LIMITATIONS OF LARVAL WALLEYE (*SANDER VITREUS*) PRODUCTION IN MICHIGAN'S INLAND WATERWAY

By

Ryan D. MacWilliams

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Fisheries and Wildlife – Master of Science

2013

ABSTRACT

LIMITATIONS OF LARVAL WALLEYE (*SANDER VITREUS*) PRODUCTION IN MICHIGAN'S INLAND WATERWAY

By

Ryan D. MacWilliams

Walleye (*Sander vitreus*) are one of the most targeted species by anglers in North America. Consequently, there is a need to understand the factors that influence year-class formation in age-0 walleye. Prey availability during the early life stages of walleye is considered the most important factor influencing the success of recruitment. I conducted a two-year study of larval walleye density, zooplankton prey availability, and fall age-0 walleye relative abundance within Michigan's Inland Waterway to document locations of larval walleye concentrations in the system and to determine if adequate prey are available to age-0 walleye. Larval walleye density in Burt Lake (mean=$2.47 \cdot 1000 m^{-3}$ SE=0.81) was 87% higher than all other study lakes, and 94% higher than Pickerel Lake, which had the lowest density (mean=$0.14 \cdot 1000 m^{-3}$ SE=0.14). The density of large-bodied zooplankton taxa (Calanoida, *Daphnia*) across all lakes was low ($2 \cdot L^{-1}$), well below the 100 Daphnids$\cdot L^{-1}$ recommended for optimal walleye survival. The relative abundance of naturally produced age-0 walleye fall fingerlings was positively related to the spring density of large-bodied zooplankton taxa and larval walleye when all lakes and years were included in the analysis. While it is likely that multiple factors influenced year-class formation in the system, the results of this study suggest that prey availability during critical early life stages limited larval walleye density and year-class formation in Michigan's Inland Waterway.

ACKNOWLEDGEMENTS

I am very grateful to my primary advisor, Brian Roth, for the guidance he provided during the duration of this project and particularly with the development of this thesis. I would also like to thank the members of my committee, Daniel Hayes and Mary Bremigan, for always providing excellent advice at a moment's notice, especially concerning the development of the code used in my analysis as well as their contributions to this manuscript. This project could not be possible without the support of funds from the Michigan Department of Natural Resources, Fisheries Division. Thank you to Tim Cwalinksi, Neil Godby, Patrick Hanchin, and many others of the Fisheries Division for their assistance in the field and the contribution of data. My field season would not have been possible without the help and guidance of Seth Herbst, as well as assistance from a number of hardworking technicians and volunteers, including Joe Parzych, Mike Rucinski, Chad Brewer, Julia Feeley, and Kevin Osantowski. Lastly, I would like to thank my colleagues in the Fisheries and Wildlife Department at MSU who provided constructive comments along the development of my project, presentations, and this thesis.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Walleye (*Sander vitreus*) is one of the most targeted species by anglers in North America. In a study of game fish species popularity, walleye ranked first or second throughout their native and introduced ranges (Quinn 1992). Walleye are targeted by approximately 0.5 million anglers over an estimated 5.5 million days per year (USDOI et al. 2001). Because of their popularity, walleye fisheries generate a considerable economic impact in North America. For example, walleye is the most targeted species in Lake Erie and Lake Winnebago where these two fisheries generate a combined value of >$800 million (USDOI et al. 2008; Winnebago County University of Wisconsin Extension 2006). Aboriginal walleye fisheries also occur in several states and provinces within the United States and Canada. Aboriginal fishing rights were retained in land treaties, including the treaties of 1836, 1837, 1842, and 1854 (Barton 2011), leading to considerable Tribal and State interest for the walleye fisheries within these Treaty-ceded territories (Godby et al. 2011). Therefore, effective management is needed in fisheries where tribal and sport fisheries are substantial.

In this study, I evaluated young-of-year walleye in the Inland Waterway of Michigan, which is comprised of four interconnected lakes in the northern Lower Peninsula and lies within the 1836 Treaty-ceded Territory (Figure 1). The waterway extends 72.4km from Lake Huron nearly to Lake Michigan, near the northern tip of the Lower Peninsula. In the system, gravid and barren female walleye have been captured in both riverine and lake habitat, suggesting that both lakes and rivers may contribute to natural recruitment

(Hanchin et al. 2005a; Hanchin et al. 2005b; Michigan Department of Natural Resources, unpublished data). However, walleye production in the system likely occurs in a few key areas, including Burt Lake, the Sturgeon River, and the Black River. Further, some walleye may employ a lake-to-river reproductive strategy, such as that found in the Maumee River (western basin of Lake Erie), the Current River (Thunder Bay, Lake Superior), and the Ottertail river (Many Point Lake, MN) (Olson and Scidmore 1962; Geiling et al. 1996; Roseman et al. 2001).

A population estimate of adult walleyes conducted in 2009 on one of these lakes (Mullett Lake) produced an adult population estimate (2,648 walleye ± 648 95% CI) that was markedly lower than an estimate conducted in 1998 (14,350 walleye ± 6,480 95% CI) (Michigan Department of Natural Resources, unpublished data). The 2009 Mullett Lake population estimate raised concerns that a decline in natural walleye recruitment in the lake may have occurred. In the early 1990s, Zebra Mussels (*Dreissena polymorpha*) invaded the Inland Waterway (Michigan Department of Natural Resources, unpublished data), potentially leading to observed reductions in chlorophyll-a in Burt and Mullett lakes (Figure 2). Results from other systems invaded by zebra mussel indicate that such reductions in primary producers could result in reduced zooplankton abundance as well, which could have negative implications for larval walleye survival. For example, phytoplankton and macrozoooplankton biomass in dreissenid invaded inland lakes in Michigan were 24% and 33% lower, respectively, than uninvaded lakes (Kissman et al. 2010). In other Michigan lakes, zebra mussels are associated with a significant decline in *Daphnia* (Kissman et al. 2010) that provide food during a critical period of larval walleye development. Additionally, after dreissenid invasion in Lake Ontario, age-0 walleye CPUE declined to 33% of catch-rates from pre-invasion years (Hoyle et al. 2008). Low larval walleye abundance and recruitment would likely necessitate intervention in the form of stocking and would be evidenced by a high proportion of stocked age-0 fish compared to naturally-produced age-0 fish. In the Inland Waterway, stocked fish represented 100% of fall age-0 walleye caught during near-shore electrofishing surveys of Mullett Lake from 1999-2002, and have subsequently remained a considerable proportion of fall age-0 walleye (Michigan Department of Natural Resources, unpublished data).

