crappie *Pomoxis nigromaculatus* (Kelling et al. 2016). Additionally, cannibalism is relatively common in Largemouth Bass populations (Reed and Parsons 1996; Dibble and Harrel 1997). Furthermore, predation on stocked Walleye has been documented, although the impact of Largemouth Bass predation appears to be negligible (Freedman et al. 2012).

Management of large piscivores, especially those introduced into new water bodies, can be a contentious issue due to potential impacts on native fish species (McMahon and Bennett 1996; Doss 2017). In Minnesota, debates over management of stocked Muskellunge center on potential impacts on Walleye and other game fish (Schroeder et al. 2007; Kerr 2011) and culminated in legislation proposing to suspend all Muskellunge stocking throughout the state and allow counties to determine stocking quotas (S.F. 3319, 2018). While declines in certain fish populations have been documented following initial stocking of Muskellunge (Siler and Beyerle 1986), multiple studies across the Muskellunge range have indicated that the community effects of introduced Muskellunge are minimal. Fayram et al. (2005) indicated no negative impacts on stocked Walleye populations, finding a positive relationship between Walleye catch per unit effort (CPUE) and Muskellunge CPUE. In Minnesota, CPUE of seven different fish species was monitored before and after Muskellunge stocking, with no significant decrease in CPUE for any species across the set of 41 lakes (Knapp et al. 2012). Further examination with additional lakes and years of data indicated that Yellow Perch relative abundance and Northern Pike average weight were both higher in lakes that were stocked with Muskellunge than in unstocked reference lakes (Knapp et al. 2020). No decreases were observed for game species following Muskellunge stocking, with the exception of

Northern Pike, which exhibited lower CPUE in lakes after the introduction and management of Muskellunge. Furthermore, an extensive review by Kerr (2016) found very little evidence to suggest negative impacts of Muskellunge on other sport fish species.

The objectives of this study were to (1) quantify diet patterns of Muskellunge, Northern Pike, Walleye, and Largemouth Bass, and (2) compare dietary overlap between these piscivores in a set of Minnesota lakes with a variety of prey fish assemblages. Emphasis was given to how the presence or absence of Cisco impacted diet patterns and niche overlap. Additionally, lakes without Muskellunge were also sampled to determine how Muskellunge presence impacts the diets of the other three targeted species.

Methods

Data Collection

Muskellunge, Northern Pike, Walleye, and Largemouth Bass were sampled from eight different Minnesota lakes (N=5 in 2019 and N=3 in 2020) during spring (April-early June), summer (July-August), and fall (September-October; Figure 1). Selected lakes were split between four treatment groups: Muskellunge and Cisco Present (Both present; BP), Muskellunge present/Cisco absent (Muskellunge only; MO), Muskellunge absent/Cisco present (Cisco only; CO), Muskellunge and Cisco absent (Both absent; BA, Table 1; Figure 2). Fish were primarily collected by boat electrofishing in shallow waters (<3 m in depth). A variety of habitats were sampled in each lake, including shoreline areas and any other shallow structure (i.e. islands, reefs, etc.). Other gears (trap nets, gill nets, and angling) were also used as part of other Department of Natural Resources standard lake surveys or to bolster sample size when electrofishing was not effective (Figure 3). All sampled fish were identified to species and measured to the nearest mm total length. Gastric lavage (Foster 1977, Kamler and Pope 2001) was used to flush stomachs of live fishes using a handmade device consisting of a battery-operated bilge pump and a garden hose with a trigger-nozzle to control pressure, similar to the design of Crossman and Hamilton (1978). Following the gastric lavage procedure, all fish were released alive. When fish were sampled in a lethal gear type (i.e. gill nets), the stomach was removed in lieu of performing gastric lavage. Furthermore, all fish collected in 2020 were euthanized via cranial concussion (AVMA 2020) and stomachs removed because the close proximity of crew members required to perform gastric lavage was not in accordance with COVID-19 prevention protocols. Additional fish were euthanized in a similar manner when freshly consumed prey items could not be removed without causing serious injury to the fish. Stomach contents were placed in a Whirl-Pak bag labeled with a unique code indicating which lake and fish the diet came from and preserved in ethanol. Total length, gear type, lake, and date of sampling were recorded on data sheets with corresponding diet codes.

In the lab, all prey items were identified to the lowest possible taxonomic group using taxonomic keys, cleithra (Traynor et al. 2010), or otoliths (Ross et al. 2005; Rypel 2008). Fish prey were measured to the nearest mm by total length, backbone length, cleithra length, or otolith length, depending on the extent of digestion. Relationships between backbone length-total length, cleithra length-total length, and otolith length-total length were developed to estimate total length of digested prey items. Length-weight regressions were then used to estimate wet weight of all fish prey items (Table 2). Invertebrate components of fish diets were processed in the lab using an image analysis system. For macroinvertebrates and zooplankton, the lengths of the first 30 individuals for each diet taxa were measured, and average length was used to estimate average wet weight based on published length-weight regressions. Average wet weight was multiplied by the number of individual prey items for each taxa in the diet to obtain total wet mass of each invertebrate taxa consumed. Prey items from each sample were then grouped by lowest possible taxon and counted to determine proportion of diet items. Up to 100 unidentifiable prey fish each year were preserved in 95% non-denatured ethanol and sent to the Aquatic Genetics Lab at the University of Minnesota for genetic sequencing (Kelling et al. 2016; L.M. Miller, Minnesota Department of Natural Resources, personal communication). Muskellunge diets were highest priority due to difficulty in reaching our targeted sample size, while other species with smaller sample size in a given lake were chosen secondarily. Prey items that could not be identified visually or by genetic sequencing were classified as “unidentifiable fish”. Any prey items that were unmeasurable due to digestion were assigned the mean wet weight of other prey items of the same taxa that were consumed from the same lake.

Data Analysis

Predator diets were pooled by lake group and season and analyzed using program R (R Core Team 2021). To quantify diet patterns of piscivores, an index of relative importance (IRI, Pinkas et al. 1971; Martin et al. 1996) was calculated for each prey category as

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

where F is the frequency of occurrence, N is the prey number, and M is the prey mass. The resulting IRI value indicates ‘importance’ for each prey category (West et al. 2003) while reducing potential bias of ‘rare and large’ or ‘small and abundant’ prey (Liao et al. 2001). The IRI value was then scaled as a percentage to allow for comparisons among predators and lake types, and 95% confidence intervals were calculated using bootstrapping methods in the boot package (Canty and Ripley 2021).

In addition to quantifying diet patterns, diet overlap among piscivores was calculated using Pianka’s (1974) index of niche overlap. Overlap was calculated as

$$O_{ij} = \frac{\sum_i^n P_{ij} \, P_{ik}}{\sqrt{\sum_i^n {P_{ij}}^2 \sum_i^n {P_{ik}}^2}}$$

where P_{ij} is the average proportion of prey type i in the diets of species j, P_{ik} is the average proportion of prey type i in the diets of species k, and n is the total number of prey types observed in the diets of both species (Pianka 1974; Kelling et al. 2016). A separate calculation was used for each different pairing of piscivores in each lake, resulting in index values between 0 and 1 for each pair. Each calculation was bootstrapped 1000 times to provide 95% confidence intervals using the pgirmess package (Giraudoux 2021). Index values greater than 0.75 indicated high diet overlap, whereas values less than 0.40 indicated low overlap (Matthews et al. 1982; Ross 1986; Kelling et al. 2016). Finally, non-parametric multi-dimensional scaling (NMDS) ordinations were used to visualize niche size and overlap among piscivores in each prey category. All piscivores with at least one diet item were included in the ordinations, which used the number of prey items (N) consumed from each prey category. Ordination plots displayed the centroid and 95% confidence interval for each predator species and were constructed using the vegan (Oksanen et al. 2020) and ellipse (Murdoch and Chow 2020) packages.

Results

Stomach contents were collected from 166 Muskellunge (285-1341 mm TL), 741 Northern Pike (144-1065 mm TL), 846 Walleye (132-770 mm TL), and 801 Largemouth Bass (104-510 mm TL) from eight Minnesota lakes. Prey items representing 29 prey categories (Table 2) were obtained from stomachs of 105 Muskellunge (63.2%), 381 Northern Pike (51.5%), 438 Walleye (51.9%), and 434 Largemouth Bass (54.4%), with up to 101 individual prey items present in a single stomach. Fish and aquatic invertebrates were by far the most important prey groups in each lake category (Figure 4); however, other organisms consumed include frogs (family Ranidae), muskrats *Ondatra zibethicus*, a ring-billed gull *Larus delawarensis*, and one mallard *Anas platyrhynchos* duckling. Relative importance of prey categories was similar between the most frequently used gears for Muskellunge, Northern Pike, and Walleye (Figure 5). Contributions of other gear types were minor and considered negligible. Similarly, other gears were rarely used to capture Largemouth Bass and any difference among gear types was considered negligible.

Quantification of Piscivore Diets

In BP lakes, Yellow Perch were the dominant prey species for Muskellunge (62.34% IRI). Other important prey categories include *Micropterus* spp. (9.18%), White Sucker (8.53%), and unidentifiable fish (8.23%). Other prey items included *Ameiurus* spp. (2.85%) and aquatic invertebrates (2.25%). In MO lakes, Northern Pike were the most important Muskellunge forage (21.68% IRI), followed by *Lepomis* spp. (13.31%), *Micropterus* spp. (9.63%), Black Crappie (7.13%), and *Ameiurus* spp. (6.96%). Additionally, many Muskellunge diets in this lake category contained unidentifiable fish (36.98%).

Northern Pike diets were dominated by some combination of Yellow Perch, Black Crappie, and *Lepomis* spp. in all four lake categories. In BP lakes, the vast majority of Northern Pike diets consisted of Yellow Perch (88.39% IRI), followed by unidentifiable fish and Cisco (4.10% and 1.62%, respectively). In MO lakes, *Lepomis* spp. (62.70%) and Black Crappie (28.56%) were most important, followed by Yellow Perch (4.53%) and unidentifiable fish (2.80%). Yellow Perch (37.46%), Black Crappie (16.84%), and *Lepomis* spp. (12.45%) were once again most common in CO lakes. Other important prey categories for Northern Pike in CO lakes included Brook Stickleback *Culaea inconstans*

(11.90%), Lake Whitefish *Coregonus clupeaformis* (9.51%), and unidentifiable fish (7.31%). The same pattern continued in BA lakes, where Northern Pike diets once again consisted primarily of Yellow Perch (47.23%) and *Lepomis* spp. (41.58%).

Similar to Northern Pike, Walleye consumed predominantly Yellow Perch, *Lepomis* spp., and Black Crappie among lake types. In BP lakes, Yellow Perch (80.98% IRI) were the most important diet item. Other prey items included unidentifiable fish (10.46%), *Lepomis* spp. (3.40%), and aquatic invertebrates (2.54%). In MO lakes, *Lepomis* spp. (69.72%) were most important, followed by Black Crappie (15.06%), Yellow Perch (5.51%), unidentifiable fish (5.34%), and cyprinids (2.09%). In CO lakes, *Lepomis* spp. (34.99%) and Yellow Perch (30.49%) were key prey sources. Unidentifiable fish (17.61%) were also common, and aquatic invertebrates (10.98%) were more important for Walleye in CO lakes than in any other lake category. In BA lakes, the majority of Walleye diets once again consisted of Yellow Perch (48.02%), and *Lepomis* spp. (31.20%).

