North American Journal of Fisheries Management

ISSN: 0275-5947 print / 1548-8675 online
DOI: 10.1002/nafm.10562

MANAGEMENT BRIEF

Are Muskellunge Affecting Fish Communities in Waters Where They Have Been Introduced? A Re-examination of Minnesota's Stocked Muskellunge Waters

Michael L. Knapp*
Minnesota Department of Natural Resources, 1601 Minnesota Drive, Brainerd, Minnesota 56401, USA

Steven W. Mero
Minnesota Department of Natural Resources, 1201 East Highway 2, Grand Rapids, Minnesota 55744, USA

David F. Staples
Minnesota Department of Natural Resources, 5463C West Broadway, Forest Lake, Minnesota 55025, USA

Abstract
Muskellunge *Esox masquinongy* are large piscivores stocked into numerous lakes in North America, but the potential effects of these stockings remains poorly understood. To investigate potential fish community changes associated with Muskellunge stocking, we contrasted catch per unit effort (CPUE) for seven fish species commonly found in Minnesota, along with mean weight for two predator species, before and after Muskellunge introduction in 36 lakes with that of paired reference lakes. Because of the known importance of Cisco *Coregonus artedi* as prey for Muskellunge, we also examined these data by separating the lakes into those with and without Cisco. Across all 36 lakes, we observed several significant differences between stocked and reference lakes. Yellow Perch *Perca flavescent* CPUE in gill nets were significantly higher after Muskellunge were introduced, as was mean weight for Northern Pike *Esox lucius*. Gill-net CPUE for Northern Pike and White Sucker *Catostomus commersonii* were both lower following Muskellunge introduction. When subsets of lakes with and without Cisco were considered, results for the 21 lakes without Cisco were similar to the results of the entire set of lakes. In the 15 lakes with Cisco, the only significant result was lower Northern Pike CPUE after Muskellunge stocking. Our results are evidence that the introduction and management of Muskellunge in these lakes has not adversely affected game fish populations.

The goal of Muskellunge *Esox masquinongy* management in Minnesota is to provide high-quality angling opportunities for trophy fish (MNDNR 2008). Stocking as a management tool has been used to restore or supplement overharvested native populations (Olson and Cunningham 1989), create new fishing opportunities through introduction, and maintain native or introduced populations where nursery and juvenile habitat has been degraded or is limited. The origin of Minnesota's modern Muskellunge program can be traced to the evaluation of four genetic strains and subsequent selection of the Mississippi River strain (also known as Leech Lake strain) for all future stocking because of its superior growth and size potential (Younk and Strand 1992). Beginning in 1982, there was a transition to stocking the Mississippi strain in both existing stocked and new waters. The new waters stocked through the 1980s represent the bulk of the expansion of the Muskellunge waters in the state (Minnesota Department of Natural Resources, unpublished data). Changes in minimum length limits to 914 mm in 1983, 1,016 mm in 1993, 1,219 mm in 2007, and 1,372 mm in 2015 were designed to address biological and social aspects of the program. Increasing minimum length limits allowed the Mississippi strain the additional time necessary to mature and have multiple years of spawning before being exposed to harvest while addressing anglers' ever-increasing desire to catch larger fish. Understanding

*Corresponding author: michael.knapp@state.mn.us
Received June 5, 2020; accepted November 18, 2020

that a trophy is uniquely defined by each angler, both Anderson and Gutreuter (1983) and Gabelhouse (1984) proposed trophy Muskellunge to be 1,270 mm and longer as a standard for fisheries management. Angler reports and Minnesota Department of Natural Resources (MNDNR) fisheries surveys have documented the subsequent increase in trophy Muskellunge throughout the 2000s (Younk and Pereira 2006; Richards 2017), and interest has grown substantially since the onset of the modern Muskellunge program in the 1980s (Wingate 1986; Leitch and Baltezore 1987; Schroeder and Fulton 2005; Schroeder et al. 2007; Wingate and Younk 2007; Schroeder 2015; Miller 2018). The observed increases in both numbers of large fish and angler interest suggest that significant progress toward the goal of developing high-quality trophy fisheries has been made.

Concurrent with the expansion and increased popularity of Muskellunge fisheries has been increased public concern about their management. In the New River, Virginia, many anglers remain concerned over the effects of Muskellunge management on the Smallmouth Bass *Micropterus dolomieu* fishery (Murphy 2017), despite results from diet and bioenergetics studies that indicated that Smallmouth Bass were a relatively minor component of Muskellunge diets (Brenden et al. 2004; Doss et al. 2017). In Minnesota, the potential impacts of stocked Muskellunge on resident fish communities is the most prevalent concern in comments from the public, but fear of attacks on swimmers, introduction of invasive species by anglers, declining property values, and crowding on the lakes are just a few other examples. These concerns have even risen to the legislative level with attempts to block new introductions and in some cases to discontinue stocking in lakes deemed biologically successful by fisheries managers. In spite of and perhaps because of the success of Muskellunge management, social aspects of management have become increasingly important in recent years. Stakeholders desiring to become more informed often demand thorough investigations be completed when new management actions are implemented or even considered (e.g., new introductions or regulation changes). Though this study does not attempt to investigate Muskellunge fisheries from a human dimensions perspective, social concerns voiced by some in the public have been the impetus for re-examining the data from lakes stocked with Muskellunge. For fisheries managers, the core issue remains one of fish community dynamics and potential species interactions with Muskellunge. Adult Muskellunge are the apex predator in systems where they are present, and fisheries management relies on good scientific information to manage these fish communities effectively.

Comments during the public input process for considering new Muskellunge waters and criticisms of an initial evaluation of the stocked Muskellunge lakes (Knapp et al. 2012) have been invaluable in guiding this study. An example of an important point from the public input process regarded what Muskellunge might consume should Cisco *Coregonus artedi* populations continue to decline due to climate change. Fisheries managers were aware of climate change considerations for all species, and Jacobson et al. (2012) documented a decline in Minnesota Cisco populations from 1980 to 2007. Managers also understood the importance of Cisco as prey for Muskellunge (Oehmcke et al. 1958) and that a number of studies found that esocid species prefer soft-rayed, fusiform-shaped prey like Cisco (Weithman and Anderson 1977; Gillen et al. 1981; Engstrom-Heg et al. 1986; Wahl and Stein 1988). In fact, the presence of Cisco has been a key consideration in lakes selected for Muskellunge stocking in Minnesota (MNDNR 2008). However, not all stocked lakes contain Cisco because their natural distribution exists in the northern half of Minnesota while Muskellunge fisheries exist throughout the state. The fact that some stocked Muskellunge lakes contained Cisco while others did not provided an opportunity to evaluate how Cisco may provide a buffer for other potential prey species. Even though there are no stocked lakes where Cisco were extirpated to evaluate, evaluating the lakes without Cisco may provide insight into questions brought from the public, should Muskellunge be a determining factor in the abundance of the other species being examined. Consequently, given the biological importance and social interest of Cisco as prey and the environmental pressure on the species, further investigation was warranted to evaluate fish community interactions in lakes stocked with Muskellunge that contained Cisco and those that did not.