Prey availability to larval fish is thought to be particularly important because it has a large effect on larval growth and survival (Houde 1987, Miller et al. 1988). For many walleye populations, year-class strength is established by late fall (Kempinger and Churchill 1972), and is dependent on variability in survival during the first year (Barton 2011). Some studies suggest that forage availability during early development of larval walleye is the most important factor influencing the effectiveness of natural recruitment (Spykerman 1974, Fielder 1992). Low forage availability can influence survival by reducing swimming speeds thereby increasing vulnerability to capture by predators (Laurence 1972; Rice et al. 1987; Jonas and Wahl 1998). Larval walleye growth rate and survival is shown to increase with crustacean zooplankton density, with optimal growth and survival rates occurring when the number of large-bodied zooplankton exceed $100 \cdot L^{-1}$ (Li and Mathias 1982; Hoxmeier et al. 2004; Peterson et al. 2005). However, adequate walleye recruitment has been observed when spring large-bodied zooplankton densities $<100 \cdot L^{-1}$ were observed. For example, Engel et al. (2000) reported densities of fall fingerlings in Escanaba Lake, Wisconsin coinciding with spring daphnia densities $<10 \cdot L^{-1}$. While an absolute threshold between zooplankton density and larval walleye survival has not been established, high walleye larvae survival is more likely when higher zooplankton densities are available to walleye during early development.

A positive relationship between zooplankton density and larval fish survival has been observed for several species (Lemly and Dimmick 1982; Mills et al. 1989; Claramunt and Wahl 2000; Engel et al. 2000; Hoxmeier et al 2004; Peterson et al. 2006). For example, in a multi-year study of walleye recruitment dynamics in Escanaba Lake, Wisconsin, Engel et al. (2000) observed that fall age-0 walleye abundance was linearly related to spring zooplankton density. Similarly, a positive relationship between large-bodied zooplankton taxa and CPUE of fall age-0 walleye was observed in a two-year study of five reservoirs in Pennsylvania (Peterson et al. 2006). Still, some studies have reported no significant relationship between walleye and zooplankton densities (Houde 1967; Partridge and DeVries 1999). This uncertainty in the role of larval forage for walleye indicates a need to develop additional quantitative field studies of walleye recruitment dynamics, examining the relationship between age-0 walleye density and spring forage availability. Such studies can help identify factors that could limit juvenile walleye survival and facilitate better prediction of walleye recruitment.

I developed and conducted a two-year study of the larval walleye density and fall age-0 walleye relative abundance within the Inland Waterway in order to better understand the locations of higher larval walleye abundance and the potential limitations to age-0 walleye recruitment within the system. The objectives of this study were to:

(1) Determine locations of larval walleye concentrations in the Inland Waterway

(2) Determine if adequate food resources exist for larval walleye, defined by the density of

large-bodied zooplankton taxa, both in terms of ambient zooplankton communities and in larval walleye diets.

(3) Examine whether biotic factors, such as zooplankton density and larval walleye density, potentially influence the relative abundance of fall age-0 walleye.

To address the first objective, I conducted a survey of the spring ichthyoplankton in the rivers and lakes of the waterway in order to determine concentrations of larval walleye in the Inland Waterway. I used Ichthyoplankton nets in each of the four study lakes and in the Black River and Sturgeon River to gather walleye larvae at night in near shore areas and from riverine sources where they are known to inhabit (Nepszy et al. 1991; Roseman et al. 2005). In order to address the second objective, I sampled zooplankton concurrently with ichthyoplankton to quantify the density of large bodied zooplankton taxa (Calanoid copepods and *Daphnia* spp.) available to larval walleye. I addressed the third objective by evaluating if metrics of zooplankton density, larval walleye density, and larval yellow perch density could predict an index of fall age-0 walleye abundance. While age-0 yellow perch are not preferred prey of age-0 walleye (Pelham et al. 2001) they are still capable of influencing walleye year class strength through the mitigation of cannibalism by adult walleye. For example, in years where age-0 yellow perch were not abundant, cannibalism among walleye in Lake Oneida contributed significantly to mortality and may have determined year class strength (Forney 1974, Forney 1976, Chevalier 1973). Finally, Fall age-0 walleye relative abundance in each of the study lakes was assessed with a complete shoreline electrofishing survey in collaboration with the Michigan Department of Natural Resources (DNR) and the Little Traverse Bay

Band of Odawa Indians (LTBB) in the fall of 2011 and 2012.

This study aims to give a better understanding of areas of larval walleye concentrations in the system as well as the limitations for natural recruitment of walleye in oligotrophic lakes. The results of this study demonstrate, *in situ*, the influence of forage availability on larval walleye density and subsequent relative abundance of fall recruits. Additionally, this work has further implications towards enhancing stocking programs in similar systems where low zooplankton density (<<100/L) could limit walleye year-class strength.

METHODS

Study Area

The Inland Waterway is a heterogenous system containing some of the largest inland lakes in the state of Michigan (Figure 1). The Inland Waterway is comprised of four lakes, Crooked Lake (area=9.5km^2, max depth=15.2m), Pickerel Lake (area= 4.4km^2, max depth=22.9m), Burt Lake (area=69.3km^2, max depth=22.3m), and Mullett Lake (area=67.6km^2, max depth=44m) (Table 1). The shoreline of the waterway is largely developed with private and commercial residences; however some undeveloped riparian land is contained within state forest and state park land. The fish community of the waterway is typical of oligotrophic waterbodies of northern Michigan and includes, but is not limited to: Bowfin (*Amia* calva), various Cyprinids, White Sucker (*Catostomus commersoni*), Black Bass (*Micropterus dolomieu, Micropterus salmoides*) and *Lepomis* sunfish, Alewife (*Alosa pseudoharengus*), Northern Pike (*Esox Lucius*), Muskellunge (*Esox masquinongy*), Burbot (*Lota lota*), Brown Bullhead (*Ameiurus nebulosus*), Longnose Gar (*Lepisosteus osseus*), Rainbow Trout (*Onchorhynchus mykiss*), Yellow Perch (*Perca flavescens*), and Walleye (Hanchin et al. 2005a; Hanchin et al. 2005b).