In addition to the fish that were key prey items for the other three predator species, crayfish (*Faxonius* spp.) and other aquatic invertebrates were much more important in diets of Largemouth Bass. In BP lakes crayfish (55.46% IRI) and aquatic invertebrates (29.08%) were dominant prey taxa, followed by Tadpole Madtom *Noturus gyrinus* (6.54%) and Yellow Perch (5.90%). While *Lepomis* spp. (63.51%) were most important in MO lakes, crayfish (16.38%) and aquatic invertebrates (5.32%) were also components of Largemouth Bass diets. In CO lakes, crayfish (65.70%) and aquatic invertebrates (14.08%) were the primary prey items, followed by Yellow Perch (11.56%) and unidentifiable fish (6.38%). Similar to MO lakes, *Lepomis* spp. (68.01%) were the most important prey in BA lakes. Other prey items included aquatic invertebrates (14.99%), Yellow Perch (7.23%), unidentifiable fish (3.68%), Black Crappie (3.17%), and crayfish (2.59%).

Diet Overlap

According to Pianka's index of niche overlap, diet overlap between Muskellunge and all other species was low in both BP (O_{ij}=0.07-0.26) and MO (O_{ij}=0.12-0.31) lake categories (Figure 6). Diet overlap was considered high between Northern Pike and Walleye in BP (O_{ij}=0.85), MO (O_{ij}=0.88), and BA (O_{ij}=0.86) lake categories.

Largemouth Bass displayed moderate overlap with Northern Pike and Walleye in MO (O_{ij}=0.42-0.64) and BA (O_{ij}=0.62-0.71) lake categories, while diet overlap was low among all other species pair/lake category combinations (Table 3).

NMDS ordinations indicated that the mechanism for low diet overlap between Muskellunge and the other piscivores was different in BP and MO lakes (Figure 7). In BP lakes, Muskellunge displayed a broad niche that fully encompassed the other three species. However, ellipses overlapped much less in MO lakes. Walleye and Northern Pike diets appeared similar in all lake categories, supporting the results of Pianka's index of niche overlap. Largemouth Bass diets appeared most variable in both size (breadth) and location, also supporting the results of Pianka's index.

Discussion

Quantification of Piscivore Diets

Muskellunge in this study consumed a broad range of prey. Although differences in importance of prey categories were apparent between lake treatment groups, the differences were not driven by consumption of Cisco (0.10% IRI) in BP lakes. While recent research using stable isotopes indicated Cisco were a dominant prey category in a deep Minnesota lake (Herwig et al. 2022), other previous research indicated only modest levels of Muskellunge predation on Cisco (Burri 1997; Kerr and Grant 2000). Cisco are typically found in the pelagic zone of relatively deep and clear lakes and have strict requirements for oxygen, temperature, and water quality (Scott and Crossman 1973; Jacobson et al. 2008). These habitat requirements can lead to differences in the aquatic community and available forage in lakes where Cisco are found (e.g. Cross 2018), which can cause changes in prey community composition and dominant prey species in diets. Differences in Muskellunge diets between BP and MO lakes were instead driven by the difference in importance of Yellow Perch between the lake groups. Yellow Perch dominated Muskellunge diets in BP lakes (62.34% IRI) but were largely inconsequential in MO lakes (0.77%), while Northern Pike, *Lepomis* spp., Black Crappie, and *Ameiurus* spp. were of greater importance in MO lakes. Additionally, White Sucker and *Micropterus* spp. were relatively important prey categories in both lake groups. The unspecialized foraging pattern observed in Muskellunge in Minnesota lakes, especially MO lakes, is consistent with previous findings throughout their native and introduced range (Hourston 1952; Parsons 1959; Bozek et al. 1999; Andrews et al. 2018). Furthermore, it is entirely possible that Cisco are important forage for Muskellunge in BP lakes. As noted in Burri (1997), electrofishing is an ineffective method to capture Muskellunge in the pelagic zone of lakes where predation on Cisco is much more likely to occur.

While Muskellunge consumed a wide array of prey, diets of Northern Pike and Walleye tended to be more specialized with diets consisting predominantly of some combination of Yellow Perch, Black Crappie, and *Lepomis* spp. Yellow Perch made up over 80% of the diets of each piscivore species in BP lakes, while Black Crappie and *Lepomis* spp. accounted for over 80% of their diet in MO lakes. Northern Pike and Walleye diets were more balanced in CO and BA lakes, where 66-95% of diets consisted of a combination of the three prey categories. The importance of Yellow Perch as forage for these species is well documented (Diana 1979; Liao 2001; Kaufman et al. 2009; Herbst et al. 2016), and abundant Walleye populations in inland lakes are capable of altering Yellow Perch population abundance and size structure (Forney 1974; Pierce and Tomcko 2003; Pierce et al. 2006). Consumption of laterally compressed prey (i.e. Black Crappie and *Lepomis* spp.) is also well documented in Minnesota (Anderson and Schupp 1986; Reed and Parsons 1996) and throughout the Upper Midwest (Beyerle 1971; Sammons et al. 1994; Scheibel et al. 2016). Similar to Muskellunge, Cisco did not appear to be a critical component of Northern Pike or Walleye diets in this study (IRI < 2%). Previous studies have observed predation on Cisco by both Walleye (Kaufman et al. 2009) and Northern Pike (Margenau et al. 1998), and evidence suggests that Cisco are more important for the largest individuals of a population for both species (Herwig et al. 2022). Furthermore, stable isotope analysis of Minnesota lakes indicates a shift to littoral energy sources in lakes where zebra mussels *Dreissena polymorpha* have been introduced (McEachran et al. 2018; Morrison et al. 2021). In this study, three of the five lakes with Cisco also have zebra mussels present, which could limit pelagic productivity and prey usage by Northern Pike and Walleye.

In contrast to the other predators, Largemouth Bass depended heavily on crayfish and other aquatic invertebrates for their diets, especially in the lake groups where Cisco were present (BP and CO; 80-85% IRI). While crayfish and other aquatic invertebrates were still common diet items in lakes where Cisco were absent (MO and BA lake groups; 18-22% IRI), *Lepomis* spp. were much more important components of Largemouth Bass diets in these systems (64-68%). Although several studies have indicated an ontogenetic shift to piscivory in juvenile Largemouth Bass (Olson 1996; Shoup and Broderius 2018), aquatic invertebrates remain a major diet for adults in many systems (Schindler et al. 1997; Pope et al. 2001; Becher et al. 2021). In Minnesota, preliminary stable isotope analyses indicated that Largemouth Bass occupied a lower trophic position than Walleye or Northern Pike, suggesting dependence on aquatic invertebrates for a substantial portion of their diet (Bethke and Schmalz 2020). A heavy reliance on crayfish has been documented in certain instances (Kelling et al. 2016; Nawrocki et al. 2020), and field and laboratory research suggests that Largemouth Bass select for crayfish as prey in clear water (Shoup and Lane 2015). Recent work in the Laurentian Great Lakes indicates that invasive dreissenid mussels not only increase water clarity, but also have the potential to benefit invasive rusty crayfish *Faxonius rusticus* populations (Glon et al. 2017), which could provide additional foraging options for Largemouth Bass in systems where all three exist.

Walleye are a popular sportfish throughout the Laurentian Great Lakes region (Miller 2018; OMNR 2020; Holsman and Scott 2021), and numerous studies have examined the impacts of predation on Walleye populations and stocking success (e.g. Fayram et al. 2005; Freedman et al. 2012; Grausgruber and Weber 2020, 2021). While Largemouth Bass predation on Walleye was not documented in this study, predation on Walleye was observed in Muskellunge (N=3), Northern Pike (N=12), and Walleye (N=5). However, importance of Walleye to predator diets was extremely low in all lake groups (%IRI=0-0.75). While Walleye have been documented in the stomachs of Muskellunge (Anderson 1948), numerous studies have indicated that Walleye are not a major component of Muskellunge diets (Bozek et al. 1999; Grausgruber and Weber 2020). On the other hand, small Walleye have been identified as marginally important diet items for Northern Pike, Largemouth Bass, and adult Walleye in some systems (Santucci and Wahl 1993; Liao et al. 2002, 2004; Grausgruber and Weber 2020, 2021). Nevertheless, results suggest Walleye are not an integral part of piscivore diets in the Minnesota lakes included in this study.

Diet Overlap

While previous studies have investigated the impacts of Muskellunge predation on other species of interest (e.g. Brenden et al. 2004; Koenig et al. 2015; Andrews et al. 2018), little is known about how Muskellunge diets compare to co-existing piscivores. While NMDS ordinations indicated shared use of prey sources, diet overlap between Muskellunge and other piscivores in this study was low (O_{ij}=0.07-0.31). This is likely due to the broad range of prey consumed by Muskellunge in comparison to the relatively narrow diets of the other predators. In Wisconsin, high densities of Muskellunge were indicative of lakes with naturally reproducing Walleye populations (Nate et al. 2003) and CPUE of both species was positively correlated (Fayram et al. 2005), suggesting direct competition between the two was unlikely. A similar relationship was observed in Minnesota, where White Sucker and Northern Pike were the only two species that experienced a decline in CPUE following Muskellunge stocking (Knapp et al. 2020). Furthermore, relative weight of Northern Pike increased in lakes where Muskellunge were stocked when compared to reference lakes (Knapp et al. 2020), despite increased Northern Pike CPUE and decreased relative weight in a broader analysis of all lakes throughout Minnesota (Bethke and Staples 2015). While diet overlap between Muskellunge and Northern Pike was low (O_{ij}=0.26-0.31), Northern Pike were present in Muskellunge diets in BP lakes and the most important component of Muskellunge diets in MO lakes (21.68% IRI), indicating Muskellunge may exert some amount of predatory control over Northern Pike populations in Minnesota lakes (Knapp et al. 2020).

High diet overlap between Walleye and Northern Pike was observed in BP (O_{ij}=0.85), MO (O_{ij}=0.88), and BA (O_{ij}=0.86) lakes. Interactions between these frequently co-occurring species have been well documented (Anthony and Jorgensen 1977; Johnson et al. 1977; Paul et al. 2021), and recent studies indicated they may occupy similar isotopic niches in some Minnesota lakes (Bethke and Schmalz 2020). Furthermore, interactions between Walleye and Largemouth Bass have been well documented in a variety of systems. While instances of shared habitat use appeared to be low (Schlagenhaft 1984), diet overlap between the two species can be high in reservoirs in the southern United States (Raborn et al. 2004). Results from Wisconsin suggest that diet overlap between Walleye and Largemouth Bass can be high (Repp 2012; Kelling et al. 2016), and interactions between the two species is expected to favor Largemouth Bass in many systems as water temperatures continue to increase (Hansen et al. 2017). However, results of this study indicated diet overlap between Walleye and Largemouth Bass in Minnesota lakes was relatively low (O_{ij}=0.20-0.64). This is supported by stable isotope analysis in northeast Minnesota lakes, which indicated low diet overlap between Largemouth Bass and both Walleye and Northern Pike due to a lower trophic position (Bethke and Schmalz 2020).

The apparent ability of Muskellunge to consume a broader range of prey compared to co-occurring piscivores led to low levels of diet overlap with the other piscivores and may contribute to stability of aquatic food webs (McMeans et al. 2016). This includes high consumption of prey categories considered ‘secondary’ (Yellow Perch) and ‘alternative’ (*Ameiurus* spp.) in Minnesota (MN DNR 2008) as well as other prey categories previously considered unimportant (Northern Pike, *Lepomis* spp., *Micropterus* spp.), despite the presence of ‘primary’ forage options (coregonids and catostomids). Furthermore, Walleye were not an important diet component of Muskellunge or any other piscivore in this study. This information suggests that Muskellunge can co-exist at current population densities with other piscivores in Minnesota lakes. Finally, diet overlap among all predator species tended to be lower in lakes where Cisco were present, despite the relative unimportance of Cisco in piscivore diets. Given recent and expected future declines in Cisco populations (Jacobson et al. 2012; Honsey et al. 2016; Renik et al. 2020), it will be critical to monitor piscivore populations and potential diet shifts in lakes where Cisco may be extirpated. This information will allow biologists to monitor prey species in systems with a variety of available forage and make management decisions to improve the health of piscivore populations.

