Minnesota Department of Natural Resources
Investigational Report 576, June 2016

Mille Lacs Lake Bioenergetics

Tyler D. Ahrenstorff

and

Beth V. Holbrook

Minnesota Department of Natural Resources
Division of Fish and Wildlife
Section of Fisheries
1601 Minnesota Drive
Brainerd, MN 56401, USA

Abstract - The Walleye (*Sander vitreus*) population in Mille Lacs Lake has declined to historically low catch rates in recent years. Other changes have also been observed in the fish community, including reduced catch rates of forage species such as Cisco (*Coregonus artedi*), and increased catch rates of Northern Pike (*Esox lucius*) and Smallmouth Bass (*Micropterus dolomieu*). Evidence suggests that declines in Walleye may be related to reduced survival of juvenile Walleye (age-0 to age-2). Predation is one mechanism that may directly affect juvenile Walleye survival. Therefore, the primary goals of this study were to evaluate consumption patterns of predators on juvenile Walleye by: 1) analyzing diet data from adult Walleye; 2) estimating lakewide Walleye consumption of preferred prey species, including juvenile Walleye, using size distributions that could result from different management policies; 3) comparing Walleye consumption patterns, including cannibalism, to estimates of available forage; and 4) analyzing stomach contents and lakewide consumption of other predatory species that may prey on juvenile Walleye, including Northern Pike and Smallmouth Bass. Our results suggested that total consumption by the Walleye population varied by only 5% between the different management policies that were evaluated, assuming equal Walleye biomass in each scenario. Forage availability did not influence total Walleye consumption estimates; however, prey availability appeared to have a significant impact on the consumption of juvenile Walleye biomass, with Cisco and spottail shiners (*Notropis hudsonius*) potentially buffering predation on juvenile Walleye by Walleye. Lastly, the Walleye population consumed considerably more food, and more juvenile Walleye, compared to Northern Pike and Smallmouth Bass populations. Overall, these results suggest that Walleye cannibalism may affect juvenile Walleye survival more than predation by other species, and Walleye cannibalism rates are likely related to forage availability.

This project was funded in part by the Federal Aid in Sport Fish Restoration (Dingell-Johnson) Program.
Completion Report, Study 665, D-J Project F-26-R Minnesota.

INTRODUCTION

Mille Lacs Lake is a system under change. Since the early 1980's, gillnet catch rates of Walleye (*Sander vitreus*) have declined to an all-time low in recent years, while gillnet catch rates of Northern Pike (*Esox Lucius*) and Smallmouth Bass (*Micropterus dolomieu*) have reached an all-time high (Jensen 2014; Kumar 2015). Over the same time-period, Cisco (*Coregonus artedi*) catch rates have declined, partly due to thermal stress (Kumar et al. 2013). Observed changes in the fish community may be related to changes in lower trophic levels, including reduced primary production caused by limits on nutrient inputs from septic systems and the establishment of zebra mussels (*Dreissena polymorpha*). Additional invasive species have also become established in the lake including Eurasian watermilfoil (*Myriophyllum spicatum*) and spiny waterflea (*Bythotrephes longimanus*) (Jensen 2014).

The declining Walleye population is of particular concern in Mille Lacs Lake, given that the local economy is heavily dependent on fishing and that at one time, Mille Lacs Lake was one of the most heavily fished and productive large lakes for Walleye in Minnesota (Radomski 2003; Jensen 2014). The Minnesota Department of Natural Resources and an independent review panel of international fisheries experts have concluded that reduced survival of juvenile Walleye (age-0 to age-2) is likely causing the decline in the Walleye population (Venturelli et al. 2014). Predation on juvenile Walleye may be one factor limiting survival but consumption dynamics of the predator community are not well understood, particularly as predator and prey populations fluctuate.

Bioenergetic models can be used to estimate average consumption rates of predatory species. Bioenergetic models use an energy mass-balance equation, in which all food consumed by a fish is expended through respiration and metabolism, excreted as waste, or incorporated into body tissue as growth (Kitchell et al. 1977; Brandt and Hartman 1993). Because metabolic functions are temperature- and weight-dependent, the size of fish and the habitat that they occupy influence consumption rates. Bioenergetic models can be coupled with actual or hypothetical population estimates to evaluate changes in total consumption by predator species populations under different hypotheses (Brandt and Hartman 1993). This technique can be used in Mille Lacs Lake, for example, to evaluate potential effects of various management policies, forage availability, and changing predator populations on consumption of juvenile Walleye to identify factors that may be influencing reduced survival of juvenile Walleye.

Fishing regulations can change the size structure of fish populations (Olson and Cunningham 1989; Lewin et al. 2006) and may have subsequent effects on consumption dynamics of the predator community. Johnson et al. (1992) predicted Walleye population size structures under five regulation scenarios, and combined it with bioenergetic estimates, to quantify how consumption might change in Lake Mendota under different regulation scenarios. The results suggested that as the minimum size limit increased and Walleye regulations became more restrictive, total biomass of prey consumed and the age-class at which maximum consumption occurred increased (Johnson et al. 1992). In Mille Lacs Lake, recent restrictive regulations designed to protect spawning stock biomass (protected slot), and tribal harvest of predominately male Walleye, have increased the size structure of the Walleye population, but it is unknown whether changes in the size distribution have altered consumption patterns of forage species.

The composition and abundance of forage species, including juvenile Walleye, may influence consumption by predators. For example, reduced Yellow Perch (*Perca flavescens*) abundance in Oneida Lake has resulted in increased cannibalization of juvenile Walleye (Forney 1974). Furthermore, cannibalism by Walleye has been known to regulate age-0 Walleye survival in Oneida Lake (Chevalier 1973; Forney 1980), and Walleye year class strength may depend on the presence of alternative prey (e.g., Yellow Perch) that buffer cannibalism (Hall and Rudstam 1999). In Mille Lacs Lake, Yellow Perch populations have fluctuated over time while Cisco populations have declined (Jensen 2014), providing a gradient of forage composition and availability with which to compare to Walleye cannibalism. If cannibalism by Walleye was related to forage availability, changes in the forage fish community could potentially affect survival rates of juvenile Walleye.

Northern Pike and Smallmouth Bass are also known to periodically feed on juvenile Walleye (Sammons et al. 1994; Wuellner et al. 2010). Sammons et al. (1994) found that larger Northern Pike consumed a larger proportion of juvenile Walleye than smaller Northern Pike, and consumption was higher in the spring and fall than in summer and winter. Wuellner et al. (2010) found that in a Missouri reservoir a minor component of the Smallmouth Bass diet consisted of Walleye, with consumption occurring throughout the spring, summer, and fall. In other systems with more abundant crayfish populations, Smallmouth Bass did not consume many Walleye and instead their diets were composed primarily of crayfish (Frey et al. 2003; Olson and Young 2003). In Mille Lacs Lake, gillnet catch rates of Northern Pike and Smallmouth Bass have been increasing (Jensen 2014), and a detailed diet study and bioenergetics modeling across all seasons and sizes of predators is necessary to examine their role in consuming juvenile Walleye.

This study combines a comprehensive diet study, with bioenergetic and population models, to evaluate how predation rates on juvenile Walleye may be influenced by several different factors, including changing management policies, forage abundances, and predator abundances. The specific objectives of this study included: 1) evaluate Walleye diets over time using data collected throughout the summers of 2006, 2007, 2008, 2013, and 2014; 2) combine diet information with bioenergetic models and hypothetical management scenarios to estimate Walleye consumption under different management policies; 3) compare estimates of Walleye cannibalism under different management policies with available forage fish abundances; and 4) examine differences in consumption between Walleye, Northern Pike, and Smallmouth Bass.

METHODS AND RESULTS

<u>Objective 1: Walleye diet analysis</u>

Methods

Walleye diets were collected in Mille Lacs Lake during each month of the summer (May – October) in 2006, 2007, 2008, 2013, and 2014. In September of each year, Walleye were collected using overnight experimental gillnet sets as part of the Mille Lacs large lake assessment. During the other months, Walleye were collected using short-term experimental gillnet sets or bottom trawls. Because Walleye diets shift based on size (Parsons 1971), we collected approximately 50 individuals from each of four size classes of Walleye (≤ 329 mm, 330 – 456 mm, 457 – 583 mm, and ≥ 584 mm). Captured Walleye were brought back to the laboratory where they were measured to total length, weighed to the nearest g, and stomachs were removed. Stomachs were then dissected and prey items were sorted into prey categories and prey categories were weighed to the nearest g. Prey categories included fishes by genus or family and age class; insects by family; and crayfish, clams, snails, and other invertebrates by order or class. When stomach contents were well digested but fish parts were present, we used bottom jaws or the cleithrum to identify each prey species consumed. If we were unable to identify the prey fish species based on bony structures, we lumped stomach contents into an unknown fish category. We calculated the proportion of each prey category consumed (by mass), for each size class of Walleye, during each month of each year.

Results

We collected 1,627 Walleye diets in 2006, 1,628 diets in 2007, 2,170 diets in 2008, 1,633 diets in 2013, and 1,128 diets in 2014. Walleye stomach contents varied by Walleye size, month, and year (Figure 1). Walleye of all size classes and during all years ate primarily Yellow Perch and unknown fish. During some years, Cisco also made up a large proportion of their diet. Some juvenile Walleye were consumed, particularly by Walleye ≥ 457 mm.