Documented walleye stocking in the Inland Waterway began in 1933 and continued sporadically through the 1950s. In Burt Lake, walleye fingerlings were stocked from 1989 through 1993 (Table 2), although not at significant densities (Hanchin et al. 2005a). Walleye fingerlings were sporadically stocked in Crooked and Pickerel Lakes from 1985-2001 at varying densities (Tables 2). While stocking of fingerlings has likely augmented the walleye populations in Crooked and Pickerel Lakes, an oxytetracycline (OTC) evaluation of

Crooked Lake in the fall of 2000 showed that natural production accounted for approximately 70% of age-0 walleyes (Hanchin et al. 2005a). Recently, walleye fingerlings have been stocked in Mullett Lake from 1999-2003 and again in 2010, 2011, and 2013 (Table 2)(Michigan Department of Natural Resources, unpublished data). Surveys of fall age-0 walleye relative abundance showed that stocked fish represented 100% of fall age-0 walleye caught during near-shore electrofishing surveys of Mullett Lake from 1999-2002, and have subsequently remained a considerable proportion of fall age-0 walleye (Michigan Department of Natural Resources, unpublished data)

Spring Ichthyoplankton and Zooplankton sampling

Ichthyoplankton and zooplankton were sampled from each the four study lakes (ichthyoplankton tows) and rivers (primarily drift nets, see details) at approximately weekly intervals from May-June (2011) and April-June (2012). I conducted a combined total of 318 ichthyoplankton tows and drifts and 271 zooplankton tows in 2011, and 590 ichthyoplankton tows and drifts and 507 zooplankton tows in 2012. Details of ichthyoplankton collection effort are presented in Tables 4-7. Larval fish were collected using a 500μm conical ichthyoplankton net with a circular 0.5 m mouth opening. A flow meter was suspended in the center of the net to measure the volume of water filtered during each tow. Sampling occurred parallel to the shoreline, in near shore areas, at depths of 1-3m, and at a speed of approximately 1-1.5$m \cdot s^{-1}$ (Engel et al. 2000; Roseman et al. 2005). The net was towed through the top 0.5m of the water column, where larval walleye are documented to be the most abundant (Engel et al. 2000). Collection occurred between 2100 and 0100 hours when the greatest number of walleye larvae are vulnerable to capture near surface water and in order to overlap capture with the period of time when walleye are known to feed and therefore allow for the analysis of gut contents (Mitro and Parrish 1997; Corbett and Powles 1986). Due to their size, Burt Lake and Mullett lakes were sampled either in two consecutive nights or in one night by two crews. Crooked and Pickerel lakes could be sampled in one night by a single crew. Burt and Mullett lakes were divided into 16 zones from a focal point in the center of the waterbody with eight zones designated to both the western and eastern shores of the lake. Four zones from a total of eight were randomly selected for sampling per shoreline, per night. Crooked and Pickerel lakes were sampled by randomly selecting 12 suitable start locations. A pool of possible start locations was created by conducting a complete shoreline survey where start locations were set for every five minutes of travel time, roughly equivalent to the distance travelled when conducting Ichthyoplankton trawls.

Zooplankton samples were collected in the lakes only. Samples were collected at the completion of each ichthyoplankton tow using a vertical tow of a Wisconsin Plankton Net (12cm diameter x 80μm). Following collection, ichthyoplankton and zooplankton samples were stored in 95% ethanol for enumeration and identification in the laboratory.

I also collected ichthyoplankton in the Black and Sturgeon rivers. In 2011, I employed ichthyoplankton tows in the Black River, with the same methods used for collection in the study lakes. A pool of possible sampling sites on the Black River were selected by conducting a complete survey of the length of the Black River from the convergence of the Black River and Cheboygan River to completion at the Alverno Dam (Figure 1). Of the total possible starting locations, 12 were randomly selected for each night of sampling. However, I made the decision to switch the ichthyoplankton collection method from tows in 2011 to drift net sampling in 2012 on the Black River due to the inherent danger of towing the poorly channelized river at night. Therefore in 2012, ichthyoplankton nets were drifted in the Black River from the Mograin Bridge, approximately 1km downstream of the Alverno Dam, the only static structure proximate to spawning areas where nets could be safely anchored. Three nets were set simultaneously in four rounds of 30-minutes. Collection occurred between 2100 and 0100 hours when the greatest number of drifting walleye larvae are vulnerable to capture at the surface of water (Mitro and Parrish 1997; Corbett and Powles 1986). The shallow depth also precluded the use of larval towing methods on the Sturgeon River. Therefore, I sampled the spring larval fish assemblage on the Sturgeon River in 2011 and 2012 by anchoring drift nets from a small bridge approximately 200 meters from the mouth of the river.

Fall near-shore electrofishing survey

I related a number of biological variables to fall age-0 walleye abundance to explore factors that have the potential to influence age-0 walleye relative abundance within the Inland Waterway. In order to accomplish this goal, I conducted a survey of fall age-0 walleye density on each study lake in order to develop an index of walleye recruitment within the system. Age-0 walleye recruitment was quantified as the relative abundance (CPUE) of age-0 walleyes in fall of each year from electrofishing surveys conducted in collaboration with MDNR Fisheries Division and Little Traverse Bay Band of Odawa Indians crews in the 2011 and 2012. The fall survey consisted of electrofishing the entire shoreline each year on all four lakes. Because stocking occurred on Mullett Lake in 2011, it was necessary to evaluate the ratio of naturally produced-to-hatchery-produced fish. Walleye captured during the survey were sacrificed in MS-222 and stored on ice until they could be transported to the laboratory. Otoliths from sacrificed walleye were removed and examined for oxytetracycline marks (indicating these fish were of hatchery origin) in order to assess recruitment of stocked and naturally produced age-0 walleye in Mullett Lake. Mean catch-per-mile of naturally produced age-0 walleye was calculated for each lake in 2011 and 2012.

