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## ARTICLE

# Diet Patterns and Niche Overlap of Muskellunge and Co-Occurring Piscivores in Minnesota Lakes

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Abstract

Muskellunge *Esox masquinongy*, Northern Pike *E. lucius*, Walleye *Sander vitreus*, and Largemouth Bass *Micropterus salmoides* are popular sport fish that often co-occur in aquatic systems. Although numerous studies have investigated interactions among these species, the simultaneous evaluation of diet patterns and niche overlap among all four species has not been conducted. Our experimental design aimed to quantify diet overlap among Muskellunge and the other piscivores, while lakes without Muskellunge were also sampled to compare the diets of the other piscivores in their presence or absence. Diets of piscivores from 10 Minnesota lakes were collected via gastric lavage and quantified using an index of relative importance. Diets of individual species were compared among seasons and predator length categories, and among-species comparisons were also conducted by season and relative to Muskellunge presence using permutational multivariate ANOVA (PERMANOVA). Muskellunge consumed a wide range of prey, whereas Northern Pike and Walleye diets consisted primarily of Yellow Perch *Perca flavescens* and centrarchids. Largemouth Bass consumed more invertebrates, especially crayfish *Faxonius* spp. No species exhibited seasonal diet shifts, but diets were different among length categories for all species except Walleye. Although nonmetric multidimensional scaling ordinations indicated shared prey use, PERMANOVA results indicated that the diets of Muskellunge and Largemouth Bass were most different from each other and the other piscivores' diets across all seasons. Conversely,

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Northern Pike and Walleye diets were similar regardless of season or Muskellunge presence. Finally, lake-scale habitat variables were correlated with piscivore diets, and Yellow Perch abundance was correlated with Walleye diets. Our results indicate that while Muskellunge, Northern Pike, Walleye, and Largemouth Bass can coexist in a variety of lakes, populations of important prey and habitat variables should be examined before management actions (e.g., stocking) are implemented to ensure adequate prey availability and to ensure that competition among these piscivores is not increased to the detriment of existing fisheries.

Investigating the diet patterns of sympatric species can provide crucial information on niche overlap and resource partitioning within aquatic ecosystems (Pianka 1974; Schoener 1974). This is especially true for apex predators, as competitive interactions and direct predation act simultaneously to structure the broader community (Kotler and Holt 1989; He and Kitchell 1990). Furthermore, top predators tend to stabilize aquatic food webs by utilizing resources from multiple habitats (McMeans et al. 2016; Keppeler et al. 2021) and can alter entire ecosystems through top-down trophic cascades (Carpenter et al. 1985; Martin et al. 2022). Understanding the trophic ecology of predatory fish can provide managers with essential information to effectively manage fisheries and the ecosystems in which they occur (Link 2002). Diet information is a cornerstone for effective ecosystem-based fisheries management approaches to understand the broader ecological impacts of managing and stocking top predators in aquatic systems (Eby et al. 2006; Link 2010; Dolan et al. 2016).

The Muskellunge Esox masquinongy is the largest member of the family Esocidae and is frequently managed for trophy angling opportunities (Casselman et al. 2017). Many Muskellunge populations throughout North America have been created and maintained by stocking, both within and outside the native range of the species (Kerr and Grant 2000; Kerr 2011). New introductions have resulted in concerns from some stakeholder groups (Schroeder et al. 2007; Murphy 2017); these concerns are often centered around potential predation on (Brenden et al. 2004; Wolter et al. 2012; Koenig et al. 2015; Andrews et al. 2018) or interspecific competition with (Kerr 2011, 2016) other popular sport fish. Although evidence suggests that Muskellunge do not negatively affect the fish community in systems where they exist (Inskip and Magnuson 1983; Fayram et al. 2005; Knapp et al. 2012, 2021) and that diet overlap with other piscivores may be low (Herwig et al. 2022), more detailed information on the diets of Muskellunge and sympatric piscivores in a range of aquatic systems would assist in their management and would help to address potential concerns.

Muskellunge, Northern Pike *E. lucius*, Walleye *Sander vitreus*, and Largemouth Bass *Micropterus salmoides* are popular sport fish that often co-occur in aquatic systems, either naturally or through stocking (Li et al. 1995; Kerr 2011, 2016; MN DNR 2016; Rypel et al. 2019). Although all four species are opportunistic predators, they tend to be

predominantly piscivorous as adults. Yellow Perch Perca flavescens are important prey for Northern Pike (Beyerle 1971; Diana 1979; Margenau et al. 1998; Pierce et al. 2003; Ahrenstorff and Holbrook 2016) and Walleve (Forney 1974; Nielsen 1980; Pierce et al. 2006; Ahrenstorff and Holbrook 2016), while Muskellunge often consume catostomids in addition to Yellow Perch (Bozek et al. 1999; Brenden et al. 2004; Woomer et al. 2012). For all three of these predators, Cisco Coregonus artedi can also serve as an important prey item in lakes where the species is abundant (Lyons and Magnuson 1987; Kaufman et al. 2009; Vivian and Frazer 2021; Herwig et al. 2022). In contrast, Largemouth Bass more frequently consume crayfish, aquatic invertebrates, and a variety of terrestrial organisms in addition to fish (Hodgson and Kitchell 1987; Hodgson and Hansen 2005; Kelling et al. 2016). Although numerous studies have investigated interactions among these predators in a variety of systems (Nate et al. 2003; Fayram et al. 2005; Knapp et al. 2012, 2021; Bethke and Schmalz 2020; Herwig et al. 2022), a simultaneous evaluation of diet patterns and niche overlap among all four species has yet to be performed.

Prey availability in aquatic systems is often influenced by relationships between habitat characteristics and the fish communities they support, as well as interactions among the various fish species present in different systems (Johnson et al. 1977; Schupp 1992; Cross 2018; Rypel et al. 2019). Physical parameters and nutrients can impact prey fish assemblages (Barbour and Brown 1974; Egertson and Downing 2004; Fischer and Quist 2019) and the habitat available to mobile predators (Jackson et al. 2001; Dolson et al. 2009), thereby dictating food chain length (Vander Zanden et al. 1999; Post et al. 2000), habitat coupling (Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002), and food web stability (McCann et al. 2005; Rooney et al. 2006). These habitat-prey interactions can have direct consequences for generalist predators whose diets are often closely tied to prey fish abundances (Knight et al. 1984; Weber et al. 2010). Although many studies have compared piscivore diets among groups of lakes (Pothoven et al. 1999; Olson and Young 2003) or among habitats within lakes (Dibble and Harrel 1997; Sass et al. 2006, 2011; Ahrenstorff et al. 2009), rarely have studies investigated the influences of lake-scale habitat and availability of important prey fish on diet patterns.



FIGURE 1. Locations of 10 lakes throughout Minnesota, where diets of piscivorous fishes were collected in 2019–2021. Black dots indicate lakes with Muskellunge present, and gray dots indicate lakes with no Muskellunge population. Physical and biological characteristics of each lake are described in Tables 1 and 2.

The goals of this study were to document and evaluate the population-wide diet patterns and niche overlap of four piscivorous species in a variety of Minnesota lakes to better understand interactions among co-occurring sport fish populations, thus helping to guide future management decisions. An understanding of what these predators eat and how their diets may overlap is important for managers because if there are substantial trophic interactions (e.g., predation or competition), changes in the population status of one species could affect the population status or fisheries of the other species. To address potential trophic interactions, our objectives were to determine whether (1) within-species diets of Muskellunge, Northern Pike, Walleye, and Largemouth Bass populations varied among seasons, by predator length, or relative to Muskellunge presence; (2) diets differed among piscivores seasonally or

in relation to Muskellunge presence; and (3) environmental variables, such as lake-scale habitat and availability of important prey fish, were correlated with the diets of predator populations.