References

Ahrenstorff, T.D., G.G. Sass, and M.R. Helmus. 2009. The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*). Hydrobiologia 623:223-233.

AVMA (American Veterinary Medical Association). 2020. AVMA guidelines for the euthanasia of animals: 2020 edition.

Anderson, L.R. 1948. Unusual items in the diet of the northern muskellunge (*Esox masquinongy immaculatus*). Copeia 1948:63.

Anderson, D.W., and D.H. Schupp. 1986. Fish community responses to northern pike stocking in Horeshoe Lake, Minnesota. Minnesota Department of Natural Resources Investigational Report 387.

Andrews, S.N., K. Zelman, T. Ellis, T. Linnansaari, and R.A. Curry. 2018. Diet of striped bass and muskellunge downstream of a large hydroelectric dam: A preliminary investigation into suspected atlantic salmon smolt predation. North American Journal of Fisheries Management 38:734-746.

Anthony, D.D., and C.R. Jorgensen. 1977. Factors in the declining contributions of walleye (*Stizostedion vitreum vitreum*) to the fishery of Lake Nipissing, Ontario, 1960-76. Journal of Fisheries Research Board of Canada 34:1703-1709.

Beaudoin, C.P., W.M. Tonn, E.E. Prepas, and L.I. Wassenaar. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. Oecologia 120:386-396.

Becher, C., S.M. Tyszko, R.D. Zweifel, J.D. Conroy, J.J. Pritt, and S.A. Ludsin. 2021. Alternative prey reduces largemouth bass predation mortality on newly stocked channel catfish fingerlings. North American Journal of Fisheries Management 41:1322-1333.

Bethke, B.J., and P.J. Schmalz. 2020. Trophic interactions and regulators of abundance of largemouth bass in northeastern Minnesota. Minnesota Department of Natural Resources Investigational Report 568.

Bethke, B.J., and D.F. Staples. 2015. Changes in relative abundance of several Minnesota fishes from 1970 to 2013. Transactions of the American Fisheries Society 144:68-80.

Beyerle, G.B. 1971. A study of two northern pike-bluegill populations. Transactions of the American Fisheries Society 1:69-73.

Bozek, M.A., T.M. Burri, and R.V. Frie. 1999. Diets of muskellunge in northern Wisconsin lakes. North American Journal of Fisheries Management 19:258-270.

Brenden, T.O., E.M. Hallerman, and B.R. Murphy. 2004. Predatory impact of muskellunge on New River, Virginia, smallmouth bass. Proceedings of the 2004 Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 58:12-22.

Burri, T.M. 1997. Food habits of muskellunge in Wisconsin. Master's thesis. University of Wisconsin-Stevens Point, Stevens Point, WI, USA

Canty, A., and B. Ripley. 2021. boot: Bootstrap R (S-Plus) functions. R package version 1.3-28.

Chapman, L.J., W.M. Mackay, and C.W. Wilkinson. 1989. Feeding flexibility in northern pike (*Esox lucius*): Fish versus invertebrate prey. Canadian Journal of Fisheries and Aquatic Sciences 46:666-669.

Cross, T.K. 2018. Large-scale habitat factors affecting fish populations in Minnesota lakes and a proposed habitat classification. Minnesota Department of Natural Resources Investigational Report 562.

Crossman, E.J., and J.G. Hamilton. 1978. An apparatus for sampling gut contents of large, living fishes. Environmental Biology of Fishes 3:297-300.

Diana, J.S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). Canadian Journal of Zoology 57:2121-2127.

Dibble, E.D., and S.L. Harrel. 1997. Largemouth bass diets in two aquatic plant communities. Journal of Aquatic Plant Management 35:74-78.

Doss, S.S. 2017. Muskellunge of the New River, Virginia: The effects of restrictive harvest regulations on population demographics and predation on sympatric smallmouth bass. Master's Thesis. Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

Fayram, A.H., M.J. Hansen, and T.J. Ehlinger. 2005. Interactions between walleyes and four fish species with implications for walleye stocking. North American Journal of Fisheries Management 25:1321-1330.

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 103:15-24.

Foster, J.R. 1977. Pulsed gastric lavage: An efficient method of removing the stomach contents of live fish. Progressive Fish Culturist 39:166-169.

Freedman, J.A., R.J.H. Hoxmeier, L.M. Einfalt, R.C. Brooks, and D.H. Wahl. 2012. Largemouth bass predation effect on stocked walleye survival in Illinois impoundments. North American Journal of Fisheries Management 32:1039-1045.

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

Giraudoux, P. 2021. pgirmess: Spatial analysis and data mining for field ecologists. R package version 1.7.0.

Glon, M.G., E.R. Larson, L.S. Reisinger, and K.L. Pangle. 2017. Invasive dreissenid mussels benefit invasive crayfish but not native crayfish in the Laurentian Great Lakes. Journal of Great Lakes Research 43:289-297.

Grausgruber, E.E., and M.J. Weber. 2020. Is bigger better? Evaluation of size-selective predation on age-0 walleye. North American Journal of Fisheries Management 40:726-732.

Grausgruber, E.E., and M.J. Weber. 2021. Using bioenergetics to estimate consumption of stocked age-0 walleye by a suite of piscivores. North American Journal of Fisheries Management 41:383-398.

Hansen, G.J.A., J.S. Read, J.F. Hansen, and L.A. Winslow. 2017. Projected shifts in fish species dominance in Wisconsin lakes under climate change. Global Change Biology 23:1463-1476.

Hartman, K.J., and F.J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. Transactions of the American Fisheries Society 121:245-260.

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: 319-333.

Herwig, B.R., M.A. Hanson, J.R. Reed, B.G. Parsons, A.J. Potthoff, M.C. Ward, K.D. Zimmer, M.G. Butler, D.W. Willis, and V.A. Snook. 2004. Walleye stocking as a tool to suppress fathead minnows and improve habitat quality in semipermanent and permanent wetlands in the prairie pothole region of Minnesota. Minnesota Department of Natural Resources Special Publication 159.

Herwig, B.R., K.D. Zimmer, D.F. Staples. 2022. Using stable isotope data to quantify niche overlap and diets of muskellunge, northern pike and walleye in a deep Minnesota lake. Ecology of Freshwater Fish 31:60-71.

Hodgson, J.R., and E.M. Hansen. 2005. Terrestrial prey items in the diet of largemouth bass, *Micropterus salmoides*, in a small north temperate lake. Journal of Freshwater Ecology 20:793-794.

Hodgson, J.R., and J.F. Kitchell. 1987. Opportunistic foraging by largemouth bass (*Micropterus salmoides)*. American Midland Naturalist 118:323-336.

Holsman, R., and A. Scott. 2021. Angler opinions about walleye fishing and management in Wisconsin. Wisconsin Department of Natural Resources Fisheries Management Report no. 159.

Hourston, A.S. 1952. The food and growth of the maskinonge (*Esox masquinongy*) in Canada waters. Journal of the Fisheries Research Board of Canada 8:347-368.

Jacobson, P.C. 1992. Analysis of factors affecting growth of northern pike in Minnesota. Minnesota Department of Natural Resources Investigational Report 424.

Jacobson, P.C. 1994. Population dynamics of large walleye in Big Sand Lake. Minnesota Department of Natural Resources Investigational Report 436.

Jacobson, P.C., T.K. Cross, J. Zandlo, B.N. Carlson, and D.P. Pereira. 2012. The effects of climate change and eutrophication on cisco *Coregonus artedi* abundance in Minnesota lakes. Advances in Limnology 63:417-427.

Jacobson, P.C., T.S. Jones, P. Rivers, D.L. Pereira. 2008. Field estimation of a lethal oxythermal niche boundary for adult ciscoes in Minnesota lakes. Transactions of the American Fisheries Society 137:1464-1474.

Johnson, M.G., J.H. Leach, C.K. Minns, and C.H. Olver. 1977. Limnological characteristics of Ontario lakes in relation to associations of walleye (*Stizostedion vitreum vitreum*), northern pike (*Esox lucius*), lake trout (*Salvelinus namaycush*), and smallmouth bass (*Micropterus dolomieui*). Journal of Fisheries Research Board of Canada 34:1592-1601.

Kamler, J.F., and K.L. Pope. 2001. Nonlethal methods of examining fish stomach contents. Reviews in Fisheries Science 9:1-11.

Kapuscinski, K.L., J.M. Farrell, and B.A. Murry. 2012. Feeding strategies and diets of young-of-the-year muskellunge from two large river ecosystems. North American Journal of Fisheries Management 32:635-647.

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

Kelling, C.J. 2014. Largemouth bass in Wisconsin: Dietary interactions with walleyes and factors regulating first-year growth and diet. Master’s thesis. University of Wisconsin-Stevens Point, Stevens Point, WI, USA.

Kelling, C.J., D.A. Isermann, B.L. Sloss, and K.N. Turnquist. 2016. Diet overlap and predation between largemouth bass and walleye in Wisconsin lakes using DNA barcoding to improve taxonomic resolution. North American Journal of Fisheries Management 36:621-629.

Kennedy, P.J., T.J. Bartley, D.M. Gillis, K.S. McCann, and M.D. Rennie. 2018. Offshore prey densities facilitate similar life history and behavioral patterns in two distinct aquatic apex predators, northern pike and lake trout. Transactions of the American Fisheries Society 147:972-995.

Kerr, S.J. 2011. Distribution and management of muskellunge in North America: An overview. Fisheries Policy Section, Biodiversity Branch. Ontario Ministry of Natural Resources.

Kerr, S.J. 2016. Feeding habits and diet of the muskellunge (*Esox masquinongy*): A review of potential impacts on resident biota. Report prepared for Muskies Canada Inc. and the Ontario Ministry of Natural Resources and Forestry.

Kerr, S.J., and R.E. Grant. 2000. Ecological impacts of fish introductions: Evaluating the risk. Fish and Wildlife Branch, Ontario Ministry of Natural Resources.

Knapp, M.L., S.W. Mero, D.J. Bohlander, D.F. Staples, and J.A. Younk. 2012. Fish community responses to the introduction of muskellunge in Minnesota lakes. North American Journal of Fisheries Management 32:191-201.

Knapp, M.L., S.W. Mero, and D.F. Staples. 2020. Are muskellunge affecting fish communities in waters where they have been introduced? A re-examination of Minnesota’s stocked muskellunge waters. North American Journal of Fisheries Management 41:229-241.

Knight, R.L. and B. Vondracek. 1993. Changes in prey fish populations in western Lake Erie, 1969-88, as related to walleye, *Stizostedion vitreum*, predation. Canadian Journal of Fisheries and Aquatic Science 50:1289-1298.

Koenig, M.K., K.A. Meyer, J.R. Kozfkay, J.M. DuPont, and E.B. Schriever. 2015. Evaluating the ability of tiger muskellunge to eradicate brook trout in Idaho alpine lakes. North American Journal of Fisheries Management 35:659-670.

Krska, R.J., and R.L. Applegate. 1982. Food of young muskellunge in a power plant cooling reservoir. Progressive Fish Culturist 44:172-173.

Lawler, G.H. 1965. The food of the pike, *Esox lucius,* in Heming Lake, Manitoba. Journal of Fisheries Research Board of Canada 22:1357-1377.