Ichthyoplankton Enumeration

Ichthyoplankton samples collected in the spring of 2011 and 2012 were enumerated under a microscope to determine the mean density of each taxon for each sampling event. All species collected in ichthyoplankton tows were identified to the lowest possible taxon. Total length was measured and gut contents of larval walleye were collected in order to assess prey selectivity during development. A General Linear Model (GLM) with waterbody and sampling year treated as categorical variables with interaction (walleye density= Waterbody | Sampling Year), and subsequent Tukey-HSD Post-Hoc testing, using the GLM procedure in SAS, were conducted to determine if spring age-0 walleye density differed significantly among waterbodies and sampling years.

Evaluation of age-0 walleye diet

The contents of the alimentary canals of YOY walleye captured with ichthyoplankton tows were evaluated to assess prey selectivity of larval walleye during development. All prey items within the gut of age-0 walleyes were identified, counted and measured (standard length). Copepod prey were identified as either Calanoid or Cyclopoid, whereas cladocerans were identified to the lowest possible taxonomic level. Age-0 walleye dietary items were to be compared with available forage to determine the selection of prey items by walleyes across the waterway. However, an insufficient number of walleyes possessed gut-contents (<90%, N=146), precluding the use of selectivity analysis.

Zooplankton Enumeration

Zooplankton samples were analyzed to determine the composition of the crustacean zooplankton community at every ichthyoplankton sampling site. Copepod nauplii and rotifers were not enumerated as they do not represent a significant portion of age-0 walleye gut contents (Hoxmeier et al 2004; Peterson et al 2006; Mathias and Li, 1982). Calanoid copepods and *Daphnia* were categorized as large-bodied zooplankton taxa in order to calculate the mean density of preferred dietary items for spring age-0 walleye (Engel et al. 2000; Houde 1967). Zooplankton samples were filtered through a ring net (80 μm) and then adjusted to a known volume. Visibly dense samples were subsampled in 1mL aliquots until a minimum of 100 individuals were counted (Hoxmeier et al 2006). Total lengths for up to ten individuals from each major group (Calanoid and Cyclopoid copepods, *Bosmina, Daphnia*) were recorded using digital imaging software (Hoxmeier et al., 2004). A GLM with Lake and sampling year treated as categorical variables with interaction, (Zooplankton density= Lake | Sampling Year) and subsequent Tukey-HSD Post-Hoc testing, using the GLM procedure in SAS, were conducted to determine if the spring zooplankton community or large-bodied taxa density differed significantly among waterbodies and sampling years.

Summer shore seining survey

A rectangular seine net measuring 15.24m X 1.22m with 0.63cm mesh was used during the month of July with the intent of developing a mid-summer index of age-0 walleye abundance. One end of the seine was anchored to the shore; the other end was deployed perpendicular to the shore and was swept around a 90-degree arc. Three replicate hauls were conducted at each sampling site, with each subsequent replicate beginning at the location on shore where the previous haul concluded. Between 5-6 sampling sites were chosen on each of the four lakes within the waterway, depending on the limitations of site quality and access. Over both sampling years, a total of 54 seine hauls were completed. No age-0 walleye were captured during 2011-2012 shore seining effort, so results are not reported for this portion of the study.

Regression analysis

I used linear regression to test for significant predictors of annual spring and fall age-0 walleye density within the waterway. These predictors were zooplankton density, larval walleye density, and larval yellow perch density. I used Pearson's Product-Moment Correlation test to determine relationships of fall age-0 walleye density with zooplankton community density, large-bodied zooplankton taxa density, spring age-0 walleye, and spring age-0 yellow perch. I also used this test to evaluate the association of spring age-0 walleye density with zooplankton community density, large-bodied zooplankton taxa density, and spring age-0 yellow perch.

RESULTS

Spring larval walleye abundance

Overall, walleye represented less than 0.2% of the ichthyoplankton community during 2011-2012 sampling (mean density=$3.56 \cdot 1000m^{-3}$ SE=1.29). Yellow Perch (mean density =$1376.15 \cdot 1000m^{-3}$ SE=164.26) and white sucker (mean density=$509.7 \cdot 1000m^{-3}$ SE=137.892) dominated the catch (Figure 3).

Larval walleye densities differed significantly across lakes (F=5.51, p= <0.001), with walleye density being highest in Burt Lake (mean=$2.47 \cdot 1000m^{-3}$ SE=0.81)(Tukey HSD, p<0.05)(Figure 4). All other lakes contained similar mean larval walleye densities (Tukey HSD, all p>0.05)(Figure 4). Walleye density in Burt Lake was on average 87% higher than all other lakes, and 94% higher than Pickerel Lake, which had the lowest walleye larvae density in the system (mean=$0.14 \cdot 1000m^{-3}$ SE=0.14) (Figure 4). No walleye were captured in Pickerel Lake in spring 2011. Within each lake, walleye densities were similar in 2011 and 2012 (Tukey HSD, all p>0.05) (Figure 4). Of the rivers sampled, the Sturgeon River had the highest point estimate of mean larval walleye density in 2011 (mean = $8.64 \cdot 1000m^{-3}$ SE=4.66)(Figure 5). The Black River had the highest point estimate of mean larval walleye density in 2012 (mean=$24.08 \cdot 1000m^{-3}$ SE=16.39)(Figure 5). However, GLM results indicated that there was no significant difference in walleye density between the rivers (F=0.69, p=0.60)(Figure 5). The density of walleye larvae captured in rivers was similar in 2011 and 2012 (Tukey HSD, all p>0.05) (Figure 5).