Studies attempting to evaluate potential impacts of stocked Muskellunge on resident fish communities remain scarce (Brenden et al. 2004; Knapp et al. 2012; Kerr 2016; Doss et al. 2017). Knapp et al. (2012) investigated whether changes in catch rates for seven important fish species occurred following the introduction of Muskellunge in 41 Minnesota lakes. Standardized fish surveys continued in these lakes, and though the authors did not observe consistent negative changes linked to the introduction of Muskellunge, they recommended further study to investigate if there might be any longer-term effects. Additional time has allowed the few younger Muskellunge populations evaluated in Knapp et al. (2012) to further mature while additional surveys provided more data for evaluation.

The broad objective of our study was to re-examine whether Muskellunge were having any measurable effects on the fish communities where they were introduced. We contrasted gill net and trap net data from standard fisheries surveys for seven species before and after the first Muskellunge stocking event in 36 lakes with that of paired reference lakes. The specific objectives were to (1) expand

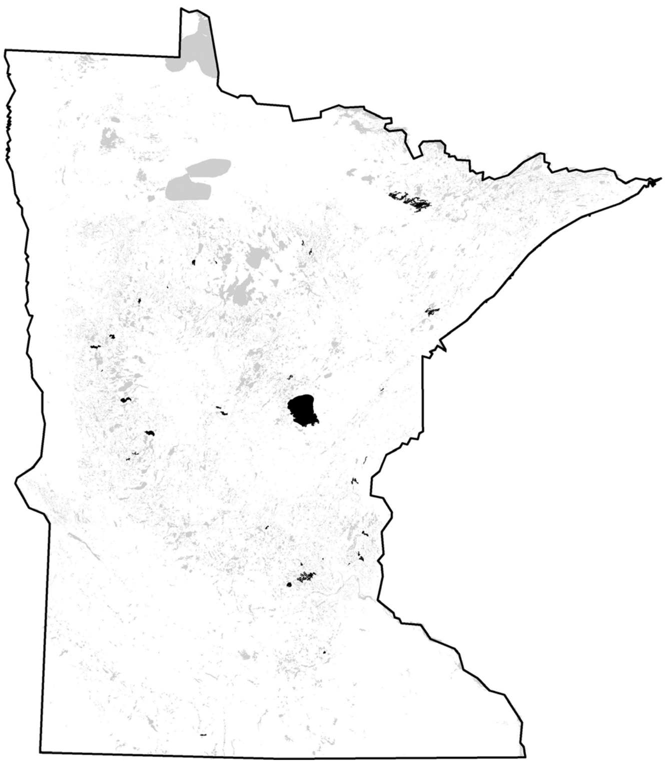

FIGURE 1. Distribution of lakes stocked with Mississippi River strain Muskellunge in Minnesota that are included in this study.

on the Knapp et al. (2012) study by incorporating 12 additional years of fisheries survey data, reference lakes, and more advanced statistical methodology; and (2) investigate potential changes in catch rates for the seven study species in lakes with and without Cisco. We postulated that if Muskellunge were negatively affecting fish communities where they have been introduced, we would observe consistent patterns of decline for many of the species being investigated.

METHODS

Study lakes and characteristics.— Knapp et al. (2012) examined 41 lakes distributed throughout Minnesota stocked with Muskellunge. A total of 36 of the original 41 lakes (Figure 1; Table 1) were included in this study. Five of the original lakes were excluded because they were either dominated by a previously stocked strain with poor growth potential (Younk and Strand 1992; Miller et al. 2012), were no longer stocked with Muskellunge, or did not have adequate fish survey data prior to stocking. Our study only examined waters stocked with Mississippi strain Muskellunge. Minnesota has an additional 60 managed Muskellunge waters, but these waters are either stocked with tiger muskellunge (Muskellunge × Northern Pike *E. lucius*) or have self-sustaining populations. Relative abundance of the seven species studied varied across these lakes and represented a range of CPUEs, thereby eliminating bias if Muskellunge effects were dependent on the prevalence of the other species.

We assumed that study lakes had established Muskellunge populations. Muskellunge have been stocked in these waters for 20–56 years (mean, 39.1 years) with 33 of the 36 lakes receiving fish for at least 30 years. This allowed evaluation of long-term changes in the fish communities. The study lakes had adequate time for multiple year classes to grow to trophy size. The 36 lakes received a mean of nine stockings during the initial 15 years. Further, we documented the presence of large Muskellunge during the time frame of this study. On average, the 36 study lakes had Muskellunge ≥1,016 mm within 13 years from the initial stocking, with an average of 8.1 surveys per lake after the initial documentation of fish this size (Table 1). All but one of the 36 study lakes had Muskellunge measuring at least 1,270 mm, observed on average 21.4 years after the initial stocking. A mean of 6.3 surveys per lake were conducted on those lakes after the initial documentation of fish ≥1,270 mm.

Muskellunge density estimates suggest that adult (≥762 mm) densities were low for the study lakes where they were available. Twenty-four of the 36 stocked lakes had adult density estimates, with 18 having biomass estimates within the past 12 years (MNDNR, unpublished data). Adult densities ranged from 0.04 to 1.40 fish/ha with a mean of 0.41/ha. Most (92%) had densities between 0.14 to 0.51 fish/ha with the highest and lowest density estimates representing the smallest and largest lakes, respectively. Biomass estimates ranged from 1.64 to 5.33 kg/ha with a mean of 3.32 kg/ha. Though density estimates were low, the fisheries in these waters consistently attract trophy Muskellunge anglers.

Survey gear and protocol.— We investigated changes in catch rates for seven species commonly sampled using standard survey methods (MNDNR 1993) as in Knapp et al. (2012). Survey data were available from as early as 1941, with 91% of the surveys occurring from 1970 through 2018. The number of years and survey frequency varied for each lake. Northern Pike, Walleye *Sander vitreus*, Yellow Perch *Perca flavescens*, White Sucker *Catostomus commersonii*, Black Crappie *Pomoxis nigromaculatus*, and Cisco were sampled using multifilament experimental gill nets. These gill nets have been a standard gear in MNDNR fisheries surveys for decades (Moyle 1950; Wingate and Schupp 1984; MNDNR 1993) and are used for sampling lakes across North America and Europe (Morgan 2002; CEN 2005; Bonar et al. 2009). Catch per unit effort has been shown to be correlated with abundance measured by other methods (Ryan 1984; Richards and Schnute 1986; Elliott and Fletcher 2001; Simpfendorfer et al. 2002; Pierce and Tomcko 2003; Pierce et al.

TABLE 1. Selected characteristics of 36 Minnesota lakes stocked with Mississippi River strain Muskellunge included in this study. Lake areas were derived from GIS in 2018. Number of surveys before and after represents the number of surveys before and after Muskellunge were stocked. Number of surveys after the first fish that was 1,016 mm and 1,270 mm was sampled are represented under the respective lengths. Year stocked represents the first substantial or regular stocking of Muskellunge.