Liao, L. 2001. Assessment of diet and consumption dynamics of the adult piscivorous fish community in Spirit Lake, Iowa. Doctoral dissertation. Iowa State University, Ames, Iowa, USA.

Liao, L., C.L. Pierce, and J.G. Larscheid. 2001. Empirical assessment of indices of prey importance in the diets of predacious fish. Transactions of the American Fisheries Society 130:583-591.

Liao, H., C.L. Pierce, and J.G. Larscheid. 2002. Diet dynamics of the adult piscivorous fish community in Spirit Lake, Iowa, USA 1995-1997. Ecology of Freshwater Fish 11:178-189.

Liao, H., C.L. Pierce, and J.G. Larscheid. 2004. Consumption dynamics of the adult piscivorous fish community in Spirit Lake, Iowa. North American Journal of Fisheries Management 24:890-902.

Mann, R.H.K. 1982. The annual food consumption and prey preferences of pike (*Esox lucius*) in the River Frome, Dorset. Journal of Animal Ecology 51:81-95.

Margenau, T.L., P.W. Rasmussen, and J.M. Kampa. 1998. Factors affecting growth of northern pike in small northern Wisconsin lakes. North American Journal of Fisheries Management 18:625-639.

Martin, G.R., L.E. Twigg, and D.J. Robinson. 1996. Comparison of the diet of feral cats from rural and pastoral Western Australia. Wildlife Research 23:475-484.

Matthews, W.J., J.R. Bek, and R. Surat. 1982. Comparative ecology of the darters *Etheostoma podostemone, E. Flabellare* and *Percina roanoka* in the Upper Roanoke River Drainage, Virginia. Copeia 1982:805-814.

McEachran, M.C., R.S. Trapp, K.D. Zimmer, B.R. Herwig, C.E. Hegedus, C.E. Herzog, and D.F. Staples. 2018. Stable isotopes indicate that zebra mussels (*Dreissena polymorpha*) increase dependence of lake food webs on littoral energy sources. Freshwater Biology 64:183-196.

McMahon, T.E., and D.H. Bennett. 1996. Walleye and northern pike: Boost or bane to northwest fisheries? Fisheries 21:6-13.

McMeans, B.C., K.S. McCann, T.D. Tunney, A.T. Fisk, A.M. Muir, N. Lester, B. Shuter, and N. Rooney. 2016. The adaptive capacity of lake food webs: From individuals to ecosystems. Ecological Monographs 86:4-19.

Miller, H.M. 2018. Fishing in Minnesota: A study of angler participation and activities. U.S. Geological Survey. Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology.

Miranda, L.E., and L.L. Pugh. 1997. Relationship between vegetation coverage and abundance, size, and diet of juvenile largemouth bass during winter. North American Journal of Fisheries Management 17:601-610.

MN DNR (Minnesota Department of Natural Resources). 2008. Long range plan for muskellunge and large northern pike management through 2020. Minnesota Department of Natural Resources, Division of Fish and Wildlife.

MN DNR (Minnesota Department of Natural Resources). 2016. Minnesota’s managed muskellunge waters. Minnesota Department of Natural Resources, Division of Fish and Wildlife.

Morrison, A.L., M.A. Thelen, S.E. Howe, K.D. Zimmer, B.R. Herwig, D.F. Staples, and M.C. McEachran. 2021. Impacts of zebra mussels (*Dreissena polymorpha*) on isotopic niche size and niche overlap among fish species in a mesotrophic lake. Biological Invasions 23:2985-3002.

Murdoch, D., and E.D. Chow. 2020. ellipse: Functions for drawing ellipses and ellipse-like confidence regions. R package version 0.4.2.

Nate, N.A., M.A. Bozek, M.J. Hansen, C.W. Ramm, M.T. Bremigan, S.W. Hewett. 2003. Predicting the occurrence and success of walleye populations from physical and biological features of northern Wisconsin lakes. North American Journal of Fisheries Management 23:1207-1214.

Nawrocki, B., A.M. McLeod, N.E. Hussey, S.F. Colborne, J. Del Papa, A.T. Fisk. 2020. Assessing trophic position quantification methods for three piscivorous freshwater fish using stable isotopes and stomach contents. Journal of Great Lakes Research 46:578-588.

Oehmcke, A.A., L. Johnson, J. Klingbiel, and C. Wistrom. 1958. The Wisconsin muskellunge; Its life history, ecology, and management. Wisconsin Department of Natural Resources Publication 225.

Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P.R. Minchin, R.B. O'Hara, G.L. Simpson, P. Solymos, M.H.H. Stevens, E. Szoecs, and H. Wagner. 2020. vegan: Community ecology package. R package version 2.5-7.

Olson, N.W. 2004. Interactions among hybrid striped bass, white bass, and walleye in Harlan County Reservoir. Master's thesis. Montana State University, Bozeman, Montana, USA.

OMNR (Ontario Ministry of Natural Resources and Forestry). 2020. 2015 survey of recreational fishing in Canada: Results for fisheries management zones of Ontario. Ontario Ministry of Natural Resources and Forestry Technical Report.

Paul, A.J., C.L. Cahill, L. MacPherson, M.G. Sullivan, and M.R. Brown. 2021. Are Alberta's northern pike populations at risk from walleye recovery? North American Journal of Fisheries Management 41:399-409.

Parsons, J.W. 1959. Muskellunge in Tennessee streams. Transactions of the American Fisheries Society 88:136-140.

Pianka, E.R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Sciences of the USA 71:2141-2145.

Pierce, R.B., and C.M. Tomcko. 2003. Effects of walleye stocking on the fish community of Lake Thirteen. Minnesota Department of Natural Resources Investigational Report 505.

Pierce, R.B., C.M. Tomcko, and M.T. Drake. 2003. Population dynamics, trophic interactions, and production of northern pike in a shallow bog lake and their effects on simulated regulation strategies. North American Journal of Fisheries Management 23:323-330.

Pierce, R.B., C.M. Tomcko, and M.T. Negus. 2006. Interactions between stocked walleyes and native yellow perch in Lake Thirteen, Minnesota: A case history of percid community dynamics. North American Journal of Fisheries Management 26:97-107.

Pinkas, L., M.S. Oliphant, and I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in Californian waters. Fisheries Bulletin 152:11-105.

Pope, K.L., M.L. Brown, W.G. Duffy, and P.H. Michaletz. 2001. A caloric-based evaluation of diet indices for largemouth bass. Environmental Biology of Fishes 61:329-339.

Porath, M.T., and E.J. Peters. 1997. Walleye prey selection in Lake McConaughy, Nebrasky: A comparison between stomach content analysis and feeding experiments. Journal of Freshwater Ecology 12:511-520.

Pothoven, S.A., B. Vondracek, and D.L. Pereira. 1999. Effects of vegetation removal on bluegill and largemouth bass in two Minnesota lakes. North American Journal of Fisheries Management 19:748-757.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Raborn, S.W., L.E. Miranda, and M.T. Driscoll. 2004. Diet overlap and consumption patterns suggest seasonal flux in the likelihood for exploitative competition among piscivorous fishes. Ecology of Freshwater Fish 13:276-284.

Reed, J.R., and B.G. Parsons. 1996. Observations of predation on small bluegill in a Minnesota centrarchid lake. Minnesota Department of Natural Resources Investigational Report 452.

Renik, K.M., M.J. Jennings, J.M. Kampa, J. Lyons, T.P. Parks, and G.G. Sass. 2020. Status and distribution of cisco (*Coregonus artedi*) and lake whitefish (*Coregonus clupeaformis*) in inland lakes of Wisconsin. Northeaster Naturalist 27:469-484.

Repp, A.J. 2012. Investigating interactions between walleye and black bass in northern Wisconsin lakes. Master's thesis. University of Wisconsin-Stevens Point, Stevens Point, Wisconsin, USA.

Ross, S.T. 1986. Resource partitioning in fish assemblages: A review of field studies. Copeia 1986:352-388.

Ross, R.M., J.H. Johnson, and C.M. Adams. 2005. Use of fish—otolith-length regressions to infer size of double-crested cormorant prey fish from recovered otoliths in Lake Ontario. Northeastern Naturalist 12:133-140.

Rypel, A.L. 2008. An inexpensive image analysis system for fish otoliths. North American Journal of Fisheries Management 28:193-197.

Sammons, S.M., C.G. Scalet, and R.M. Neumann. 1994. Seasonal and size-related changes in the diet of northern pike from a shallow prairie lake. Journal of Freshwater Ecology 9:321-329.

Santucci, V.J. Jr., and D.H. Wahl. 1993. Factors influencing survival and growth of stocked walleye (Stizostedion vitreum) in a centrarchid-dominated impoundment. Canadian Journal of Fisheries and Aquatic Science 50:1548-1558.

Sass, G.G., S.R. Carpenter, J.W. Gaeta, J.W. Kitchell, and T.D. Ahrenstorff. 2011. Whole-lake addition of coarse woody habitat: response of fish populations. Aquatic Sciences 74:255-266.

Scheibel, N.C., D.J. Dembkowski, J.L. Davis, and S.R. Chipps SR. 2016. Impacts of northern pike on stocked rainbow trout in Pactola Reservoir, South Dakota. North American Journal of Fisheries Management 36:230-240.

Schindler, D.E., J.R. Hodgson, J.F. Kitchell. 1997. Density-dependent changes in individual foraging specialization of largemouth bass. Oecologia 110:592-600.

Schlagenhaft, T.W. 1984. Interactions between walleye and largemouth bass in a west Texas reservoir. Master's thesis. Texas Tech University, Lubbock, Texas, USA.

Schroeder, S.A., D.C. Fulton, and R.A. Dodd. 2007. Managing muskie in Minnesota. U.S. Geological Survey. Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology.

Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Bulletin 184. Fisheries Research Board of Canada.

S.F. 3319. 2018. Minnesota State Senate, 90th Session.

Shoup, D.E., and C.R. Broderius. 2018. Effects of vegetation density on the ontogeny to piscivory of juvenile largemouth bass. North American Journal of Fisheries Management 38:630-638.

Shoup, D.E., and W.D. Lane. 2015. Effects of turidity on prey selection and foraging return of adult largemouth bass in reservoirs. North American Journal of Fisheries Management 35:913-924.

Siler, D.H., and G.B. Beyerle. 1986. Introduction and management of northern muskellunge in Iron Lake. Pages 257-262 *in* G. Hall, editor. Managing muskies: a treatise on the biology and propagation of muskellunge in North America. American Fisheries Society Special Publication 15, Bethesda, Maryland, USA.

Spooner, E. 2016. Muskellunge (*Esox masquinongy*) feeding habits and habitat preferences in Lake St. Clair. Master's thesis. University of Michigan, Ann Arbor, Michigan, USA.

Traynor, D., A. Moerke, R. Greil. 2010. Identification of Michigan fishes using cleithra. Great Lakes Fishery Commission Miscellaneous Publication 2010-02.

VanderBloemen, S.V., J.A. Gorne, G.G. Sass, and S.L. Shaw. 2020. Influence of cisco (*Coregonus artedi*, Lesueur) on muskellunge (*Esox masquinongy*, Mitchill) mean length, population size structure, and maximum size in northern Wisconsin lakes. Journal of Applied Ichthyology 36:159-167.

Venturelli, P.A., and W.M. Tonn. 2006. Diet and growth of northern pike in the absence of prey fishes: Initial consequences for persisting in disturbance-prone lakes. Transactions of the American Fisheries Society 135:1512-1522.

Wahl, D.H., and R.A. Stein. 1988. Selective predation by three esocids: The role of prey behavior and morphology. Transactions of the American Fisheries Society 117:142-151.