#### **METHODS**

Study site.— Predator diets were collected from 10 lakes throughout Minnesota (Figure 1). Most lakes were located within the Northern Lakes and Forests Ecoregion and the North Central Hardwood Forests Ecoregion (Omernik 1987), as many of Minnesota's Muskellunge waters are concentrated in those areas (MN DNR 2008). Lakes ranged from 121 to 2,669 ha in surface area, with maximum depths ranging from 11 to 63 m. We included six lakes with Muskellunge populations and four lakes

Lake	Surface area (ha)	Maximum depth (m)	Percent littoral area	Geometry ratio	SDI	TSI
Bald Eagle	425	11	71.6	4.03	2.03	58
Bemidji	2,669	23	28.2	3.10	1.30	52
Deer	121	13	39.6	2.59	1.50	45
Grace	348	13	39.5	3.37	1.05	49
Little Boy	588	23	32.1	2.18	1.88	46
Miltona	2,316	32	48.2	2.17	1.63	44
Pelican	1,870	21	43.5	3.13	3.08	42
Shamineau	580	16	52.0	3.19	1.95	43
South Center	338	33	67.2	1.29	2.96	56
Ten Mile	2,056	63	25.9	1.04	2.49	36

TABLE 1. Surface area (ha), maximum depth (m), percent littoral area, geometry ratio, shoreline development index (SDI), and trophic state index (TSI) for each of 10 sampled lakes in Minnesota.

without Muskellunge to explore possible influences that this predator may have on co-occurring piscivores. Lakes with abundant populations of all predators present were prioritized to improve the likelihood of reaching adequate sample sizes. Additionally, lakes that were sampled in 2020 were restricted to the area within 20 min of the city of Bemidji because COVID-19 safety and distancing protocols limited travel. Lakes were highly variable in physical characteristics and trophic status (Table 1) as well as in the overall fish community (Table 2), providing gradients with which to investigate how these factors were related to piscivore diet patterns.

*Data collection.*— Diets of Muskellunge, Northern Pike, Walleye, and Largemouth Bass were collected during spring (April–early June), summer (mid-July–mid-August), and fall (mid-September–early November) in 2019–2021 (Table 3). Each study lake was sampled within a calendar year to reduce variability in potential prey availability, with one exception: Muskellunge from Lake Bemidji were sampled 1 year after the other piscivores because COVID-19 safety and distancing protocols precluded us from handling this species during 2020. Fish were collected primarily by boat electrofishing in shallow waters (<3 m in depth). A variety of habitats were sampled in each lake, including shoreline habitats and other shallow structures (i.e., islands, reefs, etc.). Fish were also collected using other gears (trap nets, horizontal gill nets, and angling) during Minnesota Department of Natural Resources (MN DNR) population assessments or to bolster sample size when electrofishing was not effective. Piscivores were measured to the nearest millimeter TL, and gastric lavage (Foster 1977; Kamler and Pope 2001) was used to flush the stomachs of live fish by 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). When fish were sampled with gill nets, the stomach and contents were removed in lieu of gastric lavage. All fish collected in

TABLE 2. Muskellunge presence/absence and the CPUE (fish per net) of Largemouth Bass (LMB), Northern Pike (NOP), Walleye (WAE), Bluegill Lepomis macrochirus (BLG), Cisco (TLC), White Sucker Catostomus commersonii (WTS), and Yellow Perch (YEP) in Minnesota Department of Natural Resources standard survey trap nets (TN) and gill nets (GN). Data represent the most recent standard survey conducted in each lake prior to or during the year in which diets were collected.

Lake	Muskellunge	LMB TN	NOP GN	WAE GN	BLG TN	TLC GN	WTS GN	YEP GN
Bald Eagle	Present	0.09	6.20	1.80	10.09	Absent	0.00	31.00
Bemidji	Present	0.13	3.50	19.86	0.00	15.21	9.64	50.00
Deer	Absent	0.11	5.17	1.00	10.67	0.83	0.83	1.00
Grace	Absent	2.33	6.08	12.08	55.17	Absent	5.50	18.58
Little Boy	Present	0.33	9.42	7.17	6.92	1.33	0.92	22.33
Miltona	Present	1.53	3.75	5.83	35.27	0.00	0.08	12.92
Pelican	Present	2.13	5.07	15.53	16.60	0.00	0.73	37.33
Shamineau	Present	1.73	3.40	5.07	16.20	Absent	0.13	23.27
South Center	Absent	0.42	4.75	2.42	53.83	Absent	0.58	2.83
Ten Mile	Absent	0.60	8.53	7.60	14.60	0.00	0.87	4.73

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		Ν	Iuskellunge	Noi	thern Pike		Walleye	Large	emouth Bass
Lake	Year	N	Mean TL	N	Mean TL	N	Mean TL	N	Mean TL
Bald Eagle	2019	74	$1,053 \pm 147$	135	$632 \pm 131$	100	$370 \pm 118$	139	$308\pm78$
Bemidji	$2020^{a}$	94	$1,167 \pm 102$	97	$608\pm135$	98	$444\pm91$	7	$433\pm43$
Deer	2020	_	_	64	$601\pm 122$	74	$387 \pm 141$	94	$376\pm 61$
Grace	2020	_	-	106	$609\pm 69$	115	$396 \pm 112$	102	$352\pm100$
Little Boy	2019	31	$959 \pm 194$	116	$580\pm 125$	140	$408\pm130$	53	$380\pm51$
Miltona	2019	61	$1,043 \pm 222$	85	$588\pm 127$	116	$471\pm108$	120	$308\pm79$
Pelican	2021	52	$1,064 \pm 167$	164	$584 \pm 136$	173	$449\pm 140$	157	$328 \pm 103$
Shamineau	2021	56	$927\pm270$	158	$527\pm148$	212	$414 \pm 119$	149	$334\pm70$
South Center	2019	_	-	73	$634 \pm 112$	98	$460 \pm 134$	170	$320\pm90$
Ten Mile	2019	_	_	68	$568\pm 177$	107	$510\pm100$	118	$320\pm70$

TABLE 3. Total sample sizes (N) and mean TL (mm)  $\pm$  SD for Muskellunge, Northern Pike, Walleye, and Largemouth Bass collected from Minnesota lakes during 2019–2021.

<sup>a</sup>Muskellunge were sampled from Lake Bemidji in 2021 due to COVID-19 safety and distancing protocols.

2020 were euthanized via cranial concussion (AVMA 2020), and stomachs were removed in lieu of gastric lavage to comply with established COVID-19 safety and distancing protocols. When freshly consumed prey items could not be removed without causing serious injury to the fish, those individuals were also euthanized via cranial concussion. All stomach contents were placed in an individually labeled bag and preserved in ethanol.