Lake	Area (acres)	Maximum depth (ft)	Presence of Cisco (Y/N)	Number of surveys				Year stocked
				Before	After	1,016 mm	1,270 mm	
Alexander	2,709	64	Y	5	8	8	5	1988
Bald Eagle	1,047	36	N	4	11	10	5	1982
Beers	200	61	N	2	4	3	0	1977
Bemidji	6,596	76	Y	3	9	6	5	1978
Big	3,592	35	Y	2	10	9	9	1969
Cedar	1,745	105	Y	5	6	5	3	1994
Cross	925	30	N	4	10	5	4	1977
Detroit	3,067	89	Y	6	7	5	4	1989
Eagle	287	34	N	3	10	9	6	1982
East Rush	1,481	24	N	1	11	5	4	1968
Elk	303	93	Y	1	8	5	3	1982
Forest	2,271	37	N	7	9	8	7	1989
Fox	951	20	N	16	19	13	10	1999
French	876	56	N	4	10	6	4	1974
Harriet	341	87	N	4	9	6	5	1974
Independence	832	58	N	2	13	9	7	1971
Island	536	42	N	6	7	4	3	1982
Island Reservoir	8,001	94	N	2	9	4	3	1972
Little Wolf	528	24	N	5	6	4	1	1982
Lobster	1,329	65	Y	1	11	7	5	1968
Mille Lacs	128,226	42	Y	11	34	27	24	1984
Miltona	5,724	105	Y	3	14	10	7	1982
Minnetonka	14,730	113	N	2	22	19	17	1974
North Star	1,071	90	Y	6	6	4	3	1989
Oscar	1,191	25	N	3	9	5	3	1985
Owasso	375	37	N	10	6	5	4	1982
Pelican	3,962	55	Y	3	12	7	6	1978
Plantagenet	2,531	65	Y	3	7	6	5	1982
Round	127	20	N	3	3	3	na	1990
Shamineau	1,434	52	N	4	8	5	4	1988
Sugar	1,020	69	Y	1	9	7	3	1970
Vermilion	39,273	76	Y	12	34	26	21	1984
Waconia	3,080	37	N	5	12	10	10	1984
West Battle	5,565	108	Y	1	13	7	7	1963
West Rush	1,579	42	N	1	11	10	4	1968
White Bear	2,428	83	N	3	13	9	9	1975

2010) and was used as a measure of relative abundance for each species in this study. We also investigated for changes in mean weight of all Northern Pike and Walleye caught in gill nets following Muskellunge stocking, as in Knapp et al. (2012). Weights of the two predator species were assessed because size structure is another population metric that may be influenced by interspecific competition at higher trophic levels. Gill nets used during standardized fisheries surveys contained five panels of 19-, 25-, 32-, 38-, and 51-mm bar measure mesh. Each panel was 1.8 m high × 15.2 m long and sewn to the others in ascending mesh size. Bluegill *Lepomis macrochirus* and Black Crappie were also sampled using trap nets with a 19-mm bar measure mesh size, a 0.9 m high × 1.8 m wide double frame, and a 12.2-m lead. Netting effort, in terms of duration, was consistently a 24-h period, with the number of nets standardized in 1993 (MNDNR 1993) based on lake size. Individual lakes were typically sampled at the same

TABLE 2. Selected characteristics of the 35 Minnesota unstocked reference lakes included in this study. Lake areas were derived from GIS in 2018.

Lake	Area (acres)	Maximum depth (ft)	Total number of surveys	Presence of Cisco (Y/N)
Balsam	716	37	12	Y
Big Birch	2,107	81	10	Y
Big Cormorant	3,657	75	13	N
Big Marine	1,799	60	16	N
Big Pine	4,728	76	15	Y
Burntside	7,314	126	19	Y
Cedar	790	108	9	Y
Clear	429	28	13	N
Clearwater	3,187	73	7	Y
Crookneck	183	22	6	N
Deer	298	42	12	Y
Fish	238	49	10	N
Green	5,569	110	33	Y
Green	1,809	32	12	N
Hill	794	48	13	N
Kabetogama	24,034	80	28	Y
Long	285	33	13	N
Maple	831	78	11	N
Medicine	925	49	14	N
North Twin	326	59	10	N
Osakis	6,389	73	15	Y
Pine Mountain	1,612	80	13	Y
Pulaski	813	87	9	N
Round	2,860	24	12	Y
Rush	5,276	68	13	Y
Sand	527	47	13	N
Shields	940	42	12	N
South Center	835	109	16	N
South Silver	252	22	9	N
Stuart	740	49	12	Y
Sullivan	1,103	57	11	Y
Ten Mile	5,080	208	20	Y
Turtle	450	28	8	N
Villard	544	16	8	N
West Lake Sylvia	904	97	7	Y

time each year using the same net locations. Surveys occurred in June, July, and August with a frequency of roughly 3 to 5 years between surveys. Notable exceptions to this include Fox, Mille Lacs, and Vermilion lakes, which were sampled annually in September. Data for stocked and reference lakes were obtained from the MNDNR fisheries database and checked for errors by personnel from respective fisheries management areas.

Data considerations.— The initial Muskellunge stocking event was denoted for each lake as the year when fish were introduced and regularly stocked as fall fingerlings or larger (Knapp et al. 2012). Big Lake contained a very low-density native population, and a few lakes had Muskellunge introduced in very low numbers before regular stocking began. In these cases, viable populations were not established, so the effect of these few fish was assumed negligible. Surveys conducted before regular stocking began were considered prestocking surveys. Surveys in the same year as the onset of regular stocking were also considered prestocking, as they would have been completed prior to the actual fall stocking event(s). Initial Muskellunge stocking dates ranged from 1963 to 1999 (Table 1).

We also considered that if the introduction of Muskellunge was going to have an effect on the study species, an established population having multiple age-classes and size-classes would have a more definitive effect than a population shortly after the initial stockings. Therefore, we also evaluated the lakes by excluding survey data from the year of stocking until 15 years later, so those data would not influence the poststocking results.

Knapp et al. (2012) noted the challenges in using reference lakes in an evaluation of lakes specifically chosen for Muskellunge management; i.e., lakes stocked with Muskellunge were not chosen at random, but were selected based on criteria thought to support healthy Muskellunge populations. However, a reference group of ecologically similar lakes would help account for large-scale regional changes unrelated to Muskellunge stocking. To select study reference lakes, we compiled a list of candidate reference lakes for each individual stocked lake that were in the same ecological lake class (Schupp 1992), within a 50-mi radius, and within the same MNDNR fisheries management area (because most lake-specific management decisions are made at this administrative level). In two cases, a 75-mi radius was required to find a reference lake within the same lake class. A single reference lake was randomly chosen from the resulting list of lakes; the sole exception was Mille Lacs Lake, for which no similar, nonstocked lakes were available. The result was a group of reference lakes with similar distributions of chemical and physical habitats and spatial location as the group of stocked lakes (Table 2). The group of reference lakes was also similar to the group of stocked lakes in terms of management (e.g., stocked or significant natural reproduction to sustain a viable Walleye fishery), special regulations, and aquatic invasive species such as zebra mussels *Dreissena polymorpha* and Eurasian watermilfoil *Myriophyllum spicatum* (Figure 2). As with the stocked lakes, relative abundance of the species investigated varied from relatively high to very low in reference lakes. Note that this is an observational study, so correlations observed here do not necessarily infer casual relationships, and there is a possibility of unknown factors such as resiliency to change or angling pressure affecting the study results. However, the broad range of lakes selected for Muskellunge stocking and as reference lakes helped mitigate effects of these unknowns.