Wahl, D.H., and R.A. Stein. 1991. Food consumption and growth of three esocids: Field test of a bioenergetic model. Transactions of the American Fisheries Society 120:230-246.

Walrath, J.D., M.C. Quist, J.A. Firehammer. 2015. Trophic ecology of nonnative northern pike and their effect on conservation of native westslope cutthroat trout. North American Journal of Fisheries Management 35:158-177.

Ward, M.C., D.W. Willis, B.R. Herwig, S.R. Chipps, B.G. Parsons, J.R. Reed, and M.A. Hanson. 2008. Consumption estimates of walleye stocked as fry to suppress fathead minnow populations in west-central Minnesota wetlands. Ecology of Freshwater Fish 17:59-70.

West, J.M., G.D. Williams, S.P. Madon, and J.B. Zedler. 2003. Integrating spatial and temporal variability into the analysis of fish food web linkages in Tijuana Estuary. Environmental Biology of Fishes 67:297-309.

Wolter, M.H., C.S. DeBoom, C.P. Wagner, M.J. Diana, and D.H. Wahl. 2012. Evaluation of growth and survival of different genetic stocks of muskellunge: Implications for stocking programs in Illinois and the Midwest. Illinois Natural History Survey Technical Report 2012-33.

Woomer, A., R. Lorantas, and B. Ensign. 2012. Plan for management of muskellunge in Pennsylvania. Pennsylvania Fish and Boat Commission, Division of Fisheries Management.

Zimmerman, M.P. 1999. Food habits of smallmouth bass, walleyes, and northern pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. Transactions of the American Fisheries Society 128:1036-1054.

TABLES

Table 1. Surface area (ha), maximum depth (m), and lake group, as well as total sample sizes (*N*) and mean TLs (mm) with SDs (in parentheses) for Muskellunge, Northern Pike, Walleye, and Largemouth Bass collected in 2019 and 2020. Lakes are in one of four treatment groups: Muskellunge and Cisco Present (BP), Muskellunge present/Cisco absent (MO), Muskellunge absent/Cisco present (CO), Muskellunge and Cisco absent (BA).

					Muskellunge		Northern Pike		Walleye		Largemouth Bass	
Year	Lake	Area (ha)	Maximum depth (m)	Lake group	*N*	Mean TL	*N*	Mean TL	*N*	Mean TL	*N*	Mean TL
2019	Little Boy	588	23	BP	31	959 (194)	114	581 (126)	138	409 (131)	53	380 (51)
2019	Miltona	2316	32	BP	61	1043 (222)	85	588 (127)	116	471 (108)	118	307 (79)
2019	Bald Eagle	425	11	MO	74	1053 (147)	135	632 (131)	100	370 (118)	139	308 (78)
2019	Ten Mile	2056	63	CO	--	--	68	568 (177)	107	510 (100)	118	320 (70)
2019	South Center	338	33	BA	--	--	72	633 (113)	98	460 (134)	171	322 (94)
2020	Bemidji	2669	23	BP	--	--	97	608 (135)	98	444 (91)	6	440 (42)
2020	Deer	121	13	CO	--	--	64	601 (122)	74	387 (141)	94	376 (61)
2020	Grace	348	13	BA	--	--	106	609 (69)	115	396 (112)	102	352 (100)

Table 2. Common names and abbreviations used to represent 29 prey categories observed in diets of Muskellunge, Northern Pike, Walleye, and Largemouth Bass in Minnesota Lakes.

Prey category	**Abbreviation**
Amphibian	AMPH
Banded Killifish	BKF
Bird	BIRD
Black Crappie	BLC
Bowfin	BOF
Brook Silverside	BKS
Brook Stickleback	BST
Bullhead	BLH
Central Mudminnow	CNM
Cisco	TLC
Crayfish	CRAY
Cyprinidae	OTM
Darter	DAR
Invertebrates	INV
Lake Whitefish	LKW
Mammals	MAM
Micropterus spp.	MIC
Muskellunge	MUE
Northern Pike	NOP
Rock Bass	RKB
Sculpin	SCU
Sunfish	SUN
Tadpole Madtom	TPM
Trout-perch	TRP
Turtle	TUR
Unidentified fish	UNK
Walleye	WAE
White Sucker	WTS
Yellow Perch	YEP

Table 3. Pianka's index of niche overlap for predator species pairs in different lake groups.

Predators	BP Lakes	MO Lakes	CO Lakes	BA Lakes
Muskellunge – Northern Pike	0.255-	0.308-	N/A	N/A
Muskellunge - Walleye	0.264-	0.257-	N/A	N/A
Muskellunge – Largemouth Bass	0.066-	0.118-	N/A	N/A
Northern Pike - Walleye	0.847+	0.877+	0.336-	0.860+
Northern Pike – Largemouth Bass	0.268-	0.424	0.037-	0.707
Walleye – Largemouth Bass	0.119-	0.637	0.203-	0.621

- low diet overlap

+ high diet overlap

FIGURES

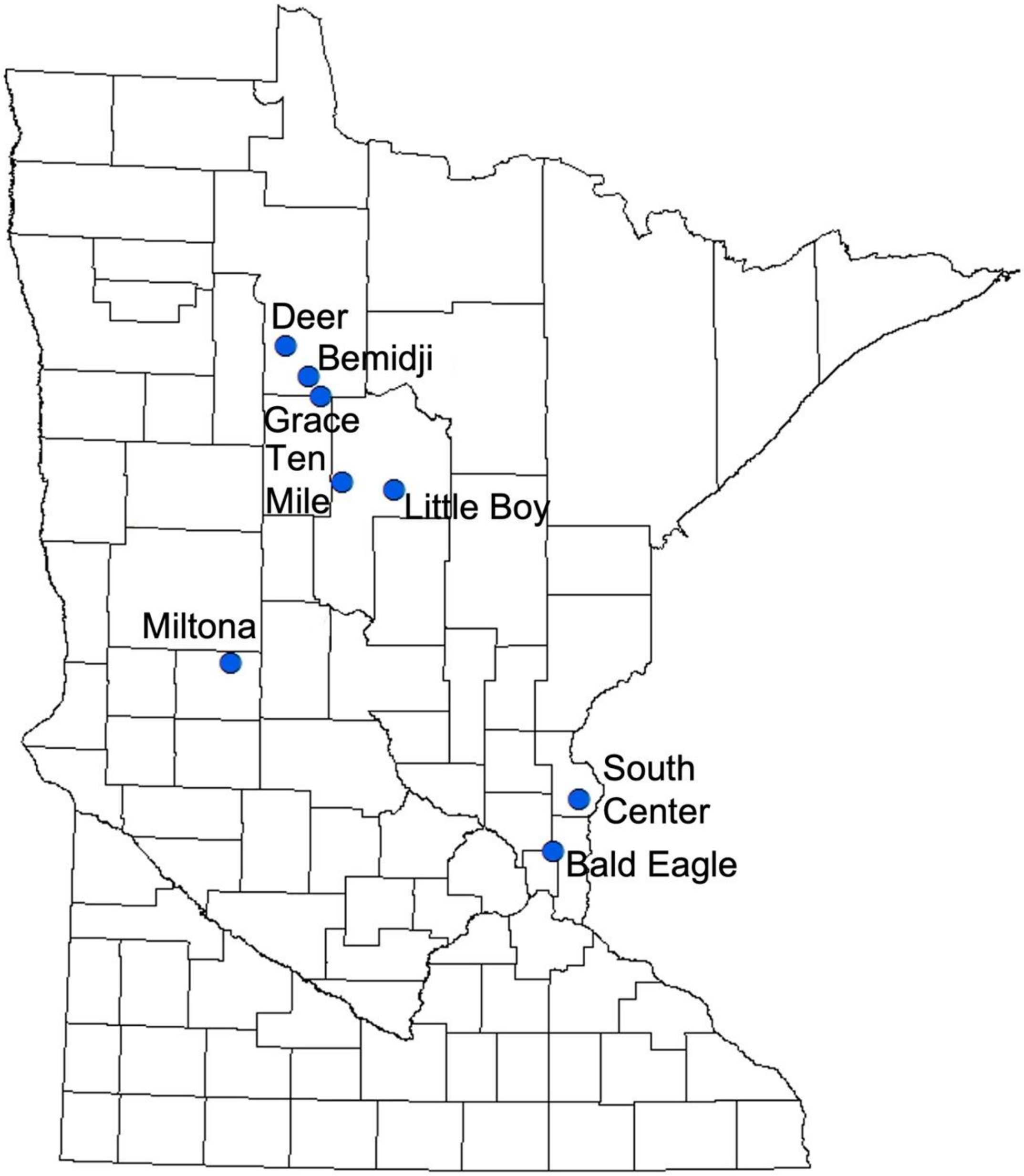

Figure 1. Map of Minnesota showing the locations of eight study lakes where piscivore stomach contents were collected.

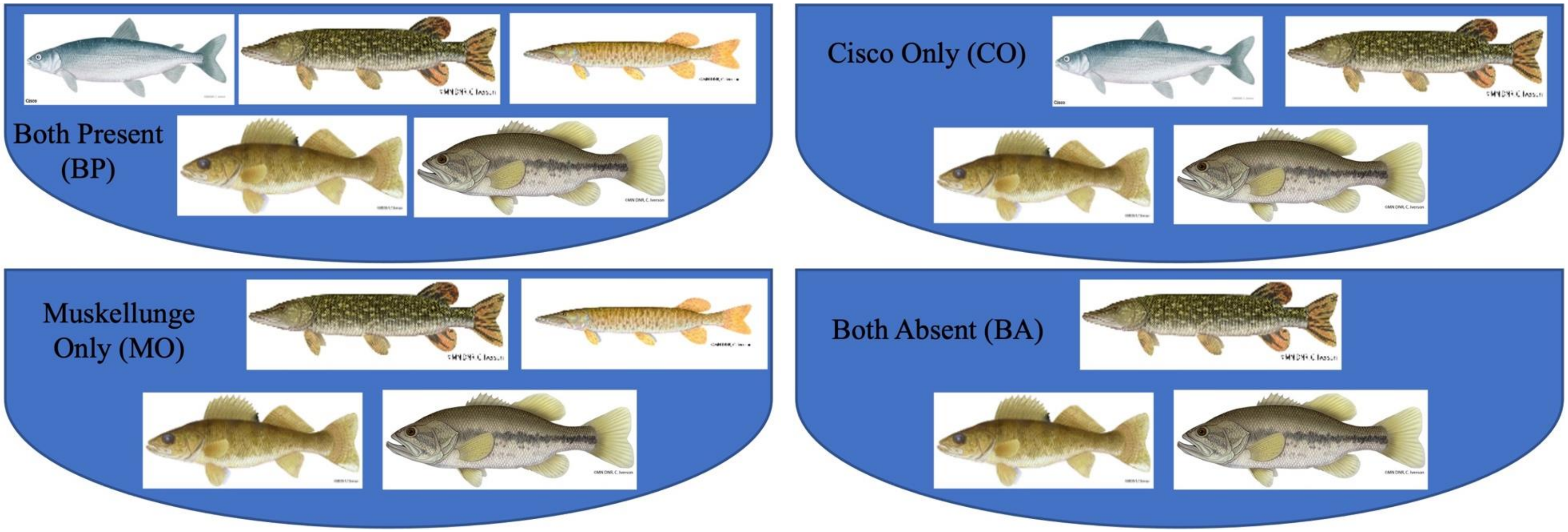

Figure 2. Experimental design where Muskellunge (present/absent) is crossed with Cisco (present/absent).