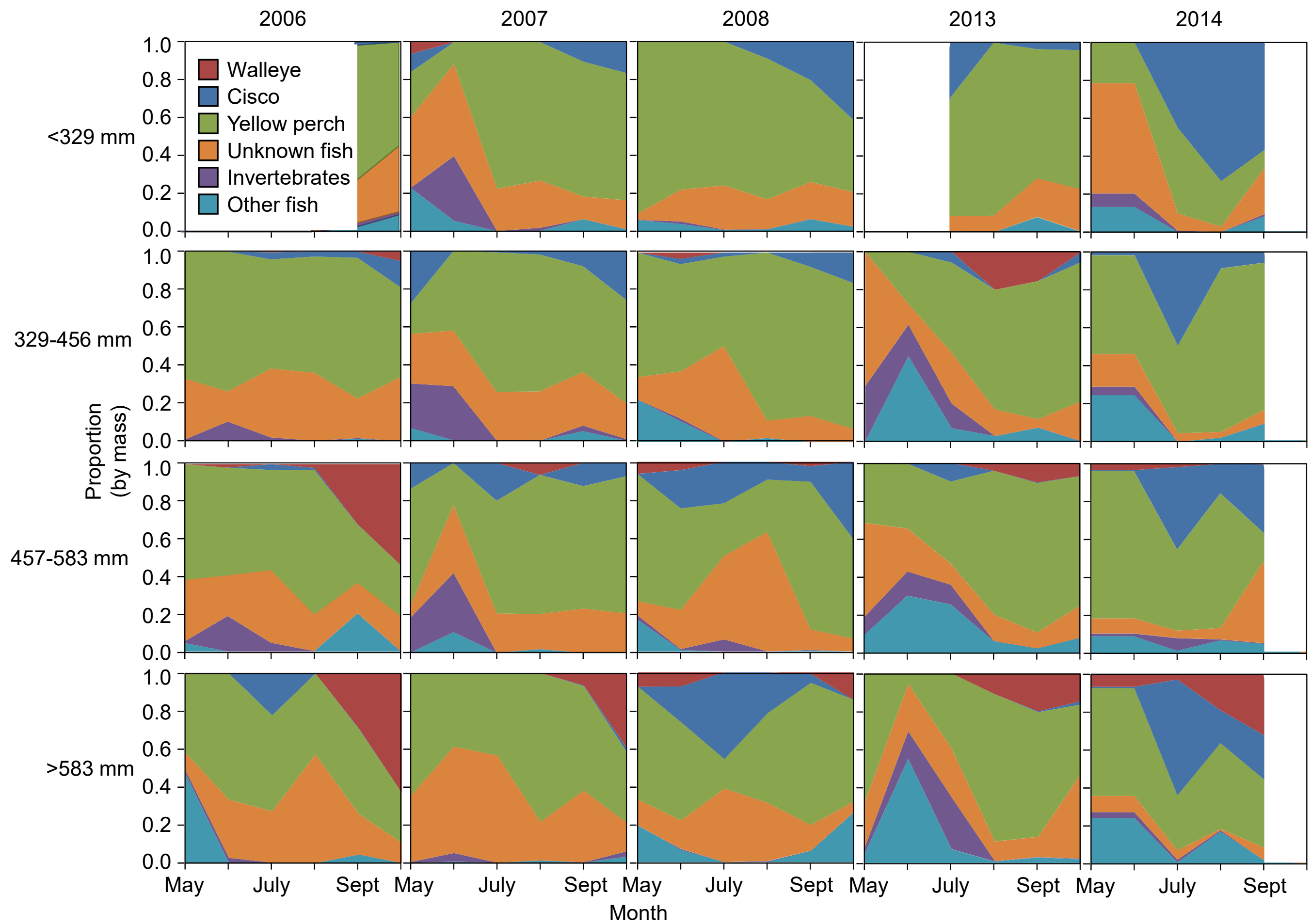

FIGURE 1. Walleye diets (proportion by mass) by month for four different size classes of Walleye (rows) collected during May – October of 2006, 2007, 2008, 2013, and 2014 (columns).

Objective 2: Estimates of Walleye consumption under different management policies

Methods

Bioenergetics model for Walleye

A bioenergetic model for Walleye was coded in R statistical software (R Core Team 2013) using the following data inputs: Walleye diets, water temperatures, and Walleye growth information to estimate age- and sex-specific average annual individual consumption from 1 October of one year to 30 September of the following year. The generalized bioenergetic model procedure is described in Figure 2. Data inputs were averaged across five years of available data (2006, 2007, 2008, 2013, and 2014) prior to being used in the model. Walleye diets were used from Objective 1. Daily water temperatures were estimated using data from a single logger located six ft below the surface in 36 ft of water, which was assumed representative of the entire water column since Mille Lacs is polymictic. Sex-specific Walleye growth was averaged across years using measured Walleye weights in September, estimated ages obtained from otoliths, and application of Von Bertalanffy growth models.

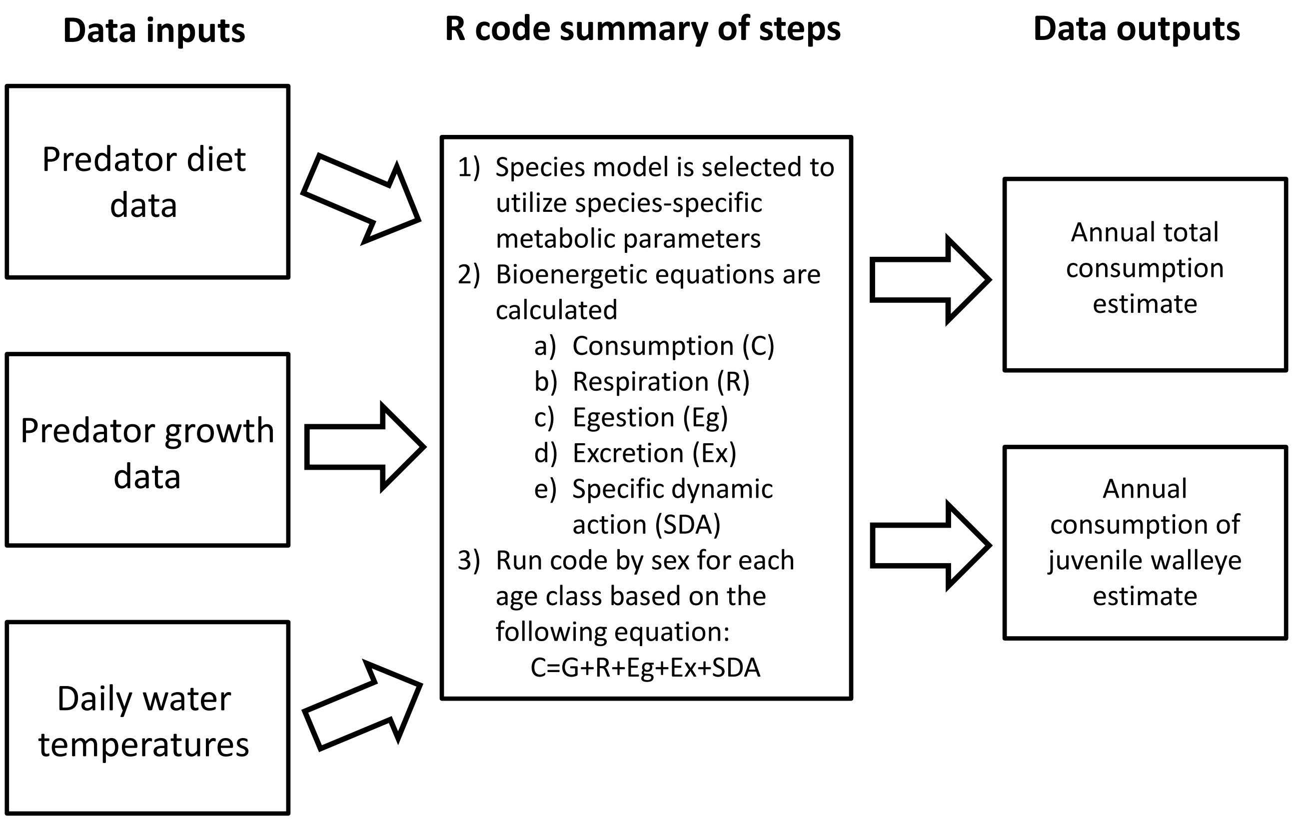

FIGURE 2. Flow chart describing data inputs, R code summary of steps, and data outputs from the bioenergetics model.

Theoretical size distributions

Three theoretical Walleye populations were created based on different management policies, including no fishing, protected 17 – 28 in slot, and standard statewide regulation scenarios. Age distribution data under each scenario were created by applying different mortality estimates. In the no fishing scenario, natural mortality was estimated for each age class based on data from previous studies on Mille Lacs Lake. In the protected slot and standard statewide regulation scenarios, natural mortality was combined with fishing mortality estimates using previously collected data on hooking mortality, angler selectivity, and the relative proportion of fish kept. Age distribution estimates were used to create hypothetical populations for each scenario by keeping the total biomass of Walleye equivalent. Therefore, total Walleye biomass did not vary between scenarios, only the distribution of biomass among age classes.

Combining bioenergetic modeling with theoretical size distributions

Hypothetical Walleye populations were combined with age- and sex-specific bioenergetic estimates to evaluate differences in total consumption between the three management scenarios.

Results

Bioenergetics model for Walleye

Walleye diets averaged across all years for the four size classes indicated that of the identified prey items, Walleye primarily consumed Yellow Perch and Cisco (Figure 3A). Diet data combined with average annual water temperature data (Figure 3B) and modeled growth of female and male Walleye (Figure 3C) were used in the bioenergetics model and indicated that average annual consumption varied by sex and age, ranging from 500 g – 5,500 g with older fish consuming more grams of prey on average than younger fish, and females consuming more than males (Figure 4).

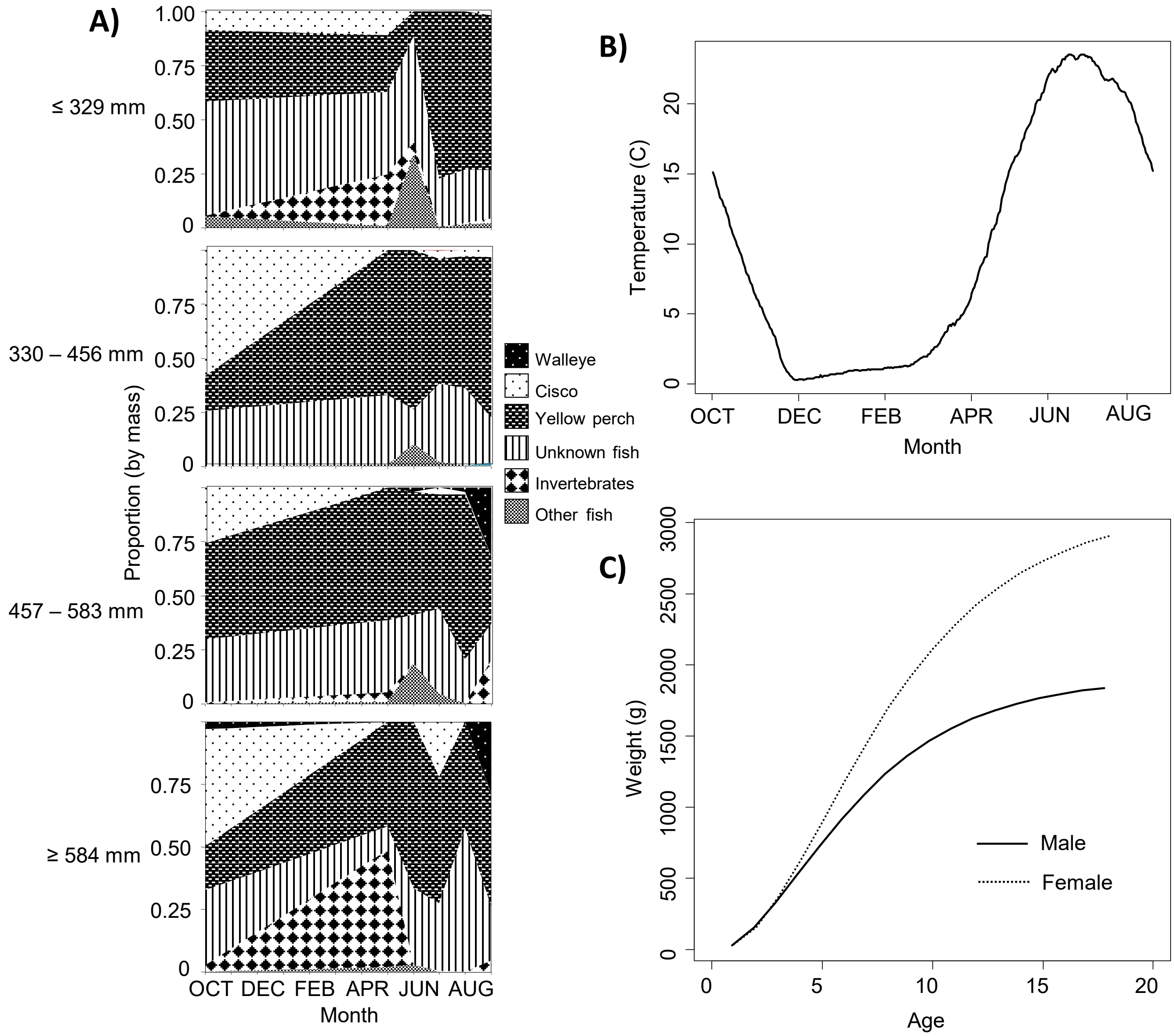

FIGURE 3. Data inputs used for bioenergetic modeling include, A) Walleye diets by month for four size ranges, B) daily water temperatures throughout the year, and C) Walleye weight at age modeled with a Von Bertalanffy growth model in September.