In the lakes sampled, peak walleye density appeared to occur earlier in 2012 than in 2011 (Figure 6). In 2011, the walleye density peaked in Burt Lake on May 21st (mean=29.16·1000m^{-3} SE =16.71), whereas in 2012, the peak density was observed on May 8th (mean=4.51·1000m^{-3} SE=1.47). This trend was also observed on Crooked Lake where, in 2011, the peak walleye density occurred on May 16th (mean=1.35·1000m^{-3} SE=0.92) and on April 28th, 2012 (mean= 3.71·1000m^{-3} SE=2.69), and in Mullett Lake, where walleye density peaked on June 5th, 2011 (mean=2.31·1000m^{-3} SE=1.57) and May 19th, 2012 (mean=1.14·1000m^{-3} SE=0.79). Results in Pickerel Lake were equivocal, as no walleyes were captured in 2011. Walleye density in the Black River peaked one week earlier in 2011 than in 2012; however this pattern was not observed in the Sturgeon River (Figure 7). In the Black River, walleye density peaked on May 13th, 2011 (mean=6.61·1000m^{-3} SE=3.15) and in 2012 on May 21st (90.35·1000m^{-3} SE=75.35). Walleye density in the Sturgeon River peaked in 2011 on May 18th (mean=21.6·1000m^{-3}) and in 2012 on May 14th (mean=38.33·1000m^{-3}).

Zooplankton Community: density and length frequency dynamics

Large-bodied zooplankton densities differed significantly across lakes (F=9.62, p<0.0001). Post-hoc analysis indicated that large-bodied zooplankton (i.e., Calanoid copepods, *Daphnia*) was significantly higher in Burt Lake (mean=1.82·L^{-1} SE=0.21, Tukey

HSD, $p<0.05$) with densities that were at least 56% higher than all other lakes (Figure 8). Additionally, the density of large-bodied zooplankton across all lakes in the waterway was higher in 2012 (mean= $1.34 \cdot L^{-1}$ SE=0.12) than 2011 (mean= $0.74 \cdot L^{-1}$ SE=0.13, Tukey HSD, $p<0.05$). A summary of the mean density of the four most common taxa is provided in Table 3.

Zooplankter mean length (all taxa) was significantly different among lakes (F=38.69, $p<0.0001$), with post-hoc analysis indicating that zooplankton in Crooked Lake (mean=0.50mm SD=0.03) were significantly larger than all other study lakes (Tukey HSD, p=<0.05)(Figure 9). Zooplankton in Mullett Lake were smaller than all other lakes (Tukey HSD, $p<0.05$, mean=0.44mm SE=0.004), but Burt and Pickerel lakes contained similar-sized zooplankton. The difference between the lake with the largest average zooplankton length (Crooked Lake) and the smallest (Mullett) was small (0.06mm). Length frequency distributions of the combined zooplankton community of the entire waterway indicate large zooplankton (≥1mm) composed <10% of the community by number, while small zooplankton (0.2mm-0.5mm) were most common (Figure 10).

Fall age-0 walleye recruitment: Annual density and regression analysis

Age-0 walleye were sampled using a near shore electrofishing survey that was designed to sample the entire shoreline of the four lakes in the waterway. Because of the sampling design, the resulting estimate of annual age-0 walleye density lacked the replication required in order to test for variance in catch data across the four lakes in the waterway. Specifically, Pickerel Lake only had one estimate, precluding the ability to assess differences in lake-specific densities. However, catch data from the survey indicated that Burt Lake had the highest CPUE of naturally produced age-0 walleye in 2011 (mean $=8.32 \cdot mile^{-1}$ SE=1.34) and 2012 (mean=$8.32 \cdot mile^{-1}$ SE=3.58), while Crooked Lake had the lowest CPUE in 2011 ($0.62 \cdot mile^{-1}$ SE= 0.23) and Pickerel Lake had the lowest CPUE in 2012 ($1.01 \cdot mile^{-1}$)(Figure 11). The mean density of naturally produced age-0 walleye captured in the study lakes was positively related to the spring density of large-bodied zooplankton taxa (r^2=0.53, p=0.042)(Figure 12) and spring density of age-0 walleye (r^2=0.67, p=0.01)(Figure 13). Fall age-0 walleye density was not significantly related to the system wide mean density of the zooplankton community (r^2=0.45, p=0.13) or the system wide mean density of spring age-0 yellow perch (r^2=0.07, p=0.52). No correlations were found between the system wide mean densities of spring age-0 walleye, spring age-0 yellow perch (r^2=0.02, p=0.75), all zooplankton taxa (r^2=0.34, p=0.13), or large-bodied zooplankton taxa (r^2=0.23, p=0.23)(Figures 14-18).

DISCUSSION

The larval period is a critical time in the development of many fish species (Blaxter 1986). As is the case with many other piscivores, walleye must rely on zooplankton prey before they can consume fishes (Colby et al., 1979). Therefore, the study of zooplankton abundance and its influence on walleye recruitment dynamics has been the focus of several laboratory and field studies (Spykerman 1974; Li and Mathias, 1982; Houde 1987; Miller et al. 1988; Fielder 1992; Hoxmeier et al. 2004). This study provides further insight into the influence of early forage base on age-0 walleye abundance and provides an example of a study design that can be used to concurrently determine the density of larval walleye and their zooplankton prey.

While it is likely that multiple abiotic and biotic factors are responsible, this study provides some evidence to support the hypothesis that low walleye larvae density in the spring and a decline in natural recruitment in Mullett Lake are consequences of inadequate forage availability to walleye during early life stages. I observed that the mean density and length of zooplankton prey was not sufficient to support high densities of walleye larvae within the waterway (Li and Mathias 1982; Hoxmeier et al. 2004; Peterson et al. 2006). During both years of this study, the density of large-bodied taxa (Calanoid copepods, *Daphnia*) across all study lakes was low ($\sim 2 \cdot L^{-1}$)(Figure 8), and well below the 100 Daphnids$\cdot L^{-1}$ generally thought to be needed for optimal walleye survival (Li and Mathias 1982; Hoxmeier et al. 2004). Similarly, *Daphnia* spp. abundance less than $10 \cdot L^{-1}$ was related to poor survival of walleye larvae in Lake Oahe, South Dakota and several Pennsylvania Reservoir (Fielder 1992; Peterson et al. 2006). However, adequate walleye recruitment has been observed when spring large-bodied zooplankton densities <<100·L^{-1} were observed. For example, Engel et al. (2000) reported densities of fall age-0 walleye >300·ha coinciding with spring daphnia densities <10·L^{-1}. While an absolute threshold between zooplankton density and larval walleye survival has not been established, high walleye larvae survival is more likely when greater densities of large-bodied zooplankton are available during early life stages.