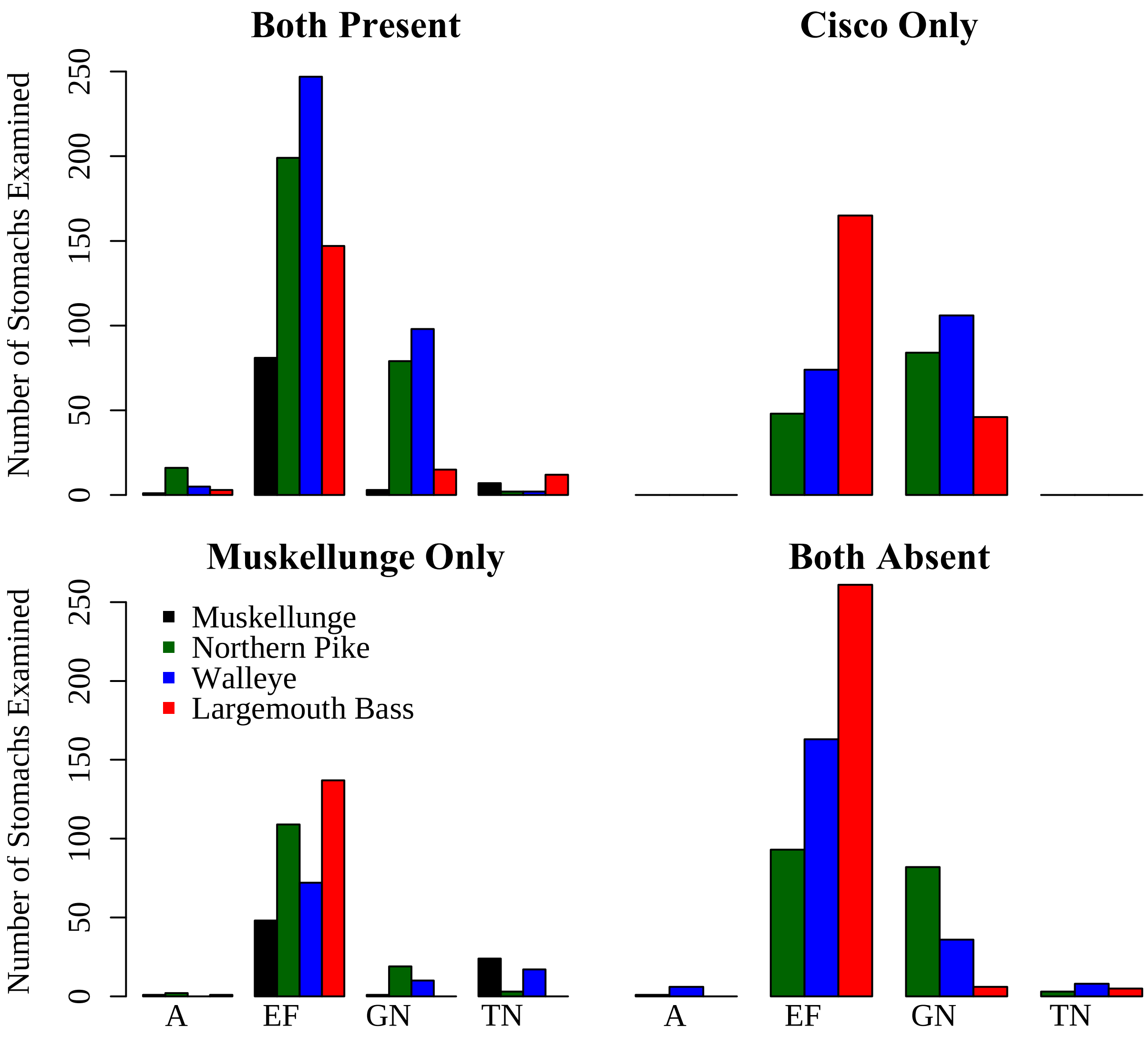

Figure 3. Number of stomachs examined from fish collected via angling (A), electrofishing (EF), gill nets (GN), and trap nets (TN).

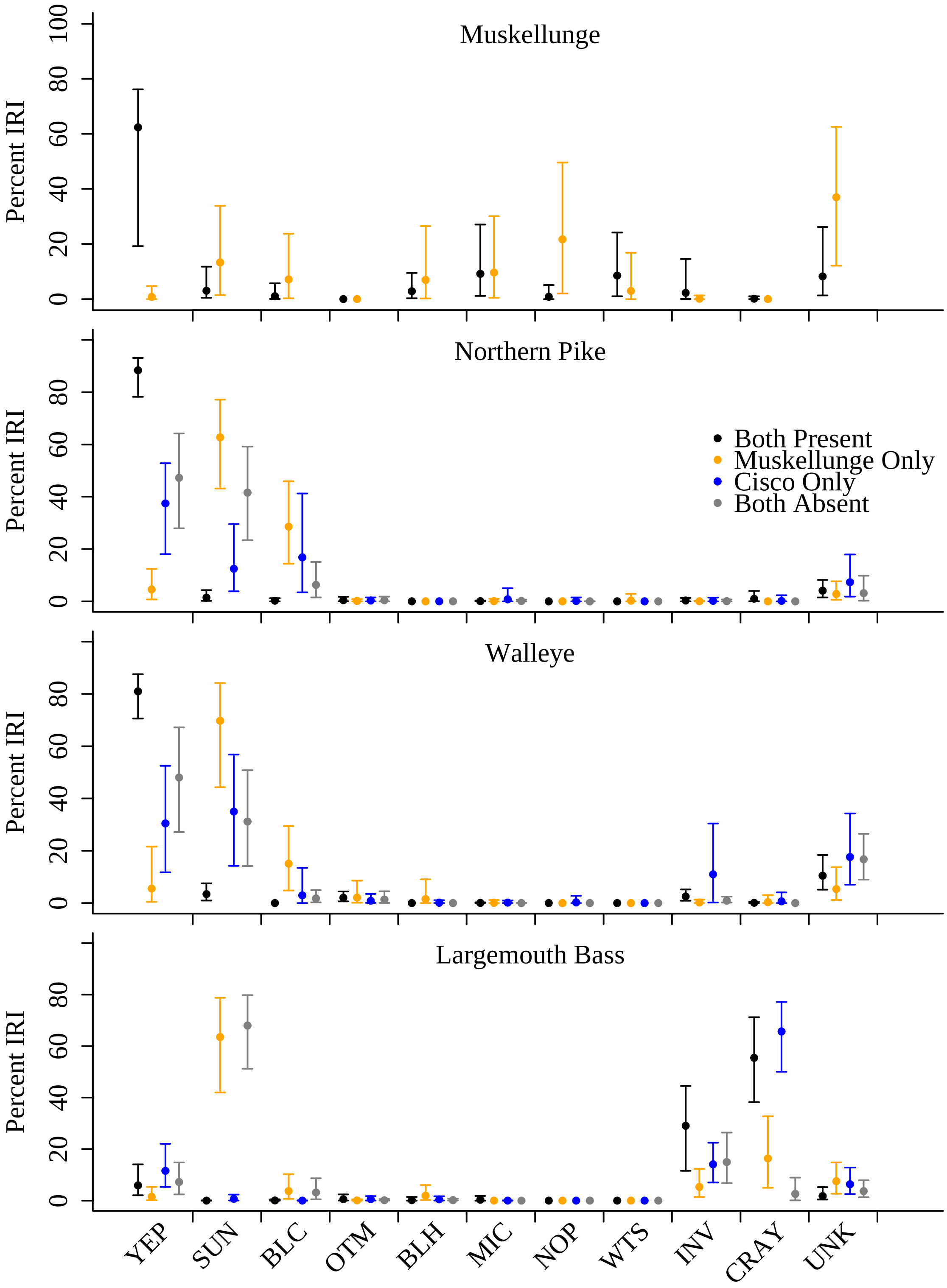

Figure 4. Percent Index of Relative Importance (IRI) values for common prey categories in piscivore diets. Error bars represent 95% confidence intervals calculated using bootstrapping methods.

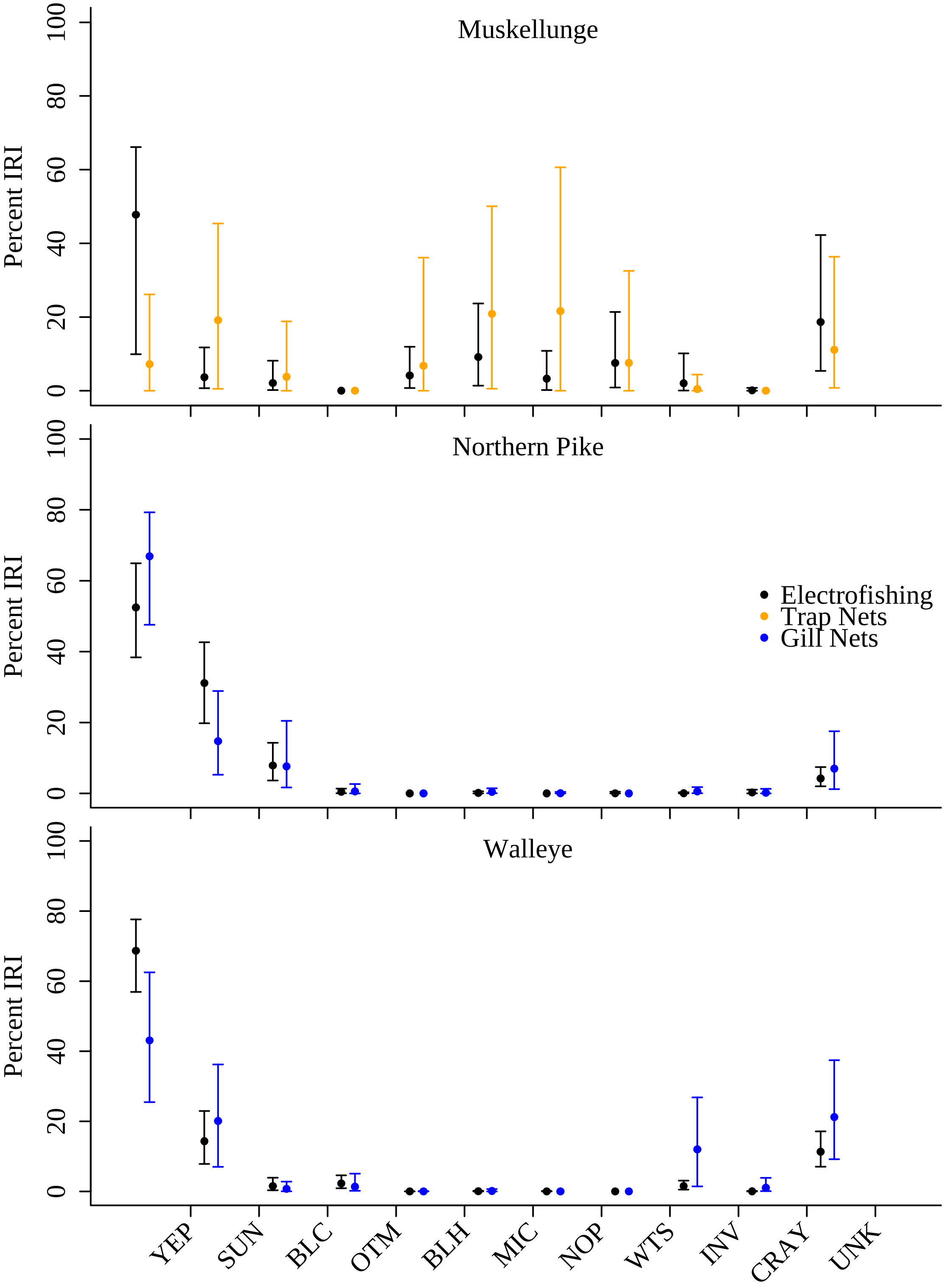

Figure 5. Percent Index of Relative Importance (IRI) values for common prey categories in piscivore diets compared across most common gears. Error bars represent 95% confidence intervals calculated using bootstrapping methods.