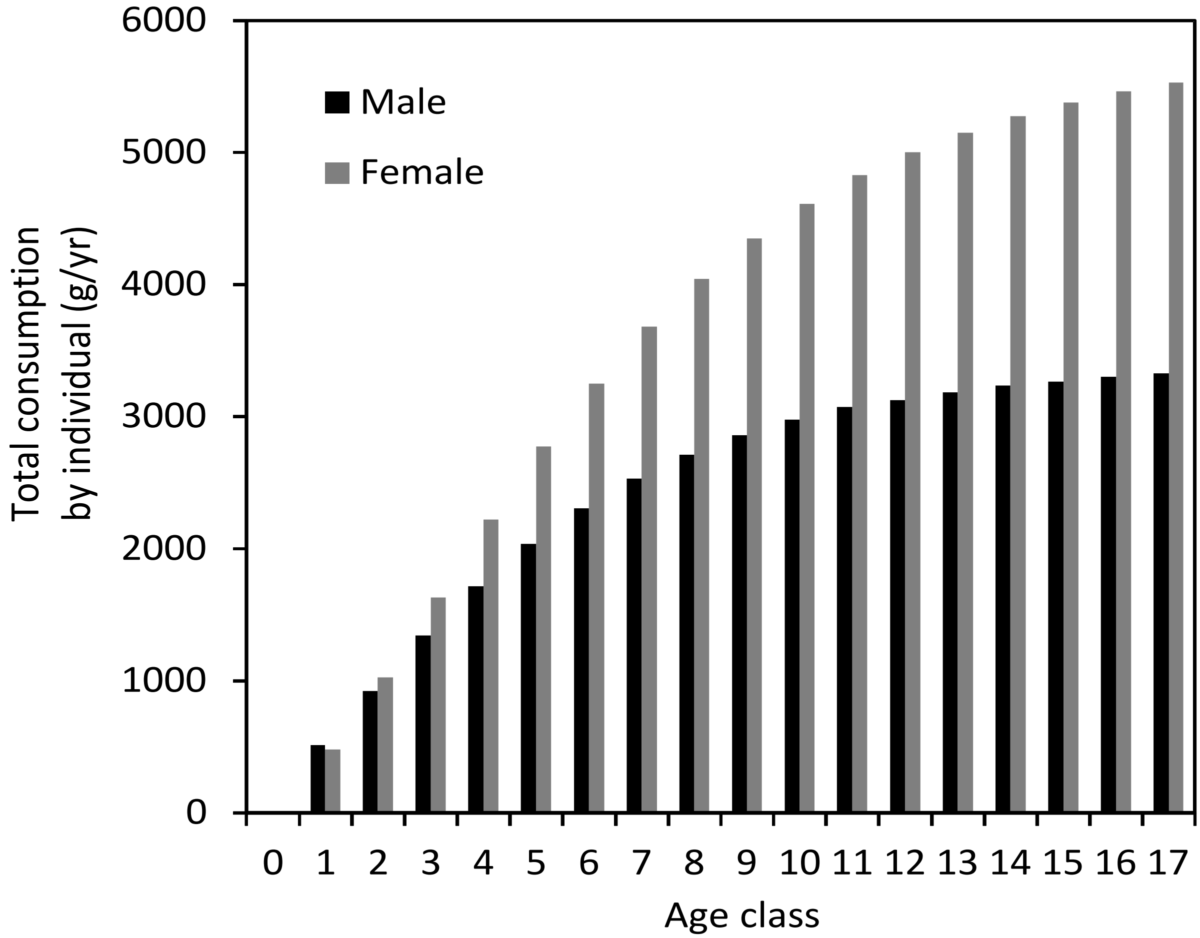

FIGURE 4. Estimated average annual consumption (g/yr) by individual Walleye by ages and sex.

Theoretical size distributions

The average number of age-1 Walleye from 1982 – present in Mille Lacs Lake was estimated using a statistical catch at age model and was used as a starting point for the no fishing population scenario. Differential mortality was applied by age class and number estimates were converted to biomass using the average weight of Walleye in each age class from 1982 – present. The overall biomass of 3,314,869 kg for the no fishing scenario was used as the fixed biomass for the other two management scenarios. Overall biomass was distributed differently among age classes based on differential mortality for the protected slot and standard statewide regulation scenarios. The total numbers of Walleye in each management scenario varied, including 5,271,907 Walleye in the no fishing scenario, 6,729,862 Walleye in the protected slot scenario, and 8,024,424 Walleye in the standard statewide regulation scenario (Figure 5).

Combining bioenergetic modeling with theoretical size distributions

When total Walleye biomass was held constant between the three scenarios, Walleye consumption by the population was highest under the standard statewide regulation scenario (9,338,355 kg/yr), followed by the protected 17 – 28 in slot (9,042,323 kg/yr), and no fishing scenarios (8,896,504 kg/yr) (Figure 6). Because specific consumption rate (g prey/g predator/day) decreases with fish size, a population with a higher proportion of smaller, younger individuals will consume a greater amount compared to a population with a higher proportion of older individuals when overall biomass is held constant (Figure 7).

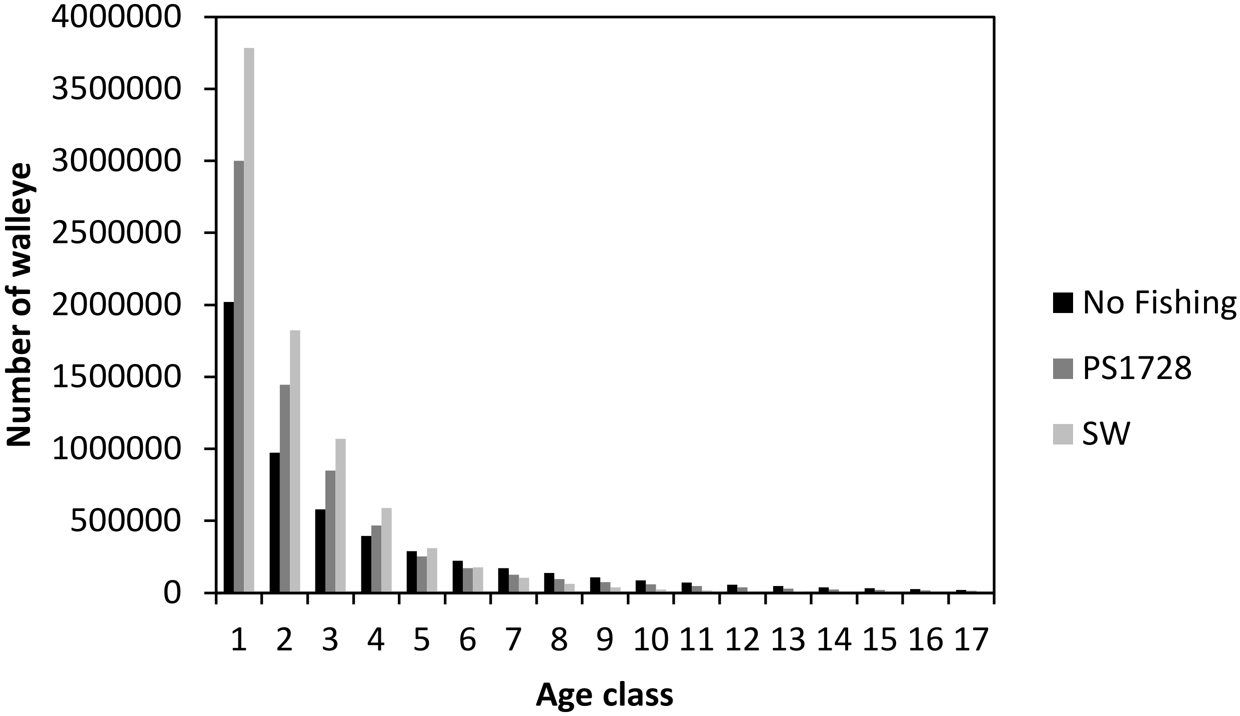

FIGURE 5. Number of Walleye by age in the no fishing, protected 17-28 in slot (PS1728), and standard statewide regulation (SW) scenarios. Walleye biomass is equal between each scenario.

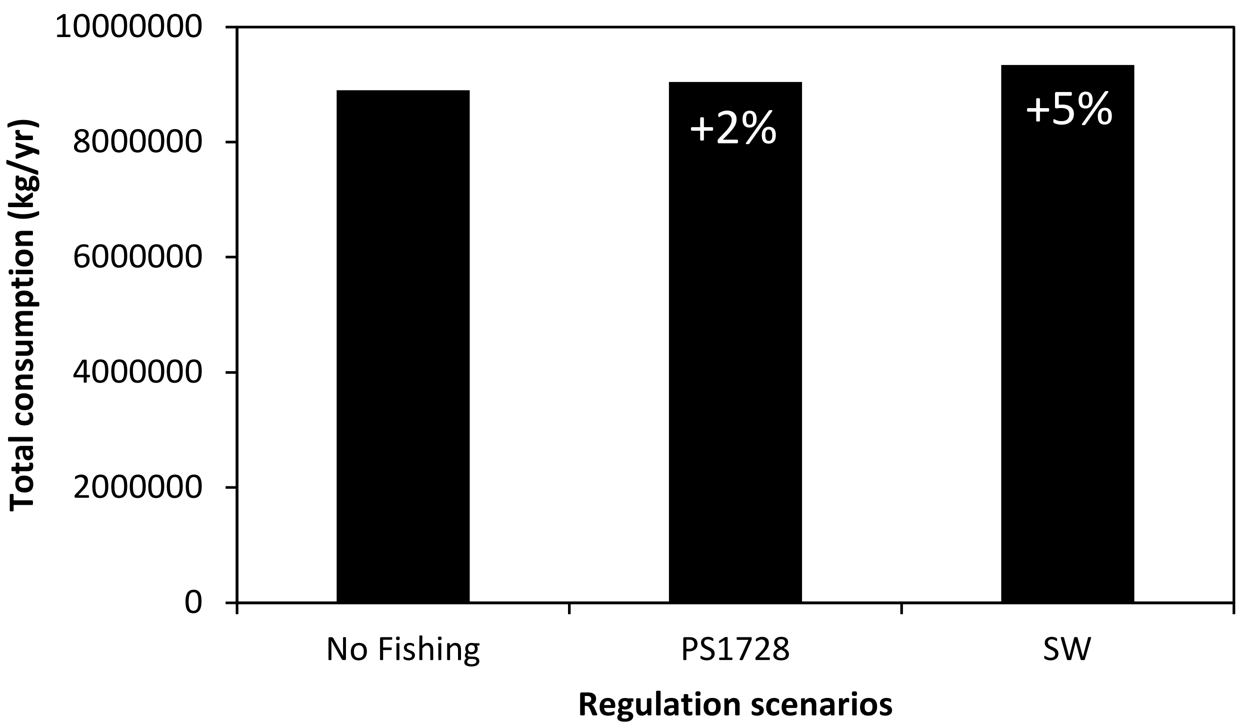

FIGURE 6. Total consumption by the Walleye population under the no fishing, protected 17 – 28 in slot (PS1728), and standard statewide regulation (SW) scenarios. Walleye biomass is equal between each scenario.