In the laboratory, all fish prey were identified to the lowest possible taxonomic group by using taxonomic keys, cleithra (Traynor et al. 2010), or otoliths (Ross et al. 2005; Rypel 2008). To reduce the uncertainty associated with unidentified prey in diet studies (Rosel and Kocher 2002; Symondson 2002), a subsample (up to 100 per year) of unidentified prey fish were identified using DNA bar coding (Ivanova et al. 2007; Kelling et al. 2016). Prey from Muskellunge diets were prioritized for DNA identification due to the frequency of empty stomachs in previous studies (e.g., Bozek et al. 1999; Andrews et al. 2018), while exceptionally large prey or diets of species with low sample sizes from a given lake were chosen secondarily. Prey fish that were not identified visually or molecularly were classified as "unidentified fish." Fish prey were measured to the nearest millimeter by TL, backbone length, cleithrum length, or otolith length depending on the extent of digestion. Relationships between TL and bony structures were developed to estimate the TLs of digested prey items (our unpublished data). Length-weight regressions were then used to estimate wet weight of all fish prey items (Table S1 available in the Supplement in the online version of this article). Any fish prey items that were identified but unmeasurable due to digestion were assigned the mean wet weight of other prev items in the same prev category that were consumed by the same predator species in the same lake. If no other items from that prey category

were documented in the same lake, then the mean wet weight of that prey category consumed by the same predator species across lakes was used instead. Unidentified fish prey that could not be measured were assigned the median weight of all prey fish consumed by the same predator species in the same lake and season. Invertebrate components of fish diets were identified to varying taxonomic levels (family, order, or species level) and were counted using an image analysis system. Up to 30 individuals of each invertebrate taxon were measured to the nearest 0.01 µm. Invertebrate lengths were used to estimate wet weight based on published regressions (Table S2), and average weight was multiplied by the total count to calculate diet biomass for each invertebrate taxon. Any invertebrate prey items that were identified but unmeasurable due to digestion were assigned the mean wet weight of other prey items of the same taxon consumed from the same lake. If no other diet items from the same taxon were collected in the same lake, then the mean wet weight of that taxon across lakes was used instead.

*Data analysis.*— 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

$$IRI = F \times (N + M),$$

where F is the percent frequency of occurrence, N is the numerical percentage, and M is the mass percentage of each prey group. The resulting IRI value indicates the "importance" for each prey category (West et al. 2003). This metric was selected to represent predator diet composition (hereafter, "diets") because it reduces potential bias due to "rare and large" or "small and abundant" prey (Liao et al. 2001) while balancing variation in feeding

Species	Substock	Stock	Quality	Preferred	Memorable	Trophy
Muskellunge	<510 (9)	510-759 (12)	760-969 (23)	970-1,069 (51)	1,070-1,269 (84)	≥1,270 (14)
Northern Pike	<350 (27)	350-529 (146)	530-709 (271)	710-859 (91)	860-1,119 (18)	≥1,120 (0)
Walleye	<250 (72)	250-379 (181)	380-509 (247)	510-629 (123)	630-759 (50)	≥760 (0)
Largemouth Bass	<200 (50)	200–299 (164)	300-379 (222)	380-509 (184)	510-629 (1)	≥630 (0)

TABLE 4. Length ranges (mm TL) of Gabelhouse (1984) length categories for Muskellunge, Northern Pike, Walleye, and Largemouth Bass. The sample size for each length category is included in parentheses.

behavior and nutritional value among individuals to represent population-wide diet patterns (Cortés 1997). The IRI values were scaled as percentages to allow for comparisons among predators and lake types.

To conduct statistical comparisons of predator diets among seasons, species, and length categories and to investigate potential effects of Muskellunge presence on the diets of other piscivores, a series of one-way permutational multivariate ANOVAs (PERMANOVAs; Anderson 2001) were performed. Within-species diet comparisons were conducted among seasons and relative to Muskellunge presence using seasonal IRI values calculated for each predator  $\times$  lake combination. Within-species comparisons were also conducted based on Gabelhouse (1984) length categories (Table 4). Because predator diets were not significantly different among seasons, the diets were pooled across seasons and stratified by length category. Between-species comparisons were then conducted among seasons and relative to Muskellunge presence using seasonal IRI values. The PERMANOVAs were conducted via the "adonis2" function in the vegan package (Oksanen et al. 2022) using Bray-Curtis dissimilarity matrices and 9,999 permutations. Bray-Curtis dissimilarity matrices were used because they provide robust measures of correlation and sample similarity (Faith et al. 1987; McCune and Grace 2002) while maintaining community structure even when presented with "joint absences" (Clarke et al. 2006), which are common in diet data. If PERMA-NOVA results were significant (P < 0.05), then the function "permutest.betadisper" with 9,999 permutations was used to test whether differences were due to differences in relative dispersion or differences in overall multivariate structure between groups (Anderson 2006). If differences between groups were not due to differences in multivariate dispersion (P > 0.05), then the "pairwise.adonis2" function from the pairwiseAdonis package (Martinez Arbizu 2017) was used to analyze pairwise comparisons. After PERMA-NOVAs were performed, nonmetric multidimensional scaling (NMDS) ordinations were constructed to visualize niche size and overlap among piscivores. The NMDS ordinations represented the overall diets and displayed ellipses representing the 95% confidence region centered on the centroids of comparison groups using the "ordiellipse" function in the vegan package within R.

Finally, the effects of environmental variables on piscivore diets were investigated. Lake-scale habitat variables (Table 1), including lake surface area, maximum depth, percent littoral area, geometry ratio, and shoreline development index (SDI; Kent and Wong 1982), were obtained (or calculated) from MN DNR files. The trophic state index (TSI; Carlson 1977), a composite metric that uses water clarity, nutrient loading, and algal biomass to estimate lake productivity, was also obtained from Minnesota Pollution Control Agency files. Potential effects of the relative abundances of Bluegill and Yellow Perch, the two most important prey fish across species and lakes, were also investigated. The trap-net CPUE of Bluegill and the gill-net CPUE of Yellow Perch were obtained from the MN DNR Fisheries' Lake Survey database. Correlations between overall diets and environmental variables were examined using the function "envfit" in the vegan package, which fits linear trends onto ordinations for continuous variables. Environmental variables were permuted 9,999 times to assess the significance of vector fits, and significant (P < 0.05) vectors were fitted to NMDS ordinations of predator diets. All statistical analyses were performed using R version 4.2.0 (R Core Team 2022).

#### RESULTS

Stomach contents from 368 Muskellunge (285–1,395 mm TL), 1,043 Northern Pike (144–1,065 mm TL), 1,178 Walleye (132–770 mm TL), and 1,105 Largemouth Bass (104–510 mm TL) were examined from 10 Minnesota lakes (Table 3). Prey items representing 30 prey categories (Appendix Table A.1) were obtained from the stomachs of 193 Muskellunge (52.4% of the total examined), 535 Northern Pike (51.3%), 633 Walleye (53.7%), and 620 Largemouth Bass (56.1%). Fish, crayfish, and other invertebrates were the dominant prey groups for all four species (Figure 2); however, organisms from the classes Mammalia, Reptilia, Amphibia, and Aves were also consumed.

## **Diet Patterns of Piscivore Species**

Muskellunge in this study consumed prey from 22 different categories, but dietary importance did not exceed 30% for any single category. The most important prey categories in terms of IRI included Yellow Perch



FIGURE 2. Percent index of relative importance (IRI) for important prey categories in the diets of Muskellunge (MUE), Northern Pike (NOP), Walleye (WAE), and Largemouth Bass (LMB) in Minnesota lakes. Prey abbreviations are defined in Table A.1. Presented prey categories include all categories that represented at least 5% of the overall diet of any predator species.