Statistical analysis.— We tested for potential effects of Muskellunge stocking across all 36 lakes as well as subsets of 15 lakes with and 21 lakes without Cisco to investigate whether fish communities responded differently in their absence. All species' CPUE and weight data were $\log_e$ transformed for analysis; zero values were replaced by a detection limit (Clarke 1998) calculated as one-half of the minimum nonzero observed CPUE for that species. A linear mixed-effects model with Gaussian error structure was used to estimate change in each species' $\log_e$ transformed CPUE or weight following Muskellunge stocking while accounting for among-lake differences and underlying temporal trends:

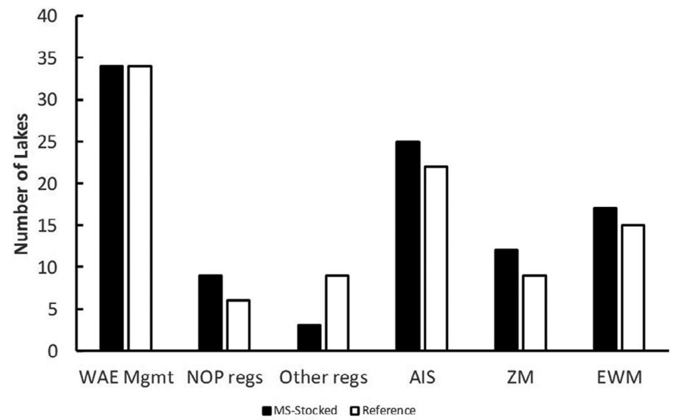

FIGURE 2. Comparison of the primary management activities and aquatic invasive species (AIS) for Minnesota lakes stocked with Mississippi River strain Muskellunge (MS-stocked) and unstocked reference lakes. Management activities include Walleye management (WAE Mgmt), Northern Pike harvest regulations (NOP regs), and other harvest regulations for Bluegill, Black Crappie, or Largemouth/Smallmouth Bass (Other regs). The AIS bars are the sum of all AIS species. The most common AIS for these lakes were one or both of either zebra mussels (ZM) and Eurasian watermilfoil (EWM), so they are also presented separately.

$$\log_e(\text{CPUE or Weight}) \sim \text{Group} \times \text{Stocking Status} + (1|\text{Lake}) + (1|\text{Year}) + Error,$$

where Group is a two-level indicator variable for stocked or reference group and Stocking Status is a two-level pre/-post stocking indicator variable in which reference lakes were considered poststocking after Muskellunge were introduced to their paired stocked lake. The model contained two random effect explanatory variables, Lake and Year, both assumed to be normally distributed. The Lake effect was included to account for inherent differences among lakes in average $\log_e$ CPUE or weight, while the Year effect was included to account for annual fluctuations and underlying temporal trends in catch rates and weights common to all lakes in the study (e.g., the statewide increase in Walleye CPUE 1970–2013 found in Bethke and Staples 2015). The fixed effects in the model are a before–after control–impact design (reviewed by Smith 2002), in which a significant interaction between Group and Stocking Status indicates a different response between stocked and reference lakes following the stocking date. Tests for significance used $\alpha = 0.05$, and P-values for the interaction estimates were calculated with degrees of freedom df = 35, the number of stocked lakes minus 1 (df = 14 and 20 for subsets with and without Cisco, respectively). To visually show the relative changes between stocked and reference lakes, the fitted models were used to estimate 95% confidence intervals of poststocking changes for each study group.