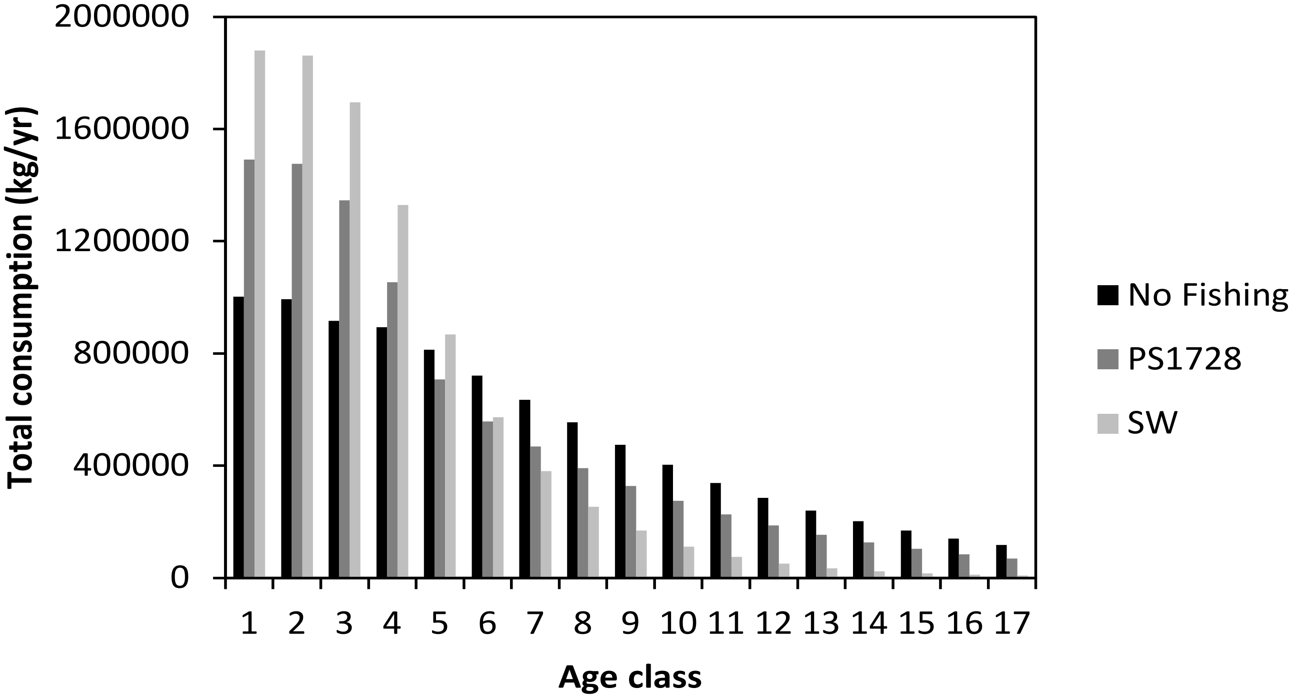

FIGURE 7. Total consumption by age under the no fishing, protected 17 – 28 in slot (PS1728), and standard statewide regulation (SW) scenarios. Walleye biomass is equal between each scenario.

OBJECTIVE 3: Estimates of Walleye cannibalism under different forage fish abundances and management policies

Methods

Walleye consumption of juvenile Walleye

We calculated the proportion of the diet of adult Walleye made up of juvenile Walleye (by mass) using bioenergetics for the years when monthly diet data were collected (2006 – 2008, and 2013 – 2014) using four Walleye size categories: ≤ 329 mm (< age-3), 330 – 456 mm (age-3 to -5), 457 – 583 mm (age-6 to -11), and ≥ 584 mm (> age-11). We also calculated the proportion of the diet of adult Walleye made up of juvenile Walleye for the years when only September diet data were collected (2006 – 2015) using the same four Walleye size categories.

Walleye consumption of juvenile Walleye compared to forage fish abundance

Forage fish biomass was evaluated using small mesh gillnets (2.5 ft wide panels each of 1/4-, 5/16-, 3/8-, 1/2-, 5/8-, and 3/4- in bar measure mesh) set 45 times throughout the lake each September from 2006 to 2015. Estimates of the proportion of the adult Walleye diet made up of juvenile Walleye were compared with forage fish biomass using linear regression for the month of September in the years 2006 – 2015 when both sets of data were available.

Walleye consumption of juvenile Walleye under low and high forage scenarios using different theoretical size distributions

Total consumption of juvenile Walleye under high and low forage scenarios were estimated using different theoretical size distributions. First, the number of juvenile Walleye consumed during September of each year was calculated by combining total consumption estimates with the diet composition estimated for each age of adult Walleye. Next, we combined the consumption estimates of juvenile Walleye for each year from 2006 – 2015 with the three hypothetical populations described in Objective 2. The three years with the highest forage availability and the three years with the lowest forage availability were identified using forage data during this same time-period. The total number of juvenile Walleye consumed for each of the three management scenarios (no fishing, protected 17 – 28 in slot, and general statewide regulation) was then averaged for the three years with highest and lowest forage availability.

Results

Walleye consumption of juvenile Walleye

Juvenile Walleye composed ≤ 5% of the total diet of adult Walleye (by mass) each year (Figure 8), though the proportion varied among years when monthly diet data were collected (2006 – 2008, 2013 – 2014). The diets of larger Walleye (≥ 457 mm) contained a larger proportion of juvenile Walleye than the diets of smaller Walleye (< 457 mm) (Figure 9).

In the years when September diet data were collected (2006 – 2015), juvenile Walleye consistently made up ≤ 10% of the total consumption by adult Walleye during that month (Figure 10).

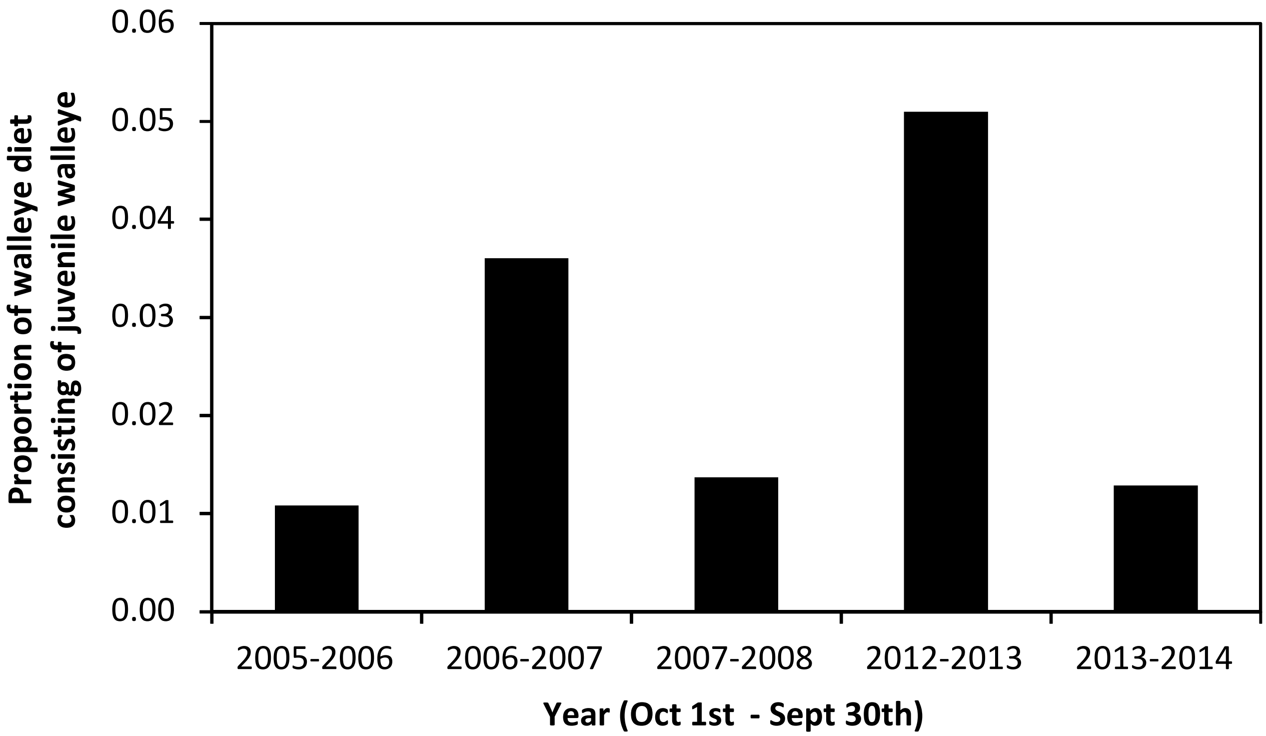

FIGURE 8. The proportion of the adult Walleye diet made up of juvenile Walleye, estimated using bioenergetics, over the course of the year for five years we collected monthly diet data during the summer.