(IRI = 27.1%), catostomids (10.5%), and invertebrates (10.1%). Other, less important prey in terms of IRI included bullheads *Ameiurus* spp. (IRI = 8.3%), Northern Pike (6.2%), black bass Micropterus spp. (6.1%), and sunfish Lepomis spp. (5.0%). Additionally, many Muskellunge diets contained unidentifiable fish (IRI = 23.2%) due to inefficiencies in extracting DNA from the predominantly bony material contained in many of these samples (Loren Miller, MN DNR, personal communication). Despite occurring in four of the six study lakes where Muskellunge were also present, Cisco were unimportant in the diets of Muskellunge (IRI = 0.44%). Muskellunge diets were not significantly different across seasons (P = 0.141) but were significantly different among length categories (P = 0.016; Table 5), and differences were not caused by variation in multivariate dispersion (P = 0.679; Table A.2). Pairwise comparisons indicated that stock-size individuals had different diets than preferred-, memorable-, and trophy-size individuals (Table 6). Additionally, the diets of memorable-size Muskellunge were also different than those of substock- and quality-size fish. In general, the dietary importance of invertebrates and catostomids increased with Muskellunge size, whereas Yellow Perch, Micropterus spp., and Lepomis spp. were more important for smaller Muskellunge (Figure 3).

Northern Pike consumed prey from 23 different categories, but their diets were dominated by only two groups. Yellow Perch were the most important prey item in terms of IRI (50.6%), followed by *Lepomis* spp. (28.7%). Unidentifiable fish (IRI = 7.6%) and Black Crappie *Pomoxis* 

TABLE 5. Results of permutational multivariate ANOVA tests for within-species differences in predator diets based on season, Gabelhouse (1984) length category (defined in Table 4), and Muskellunge presence in Minnesota lakes. Significant results (P < 0.05) are indicated by an asterisk (\*).

Predator	Predictor	df	F-statistic	P-value
Muskellunge	Season	2	1.469	0.139
C	Length category	5	1.574	0.016*
Northern	Season	2	1.386	0.181
Pike	Muskellunge presence	1	1.019	0.377
	Length category	4	1.760	0.027*
Walleye	Season	2	0.707	0.646
,	Muskellunge presence	1	1.947	0.112
	Length category	4	1.008	0.431
Largemouth	Season	2	1.435	0.186
Bass	Muskellunge presence	1	1.329	0.255
	Length category	4	2.230	0.004*

nigromaculatus (6.0%) were less important in terms of IRI. However, no other categories contributed even 2% IRI to Northern Pike diets. This again included Cisco (IRI = 0.13%) despite their presence in 6 of the 10 total study lakes. Diets of Northern Pike were not significantly different across seasons (P = 0.181) but were significantly different among length categories (P = 0.027; Table 5), and differences were not caused by variation in multivariate dispersion (P = 0.106; Table A.2). Diets of Northern Pike in the memorable size-class were different from those of stock- and quality-size individuals, and the diets of substock-size Northern Pike were also different than the diets of preferred-size fish (Table 6). Dietary importance of centrarchids generally increased with Northern Pike size, while Yellow Perch were more important for smaller size-classes (Figure 3). Diets of Northern Pike were not significantly different relative to Muskellunge presence (P = 0.377; Table 5).

Walleye consumed prey from 24 different categories, but their diets were similarly dominated by the same taxa as Northern Pike. Yellow Perch (IRI = 65.5%) and *Lepomis* spp. (16.3%) were the most important prey in terms of IRI, followed by unidentifiable fish (9.5%), invertebrates (6.1%), and cyprinids (1.5%). Once again, Cisco were not an important component of Walleye diets (IRI <0.01%). Walleye diets were not significantly different across seasons (P = 0.646), among size-classes (P = 0.431), or relative to Muskellunge presence (P = 0.112; Table 5).

Largemouth Bass consumed prey from 23 different categories and were much less piscivorous than the other predators included in this study, instead consuming more

TABLE 6. Results of pairwise permutational multivariate ANOVA tests for within-species differences in predator diets based on Gabelhouse (1984) length categories (defined in Table 4). Significant differences (P < 0.05) are indicated by an asterisk (\*). No Northern Pike or Largemouth Bass in the "trophy" size category were sampled in this study (indicated by N/A).

	Muskel	lunge	Norther	n Pike	Largemou	uth Bass
Length category pair	F-statistic	<i>P</i> -value	F-statistic	P-value	F-statistic	P-value
Substock-stock	1.746	0.151	1.229	0.282	0.700	0.655
Substock-quality	0.986	0.450	2.103	0.066	1.709	0.148
Substock-preferred	0.775	0.665	2.166	0.042*	5.017	0.002*
Substock-memorable	2.055	0.029*	1.787	0.086	1.106	0.449
Substock-trophy	1.176	0.301	N/A	N/A	N/A	N/A
Stock-quality	1.229	0.292	0.364	0.838	1.062	0.350
Stock-preferred	2.120	0.046*	2.185	0.066	5.142	0.001*
Stock-memorable	2.597	0.015*	2.687	0.032*	1.902	0.098
Stock-trophy	2.024	0.023*	N/A	N/A	N/A	N/A
Quality-preferred	1.028	0.398	1.853	0.100	1.508	0.235
Quality-memorable	3.045	0.007*	2.639	0.023*	1.469	0.179
Quality-trophy	1.952	0.076	N/A	N/A	N/A	N/A
Preferred-memorable	0.907	0.503	0.501	0.853	2.741	0.094
Preferred-trophy	1.184	0.283	N/A	N/A	N/A	N/A
Memorable-trophy	1.204	0.298	N/A	N/A	N/A	N/A

invertebrates. All invertebrates made up 67% of Largemouth Bass diets in terms of IRI, with cravfish Faxonius spp. accounting for nearly half of that contribution (31%)overall). Important fish prey in terms of IRI included Lepomis spp. (IRI = 17.5%), Yellow Perch (8.4%), and unidentifiable fish (4.5%). Diets of Largemouth Bass did not vary seasonally (P = 0.186) but were significantly different among size-classes (P = 0.004; Table 5), and differences were not caused by variation in multivariate dispersion (P = 0.104; Table A.2). Specifically, diets of preferred-size Largemouth Bass were different from those of substock- and stock-size fish (Table 6). Dietary importance of cravfish and other invertebrates increased with increasing Largemouth Bass size, while the importance of centrarchids and Yellow Perch decreased (Figure 3). Diets of Largemouth Bass were not significantly different relative to Muskellunge presence (P = 0.255; Table 5).

## **Diet Overlap among Piscivore Species**

Diets of Muskellunge, Northern Pike, Walleye, and Largemouth Bass were significantly different from each other both within and among seasons (Table 7; Figure 4), and differences were not caused by variation in multivariate dispersion ( $P \ge 0.200$ ; Table A.2). Diets of Muskellunge were different from those of all other species across and within seasons, with just one exception; Muskellunge and Walleye diets were statistically similar in spring (P = 0.130; Table 8), when the importance of Yellow Perch was highest for Muskellunge. Diets of Largemouth Bass were significantly different from those of all other piscivores among and within all seasons ( $P \le 0.050$ ; Table 8), largely driven by the importance of crayfish and other invertebrates in the Largemouth Bass diets. Conversely, the diets of Northern Pike and Walleye were not significantly different within or among seasons ( $P \ge 0.108$ ; Table 8), as Yellow Perch and Lepomis spp. were important for both species across seasons.