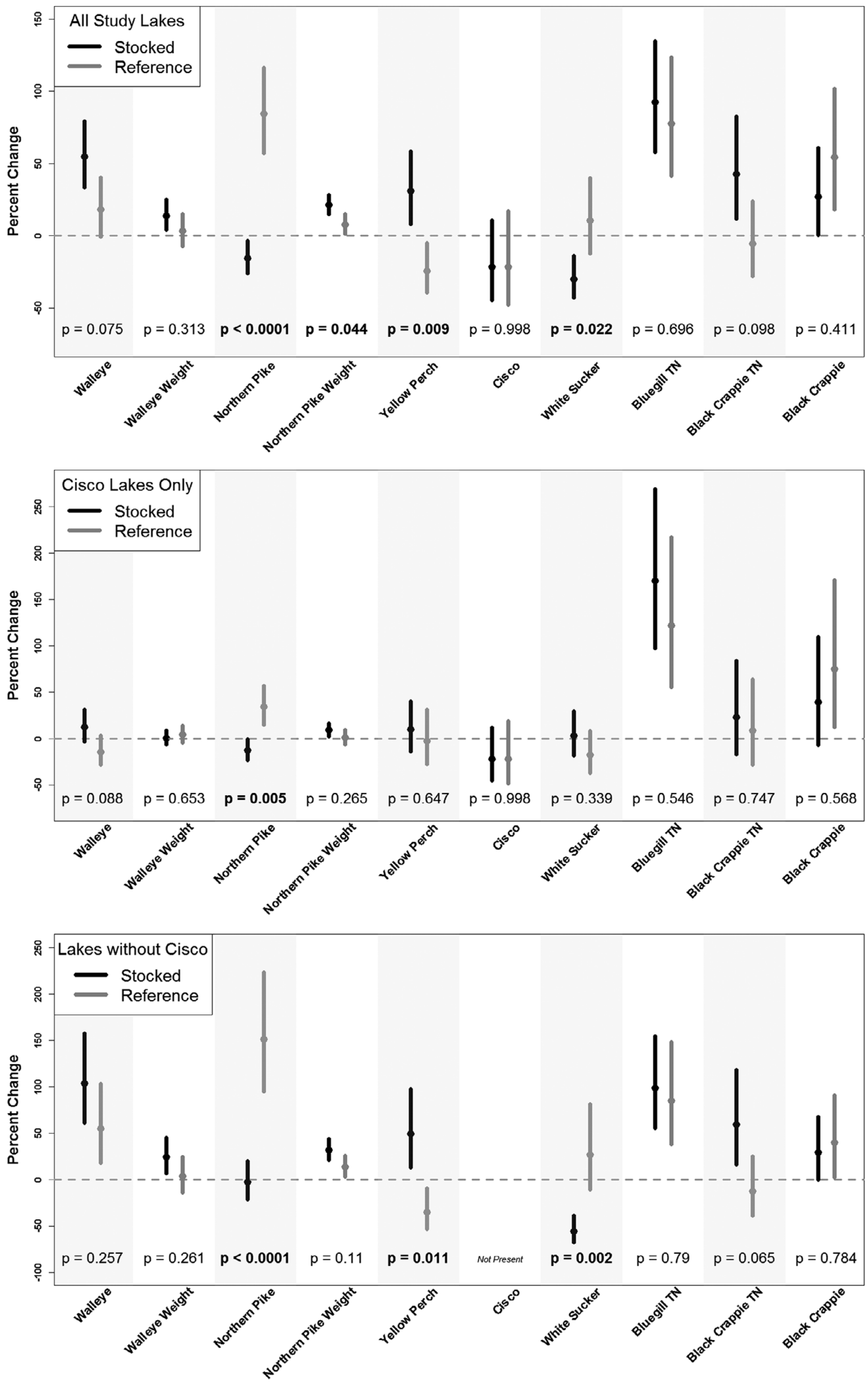

FIGURE 3. Estimated percent change and associated 95% confidence intervals for changes in catch rate or weight associated with the introduction of Muskellunge in 36 Minnesota lakes along with subsets of lakes with and without Cisco. The *P*-values for the treatment group by stocking status interaction test from the mixed effects model are provided with the significant results in bold. Species sampled by trap net are noted as "TN;" all others were sampled in gill nets.

Because not all lakes were sampled within a given year, the annual average of CPUE or weights across each year's sampled lakes is not representative of the typical value for the stocked or reference groups as a whole. Therefore, to visually display the temporal changes in the study groups across the study period, a simplified version of the linear mixed-effects model with the Group and Stocking Status fixed effects removed was fit to both study groups independently and used to estimate median annual CPUE (or weights) for plotting purposes. All analyses were performed with statistical program R (R Core Team 2020); mixed-effects models were fit using the lmer() function in the lme4 package (Bates et al. 2015).

RESULTS

Differences in Stocked and Reference Lakes before and after Muskellunge Stocking

Analysis of the 36 lakes with the before–after control–impact model resulted in significant differences following Muskellunge introduction for 4 of the 10 species metrics measured (Figure 3). Northern Pike CPUE was significantly lower and mean weight significantly higher following Muskellunge introduction across all 36 lakes relative to the reference lakes. Functionally, median Northern Pike CPUE was relatively constant in stocked lakes, while CPUE increased in the reference lakes over time (Figure 4). Similarly, median weight of Northern Pike was relatively constant in reference lakes, and it increased in stocked lakes (Figure 3). Other significant changes included increases in Yellow Perch CPUE and declines in White Sucker CPUE across all 36 lakes after stocking compared to changes observed in the reference lakes (Figure 3). In the case of White Sucker CPUE, lakes in both study groups generally declined over the past 30 years (Figure 4), but the stocked lakes showed evidence of a stronger decline associated with Muskellunge stocking. Walleye CPUE and mean weight as well as CPUE for Cisco, Bluegill, and Black Crappie had no significant difference following the introduction of Muskellunge relative to reference lakes (Figures 3 and 4).

When data from the initial 15 years following Muskellunge stocking were excluded, the results were the same as the before–after control–impact comparison with all available data with a single exception. We observed a significant ($P = 0.015$) increase for Walleye CPUE in stocked lakes relative to the reference lakes when a 15-year gap was used. Due to the similarity in results, we chose to focus on the results from the method most similar to Knapp et al. (2012) to alleviate redundancy while reflecting new methods and information.

Differences in Lakes with and without Cisco

In the 15 lakes where Cisco were present, Northern Pike CPUE was lower relative to reference lakes after Muskellunge were stocked (Figure 3). This was the only significant change in this group of lakes. As with changes in Northern Pike CPUE for the other two lake groups, stocked lakes remained relatively stable while Northern Pike CPUE in reference lakes increased.

Significant differences were detected in three of the nine species metrics in lakes without Cisco (Figure 3). Northern Pike CPUE was lower after Muskellunge stocking relative to reference lakes, and while mean Northern Pike weight was higher after Muskellunge stocking, the difference was not significant ($P = 0.11$; Figure 3). Yellow Perch CPUE was significantly higher poststocking compared to reference lakes in the 21 lakes without Cisco, while White Sucker CPUE was significantly lower (Figure 3). Mean weight for Walleye and Northern Pike as well as CPUE for Walleye, Bluegill, and Black Crappie were not significantly different following the introduction of Muskellunge relative to reference lakes (Figure 3).

DISCUSSION

Our results support the findings of Knapp et al. (2012), which demonstrated that the introduction and management of Muskellunge has not adversely affected game fish populations in Minnesota lakes. Interactions between Walleye and Muskellunge were of particular interest because Walleye are the most sought-after species in Minnesota (Miller 2018). Walleye fisheries contribute substantially to local tourism-based economies and are therefore intensively managed (Isermann and Parsons 2011). Our study found no significant decline in Walleye CPUE or mean weight related to Muskellunge stocking. In fact, for all three lake groupings, Walleye catch rates were higher after Muskellunge stocking, though the results were not statistically significant. Knapp et al. (2012) also found no significant difference in Walleye CPUE across 41 Minnesota lakes after Muskellunge stocking was initiated and noted that many of the study lakes were some of the best Walleye fisheries in the state. Similarly, Kerr (2016) noted that 63% of Ontario's inland Muskellunge waters also contained Walleye, and Nate et al. (2003) found that Wisconsin lakes with self-sustaining Walleye populations were associated with high Muskellunge densities. Furthermore, previous work in Wisconsin lakes has shown that direct competition and predation are unlikely to occur with these species (Bozek et al. 1999; Fayram et al. 2005).

Consistent with the results of Knapp et al. (2012), Northern Pike CPUE in stocked lakes remained stable following Muskellunge introduction while pike CPUE increased within reference lakes, a trend consistent with the