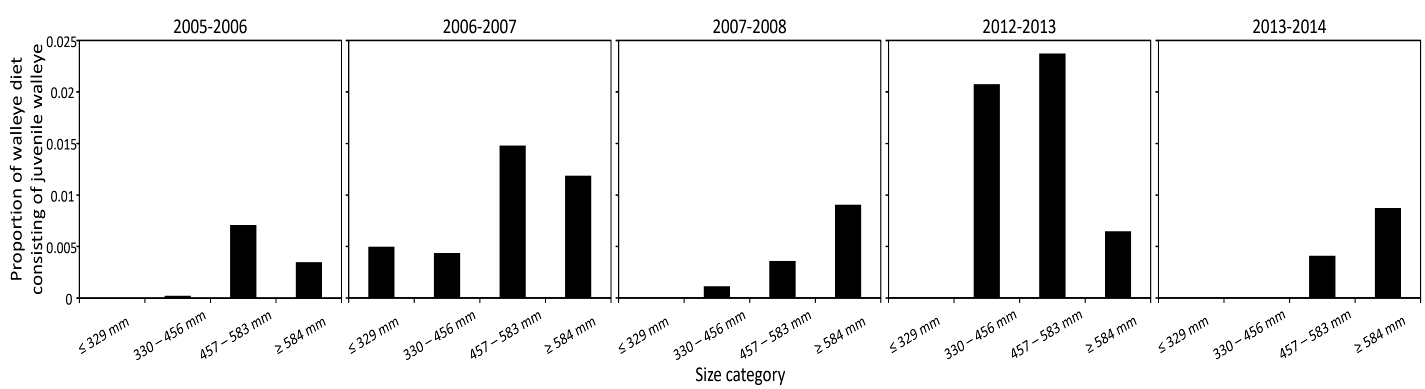

FIGURE 9. The proportion of the adult Walleye diet, by different size categories, made up of juvenile Walleye, estimated using bioenergetics, over the course of the year for five years we collected monthly diet data during the summer.

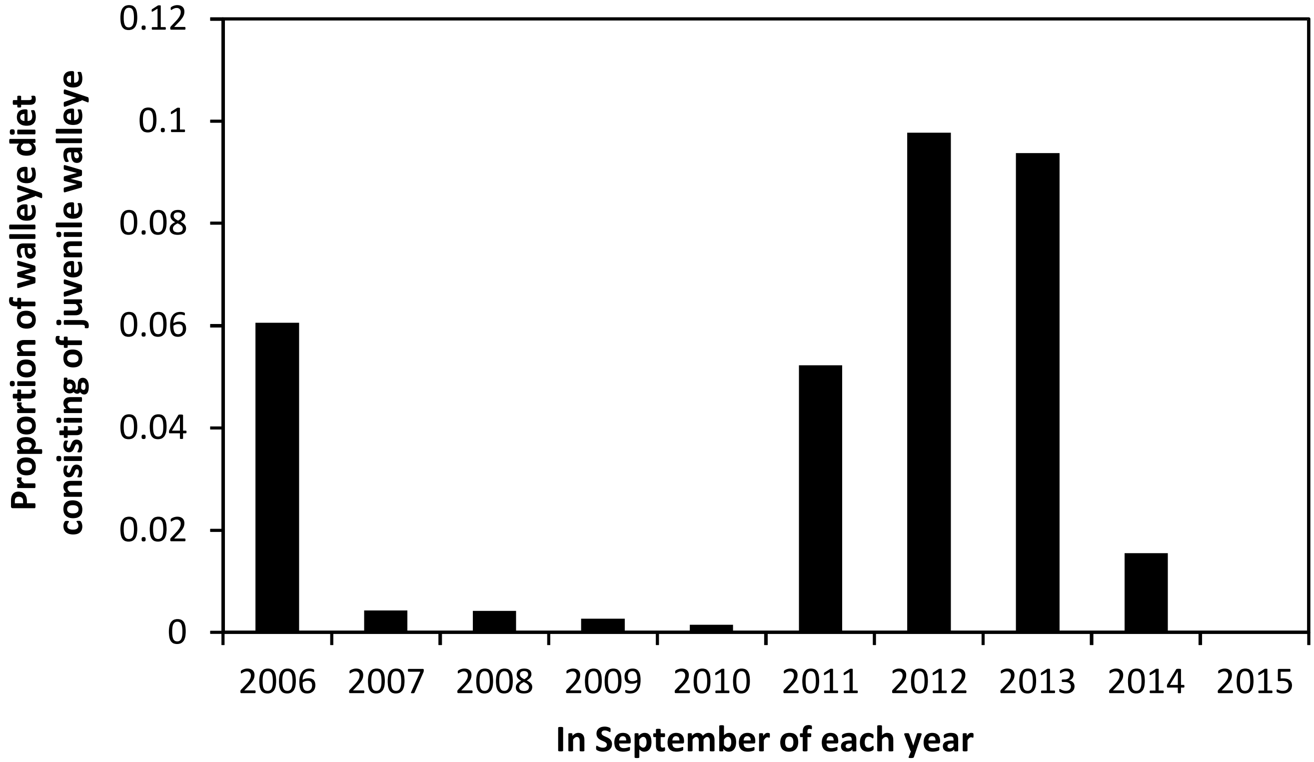

FIGURE 10. The proportion of the adult Walleye diet made up of juvenile Walleye, estimated using bioenergetics, over the course of one month (Sept 1st – 30th) from 2006 – 2015.

Walleye consumption of juvenile Walleye compared to forage fish abundance

Forage fish biomass varied for each species within each year from 2006 – 2015 (Figure 11). The proportion of the adult Walleye diet made up of juvenile Walleye was not significantly related with log transformed total prey biomass, age-1 Walleye biomass, and age-0 and age-1 Yellow Perch biomass using linear regression (Figure 12). The proportion of the adult Walleye diet made up of juvenile Walleye was significantly related with log transformed age-0 Walleye biomass (P < 0.05), age-0 and age-1 Cisco biomass (P < 0.05), and spottail shiner (*Notropis hudsonius*) biomass using linear regression (P < 0.05) (Figure 12). These results suggest that when more Cisco and spottail shiners were present in September, a lower proportion of the adult Walleye diet consisted of age-0 Walleye in September.

Walleye consumption of juvenile Walleye under low and high forage scenarios using different theoretical size distributions

A lower proportion of the adult Walleye diet was made up of juvenile Walleye, on average, during the three years of highest forage availability (2009, 2010, and 2015) compared with the three years of lowest forage availability (2006, 2007, and 2012) (Figure 13). When scaled to the three hypothetical populations (no fishing, protected 17 – 28 in slot, and general statewide regulation) for the low forage availability years, highest consumption of juvenile Walleye was predicted under the no fishing regulation, followed by the protected slot and general statewide regulation (Figure 13). As expected, during the high forage availability years, fewer juvenile Walleye were consumed for all three hypothetical scenarios, with the statewide regulation scenario resulting in the fewest juvenile Walleye consumed (Figure 14).

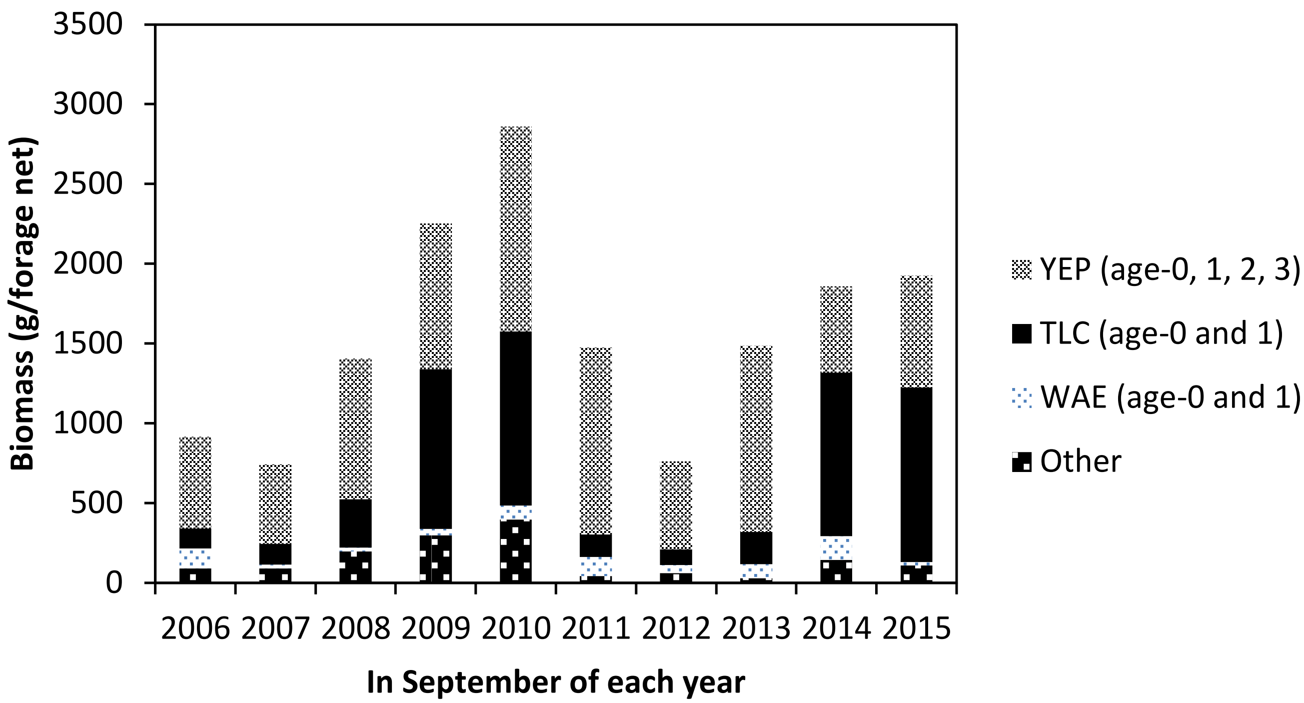

FIGURE 11. Biomass (g/forage net) of dominant forage species measured in September of each year.