Diets of Northern Pike, Walleye, and Largemouth Bass were significantly different from each other in lakes with and without Muskellunge (Table 9; Figure 5), and differences were not caused by variation in multivariate dispersion ( $P \ge 0.390$ ; Table A.3). Again, the diets of Largemouth Bass were significantly different from those of Walleye and Northern Pike in lakes with and without Muskellunge ( $P \le 0.028$ ; Table 10). On the other hand, Northern Pike and Walleye diets were not significantly different ( $P \ge 0.069$ ) regardless of Muskellunge presence.

#### **Effects of Environmental Variables**

Diets of all predator populations were significantly correlated with at least one of the tested environmental variables (Table 11). Muskellunge diets were correlated with percent littoral area (P = 0.022,  $r^2 = 0.427$ ). Northern Pike diets were related to lake surface area (P = 0.002,  $r^2 = 0.369$ ), percent littoral area (P = 0.002,  $r^2 = 0.380$ ), TSI (P = 0.003,  $r^2 = 0.340$ ), and SDI (P = 0.041,  $r^2 = 0.213$ ). Walleye diets were related to Yellow Perch CPUE (P = 0.023,  $r^2 = 0.240$ ) and percent littoral area (P = 0.032,  $r^2 = 0.222$ ). Largemouth Bass diets were related to surface area (P = 0.036,  $r^2 = 0.237$ ), percent littoral area (P < 0.001,  $r^2 = 0.498$ ), TSI (P = 0.005,  $r^2 = 0.346$ ), and SDI (P = 0.049,  $r^2 = 0.213$ ). Larger



FIGURE 3. Percent index of relative importance (IRI) for a subset of prey categories in the diets of (A) Muskellunge, (B) Northern Pike, (C) Walleye, and (D) Largemouth Bass separated by Gabelhouse (1984) length categories (defined in Table 4) in Minnesota lakes. Prey abbreviations are defined in Table A.1. Presented prey categories include all categories that represented at least 5% of the overall diet of any predator species.

TABLE 7. Results of permutational multivariate ANOVA tests for among-species differences in predator diets within individual seasons and across all seasons. Significant differences (P < 0.05) are indicated by an asterisk (\*).

Season	df	F-statistic	<i>P</i> -value
Spring	3	4.479	$1 \times 10^{-4*}$
Summer	3	3.273	$3 \times 10^{-4}$ *
Fall	3	3.196	$2 \times 10^{-4}$ *
Combined seasons	3	7.778	$1 \times 10^{-4}$ *

percent littoral area, TSI, and SDI values generally indicated an increased importance of centrarchids in the diets of the piscivores for which these variables were significant, whereas larger surface area corresponded with a decreased dietary importance of centrarchids (Figure 6). Finally, higher Yellow Perch CPUE corresponded with a higher importance of Yellow Perch in Walleye diets.

## DISCUSSION

#### **Diet Patterns of Piscivore Species**

Muskellunge consumed a wide range of prey in this study—a pattern that is consistent with other diet studies throughout the native and introduced range of the species (Hourston 1952; Parsons 1959; Andrews et al. 2018). In Wisconsin lakes, Yellow Perch and catostomids were the



FIGURE 4. Nonmetric multidimensional scaling (NMDS) ordinations of Largemouth Bass (LMB), Muskellunge (MUE), Northern Pike (NOP), and Walleye (WAE) diets in (A) spring, (B) summer, (C) fall, and (D) combined seasons. Ellipses represent the 95% CIs centered on centroids of each species' overall diet in multivariate space, and prey categories are presented in gray text. Prey abbreviations are defined in Table A.1.

TABLE 8. Results of pairwise permutational multivariate ANOVA tests for among-species differences in predator diets within seasons and across all seasons. Significant differences (P < 0.05) are indicated by an asterisk (\*).

	Spr	ing	Sum	ner	Fa	11	Combined seasons	
Species pair	F-statistic	<i>P</i> -value	F-statistic	<i>P</i> -value	F-statistic	<i>P</i> -value	F-statistic	P-value
Muskellunge–Northern Pike	3.853	$9 \times 10^{-4*}$	5.267	0.010*	2.881	0.001*	8.007	$1 \times 10^{-4}$
Muskellunge–Walleye	1.711	0.130	4.296	0.003*	4.487	0.005*	5.860	$1 \times 10^{-4}$
Muskellunge–Largemouth Bass	4.310	$5 \times 10^{-4}$ *	4.533	0.002*	4.433	0.002*	7.422	$1 \times 10^{-4}$
Northern Pike–Walleye	1.697	0.141	0.649	0.596	0.715	0.613	1.840	0.108
Northern Pike–Largemouth Bass	9.981	$1 \times 10^{-4}$	3.337	0.007*	3.345	0.018*	12.664	$1 \times 10^{-4}$
Walleye-Largemouth Bass	5.724	$3 \times 10^{-4}$ *	2.466	0.006*	3.993	0.050*	10.716	$1 \times 10^{-4}$

most important prey in Muskellunge diets (IRI = 56%; Bozek et al. 1999), while catostomids tended to be most important for larger individuals, especially in river systems (Deutsch 1986; Brenden et al. 2004). The same prey groups were also most important in this study, but they only constituted roughly 38% of the diet in terms of IRI. However, the dietary importance of catostomids did increase with increasing Muskellunge size. Moreover, only three Walleye were observed in Muskellunge diets during this study, accounting for less than 0.07% of the total diet in terms of IRI. For comparison, six Muskellunge were observed in the diets of other Muskellunge (IRI = 0.62%). These results are similar to previous Muskellunge diet studies (Bozek et al. 1999; Wolter et al. 2012; Grausgruber

TABLE 9. Results of permutational multivariate ANOVA tests for among-species differences in diets of Northern Pike, Walleye, and Large-mouth Bass relative to Muskellunge presence/absence in Minnesota lakes. Significant differences (P < 0.05) are indicated by an asterisk (\*).

Lake group	df	F-statistic	<i>P</i> -value
Muskellunge present	2	6.658	$1 \times 10^{-4*}$
Muskellunge absent	2	3.110	0.002*





FIGURE 5. Nonmetric multidimensional scaling (NMDS) ordinations of Largemouth Bass (LMB), Northern Pike (NOP), and Walleye (WAE) diets in (A) lakes with Muskellunge and (B) lakes without Muskellunge. Ellipses represent the 95% CIs centered on the centroids of each species' overall diet in multivariate space, and prey categories are presented in gray text. Prey abbreviations are defined in Table A.1.

and Weber 2020) and provide further evidence that Walleye are not important components of Muskellunge diets. The importance of invertebrates in Muskellunge diets was higher than expected, and the higher invertebrate importance for larger Muskellunge was even more surprising. Although previous research has provided little evidence of invertebrate prey being important in the diets of Muskellunge, several studies have reported invertebrates to be

TABLE 10. Results of pairwise permutational multivariate ANOVA tests for among-species differences in diets of Northern Pike, Walleye, and Largemouth Bass relative to Muskellunge presence/absence in Minnesota lakes. Significant differences (P < 0.05) are indicated by an asterisk (\*).