This study also corroborates results from previous experiments that reported a positive relationship between zooplankton density and larval fish density (Lemly and Dimmick 1982; Mills et al. 1989; Claramunt and Wahl 2000; Engel et al. 2000; Hoxmeier et al 2004; Peterson et al. 2006). Hoxmeier et al. (2004) demonstrated that walleye larvae reach optimal survival and growth rates in experimental tanks and rearing ponds when large-bodied zooplankton densities exceed 100·L^{-1}. Similarly, Peterson et al. (2006) observed in a study of five Pennsylvania impoundments that zooplankton density was positively related to fall catch of age-0 walleye and that young-of-year catch in the fall was low (<10 individuals) when spring zooplankton densities were below 50·L^{-1}.

Walleye larvae represented a small portion of the ichthyoplankton community in the waterway during the spring of 2011 and 2012 (Figure 3). Yellow perch were the most abundant ichthyoplankton species observed during the study and were nearly 100 times more abundant than walleye. It is likely that yellow perch larvae in the waterway were able to grow and survive on the extant zooplankton community, which was dominated by small zooplankters (< 0.5mm). Yellow Perch larvae (<10mm) rely almost exclusively on copepod nauplii and small copepods (< 0.5mm) during early life stages (Schael et al. 1991; Bremigan et al. 2003). In contrast, walleye larvae experience slow growth rates when feeding on small zooplankton (<1mm)(Crowder et al. 1987; Johnston and Mathias, 1994). When transitioning to exogenous feeding, walleye larvae require high densities of small zooplankton (200-800$\cdot L^{-1}$) in order to attain maximum consumption rates, while those feeding on large zooplankton (> 1mm) require lower densities (20-300$\cdot L^{-1}$) to achieve optimal growth and survival (Johnston et al. 1994). However, zooplankton densities in this system were low, and neither large zooplankton nor small zooplankton approached optimal densities for walleye (Figure 10).

Along with prey density, prey size is a factor that can influence walleye recruitment success. Walleye forage in a manner that optimizes growth (Mathias and Li 1982; Fox 1989). Several studies indicate that fish larvae selectively consume large zooplankton, relative to gape size, in order to maintain the highest reward rate relative to foraging costs (Mittlebach 1981; Mills et al. 1984; Li et al. 1985; and Confer and O'Bryan 1989). First feeding walleye in Oneida Lake consumed zooplankton as large as was allowed by their mouth gape (0.93-1.5mm gape for 10-13mm fish)(Graham and Sprules 1992). In this study, system-wide mean zooplankter length was <0.50mm, with small zooplankton (0.2mm-0.5mm) most common, and zooplankton > 1.0mm representing <10% of the community (Figure 10). This suggests that large zooplankton in all of the study lakes are not sufficiently abundant to support high walleye survival. While I found significant differences in mean zooplankton length among the study lakes, the difference between the lake with the largest average zooplankton length (Crooked Lake) and the smallest (Mullett) was small (0.06mm) and is not likely to be biologically significant given the lack of studies that report zooplankton size information at the μm scale. Therefore, it is likely that the combination of low zooplankton density ($<2 \cdot L^{-1}$) and small zooplankter size (<0.50mm) could limit first feeding walleye survival within the waterway.

The high proportion of empty alimentary canals observed in larval walleye during this study adds support to the conclusion that zooplankton density in the waterway is inadequate to support high survival of larval walleye. The low number of larval walleye captured during this study coupled with the high proportion of empty alimentary canals (> 90%) across all four lakes precluded the use of diet analysis in this study. However, the high proportion of empty alimentary canals suggests that larval walleye within the waterway are not feeding and may be experiencing deleterious effects of starvation brought about by inadequate prey availability (Mion et al. 1998). Similarly, larval walleye feeding success was compromised by low zooplankton densities (<1 individual$\cdot L^{-1}$) in the Maumee River, Ohio where >90% of larval walleye guts were empty (Mion et al. 1998). In contrast, all walleye fry captured in Clear Lake, Iowa contained gut contents when zooplankton density exceeded $100 \cdot L^{-1}$ (Bulkley et al.1976).

While forage conditions throughout the waterway appeared inadequate to support high larval walleye survival, differences in zooplankton density did exist among the study lakes. Further, these differences were positively related to walleye recruitment within the system. Therefore, this study provides evidence that walleye year-class formation is influenced in part by forage availability, even across a narrow range of large-bodied zooplankton densities (< 5 zooplankters$\cdot L^{-1}$). For example, Burt Lake had higher zooplankton densities and fall young-of-year walleye catch rates in 2011 and 2012 in comparison to the other study lakes (Figure 8). This paralleled higher walleye larvae density in spring (Figure 11), which is indicative of higher larval hatch abundance, higher larval survival rates, or both. Furthermore, a significant positive relationship between fall age-0 walleye CPUE and zooplankton density, monitored in four lakes over a 2-year period, adds further support to the hypothesis that zooplankton prey availability during critical early life stages influences larval walleye survival and hence year-class formation of juvenile walleyes (Figure 12).

While the evidence suggests that inadequate forage may indicate low larval walleye survival within the system, several alternative hypotheses remain. First, it is possible that annual variability in egg production (based on spawning adult abundance and fecundity estimates) was responsible for the low densities of walleye larvae that I observed. There has been no recent survey of walleye egg production in the waterway to determine if low egg production is contributing to low larval walleye densities. However, because annual variability in walleye egg production is generally low relative to variability in fall age-0 walleye abundance, first year survival typically drives variability in year-class strength (Barton 2011). Further, predation on walleye eggs is common and has the potential to affect walleye recruitment success in aquatic systems. Corbett and Powles (1986) observed that yellow perch and white suckers preyed upon walleye eggs, but the authors did not provide an assessment of its effect on walleye recruitment. Similarly, Roseman et al. (1996) found that 86% of White Perch (*Morone americana*) had consumed walleye eggs. Post et al. (2002) surmised that declining recreational species abundance could lead to compensatory increases in forage species, which may limit the ability of recreational species to recover due to the suppression of juveniles through predation and competition.