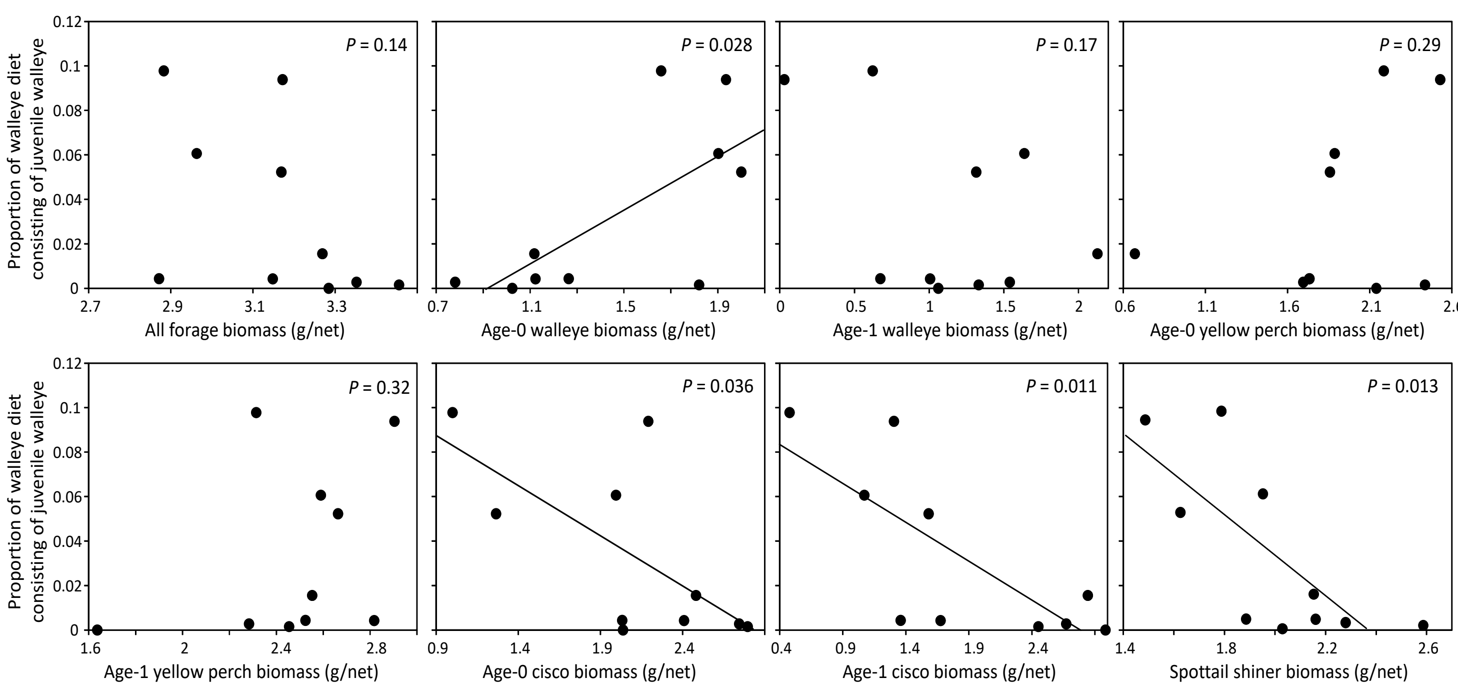

FIGURE 12. Comparisons between the proportion of the adult Walleye diet made up of juvenile Walleye and the log transformed biomass of various forage species during September of 2006 – 2015. The lines and P-values represent the results of linear regressions.

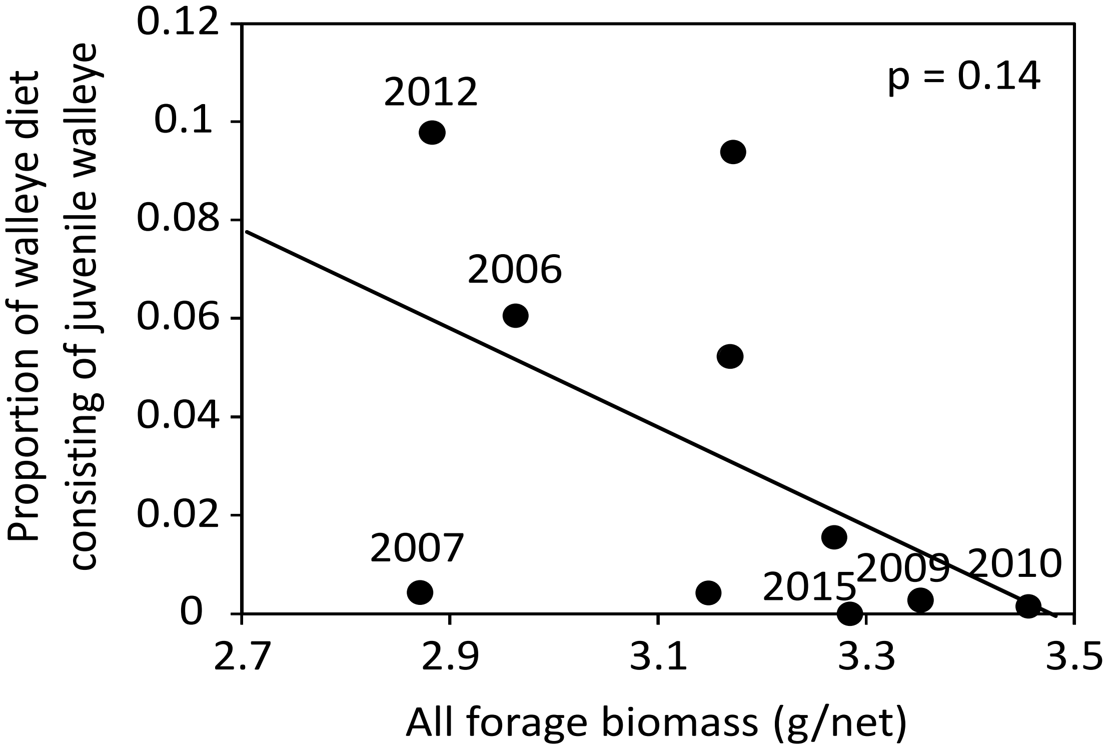

FIGURE 13. Comparison between the proportion of the adult Walleye diet made up of juvenile Walleye and the log transformed biomass of forage species in September of 2006 – 2015. The three lowest forage years were 2006, 2007, and 2012 while the three highest were 2009, 2010, and 2015.

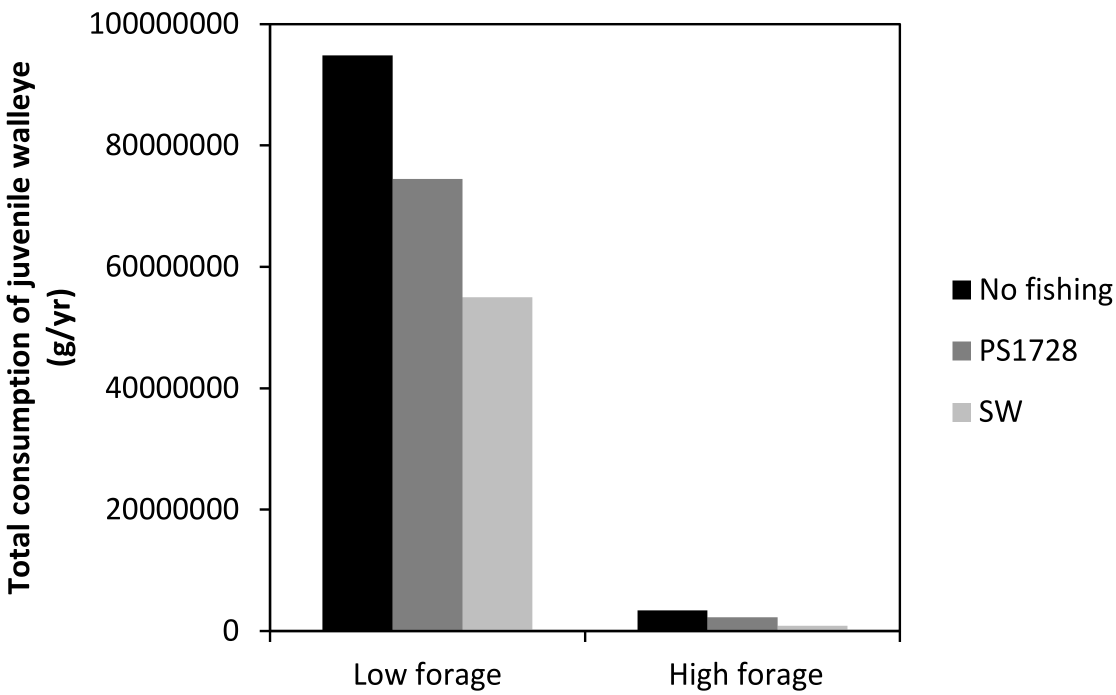

FIGURE 14. Total consumption of juvenile Walleye estimates during low or high forage availability for three hypothetical management scenarios (no fishing, protected 17 – 28 in slot, and general statewide regulation).

OBJECTIVE 4: Preliminary examination of stomach contents and initial calculation of consumption for Northern Pike and Smallmouth Bass

Methods

Bioenergetics model for Northern Pike and Smallmouth Bass

The Walleye bioenergetic model was modified for Northern Pike and Smallmouth Bass by changing metabolic parameters (Table 1) and using species-specific input data. Northern Pike and Smallmouth Bass diets were collected monthly during the summer (May – October) of 2013 and 2014 in all areas of Mille Lacs Lake. Fish were collected using either standard gillnets (6 ft deep by 250 ft long; 50 ft wide panels each of 0.75-, 1-, 1.25-, 1.5-, and 2-in bar mesh) or Northern Pike gillnets (6 ft deep by 300 ft long; 100 ft wide panels each of 1.5-, 2-, and 2.5-in bar mesh). Sampling continued each month until up to 50 fish were collected in each of four categories: Northern Pike ≤ 635 mm, Northern Pike > 635 mm, Smallmouth Bass ≤ 305 mm, and Smallmouth Bass > 305 mm. Fish that were collected were brought back to the lab where stomachs were removed, and contents were identified, counted, measured, and weighed, as in the Walleye diet analyses in Objective 1.

TABLE 1. Bioenergetic parameters used for Walleye (Kitchell et al. 1977), Northern Pike (Bean 2010), and Smallmouth Bass (Shuter and Post 1990).

Parameter	Walleye	Northern Pike	Smallmouth Bass
Consumption			
Equation	2	2	2
CA	0.25	0.2045	0.25
CB	-0.27	-0.18	-0.31
CQ	2.3	2.59	3.8
CTO	22	24	29
CTM	28	34	36
Respiration			
Equation	2	2	2
RA	0.0108	0.0153	0.009
RB	-0.2	-0.3954	-0.21
RQ	2.1	2.29	3.3
RTO	27	28.5	30
RTM	32	30	37
ACT	1	1.849	2
SDA	0.172	0.14	0.16
Egestion/Excretion			
Equation	2	1	1
FA	0.158	0.2	0.104
FB	-0.222	-	-
FG	0.631	-	-
UA	0.0253	0.07	0.068
UB	0.58	-	-
UG	-0.299	-	-

Total consumption by Walleye, Northern Pike, and Smallmouth Bass

Year- and species-specific diet data, growth, and water temperatures were used to estimate annual average individual consumption from 1 October of one year to 30 September of the following year. Individual age- and sex-specific consumption estimates were then multiplied by population estimates for each species to calculate total annual lake wide population consumption for each species. Population estimates of Northern Pike and Smallmouth Bass were estimated using a mark-recapture population estimate during 2013 and 2014. We also included Walleye population consumption estimates for 2012 – 2013 and 2013 – 2014 to provide a more comprehensive comparison of total consumption between species.

Consumption of juvenile Walleye by Walleye, Northern Pike, and Smallmouth Bass

We estimated Walleye, Northern Pike, and Smallmouth Bass population consumption of juvenile Walleye by combining population total consumption estimates with the proportion of the Walleye, Northern Pike, and Smallmouth Bass diet consisting of juvenile Walleye.

Results

Bioenergetics model for Northern Pike and Smallmouth Bass

We collected 1,029 Northern Pike diets in 2013 and 2014 and 514 Smallmouth diets over the same time-period. Northern Pike diets consisted primarily of Yellow Perch, with larger Northern Pike (> 635 mm) also consuming some Cisco (Figure 15). Smallmouth Bass diets were dominated by crayfish and Cisco throughout much of the summer (Figure 16).