	Muskellun	ge present	Muskellunge absent			
Species pair	F-statistic	<i>P</i> -value	F-statistic	P-value		
Northern Pike–Walleye	0.616	0.637	2.161	0.069		
Northern Pike– Largemouth Bass	10.096	$1 \times 10^{-4}$	4.125	0.001*		
Walleye– Largemouth Bass	10.066	$1 \times 10^{-4}$	2.927	0.028*		

important prey for Northern Pike, even at larger sizes (Chapman et al. 1989; Beaudoin et al. 1999; Venturelli and Tonn 2006). Additional important prey categories in our study included bullheads Ameiurus spp., Northern Pike, black bass Micropterus spp., and sunfish Lepomis spp.; these prey categories are often regarded as "alternate" or unimportant when managing Muskellunge populations (MI DNR 2004; MN DNR 2008; Pearson 2018). The dietary importance of Northern Pike may be of particular interest to managers, as Northern Pike populations continue to increase in abundance while their size structure declines (Goeman et al. 1993; Bethke and Staples 2015). Although Northern Pike have been observed in Muskellunge stomachs previously (Bozek et al. 1999), cannibalism by large Northern Pike on small individuals has been documented more frequently (Lawler 1965; Grimm 1981b, 1983; Nilsson and Brönmark 2000; Lysack 2004), which can lead to top-down control of the abundance of small individuals (Grimm 1981a; Grimm and Klinge 1996). Our results indicate that Muskellunge predation could serve a similar role, and future research should further investigate potential changes in Northern Pike populations in response to Muskellunge stocking (Knapp et al. 2021).

Diets of Northern Pike and Walleye were less diverse than Muskellunge diets. Yellow Perch served as the dominant prey for both species, accounting for over 50% of the diets. Previous studies have observed similar reliance on Yellow Perch by both predators (Diana 1979; Liao et al. 2002, 2004; Kaufman et al. 2009). *Lepomis* spp. were the second most important prey and accounted for 16% and 29% of Walleye and Northern Pike diets, respectively. Reed and Parsons (1996) found that adult Bluegill dominated Northern Pike diets in a Minnesota lake, whereas

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TABLE 11. Environmental variables (with their abbreviations),  $r^2$  values, and *P*-values for environmental vector fits on nonmetric multidimensional scaling ordinations for diet patterns of four piscivores in Minnesota lakes. Geometry ratio serves a scaled ratio of surface area: maximum depth (i.e., small, deep lakes have a low geometry ratio, while large, shallow lakes have a high geometry ratio). Shoreline development index indicates a lake's deviation from a circular shape (i.e., circular shapes have lower index values, while irregularly shaped lakes with numerous bays have high index values). Significant explanatory variables (P < 0.05) are indicated by an asterisk (\*).

		Musk	kellunge	Northern Pike		Walleye		Largemouth Bass	
Variable	Abbreviation	$r^2$	P-value	$r^2$	P-value	$r^2$	P-value	$r^2$	<i>P</i> -value
Bluegill trap-net CPUE	BG	0.184	0.241	0.018	0.782	0.019	0.773	0.186	0.073
Yellow Perch gill-net CPUE	YP	0.213	0.188	0.066	0.394	0.240	0.023*	0.126	0.190
Surface area	SA	0.183	0.246	0.369	0.002*	0.184	0.063	0.237	0.036*
Maximum depth	MD	0.037	0.774	0.192	0.052	0.191	0.053	0.051	0.523
Trophic state index	TSI	0.073	0.580	0.340	0.003*	0.041	0.564	0.346	0.005*
Percent littoral area	PLA	0.427	0.022*	0.380	0.002*	0.222	0.032*	0.498	$3 \times 10^{-4}$ *
Geometry ratio	GR	0.077	0.569	0.036	0.595	0.119	0.175	0.033	0.663
Shoreline development index	SDI	0.233	0.158	0.213	0.041*	0.182	0.068	0.213	0.049*



FIGURE 6. Nonmetric multidimensional scaling (NMDS) ordinations of (A) Muskellunge, (B) Northern Pike, (C) Walleye, and (D) Largemouth Bass diets in lakes with and without Muskellunge. Ellipses represent the 95% CIs centered on the centroids of overall diets by lake type in multivariate space, black arrows represent environmental variables that were correlated with predator diets, and prey categories are presented in gray text. Vector abbreviations are defined in Table 11, and prey abbreviations are defined in Table A.1.

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Walleye consumed far fewer Bluegill. However, a Wisconsin study indicated that Lepomis spp. constitute a large portion of Walleye diets in certain systems (Kelling et al. 2016). Northern Pike also consumed Black Crappie, similar to observations during previous studies in Minnesota (Reed and Parsons 1996), South Dakota (Sammons et al. 1994), and Wisconsin (Margenau et al. 1998). Furthermore, the dietary importance of centrarchids generally increased with increasing Northern Pike size, similar to previous studies in Nebraska (Paukert et al. 2003) and South Dakota (Sammons et al. 1994). Finally, invertebrate prey contributed to the diets of Northern Pike and Walleye, although the relative importance of this prey category was relatively low. In fact, invertebrates were of substantially lower relative importance in the present study than in previously reported findings for both Northern Pike (Chapman et al. 1989; Beaudoin et al. 1999; Venturelli and Tonn 2006) and Walleye (Frey et al. 2003; Herbst et al. 2016).

Surprisingly, Cisco were not an important component of the diets for Muskellunge, Northern Pike, or Walleye. This pelagic prey species has been well documented in the diets of Walleye (Lyons and Magnuson 1987; Kaufman et al. 2009; Vivian and Frazer 2021) and is often considered a primary driver of predator growth rates in systems where they are present (Jacobson 1992, 1994; Kaufman et al. 2009; Kennedy et al. 2018; VanderBloemen et al. 2020). Furthermore, Cisco were identified as a major contributor to the diets of Muskellunge and large Northern Pike and Walleye in one Minnesota lake based on stable isotope analyses, with models suggesting that Cisco constituted nearly half of the energy assimilated by Muskellunge (Herwig et al. 2022). Additionally, the CPUE of White Sucker decreased following Muskellunge stocking in 21 lakes without Cisco while no change was documented in 15 lakes where Cisco were present, which could indicate that Muskellunge prefer Cisco to White Sucker as prey when both species are available (Knapp et al. 2021). Those results support current guidance for new Muskellunge introductions in Minnesota, which indicates that lakes with healthy coregonid populations should be prioritized because these prey populations likely serve as primary diet items (MN DNR 2008). In contrast, our results indicate that Cisco presence alone is not indicative of their importance in the diets of Muskellunge or other predators. However, it is also possible that Cisco were not important in predator diets because our sampling occurred primarily in the shallow littoral areas of lakes. Cisco have strict oxygen, temperature, and water quality requirements, which tend to restrict their populations to the pelagic zone throughout the open-water period (Scott and Crossman 1973; Jacobson et al. 2008); this may have limited our ability to detect Cisco in diets collected from shallow waters. Future research should attempt to quantify the contribution of Cisco to predator diets outside of the littoral zone. This is especially crucial as Cisco populations have broadly declined in recent years (Jacobson et al. 2008, 2012; Honsey et al. 2016; Renik et al. 2020), a change that could result in dramatic shifts in aquatic food webs.

While other predators were highly piscivorous, Largemouth Bass depended heavily on cravfish and other aquatic invertebrates for their diets. Lepomis spp. were the most important fish in Largemouth Bass diets. Several studies have indicated an ontogenetic shift to piscivory in juvenile Largemouth Bass (Olson 1996; Shoup and Broderius 2018), even as aquatic invertebrates remained a major diet item for adults in other 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 (i.e., lower TSI value; Shoup and Lane 2015). Furthermore, the dietary importance of crayfish tended to increase with increasing Largemouth Bass size, similar to results reported by Olson and Young (2003).