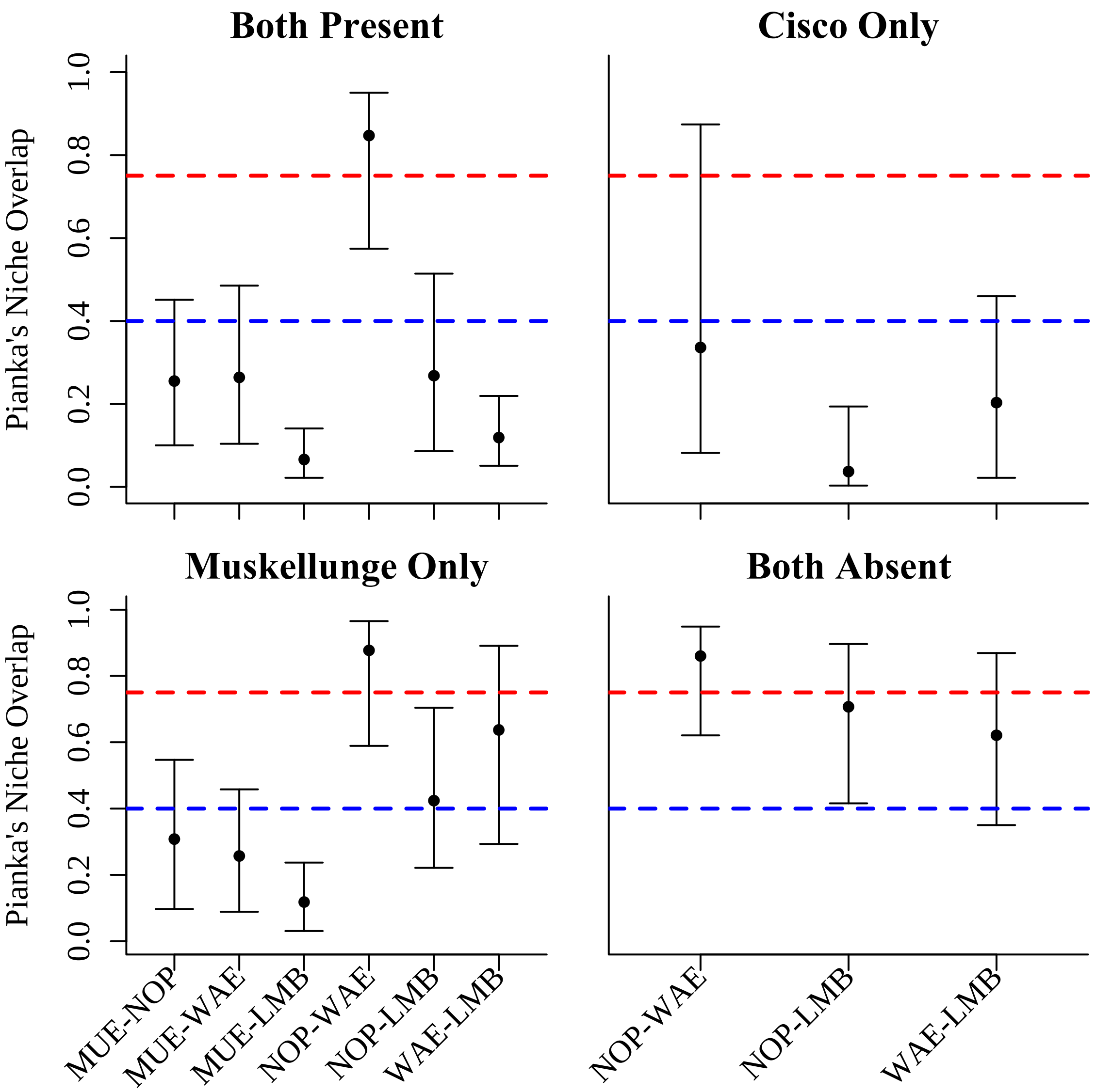

Figure 6. Pianka’s index of niche overlap for Muskellunge (MUE), Northern Pike (NOP), Walleye (WAE), and Largemouth Bass (LMB) collected from eight Minnesota lakes in 2019-2020. Error bars represent 95% confidence intervals calculated by bootstrapping method. Horizontal lines at 0.75 (red) and 0.40 (blue) represent high and low diet overlap, respectively, following the methods of Kelling et al. (2016).

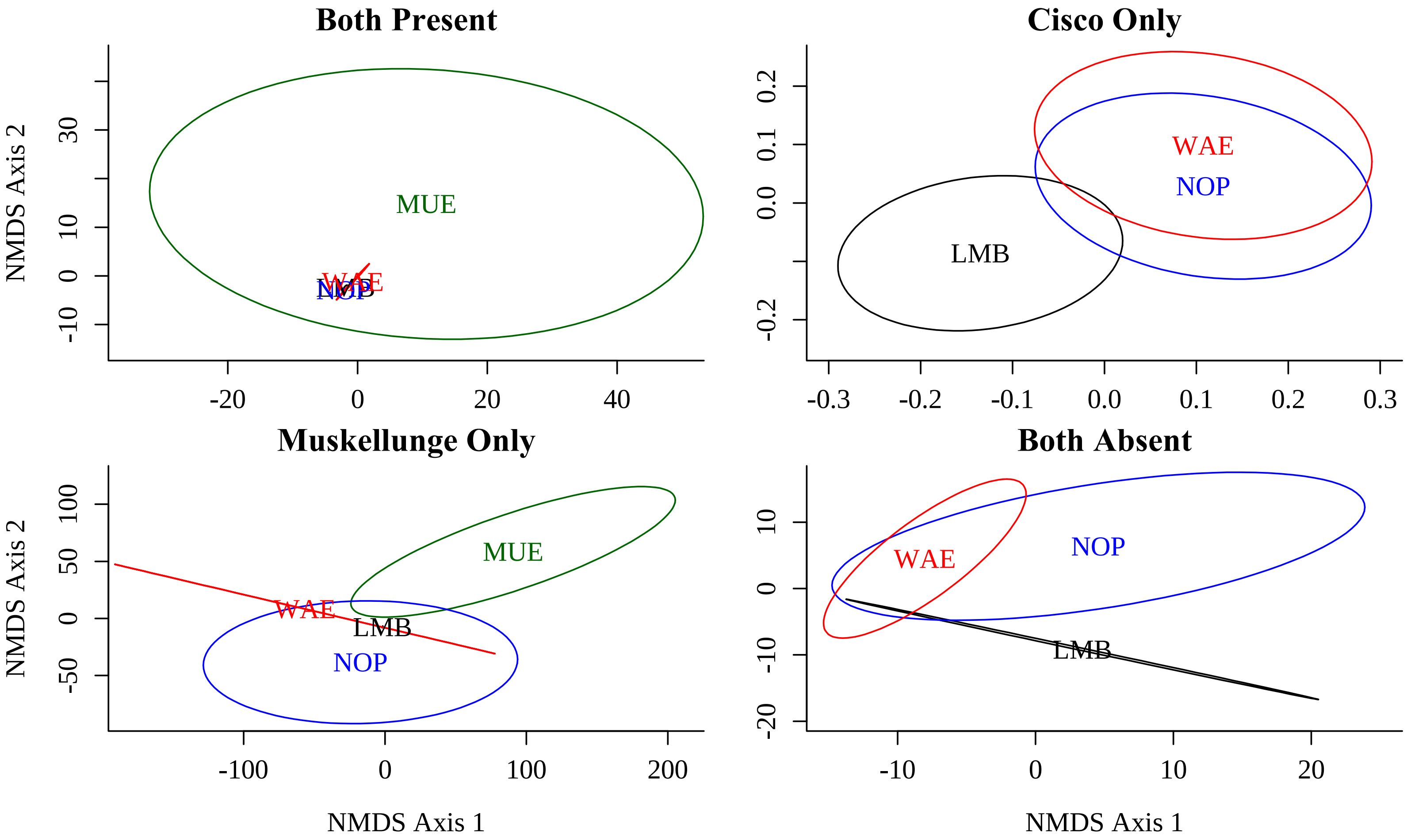

Figure 7. Non-metric multi-dimensional scaling (NMDS) ordinations based on number of items in each prey category for Muskellunge (MUE), Northern Pike (NOP), Walleye (WAE), and Largemouth Bass (LMB). Species codes represent the centroid of each species diet, and ellipses represent 95% confidence intervals.

APPENDIX A

Appendix A. Prey category, scientific name, and coefficients for equations used to estimate weight (W, g) from total length (TL, mm) for fish prey. The standard equation is: $\log_{10}W = a + b \times \log_{10}TL$

Prey category	Scientific name	*a*	*b*	Source
Banded Killifish	*Fundulus diaphanus*	-5.566	3.326	Schneider et al. 2000
Black Crappie	*Pomoxis nigromaculatus*	-5.271	3.200	Bozek et al. 1999
Bowfin	*Amia calva*	-4.899	2.960	Schneider et al. 2000
Brook Silverside	*Labidesthes sicculus*	-4.100	2.346	Miller et al. 2015
Brook Stickleback	*Culaea inconstans*	-5.000	2.932	Kapuscinski et al. 2012
Bullhead	*Ameiurus melas*	-5.257	3.097	Bozek et al. 1999
	Ameiurus natalis	-4.792	2.973	Carlander 1969
	Ameiurus nebulosus	-5.061	3.065	Carlander 1969
Central Mudminnow	*Umbra limi*	-4.848	2.925	Schneider et al. 2000
Cisco	*Coregonus artedi*	-5.304	3.073	Bozek et al. 1999
Cyprinidae	*Cyprinella spiloptera*	-5.150	3.044	Kapuscinski et al. 2012
	Notemigonus crysoleucas	-5.248	3.082	Schneider et al. 2000
	Notropis atherinoides	-5.379	3.114	Atkinson et al. 2015
	Notropis hudsonicus	-2.044	2.989	Carlander 1969
	Notropis spp.	-5.243	3.088	Schneider et al. 2000*
	Pimephales notatus	-5.709	3.390	Schneider et al. 2000
	Pimephales promelas	-5.033	3.077	Schneider et al. 2000
	Semotilus atromaculatus	-4.848	2.925	Schneider et al. 2000
Darter	*Etheostoma exile*	-5.518	3.279	Schneider et al. 2000*
	Etheostoma flabellare	-5.518	3.279	Schneider et al. 2000*
	Etheostoma microperca	-5.294	3.145	Hatch 1986*
	Etheostoma nigrum	-5.404	3.198	Schneider et al. 2000
	Percina caprodes	-5.490	3.236	Schneider et al. 2000
	Unidentifiable	-5.518	3.279	Schneider et al. 2000*
Lake Whitefish	*Coregonus clupeaformis*	-5.813	3.289	Carlander 1969*
Micropterus spp.	*Micropterus dolomieu*	-4.758	3.007	Bozek et al. 1999
	Micropterus salmoides	-5.215	3.140	Bozek et al. 1999
Muskellunge	*Esox masquinongy*	-6.658	3.491	Younk and Strand 1992
Northern Pike	*Esox lucius*	-5.552	3.122	Bozek et al. 1999
Rock Bass	*Ambloplites rupestris*	-4.724	2.987	Bozek et al. 1999
Sculpin	*Cottus bairdii*	-5.299	3.252	Schneider et al. 2000
	Cottus cognatus	-5.299	3.252	Schneider et al. 2000
Sunfish	*Lepomis cyanellus*	-5.176	3.206	Carlander 1977*
	Lepomis gibbosus	-5.142	3.208	Carlander 1977*

	Lepomis macrochirus	-5.286	3.201	Bozek et al. 1999
Tadpole Madtom	*Noturus gyrinus*	-5.040	3.102	Schneider et al. 2000
Trout-perch	*Percopsis omiscomaycus*	-4.965	3.000	Schneider et al. 2000
Unidentified fish	*Unidentifiable to any taxon*	-5.079	3.056	Kapuscinski et al. 2012
Walleye	*Sander vitreus*	-5.142	3.036	Schneider et al. 2000
White Sucker	*Catostomus commersoni*	-5.077	3.059	Bozek et al. 1999
Yellow Perch	*Perca flavescens*	-5.335	3.173	Schneider et al. 2000

* average of multiple equations

APPENDIX B

Appendix B. Prey taxa, weight equations, and dry:wet weight conversions (if applicable) for invertebrate prey.