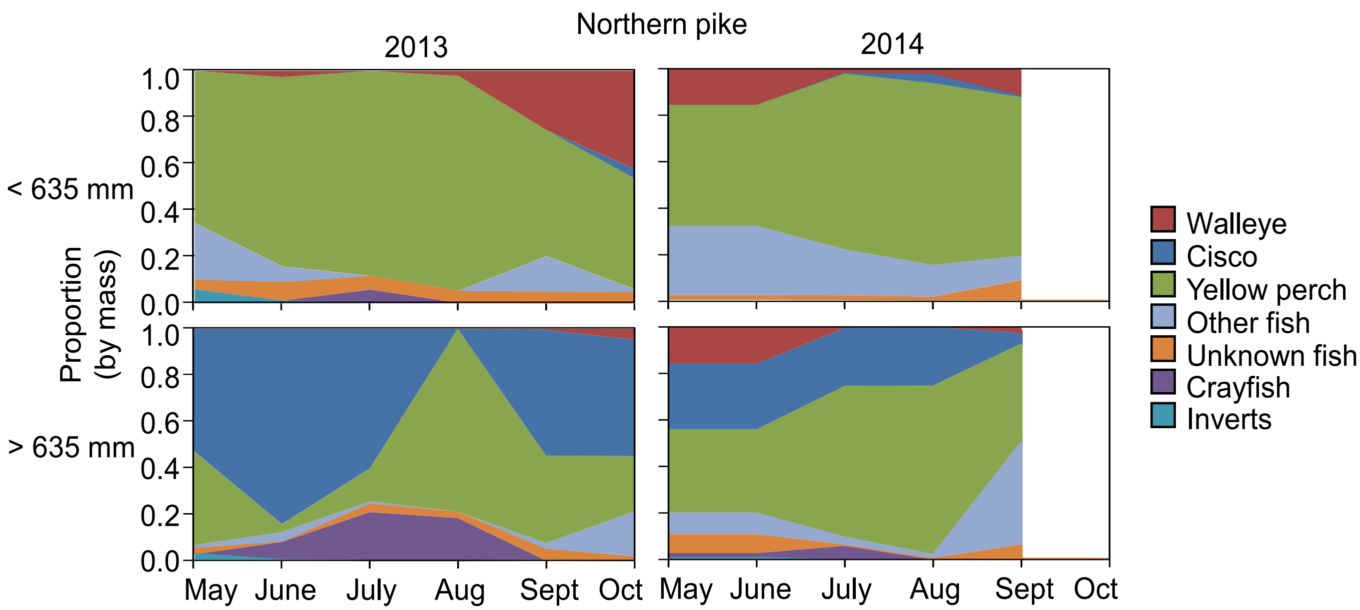

FIGURE 15. Diets (proportion by mass) of Northern Pike less than and greater than 635 mm throughout the summer of 2013 and 2014.

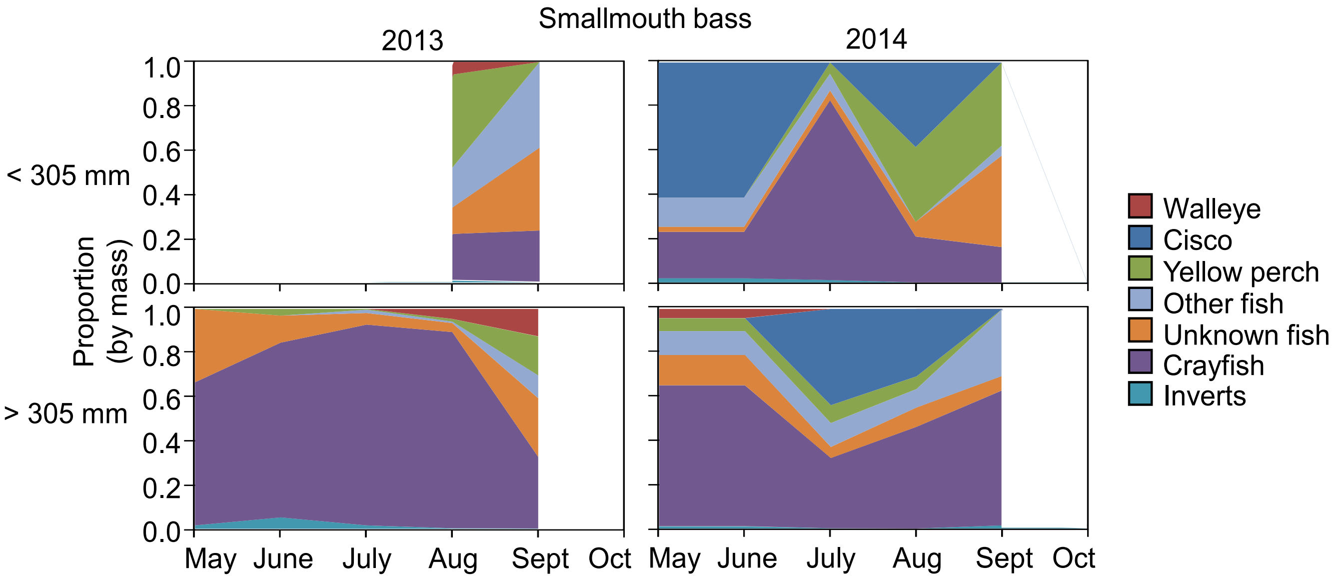

FIGURE 16. Diets (proportion by mass) of Smallmouth Bass less than and greater than 305 mm throughout the summer of 2013 and 2014.

Total consumption by Walleye, Northern Pike, and Smallmouth Bass

From October 1st of 2012 to September 30th of 2013, the Walleye population consumed the most food (1,335.4 million g/yr), followed by the Northern Pike (159.9 million g/yr) and Smallmouth Bass (28.2 million g/yr) populations (Figure 17). From October 1st of 2013 to September 30th of 2014, the Walleye population consumed 2,271.0 million g/yr, followed by the Northern Pike (170.0 million g/yr) and Smallmouth Bass (27.8 million g/yr) populations (Figure 17). While bioenergetic consumption estimates certainly influence these results, differences in population estimates were the primary driver of differences between species. Population size of individuals age-1+, estimated on January 1st of a given year, were 944,255 in 2013 and 3,713,265 in 2014 for Walleye (there was a strong year class of age-1 Walleye in 2014), about 75,000 Northern Pike in 2013 and 2014, and 32,000 Smallmouth Bass in 2013 and 2014.

Consumption of juvenile Walleye by Walleye, Northern Pike, and Smallmouth Bass

From October 1st of 2012 to September 30th of 2013, the Walleye population consumed the most juvenile Walleye (68.0 million g/yr), followed by the Northern Pike (8.2 million g/yr) and Smallmouth Bass (1.2 million g/yr) populations (Figure 18). From October 1st of 2013 to September 30th of 2014, the Walleye population consumed the most juvenile Walleye (29.2 million g/yr), followed by the Northern Pike (13.2 million g/yr) and Smallmouth Bass (0.3 million g/yr) populations (Figure 18).

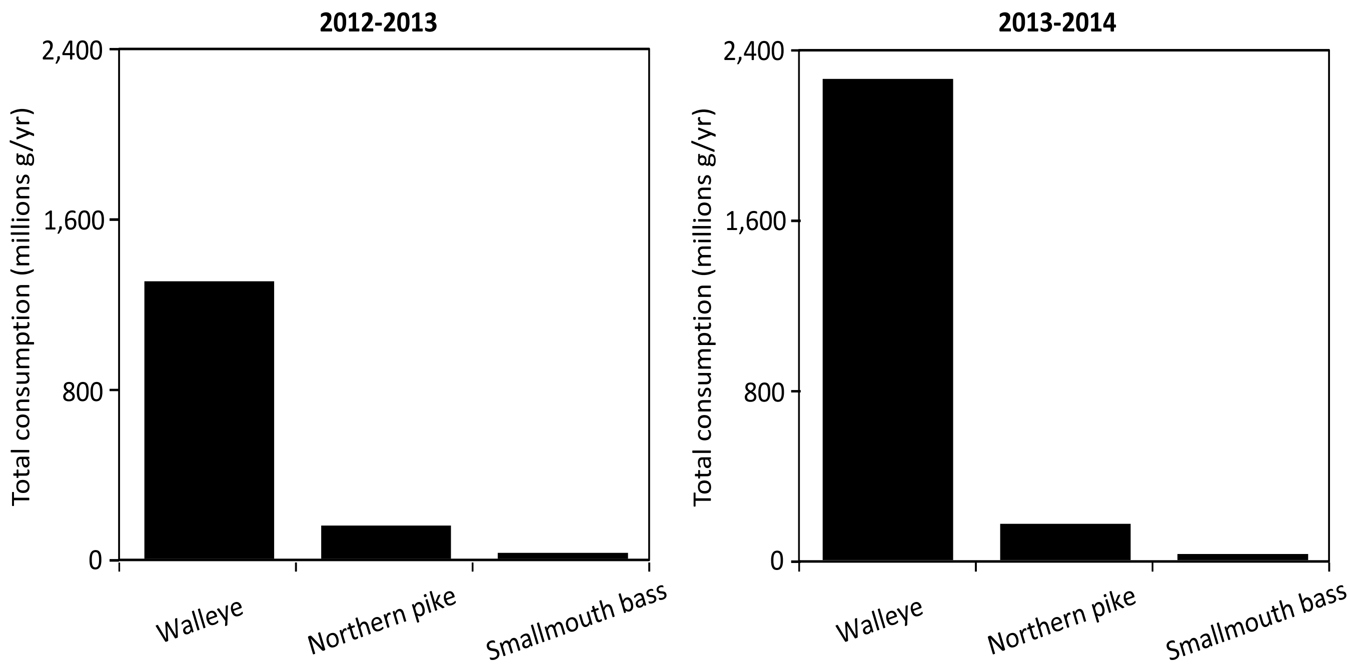

FIGURE 17. Total consumption by the Walleye, Northern Pike, and Smallmouth Bass populations from October 1st to September 30th of 2012 – 2013 and 2013 – 2014.