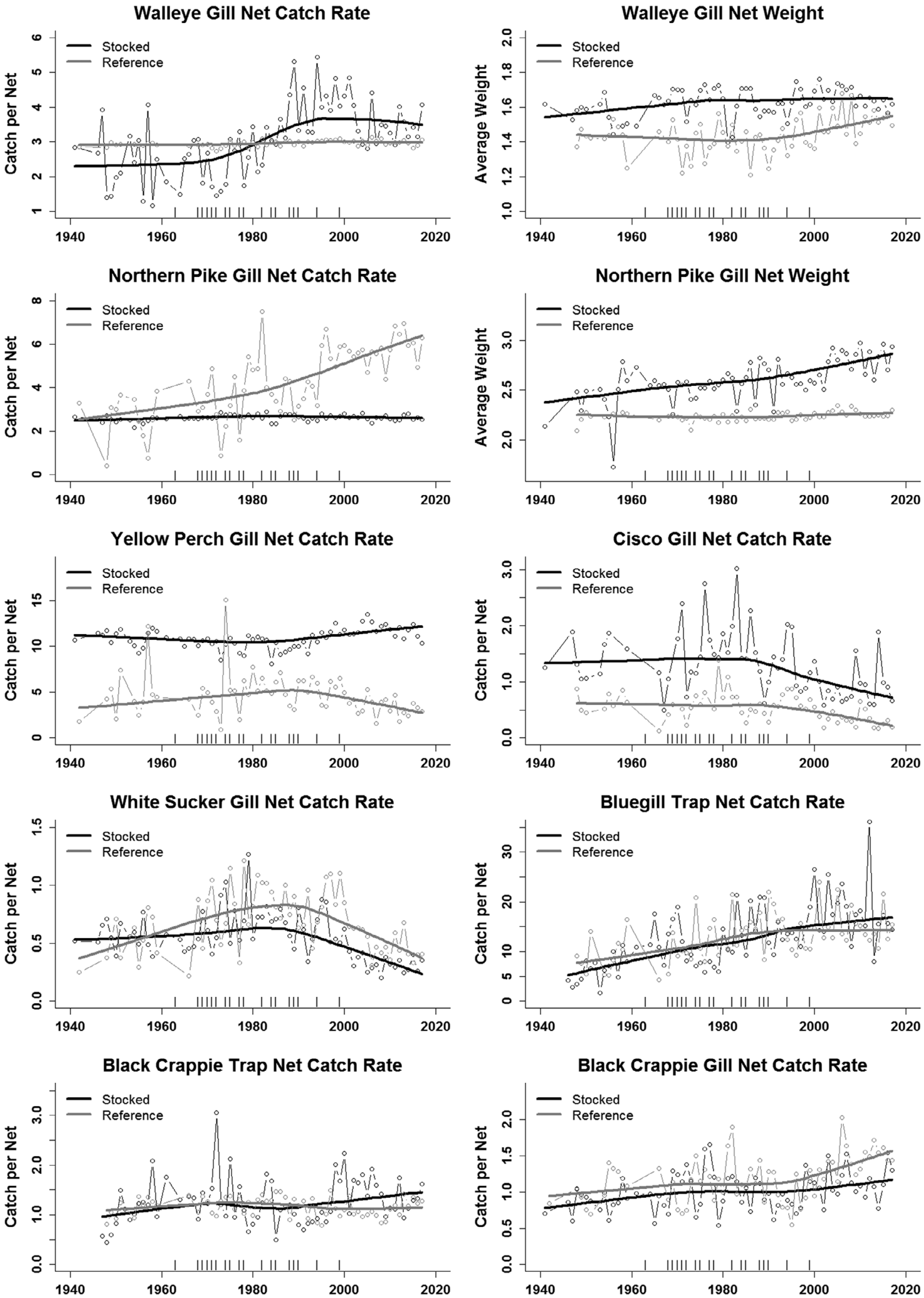

FIGURE 4. Time series plots of mixed-effects model predictions of annual median CPUE for Minnesota lakes stocked with Mississippi River strain Muskellunge and unstocked reference lake groups. Open circles are annual estimates; thicker lines are locally weighted scatterplot smoothing of the annual estimates over time. Vertical bars above horizontal axis represent initial stocking dates within the stocked lake group.

documented increase across Minnesota lakes from 1970 to 2013 (Bethke and Staples 2015). The stability of CPUE and the observed increase in mean weight associated with Muskellunge stocking are desirable attributes for Northern Pike populations. Northern Pike are considered to have a competitive advantage over Muskellunge because they appear to have a much broader and adaptable reproductive strategy that allows them to use more diverse spawning habitat, become sexually mature at early ages, and reproduce at much higher rates (Inskip 1986; Farrell and Werner 1995; Pierce 2012). Our data suggest that low-density Muskellunge populations may help moderate the abundance of smaller Northern Pike, though defining the mechanisms for this is beyond the scope of this study.

Yellow Perch are one of the most important prey items for Muskellunge throughout their range (Hourston 1952; Gammon and Hasler 1965; Inskip and Magnuson 1986; Bozek et al. 1999), and they are also important in the diets of Northern Pike and Walleye (Parsons 1971; Scott and Crossman 1973; Forney 1974; Diana 1979; Pierce et al 2006). While reference lakes mirrored the statewide decline in Yellow Perch CPUE (Bethke and Staples, 2015), it is noteworthy that Yellow Perch CPUE was significantly higher relative to reference lakes after Muskellunge introduction even in lakes without Cisco, a scenario where potentially more predation may be directed towards Yellow Perch. It appears that Yellow Perch CPUE was influenced more by reduced predation from Northern Pike than direct predation by stocked Muskellunge.

Cisco CPUE showed declined in both stocked and reference lakes, though there was no significant change in catch rates related to Muskellunge introduction. These results parallel the declining trend observed statewide in Minnesota that likely reflects changing climatic conditions that disfavor coldwater species like Cisco (Jacobson et al. 2012). The results are also evidence that Muskellunge, as managed in Minnesota, are not the cause of the Cisco decline in waters where they have been introduced.

Lakes with Cisco did not experience a decline in White Sucker CPUE related to Muskellunge stocking, indicating that the lakes without Cisco had a strong influence on the combined data set. Given the importance of soft-rayed, fusiform-shaped prey such as White Suckers in Muskellunge diets (Oehmcke et al. 1958; Bozek et al. 1999), it is not surprising that White Sucker would be consumed by Muskellunge, especially in lakes without Cisco. This corroborates previous studies such as Knapp et al. (2012), who observed a decline in the temporal trend in White Sucker CPUE across 41 lakes, most of which were included in this study. Siler and Beyerle (1986) also attributed a decline in White Sucker CPUE to a high-density Muskellunge population of 5.4 mature fish/ha.

Bluegill gill-net and trap-net CPUE has increased throughout Minnesota from 1970 to 2013 (Bethke and Staples 2015). While our study found that both stocked and reference lakes experienced increased CPUE for Bluegill, we observed no significant differences between the groups, suggesting that the broader changes observed in Bluegill populations in Minnesota appear to be independent of Muskellunge management. Wolter et al. (2012) reported Bluegill as the primary prey for Muskellunge in the absence of soft-rayed prey but found no evidence that Muskellunge had any detrimental effect on Bluegill CPUE. Attempts to control Bluegill via stocking Muskellunge (Snow 1968) and hybrid Muskellunge (Storck and Newman 1992) have proven unsuccessful, which suggests that Muskellunge and Bluegill interactions are minimal.

Our study confirms the findings of Knapp et al. (2012), who found no changes in Black Crappie gill-net or trap-net CPUE for 41 stocked Muskellunge lakes. This is not unexpected, given that Muskellunge prefer soft-rayed fusiform prey, as noted earlier. However, our findings contrast with Siler and Beyerle (1986), who observed a decline in Black Crappie trap-net catches, which they associated with a high-density Muskellunge population.