Taxon	**Weight equation**	**Dry:wet conversion**
Anisoptera	$\mathrm{DW} = 0.0139 * L^{2.78}$ (Smock 1980)	20 (Cummins and Wuycheck 1971)
Arachnida	$WW = -1.874 + 2.733 * \ln BL$ (Edwards and Gabriel 1998)	N/A
Ceratopogonidae	$\log_{10} DW = 0.41 + 2.41 * \log_{10} HW$ (Méthot et al. 2012)	8.5 (Cummins and Wuycheck 1971)
Chironomidae	$\log_{10} DW = 0.19 + 2.3 * \log_{10} HW$ (Méthot et al. 2012)	8.5 (Cummins and Wuycheck 1971)
Coleoptera	$\mathrm{DW} = 0.1529 * L^{2.18}$ (Smock 1980)	20 (Cummins and Wuycheck 1971)
Corixidae	$\log_{10} DW = -2.33 + 3.31 * \log_{10} BL$ (Méthot et al. 2012)	20 (Cummins and Wuycheck 1971)
Diptera	$\log_{10} DW = 0.19 + 2.3 * \log_{10} HW$ (Méthot et al. 2012)	8.5 (Cummins and Wuycheck 1971)
Dreissena polymorpha	$\ln DW = -9.622 + 2.864 * \ln BL$ (Hetherington et al. 2019)	37 (Rudstam and Gandino 2019)
Ephemeroptera	$\mathrm{DW} = 0.0066 * L^{2.88}$ (Smock 1980)	20 (Cummins and Wuycheck 1971)
Faxonius rusticus	$\mathrm{WW} = 3.0961 * \mathrm{CAL} - 3.6979$ (Anderson and Simon 2015)	N/A
Faxonius virilis	$\mathrm{WW} = (2.129 * \mathrm{CAL}) - 5.44$ (Simon and Stewart 2014)	N/A
Gammaridae	$\mathrm{DW} = 0.0015 * L^{3.01}$ (K.D. Zimmer, University of St. Thomas, unpublished data)	26 (Cummins and Wuycheck 1971)
Gyrinidae	$\mathrm{DW} = 0.1529 * L^{2.18}$ (Smock 1980)	20 (Cummins and Wuycheck 1971)
Hirudinea	$\mathrm{DW} = 0.019 * L^{2.1083}$ (K.D. Zimmer, unpublished data)	20 (Driver et al. 1974)
Hyalella	$\mathrm{DW} = 0.0038 * L^{2.82}$ (K.D. Zimmer, unpublished data)	26 (Cummins and Wuycheck 1971)
Hydrachnidia	$\mathrm{DW} = 0.1232 * L^{2.166}$ (K.D. Zimmer, unpublished data)	20 (Cummins and Wuycheck 1971)
Hymenoptera	$\mathrm{DW} = 0.016 * L^{2.55}$ (Schoener 1980)	20 (Cummins and Wuycheck 1971)
Lepidoptera	$\mathrm{DW} = 0.014 * L^{2.55}$ (Schoener 1980)	20 (Cummins and Wuycheck 1971)
Nepidae	$\mathrm{DW} = 0.0314 * L^{2.4}$ (Smock 1980)	20 (Cummins and Wuycheck 1971)
Oligochaeta	$\mathrm{DW} = 0.0005476 * BL^{2.86}$ (Méthot et al. 2012)	8.5 (Cummins and Wuycheck 1971)
Planorbidae	$\log_{10} DW = -1.12 + 2.9 * \log_{10} SW$ (Méthot et al. 2012)	29 (Driver et al. 1974)

Sididae	$\mathrm{DW} = 7.798 * L^{2.189}$ (McCauley 1984)	11 (Hewett and Johnson 1992)
Trichoptera	$\mathrm{DW} = 0.0019 * L^{3.12}$ (Smock 1980)	20 (Cummins and Wuycheck 1971)
Unionidae	$\mathrm{DW} = 0.000298 * SL^{2.79}$ (Atkinson et al. 2020)	37 (Rudstam and Gandino 2019)
Valvatidae	$\log_{10} DW = -0.93 + 3.18 * \log_{10} SH$ (Méthot et al. 2012)	29 (Driver et al. 1974)
Viviparus georgianus	$\ln WW = (3.09 * \ln BL) - 7.97$ (Obaza and Ruehl 2013)	N/A
Zygoptera	$\mathrm{DW} = 0.0139 * L^{2.78}$ (Smock 1980)	20 (Cummins and Wuycheck 1971)

APPENDIX C

Appendix C. Body part measured, units of length measurements, and units of mass predictions for invertebrate prey.

Taxon	Body part measured	Length units	Mass units
Anisoptera	Body length	um	mg
Arachnida	Body length	mm	mg
Ceratopogonidae	Head width	um	mg
Chironomidae	Head width	um	mg
Coleoptera	Body length	um	mg
Corixidae	Body length	um	mg
Diptera	Head width	um	mg
Dreissena polymorpha	Shell width	mm	g
Ephemeroptera	Body length	um	mg
Faxonius rusticus	Carapace length	mm	g
Faxonius virilis	Carapace length	mm	g
Gammaridae	Back length	um	mg
Gyrinidae	Body length	um	mg
Hirudinea	Body length	um	mg
Hyalella	Back length	um	mg
Hydrachnidia	Greatest width	um	mg
Hymenoptera	Body length	mm	mg
Lepidoptera	Body length	mm	mg
Nepidae	Body length	um	mg
Oligochaeta	Body length	um	mg
Planorbidae	Shell width	um	mg
Sididae	Greatest length	mm	mg
Trichoptera	Head width	um	mg
Unionidae	Shell width	mm	g
Valvatidae	Shell height	mm	mg
Viviparus georgianus	Operculum length	mm	g
Zygoptera	Body length	um	mg

REFERENCES

Anderson, W.E., and T.P. Simon. 2015. Length-weight relationship, body morphometrics, and condition based on sexual stage in the rusty crayfish, *Orconectes rusticus* Girard, 1852 (Decapoda, Camaridae) with emphasis on management implications. Fisheries and Aquaculture Journal 6:1-7.

Atkinson, T., S. Desrosiers, T. Townsend, and T.P. Simon. 2015. Length-weight relationships of the emerald shiner (*Notropis atherinoides* – Rafinesque, 1818) in the western basin of Lake Erie. Ohio Journal of Science 114:27-35.

Atkinson, C.L., T.B. Parr, B.C. van Ee, D.D. Knapp, M. Winebarger, K.J. Madoni, and W.R. Haag. 2020. Length-mass equations for freshwater unionid mussel assemblages: Implications for estimating ecosystem function. Freshwater Science 39:377-392.

Bozek, M.A., T.M. Burri, and R.V. Frie. 1999. Diets of muskellunge in northern Wisconsin lakes. North American Journal of Fisheries Management 19:258-270.

Carlander, K.D. 1969. Handbook of freshwater fishery biology, volume 1. Iowa State University Press, Ames, Iowa, USA.

Carlander, K.D. 1977. Handbook of freshwater fishery biology, volume 2. Iowa State University Press, Ames, Iowa, USA.

Cummins, K.W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. Internationale Vereinigung für Theoretische und Angewandte Limnologie: Milleilungen 18(1):1-158.

Driver, E.A., L.G. Sugden, R.J. Kovach. 1974. Calorific, chemical and physical values of potential duck foods. Freshwater Biology 4:281-292.

Edwards, R.L., and W.L. Gabriel. 1998. Dry weight of fresh and preserved spiders (Araneida: Labidognatha). Entomological News 109:66-74.

Hatch, J.T. 1986. Life history of the least darter in Dinner Creek, Becker County, Minnesota. Final report submitted to the Nongame Wildlife Program, Minnesota Department of Natural Resources.

Hetherington, A.L., L.G. Rudstam, R.L.Schneider, K.T. Holeck, C.W. Hotaling, J.E. Cooper, and J.R. Jackson. 2019. Invader invaded: population dynamics of zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis* *bugensis*) in polymictic Oneida Lake, NY, USA (1992-2013). Biological Invasions 21:1529-1544.

Hewett, S.W., and B.L. Johnson. 1992. Fish bioenergetics model 2. University of Wisconsin, Sea Grant Institute. Technical Report WIS-SC-92-250.

Kapuscinski, K.L., J.M. Farrell, and B.A. Murry. 2012. Feeding strategies and diets of young-of-the-year muskellunge from two large river ecosystems. North American Journal of Fisheries Management 32:635-647.

McCauley, E. 1984. The estimation of the abundance and biomass of zooplankton in samples. Pages 228-265 *in* J.A. Downing and F.H. Rigler, editors. A manual on methods for the assessment of secondary productivity in freshwaters, 2nd edition. Blackwell Scientific Publications, Boston, MA, USA.

Méthot, G., C. Hudon, P. Gagnon, B. Pinel-Alloul, A. Armellin, and A. Tourville Poirier. 2012. Macroinvertebrate size-mass relationships: How specific should they be? Freshwater Science 31:750-764.

Miller, S.J., D.T. VanGenechten, C.E. Cichra. 2015. Length-weight relationships and an evaluation of fish-size and seasonal effects on relative condition (Kn) of fishes in the Wekiva River, Florida. Florida Scientist 78:1-19

Obaza, A., and C.B. Ruehl. 2013. Regressions for estimating gastropod biomass with multiple shell metrics. Malacologia 56:343-349.

Rudstam, L.G., and C.J. Gandino. 2019. Zebra and quagga mussels in Onondaga Lake, New York. Onandaga Lake Ambient Monitoring Program Annual Report, Onondaga County, New York, USA.

Schneider, J.C., P.W. Laarman, and H. Gowing. 2000. Length-weight relationships. Chapter 17 *in* J.C. Schneider, editor. Manual of fisheries survey methods II: with periodic updates. Michigan Department of Natural Resources, Fisheries Special Report 25, Ann Arbor, Michigan, USA.

Schoener, T.W. 1980. Length-weight regressions in tropical and temperate forest-understory insects. Annals of the Entomological Society of America 73:106-109.

Simon, T.P., and C.R. Stewart. 2014. Growth, length-weight relationships, and condition associated with gender and sexual stage in the invasive northern crayfish, *Orconectes virilis* Hagen, 1870 (Decapoda, Cambaridae). Proceedings of the Indiana Academy of Science 123:196-203.

Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology 10:375-383.

Younk, J.A., and R.F. Strand. 1992. Performance evaluation of four muskellunge *Esox masquinongy* strains in two Minnesota lakes. Minnesota Department of Natural Resources Investigational Report 418.