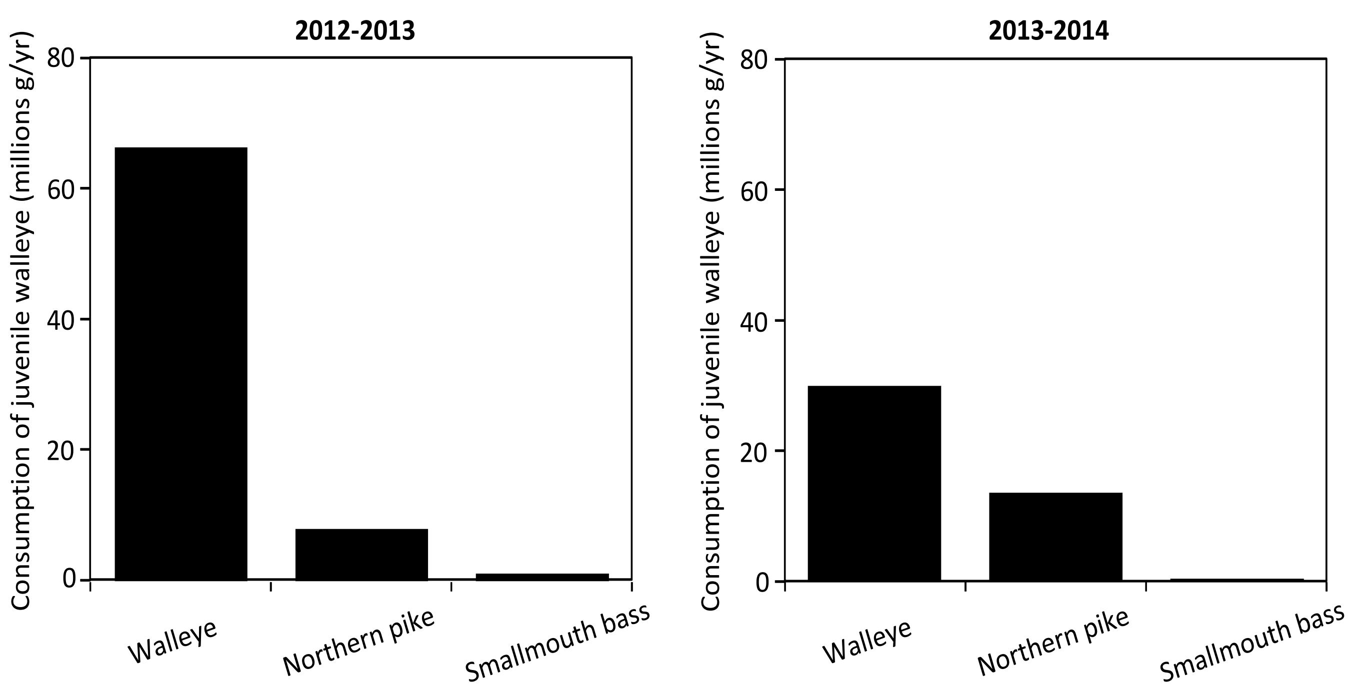

FIGURE 18. Consumption of juvenile Walleye by the Walleye, Northern Pike, and Smallmouth Bass populations from October 1st to September 30th of 2012 – 2013 and 2013 – 2014.

DISCUSSION

Evidence suggests the Walleye decline in Mille Lacs Lake has likely been caused by reduced survival of juvenile Walleye (age-0 to age-2) (Venturelli et al. 2014). While previous studies have found that juvenile Walleye are consumed by Walleye (Forney 1980), Northern Pike (Sammons et al. 1994; Margenau et al. 1998), and Smallmouth Bass (Wuellner et al. 2010), this is the first study to evaluate consumption patterns related to regulation policies, forage availability, and differences between predator populations in the same system.

Walleye diets are known to vary monthly, annually, and across Walleye sizes (Forney 1974; Hartman and Margraf 1992); therefore, we similarly characterized Walleye diets across a gradient of Walleye size classes each month of the summer over the course of five years, resulting in one of the most comprehensive diet studies found in the scientific literature (N = 8,186 diets). Consistent with Walleye diets in Oneida Lake, Walleye in Mille Lacs Lake consumed primarily age-0 Yellow Perch across all Walleye sizes, months, and years (Forney 1974). Consumption of other prey species, such as Cisco and juvenile Walleye, showed more variation across Walleye sizes, months, and years. We found a higher proportion of invertebrates in Walleye diets in the spring and a higher proportion of juvenile Walleye in stomachs of larger Walleye in the fall, results similar to those in Oneida Lake (Forney 1974).

Between the three different regulation policies evaluated (no fishing, protected 17 – 28 in slot, statewide regulation), there was less than a 5% difference in total Walleye consumption. The primary reason for the differences in overall consumption is that bioenergetic specific consumption rate (g prey/g predator/day) decreases with fish size, so a population with a higher proportion of smaller, younger individuals will consume a greater amount compared to a population with a higher proportion of older individuals when overall biomass is held constant. Using equal biomass between regulations allowed for a more direct comparison of the effect of size distributions on consumption estimates; however, it is possible that biomass could change under different regulation scenarios and consequently affect consumption. Johnson et al. (1992) used methods similar to those of this study, but allowed biomass to vary in their regulation simulations, and found that consumption by the Walleye population in Lake Mendota increased with regulations that were more restrictive, primarily because Walleye biomass increased. In Mille Lacs Lake, overall biomass of Walleye has decreased over time. Although fishing regulations changed over this same time-period, other system changes have also occurred, including reductions in primary productivity due to decreased nutrient inputs and the infestation of zebra mussels. Currently it is not known how production at lower trophic levels is related to production at higher trophic levels. Understanding these linkages would enable more accurate modeling of the effects of regulation change on consumption.

There was a positive correlation between gillnet biomass per unit effort (BPUE) of age-0 Walleye and the proportion of the adult Walleye diet consisting of juvenile Walleye, indicating that more age-0 Walleye were consumed as they comprised more of the forage base. More interestingly, gillnet BPUE of age-0 Cisco, age-1 Cisco, and spottail shiners, was significantly ($P < 0.05$) negatively correlated with the proportion of the adult Walleye diet consisting of juvenile Walleye. These results suggest that Cisco and shiners may have acted as a buffer for Walleye cannibalization, because there was no significant relationship between gillnet BPUE of juvenile Walleye compared to Cisco and shiners ($P > 0.05$). While these results only included data during September from 2006 – 2015, and consumption patterns could have varied during other months, September was the month when the majority of the juvenile Walleye were consumed. Other studies on Oneida Lake have suggested that Yellow Perch buffer Walleye cannibalism (Forney 1974; Hall and Rudstam 1999); however, in the present study, age-0 and age-1 Yellow Perch gillnet BPUE was not significantly correlated with the proportion of the adult Walleye diet consisting of juvenile Walleye. Perhaps the lack of Cisco in Oneida Lake contributes to the observed differences.

In Mille Lacs Lake, Walleye consumed considerably more forage, including juvenile Walleye, than Northern Pike and Smallmouth Bass. Although species-specific bioenergetics consumption estimates were factored into these calculations, the majority of the difference in consumption was due to differences in population estimates. While Northern Pike and Smallmouth Bass catch rates have increased in Mille Lacs Lake recently (Jensen 2014), population estimates of these species remained considerably less abundant than Walleye. Smallmouth Bass and Northern Pike also did not consume on average large proportions of juvenile Walleye. Smallmouth Bass diets were dominated by crayfish, as noted in other studies (Frey et al. 2003; Olson and Young 2003), with only a minor component of their diet consisting of juvenile Walleye. Northern Pike diets were dominated by Yellow Perch, as in other north temperate lakes (Margenau et al. 1998; Soupir et al. 2000). In Mille Lacs Lake, Northern Pike ≤ 635 mm consumed a higher proportion of juvenile Walleye compared to Northern Pike > 635 mm that consumed a higher proportion of Cisco.

Overall, this study evaluated the complex consumption dynamics of the predator community in Mille Lacs Lake, and has helped clarify how various factors may affect predation rates on juvenile Walleye. Of the factors we evaluated, prey availability appeared to have the largest impact on the consumption of juvenile Walleye biomass, with Cisco and spottail shiners potentially buffering predation of juvenile Walleye. Although juvenile Walleye were consumed by all three predatory species in this study (Walleye, Northern Pike, and Smallmouth Bass), consumption estimates were highest for Walleye, a result largely due to differences in population estimates. This result suggests that while all three predatory species may affect juvenile Walleye survival to some extent, Walleye were likely the main consumer of juvenile Walleye during the years of this study.

REFERENCES

Bean, N. J. 2010. An improved bioenergetics model for Northern Pike (*Esox lucius*) of Box Canyon Reservoir, Pend Oreille River, Washington. Eastern Washington University.

Brandt, S. B. and K. J. Hartman. 1993. Innovative approaches with bioenergetics models: future applications to fish ecology and management. Transactions of the American Fisheries Society 122:731-735.

Chevalier, J. R. 1973. Cannibalism as a factor in first year survival of Walleye in Oneida Lake. Transactions of the American Fisheries Society 102:739-744.

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.

Forney, J. L. 1980. Evolution of a management strategy for the Walleye in Oneida Lake, New York. NY Fish Game J 27:105-141.

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

Hall, S. R. and L. G. Rudstam. 1999. Habitat use and recruitment: a comparison of long-term recruitment patterns among fish species in a shallow eutrophic lake, Oneida Lake, NY, USA. Hydrobiologia 408:101-113.

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

Jensen, E. 2014. Large Lake Assessment Report for Mille Lacs Lake - 2014. Minnesota Department of Natural Resources.

Johnson, B. M., C. Luecke, R. S. Stewart, M. D. Staggs, S. J. Gilbert, and J. F. Kitchell. 1992. Forecasting effects of harvest regulations and stocking of Walleyes on prey fish communities in Lake Mendota, Wisconsin. North American Journal of Fisheries Management 12:797-807.

Kitchell, J. F., D. J. Stewart, and D. Weininger, 1977. Applications of a bioenergetics model to Yellow Perch (*Perca flavescens*) and Walleye (*Stizostedion vitreum vitreum*). Journal of the Fisheries Research Board of Canada 34:1922-1935.

Kumar, R., 2015. Ecosystem based management for Mille Lacs Lake, Minnesota under changing environmental conditions. The University of British Columbia.

Kumar, R., S. J. D. Martell, T. J. Pitcher, and D. A. Varkey. 2013. Temperature-driven decline of a Cisco population in Mille Lacs Lake, Minnesota. North American Journal of Fisheries Management 33:669-681.

Lewin, W., R. Arlinghaus, and T. Mehner. 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Reviews in Fisheries Science 14:305-367.

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

Olson, D. E. and P. K. Cunningham. 1989. Sport-fisheries trends shown by an annual Minnesota fishing contest over a 59-year period. North American Journal of Fisheries Management 9:287-297.

Olson, M. H. and B. P. Young. 2003. Patterns of diet and growth in co-occurring populations of Largemouth Bass and Smallmouth Bass. Transactions of the American Fisheries Society 132:1207-1213.

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.

Radomski, P. 2003. Initial attempts to actively manage recreational fishery harvest in Minnesota. North American Journal of Fisheries Management 23:1329-1342.

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

Shuter, B. J. and J. R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

Soupir, C. A., M. L. Brown, and L. W. Kallemeyn. 2000. Trophic ecology of Largemouth Bass and Northern Pike in allopatric and sympatric assemblages in northern boreal lakes. Canadian Journal of Zoology 78:1759-1766.

Venturelli, P., J. Bence, T. Brenden, N. P. Lester, and L. G. Rudstam. 2014. Mille Lacs Lake Walleye Blue Ribbon panel data review and recommendations for future data collection and management. Report submitted to Minnesota Department of Natural Resources.

Wuellner, M. R., S. R. Chipps, D. W. Willis, and W. E. Adams, 2010. Interactions between Walleyes and Smallmouth Bass in a Missouri river reservoir with consideration of the influence of temperature and prey. North American Journal of Fisheries Management 30:445-463.