Yellow perch are abundant in the Inland waterway, representing 77% of total angler catch according to a 2001 summer angler survey (Hanchin et al. 2005), and have the potential to consume walleye eggs, particularly in Mullett Lake where adult walleye abundance has declined. However, it is unknown whether walleye egg predation occurs at a significant level in the waterway. Roseman et al. (1996) held that walleye egg predation may only affect recruitment in years with low spring temperatures and slow warming rates, prolonging egg development and increasing the time that egg predator spawning overlaps with walleye spawning. However, there has not been substantial evidence of population-level effects of walleye egg predation showing a negative effect on recruitment success (Barton 2011). It is also possible that recruitment within the system could be influenced by predation on larval and/or juvenile walleye. Juvenile walleye can be prey for several cohabiting fish species including top predators such as northern pike, smallmouth bass, and largemouth bass among others. Larval walleye can be consumed as well by planktivores such as black crappie, white crappie, alewife, white perch, and yellow perch (Schneider and Leach 1977; Colby et al. 1979; Brooking et al. 1998). Alewives in particular have been documented as effective predators of numerous species native to the Great Lakes (Kohler and Ney 1980; Brandt *et al.* 1987), and have been observed to prey intensely upon walleye (Brooking *et al.* 1998). If alewife were feeding on larvae, I would expect other vulnerable species, particularly yellow perch to also show signs of population decline. However, yellow perch are one of the most abundant species in the Inland Waterway, representing 77% of total angler catch according to a 2001 summer angler survey (Hanchin et al. 2005) and dominating ichthyoplankton tow catches (>350 times more abundant than walleye).

While proximal causes for low zooplankton density and community size-structure are numerous, the establishment and expansion of dreissenid mussels and other non-native planktivores may play a role. Dreissenid invasion has been associated with reductions in productivity, and zooplankton abundance (Hoyle et al. 2008; Kissman et al. 2010). In one study, Michigan lakes invaded by dreissenids showed declines in Chl-a, phytoplankton biomass, and *Daphnia* biomass of 21%, 24%, and 40%, respectively when compared with non-invaded lakes (Kissman et al. 2010). Similarly, the zebra mussel invasion in the Inland Waterway coincided with a decline in primary productivity (Chl-a), increased water clarity, and increased reliance on stocking in the Inland Waterway. Invasions of rainbow smelt and alewife could also contribute to low zooplankton size in Burt and Mullett Lake. For example, Brooks and Dodson (1963) and Beisner et al. (2003) demonstrated that invasive planktivores have the potential to reduce the density and size, as well as alter the composition of zooplankton communities. Alewives are effective planktivores and are believed to restructure zooplankton communities through selective predation, reducing the size and abundance of large-bodied zooplankton taxa, and are therefore direct competitors with walleye fry (Wells 1970; Schneider and Leach 1977). However, at the time of this study, it is uncertain whether Alewife abundance in the system is high enough to cause deleterious effects on the walleye population. Furthermore, alewife have not been captured in Crooked Lake or Pickerel Lake. Consequently, I find it unlikely that alewife are responsible for the low forage availability observed in those lakes.

The present study parallels the work by Engel et al. (2000) while also increasing the frequency and duration of annual sampling effort in a system including four study lakes and two rivers. In addition, we chose to collect zooplankton samples concurrently with ichthyoplankton, instead of sampling at the deepest site in the water body. Our methodology allowed us to assess the forage availability at the site of walleye larvae capture. In both the present study and Engel et al. (2000), large-bodied zooplankton densities within Escanaba Lake and the Inland Waterway were low ($<10 \cdot L^{-1}$). Additionally, Engel et al. (2000) also observed a positive relationship between fall age-0 walleye abundance and spring walleye larvae density, as well as spring zooplankton density. Unfortunately, it is impossible to compare the density of spring age-0 walleye between these two studies, due to differences in unit reporting (walleye$\cdot$1000m^{-3} in the present study versus walleye$\cdot$1000 revolutions of a flow meter^{-1} in Engel et al. 2000).

The highest densities of juvenile walleye in the Inland Waterway were observed in the Black River and Sturgeon River (~100m from Burt Lake), suggesting that river-spawned walleye contribute to natural reproduction in the system. However, because I did not estimate the total abundance of larval walleye from river and lake origins, I cannot comment on the extent that rivers contribute larval walleye to the waterway. Observation of riverine habitat indicated large sections of coarse gravel-cobble substrate suitable for walleye spawning (Dustin and Jacobson 2003; Kelder and Farrell 2009; Ivan et al. 2010; Chalupnicki et al. 2010). Gravid and barren female walleyes were marked in the Black River and the Sturgeon River and recaptured within the lakes proper during 2011 and 2012 mark-recapture surveys (Michigan Department of Natural Resources, unpublished data). These findings suggest that some walleye within the system employ a lake-to-river reproductive strategy. This reproductive strategy is found elsewhere, including the Maumee River and the western basin of Lake Erie, the Current River and Thunder Bay, Lake Superior, and the Ottertail river and Many Point Lake, MN (Olson and Scidmore 1962; Geiling et al. 1996; Roseman et al. 2001) and in some systems can provide a significant contribution to larvae populations in recipient lakes. For example, Roseman et al. (2001) observed that 90% of walleye larvae collected in western Lake Erie in a 1998 study were found in sites closest to Maumee Bay, indicating that a large portion of walleye larvae were of Maumee River origin. Similarly, 75% of adult walleye in Black Bay, Lake Superior captured during an individual-based genetic analysis from 2004-2010 were found to have originated from native populations in the Black Sturgeon River (Garner et al. 2013).

While I did not find a statistical difference in larval walleye density between the rivers sampled in this study, I observed that the average larval walleye density in the rivers was higher than what was observed in the four study lakes. The contribution of river-spawned walleye fry to the system highlights the importance of identifying and maintaining quality riverine spawning habitat as well as connectivity in systems where walleye utilize a lake-river reproductive strategy (Wilson et al. 2007). While it is likely that some of the walleye larvae found in the lakes were from riverine sources, we cannot be certain the magnitude of this contribution based on the present study. Further assessment of this question, perhaps using otolith microchemistry techniques, may allow managers to determine the natal origin of walleye within the system. Otolith microchemistry has been successfully used to distinguish unique spawning populations within the Great Lakes for several species including yellow perch, cisco (*Coregonus artedi*), and sea lamprey (*Petromyzon marinus*)(Bronte et al. 1996; Brazner et al. 2004; Brothers and Thresher 2004; Dufour et al. 2008; Whitledge 2009). These techniques were also used successfully by Pangle et al. (2010) to classify yellow perch larvae to natal embayments and tributaries in

Lake Erie with high accuracy.