We recognize that numerous factors other than Muskellunge stocking could affect fish population characteristics in Minnesota lakes (Jackson et al. 2001; Lester et al. 2004; Cross and McInerny 2005; Jacobson et al. 2012). Furthermore, we recognize that using CPUE data assumes that catchability is similar over time and that potential changes within lakes and on the landscape may challenge this assumption. However, our inclusion of reference lakes of the same ecological classification, similar geographic location, management strategies, and aquatic invasive species presence to account for underlying large-scale changes mitigates this challenge and further strengthens the inference about changes in lakes stocked with Muskellunge.

While the social challenges of managing Muskellunge may never cease to exist (Murphy 2017), studies such as ours are useful to inform decisions made by fisheries managers and provide context to discussions with their constituents. Our results indicate that trophy Muskellunge were present in the stocked lakes, and their presence has not adversely affected game fish populations in these waters, substantiating the conclusions of Knapp et al. (2012) while including 12 additional years of data and reference lakes. Our study was based on the Mississippi strain of Muskellunge stocked in Minnesota lakes, but results should be of interest to fisheries managers elsewhere because the study lakes represent a broad range of habitats, likely similar to many throughout the native and introduced range of Muskellunge. Separating the lakes into those with and without Cisco provided insight into what Muskellunge might consume should Cisco become extirpated, and our results should help alleviate concerns fisheries managers or stakeholders may have regarding potential declines in Cisco (Jacobson et al. 2012) that may lead to negative effects on other species. We suggest that if Muskellunge in our study lakes were the predominant factor affecting other species in the fish community, we would expect to observe declines in relative abundance in the lakes without Cisco, particularly because we documented significantly lower White Sucker CPUE. Yet, we observed no negative changes associated with the introduction of Muskellunge for the other study species. These observations imply that despite the ability of Muskellunge to attain great sizes, the densities present in this study are not sufficient to shape the fish communities through predation. Though there remains much to be learned about Muskellunge life history and their place within a fish community (e.g., stock–recruitment relationships, density-dependent effects, spatial requirements related to behavior and lake habitat/morphometry), these data show that Muskellunge stocking has not had consistent negative effects on game fish populations in Minnesota, and for several metrics it was associated with beneficial changes.

ACKNOWLEDGMENTS

We thank M. Gorsuch and numerous individuals in area fisheries offices throughout Minnesota for providing and validating data for this project. Members of the Muskie Technical Committee contributed suggestions and discussion of ideas for this project. A. Carlson, M. Habrat, J. Hoxmeier, L. Miller, and P. Schmalz provided critical review of earlier versions of this manuscript. D. Isermann and two anonymous reviewers also provided helpful comments that improved this manuscript. There is no conflict of interest declared in this article.

REFERENCES

Anderson, R. O., and S. J. Gutreuter. 1983. Length, weight, and associated structural indices. Pages 283–300 *in* L. R. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software [online serial] 67(1).

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.

Brenden, T. O., E. M. Hallerman, and B. R. Murphy. 2004. Predatory impact of Muskellunge on New River, Virginia, Smallmouth Bass. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 58:12–22.

Bonar, S. A., W. A. Hubert, and D. W. Willis, editors. 2009. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.

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.

CEN (Comité Européen de Normalisation). 2005. Water quality sampling of fish with multi-mesh gill nets. European Committee for Standardization, EN 14757:2005, Brussels.

Clarke, J. U. 1998. Evaluation of censored data methods to allow statistical comparisons among very small samples with below detection limit observations. Environmental Science & Technology 32:177–183.

Cross, T. K., and M. C. McInerny. 2005. Spatial habitat dynamics affecting Bluegill abundance in Minnesota bass–panfish lakes. North American Journal of Fisheries Management 25:1051–1066.

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.

Doss, S. S., B. R. Murphy, V. J. DiCenzo, L. Costello, and J. A. Williams. 2017. Can they play nicely? Creating and managing a two-predator system [extended abstract]. Pages 595–599 *in* K. L. Kapuscinski, T. D. Simonson, D. P. Crane, S. J. Kerr, J. S. Diana, and J. M. Farrell, editors. Muskellunge management; fifty years of cooperation among anglers, scientists, and fishery biologists. American Fisheries Society, Symposium 85, Bethesda, Maryland.

Elliot, J. M., and J. M. Fletcher. 2001. A comparison of three methods for assessing the abundance of Arctic Charr, *Salvilinus alpinus*, in Windermere (northwest England). Fisheries Research 53:39–46.

Engstrom-Heg, R., R. T. Colesante, and G. A. Stillings. 1986. Prey selection by three esocid species and a hybrid esocid. Pages 189–194 *in* G. E. Hall, editor. Managing muskies: a treatise on the biology and propagation of Muskellunge in North America. American Fisheries Society, Special Publication 15, Bethesda, Maryland.

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.

Ferrell, J. M., and R. G. Werner. 1995. Contribution of natural reproduction and stocking to fall age-0 esocid abundance in Rose Bay, St. Lawrence River. Pages 99–104 *in* Managing muskies in the ‘90s. Ontario Ministry of Natural Resources, Southern Region Science and Technology Transfer Unit Workshop Proceedings, WP-007, Peterborough.

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.

Gabelhouse, D. W. Jr. 1984. A length-categorization system to assess fish stocks. North American Journal of Fisheries Management 4:273–285.

Gammon, J. R., and A. D. Hasler 1965. Predation by introduced Muskellunge on perch and bass, I: years 1–5. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 54:249–272.

Gillen, A. L., R. A. Stein, and R. F. Carline. 1981. Predation by pellet-reared tiger muskellunge on minnows and Bluegills in experimental systems. Transactions of the American Fisheries Society 110:197–209.

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

Inskip, P. D. 1986. Negative associations between abundances of Muskellunge and Northern Pike: evidence and possible explanations. Pages 135–150 *in* G. E. Hall, editor. Managing muskies: a treatise on the biology and propagation of Muskellunge in North America. American Fisheries Society, Special Publication 15, Bethesda, Maryland.

Inskip, P. D., and J. J. Magnuson. 1986. Fluctuations in growth rate and condition of Muskellunge and Northern Pike in Escanaba Lake, Wisconsin. Pages 176–188 *in* G. E. Hall, editor. Managing muskies: a treatise on the biology and propagation of Muskellunge in North America. American Fisheries Society, Special Publication 15, Bethesda, Maryland.

Isermann, D. A., and B. G. Parsons. 2011. Harvest regulations and sampling. Pages 403–422 *in* B. A. Barton, editor. Biology, management, and culture of Walleye and Sauger. American Fisheries Society, Bethesda, Maryland.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157–170.

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

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 and the Ontario Ministry of Natural Resources and Forestry, Peterborough.

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 into Minnesota lakes. North American Journal of Fisheries Management 32:191–201.

Leitch, J. A., and J. F. Baltezore. 1987. Attitudes of Minnesota anglers. Final report to Minnesota Department of Natural Resources, Division of Fish and Wildlife, St. Paul.