Piscivore diets were consistent among seasons in this study. While seasonal differences in Muskellunge diets tend to be limited (Bozek et al. 1999; Brenden et al. 2004), seasonal diet variation is more common for the other species. The important prey of Northern Pike tend to fluctuate among different prey fish species throughout the year (Lawler 1965; Paukert et al. 2003), whereas Walleye and Largemouth Bass tend to consume fewer invertebrates and more fish from spring to fall (Hodgson et al. 1997; Ahrenstorff and Holbrook 2016; Herbst et al. 2016). However, many previous studies have used single diet metrics (e.g., percent composition by number or weight) rather than a composite metric (but see Sammons et al. 1994, Liao et al. 2002, and Frey et al. 2003 for exceptions). These single metrics tend to reflect predator feeding behaviors or the caloric contribution of prey items rather than population-wide diet patterns (Macdonald and Green 1983; Cortés 1997). Our results may indicate that broad diet patterns within populations remain consistent across seasons despite potential variation in individual behaviors.

None of the piscivores examined in this study had significantly different diets in lakes with Muskellunge versus lakes without Muskellunge. Although the native ranges of these species overlap substantially, Muskellunge have also been introduced into a wide variety of systems (Kerr 2011), creating the potential for increased interactions among species (Kerr and Grant 2000). To our knowledge, this study is the first to examine the diet patterns of sympatric piscivores in lakes with and without Muskellunge. The consistent diet patterns observed suggest no effects—either direct or indirect—of Muskellunge on feeding patterns of the species examined and provide further evidence that Muskellunge do not negatively affect co-occurring fish populations (Inskip and Magnuson 1983; Fayram et al. 2005; Knapp et al. 2012, 2021).

#### **Diet Overlap among Piscivore Species**

Predation by Muskellunge on other species of interest has been investigated in previous studies (e.g., Brenden et al. 2004; Koenig et al. 2015; Andrews et al. 2018), but little is known about how Muskellunge diets compare to those of sympatric piscivores. Although NMDS ordinations indicated the shared use of prey sources, PERMA-NOVA results suggested that Muskellunge diets were significantly different from the diets of the other piscivores included in this study across seasons. These differences were probably due to the broad range of prey that were important for Muskellunge in comparison with the more specialized diet patterns of the other piscivores. This was likely facilitated by Muskellunge being substantially larger than the other species in all lakes; thus, Muskellunge were able to consume larger and more varied prey items (Gaeta et al. 2018). Previous research in Wisconsin indicated that direct competition between Muskellunge and Walleye was unlikely (Nate et al. 2003; Fayram et al. 2005), and multiple studies in Minnesota failed to document declines in the relative abundance or average weight of Walleye in relation to Muskellunge stocking (Knapp et al. 2012, 2021). Conversely, Northern Pike CPUE was significantly lower and mean weight was significantly higher after Muskellunge stocking compared to reference lakes (Knapp et al. 2021). The authors (Knapp et al. 2021) noted that the Northern Pike CPUE in the Muskellunge-stocked lakes was relatively stable, whereas it increased in reference lakes. The trend of increasing Northern Pike CPUE was consistent with statewide trends in Minnesota from 1970 to 2013 (Bethke and Staples 2015), making the stable pattern in Muskellunge-stocked lakes more notable. Given the relative importance of Northern Pike in Muskellunge diets (IRI = 6.2%), it is possible that Muskellunge may be exerting some level of predatory control over Northern Pike in some Minnesota lakes and could provide an additional option for managers aiming to improve Northern Pike size structure (Pierce 2010; Bethke et al. 2021).

The diets of Muskellunge were different from those of the other piscivores across seasons, whereas differences between the diets of Muskellunge and Walleye were not significant during the spring sampling period. During this period, Yellow Perch were the most important prey item for both predators. Yellow Perch tend to spawn in shallow water shortly after ice-out (Becker 1983), leaving them vulnerable to predation by other fishes as well as piscivorous birds (Beylea et al. 1999). Numerous studies have indicated that adult Yellow Perch are important prey for Walleye during spring (Kelso 1973; Forney 1974; Herbst et al. 2016), and Yellow Perch were more important than all other categories except catostomids for Muskellunge in Wisconsin lakes (Bozek et al. 1999). However, both predators exhibited diverse diets during the spring in this study. Wahl and Stein (1991) similarly documented increased diet diversity during spring for Muskellunge and other esocids. The generalized diet patterns of Muskellunge and Walleye in spring, along with the significantly different diets in other seasons and across all seasons, suggest that competition between these two predator species is unlikely.

Similar to Muskellunge, the diets of Largemouth Bass were significantly different from those of the other piscivores across all seasons, and Largemouth Bass diets did not differ in relation to Muskellunge presence in this study. Our results are consistent with another Minnesota study, which found that Largemouth Bass occupied a lower trophic position and had low isotopic overlap with Walleye and Northern Pike (Bethke and Schmalz 2020). However, research in Wisconsin indicated that diet overlap between Largemouth Bass and Walleye can be high at times (Kelling et al. 2016) and that Walleye populations can be negatively influenced by Largemouth Bass (Fayram et al. 2005). Interactions between these two piscivores are expected to favor Largemouth Bass in many systems as water temperatures continue to increase due to global climate change (Hansen et al. 2017), which could lead to a disconnect between angler preferences and ecological constraints (Feiner et al. 2022). Lepomis spp. and invertebrates were important components of the diets for both predators, indicating that niche overlap may increase if other resources become scarce (i.e., Yellow Perch; Holbrook et al. 2022).

In contrast, the diets of Walleve and Northern Pike were similar across all seasons and regardless of Muskellunge presence. Diet similarities in this study were largely driven by the importance of Yellow Perch and Lepomis spp. for Walleye and Northern Pike, consistent with previous studies in the region (e.g., Anderson and Schupp 1986; Reed and Parsons 1996; Liao et al. 2002, 2004; Herbst et al. 2016). Interactions between these frequently cooccurring piscivores, including both direct predation and competition, have been well documented throughout their ranges (Anthony and Jorgensen 1977; Johnson et al. 1977; McMahon and Bennett 1996; Fayram et al. 2005; Paul et al. 2021). Recent studies have indicated that Walleye and Northern Pike occupy somewhat similar isotopic niches in Minnesota lakes (Bethke and Schmalz 2020; Herwig et al. 2022), and higher levels of overlap resulted from increased use of littoral energy following lake

infestation with zebra mussels *Dreissena polymorpha* (McEachran et al. 2018; Morrison et al. 2021). Recent work has revealed substantial changes in the abundance and size structure of Yellow Perch populations in Minnesota lakes (Holbrook et al. 2022), which could lead to increased competition between Walleye and Northern Pike if the resource becomes limiting. Interactions between these two piscivores should be monitored closely as aquatic systems continuously change and adapt.

## **Effects of Environmental Variables**

Several habitat variables were related to the diets of the piscivores in this study. We found significant correlations between the percent littoral area within study lakes and the diets of all piscivores examined; surface area, TSI, and SDI also were related to the diets of Northern Pike and Largemouth Bass. The direction of these vectors on NMDS ordinations indicated a correlation with the importance of centrarchids, especially Lepomis spp., for all predators. More specifically, centrarchids tended to be more important in lakes with higher percent littoral area, higher TSI, and higher SDI, but they were less important in lakes with larger surface area. Lakes with large littoral zones (i.e., high percent littoral area and SDI) are more likely to produce large year-classes of Bluegill (Theiling 1990), but strong year-classes are less likely in large, deep lakes (Tomcko and Pierce 2001, 2005). Furthermore, juvenile growth rates and length at age tend to be higher in more productive waters (i.e., higher TSI), while increased overall growth and size structure are often associated with clearer water (i.e., lower TSI; Snow and Staggs 1994; Tomcko and Pierce 2005; Hoxmeier et al. 2009). Consequently, the combination of these three habitat variables likely resulted in abundant Lepomis populations that grew quickly to suitable prey size but rarely exceeded the gape limitations of predators.

In addition to the effects of lake-scale habitat on predator diets, the gill-net CPUE of Yellow Perch was also correlated with Walleye diets in this study. Higher Yellow Perch CPUE corresponded with increased importance of Yellow Perch in Walleye diets and provides further evidence of the well-documented predator-prey dynamics between these two species (Forney 1974; Nielsen 1980; Pierce et al. 2006; Ahrenstorff and Holbrook 2016). Although similar dynamics have been observed between Yellow Perch and Northern Pike (Paukert and Willis 2003; Paukert et al. 2003; Dembkowski et al. 2017), Yellow Perch CPUE was not correlated with the diets of Northern Pike in this study. Furthermore, the trap-net CPUE of Bluegill was not a significant variable for any predator despite Bluegill serving as important prey and despite the strong correlations between habitat variables and the dietary importance of centrarchids for all predators. Although CPUE is widely used by managers and researchers as a measure of relative population abundance (Ney 1999; Hubert et al. 2012), factors such as fish size and habitat availability can also influence catch rates in passive gears (Rudstam et al. 1984; Jackson and Harvey 1997; Anderson 1998; Pierce et al. 2010). Similarly, fish size and habitat can also influence predator diet patterns in addition to potential effects of prey fish abundance (Sass et al. 2006; Ahrenstorff et al. 2009; Middaugh et al. 2013; Gaeta et al. 2018). Our results suggest that lake-scale habitat may provide additional information to managers in identifying important prey items for predators included in this study beyond the relative abundance of key prey species.

#### Management Implications

Muskellunge, Northern Pike, Walleye, and Largemouth Bass coexist naturally and through stocking in a variety of aquatic systems throughout the region and beyond (Li et al. 1995: Kerr 2011, 2016: MN DNR 2016: Rvpel et al. 2019). These species are all top predators; thus, the potential exists for competition, predation, and community shifts as well as broader ecosystem consequences (as reviewed by Eby et al. 2006). Recognition of these tradeoffs has increased in recent years, and ecosystem-based fisheries management approaches have increased in popularity with various management agencies (Link 2010; Dolan et al. 2016). Diet studies such as ours provide critical information on potential trophic interactions among top predators and their prey. This information is particularly powerful when combined with the population-level monitoring performed by various management agencies (e.g., Knapp et al. 2021).

Despite abundant evidence that other popular sport fish are not important components of Muskellunge diets (Bozek et al. 1999; Brenden et al. 2004; Wolter et al. 2012; Andrews et al. 2018) and despite numerous studies indicating that Muskellunge management does not negatively influence other fish populations (Nate et al. 2003; Fayram et al. 2005; Knapp et al. 2012, 2021), concerns regarding new introductions and management of this species are relatively common (Schroeder et al. 2007; Murphy 2017). However, investigations into the potential indirect effects of Muskellunge on other piscivores have been lacking up to this point. In this study, we documented Muskellunge populations with diverse diet patterns that were less specialized than and significantly different from the diets of other predators and we provided evidence that the diets of Northern Pike, Walleye, and Largemouth Bass were not significantly different between lakes with Muskellunge and those without Muskellunge. To our knowledge, this is the first study to simultaneously evaluate the diets of these sympatric piscivores, and it provides further evidence that Muskellunge have little direct or indirect effect on the populations of these

species. Finally, we showed that environmental variables related to lake size, morphometry, and productivity were strongly correlated with the diets of all four predator species, thus generating valuable information concerning predator diets for use by resource managers that are unable to collect their own diet data. Our results indicate that while Muskellunge, Northern Pike, Walleye, and Largemouth Bass can coexist in a variety of lakes, populations of important prey taxa and lake-wide habitat variables should be considered before management actions (e.g., fish stocking) are implemented to ensure that prey availability is adequate and to ensure that potential competition among these piscivores is not increased to the detriment of existing fisheries.

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#### SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

## Appendix A: Prey Abbreviations and Permutation Tests of Multivariate Dispersion

TABLE A.1. Common names and abbreviations used to represent 30 prey categories observed in the diets of Muskellunge, Northern Pike, Walleye, and Largemouth Bass in Minnesota lakes.

Prey category	Abbreviation
Amphibians	AMP
Banded Killifish Fundulus diaphanus	BKF
Birds	BRD
Black Crappie Pomoxis nigromaculatus	BLC
Bowfin Amia calva	BOF
Brook Silverside Labidesthes sicculus	BKS
Brook Stickleback Culaea inconstans	BST
Bullheads Ameiurus spp.	BLH
Catostomidae	OTS
Central Mudminnow Umbra limi	CNM
Cisco Coregonus artedi	TLC
Crayfish	CRA
Cyprinidae	OTM
Darters Etheostoma spp.	DAR
Invertebrates	INV
Lake Whitefish Coregonus clupeaformis	LKW
Logperch Percina caprodes	LGP
Mammals	MAM
Black bass Micropterus spp.	MIC
Muskellunge Esox masquinongy	MUE
Northern Pike Esox lucius	NOP
Rock Bass Ambloplites rupestris	RKB
Sculpins Cottus spp.	SCU
Sunfish Lepomis spp.	SUN
Tadpole Madtom Noturus gyrinus	TPM
Trout-perch Percopsis omiscomaycus	TRP
Turtles	TUR
Unidentified fish	UNK
Walleye Sander vitreus	WAE
Yellow Perch Perca flavescens	YEP

TABLE A.2. Response and predictor variables, df, *F*-statistics, and *P*-values for permutation tests of multivariate dispersion among piscivore diets in Minnesota lakes. These results (P > 0.05) indicate that significant permutational multivariate ANOVA results were driven by differences in overall diets rather than differences in multivariate dispersions.

Response variable	Predictor variable	df	F-statistic	<i>P</i> -value
Predator diets	Spring	3	1.109	0.355
	Summer	3	0.092	0.964
	Fall	3	1.364	0.275
	Combined seasons	3	1.578	0.200
Muskellunge diets	Length category	5	0.618	0.679
Northern Pike diets	Length category	4	2.044	0.106
Largemouth Bass diets	Length category	4	2.063	0.104

TABLE A.3. Lake group, df, *F*-statistics, and *P*-values for permutation tests of multivariate dispersion among diets of Northern Pike, Walleye, and Largemouth Bass in Minnesota lakes. These results (P > 0.05) indicate that significant permutational multivariate ANOVA results were driven by differences in overall diets rather than differences in multivariate dispersions.

Lake group	df	F-statistic	P-value	
Muskellunge present	2	0.537	0.599	
Muskellunge absent	2	0.959	0.390	