Lester, N., A. Dextrase, R. Kushneriuk, M. Rawson, and P. Ryan. 2004. Light and temperature: key factors affecting Walleye abundance and production. Transactions of the American Fisheries Society 133:588–605.

Miller, L. M., S. W. Mero, and J. A. Younk. 2012. The impact of stocking on the current ancestry in 20 native and introduced Muskellunge populations in Minnesota. Transactions of the American Fisheries Society 141:1411–1423.

Miller, H. M. 2018. Fishing in Minnesota: a study of angler participation and activities 2018. Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, Final Report to the Minnesota Department of Natural Resources, University of Minnesota, St. Paul.

MNDNR (Minnesota Department of Natural Resources). 1993. Manual of instructions for lake survey. MNDNR, Division of Fish and Wildlife, Section of Fisheries, Special Publication 147, St. Paul.

MNDNR (Minnesota Department of Natural Resources). 2008. Long-range plan for Muskellunge and large Northern Pike through 2020. MNDNR, Division of Fish and Wildlife, Section of Fisheries, St. Paul.

Morgan, G. E. 2002. Manual of instructions: fall Walleye index netting. Cooperative Freshwater Ecology Unit, Department of Biology, Laurentian University, Sudbury, Ontario.

Moyle, J. B. 1950. Gill nets for sampling fish populations in Minnesota waters. Transactions of the American Fisheries Society 79:195–204.

Murphy, B. R. 2017. Haters gonna hate (*Esox* edition): user-group conflicts and vigilante justice in the age of social media. Pages 591–593 *in* K. L. Kapuscinski, T. D. Simonson, D. P. Crane, S. J. Kerr, J. S. Diana, and J. M. Farrell, editors. Muskellunge management; fifty years of cooperation among anglers, scientists, and fishery biologists. American Fisheries Society, Symposium 85, Bethesda, Maryland.

Nate, N. A., M. A. Bozek, M. J. Hansen, C. W. Ramm, M. T. Bremigan, and 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.

Oehmcke, A. A., L. Johnson, J. Klingbiel, and C. Wistrom. 1958. The Wisconsin Muskellunge—its life history, ecology, and management. Wisconsin Conservation Department, Publication 225, Madison.

Olson, D. E., and P. K. Cunningham 1989. Sport fisheries trends shown by an annual Minnesota fishing contest over a 58-year period. North American Journal of Fisheries Management 9:287–297.

Parsons, J. W. 1971. Selective food preferences of Walleyes of the 1959 year class in Lake Erie. Transactions of the American Fisheries Society 100:474–485.

Pierce, R. B. 2012. Northern Pike ecology, conservation, and management history. University of Minnesota Press, Minneapolis.

Pierce, R. B., and C. M. Tomcko. 2003. Variation in gill-net and angling catchability with changing density of Northern Pike in a small Minnesota lake. Transactions of the American Fisheries Society 132:771–779.

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.

Pierce, R. B., C. M. Tomcko, D. L. Pereira, and D. F. Staples. 2010. Differing catchability among lakes: the influence of lake basin morphometry and other factors on gill-net catchability of Northern Pike. Transactions of the American Fisheries Society 139:1109–1120.

R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Richards, K. 2017. The Muskies, Inc. Lunge Log database: 370,000 Muskellunge and growing [extended abstract]. Pages 33–36 *in* K. L. Kapuscinski, T. D. Simonson, D. P. Crane, S. J. Kerr, J. S. Diana, and J. M. Farrell, editors. Muskellunge management: fifty years of cooperation among anglers, scientists, and fishery biologists. American Fisheries Society, Symposium 85, Bethesda, Maryland.

Richards, L. J., and J. T. Schnute. 1986. An experimental and statistical approach to the question: is CPUE an index of abundance? Canadian Journal of Fisheries and Aquatic Sciences 43:1214–1227.

Ryan, P. M. 1984. Fyke net catches as indices of the abundance of Brook Trout, *Salvelinus fontinalis*, and Atlantic Salmon, *Salmo salar*. Canadian Journal of Fisheries and Aquatic Sciences 41:377–380.

Schroeder, S. A. 2015. Fishing and fish habitat in Minnesota: a study of anglers' opinions and activities. University of Minnesota, Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, Final Report to the Minnesota Department of Natural Resources, University of Minnesota, St. Paul.

Schroeder, S. A., and D. C. Fulton. 2005. Fishing in Minnesota: a study of angler participation and activities. Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, Final Report to the Minnesota Department of Natural Resources, University of Minnesota, St. Paul.

Schroeder, S. A., D. C. Fulton, and R. A. Dodd. 2007. Managing muskie in Minnesota. Minnesota Cooperative Fish and Wildlife Research Unit, Department of Fisheries, Wildlife, and Conservation Biology, Final Report to the Minnesota Department of Natural Resources, University of Minnesota, St. Paul.

Schupp, D. H. 1992. An ecological classification of Minnesota lakes with associated fish communities. Minnesota Department of Natural Resources, Section of Fisheries, Investigational Report 417, St. Paul.

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

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

Simpfendorfer, C. A., R. E. Hueter, U. Bergman, and S. M. H. Connett. 2002. Results of a fishery-independent survey for pelagic sharks in the western North Atlantic, 1977–1994. Fisheries Research 55:175–192.

Smith, E. 2002. BACI design. Pages 141–148 *in* A. H. El-Shaarawi and W. W. Piegorsch, editors. Encyclopedia of environmetrics, volume 1. Wiley, Chichester, UK.

Snow, H. E. 1968. Stocking of Muskellunge and Walleye as a panfish control practice in Clear Lake, Sawyer County. Wisconsin Department of Natural Resources, Research Report 38, Madison.

Storck, T. W., and D. L. Newman. 1992. Contribution of tiger muskellunge to the sport fishery of a small, centrarchid-dominated impoundment. North American Journal of Fisheries Management 12:213–221.

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.

Weithman, A. S., and R. O. Anderson. 1977. Survival, growth, and prey of Esocidae in experimental systems. Transactions of the American Fisheries Society 106:424–430.

Wingate, P. J. 1986. Philosophy of Muskellunge management. Pages 199–202 *in* G. E. Hall, editor. Managing muskies: a treatise on the biology and propagation of Muskellunge in North America. American Fisheries Society, Special Publication 15, Bethesda, Maryland.

Wingate, P. J., and D. H. Schupp. 1984. Large lake sampling guide. Minnesota Department of Natural Resources, Special Publication 140, St. Paul.

Wingate, P. J., and J. A. Younk. 2007. A program for successful Muskellunge management—a Minnesota success story. Environmental Biology of Fishes 79:163–169.

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. Final Report to the Illinois Natural History Survey, Champaign.

Younk, J. A., and D. L. Pereira. 2006. An examination of Minnesota's Muskellunge waters. Environmental Biology of Fishes 79:125–136.

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, Section of Fisheries, Investigational Report 418, St. Paul.