Walleye larvae density was higher in Burt Lake than any other lake within the waterway (Figure 4), peaking in late May in 2011 and early May in 2012 (Figure 6). This timing difference between years was also observed in Crooked and Mullett lakes and can be attributed to an unusually early ice-off in 2012. Walleye density in Burt Lake was on average 87% higher than all other lakes, and 94% higher than Pickerel Lake, which had the lowest walleye larvae density in the system (Figure 4). While the percent difference in walleye density appears to be considerable, it is important to emphasize that the difference between the waterbody with the highest walleye density (Burt Lake) and the waterbody with the lowest (Pickerel Lake) was small (< $2.5 \cdot 1000m^{-3}$). While significant differences in walleye production within the waterway exist, system wide spring age-0 walleye density was very low and is comparable to other systems that have experienced poor recruitment. For example, the mean density of walleye fry in western Lake Erie from first hatch through the end of May of 1995 was $2.0 \cdot 1000m^{-3}$, which at the time of the study was the second smallest since 1983 (Roseman 1997; Rosemen et al. 2005). However, peak densities of walleye larvae have been reported between $167\text{-}273 \cdot 1000m^{-3}$ in the Maumee and Sandusky Bay, Lake Erie (Mion et al. 1998). Similarly, Noble (1972) observed peak densities of walleye produced in Billington Bay, Lake Oneida from between $800 \cdot 1000m^{-3}$- $900 \cdot 1000m^{-3}$ in the spring of 1996.

To my knowledge, this study is the first to document a positive relationship between zooplankton density and fall walleye abundance in a waterway where prey availability across all lakes is scarce (<< 10·L^{-1}). While some studies failed to find a relationship between walleye fry survival and forage abundance (Houde 1967; Partridge and DeVries 1999; Quist et al. 2004), the present study provides further evidence in support of the hypothesis that spring zooplankton density has the potential to influence larval survival and year-class formation of age-0 walleye (Lemly and Dimmick 1982; Mills et al. 1989; Claramunt and Wahl 2000; Engel et al. 2000; Hoxmeier et al 2004; Peterson et al. 2006).

Management implications and research needs

The relationship between zooplankton prey abundance and walleye larvae abundance could be applied to create predictive models of juvenile walleye abundance or survival in similar systems. The development of such models could allow managers to predict year-class strength, and help to identify if augmenting natural reproduction through stocking or other means is necessary.

Prey availability should be when making decisions related to stocking walleye fry. Information on spring zooplankton abundance, provided through similar surveys, could help managers decide the number of walleye to stock and whether to stock larger fingerlings rather than fry. Based on the current condition of spring forage availability (i.e. low density and small size of zooplankton prey) within the Inland Waterway, it is not recommended that stocking of walleye fry occur. Rather, stocking late spring and fall fingerlings that rely on benthic invertebrates and forage fish rather than zooplankton, would likely result in higher stocking success and thus augment natural reproduction.

APPENDICES

APPENDIX A: Results of spring and fall sampling efforts and supporting figures and tables

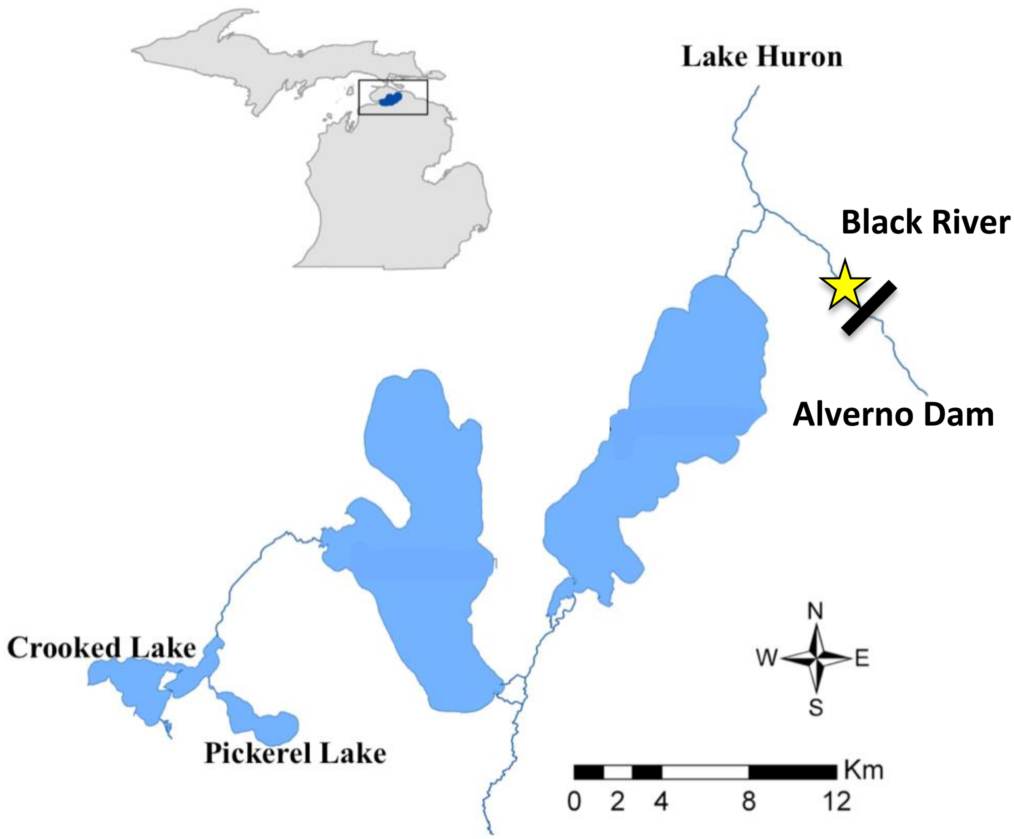

Figure 1: The Inland Waterway of northern Michigan. Sites where drift net sampling occurred on the Black River and Sturgeon River are labeled with a star. The Alverno Dam is also marked on the map (black bar), which represents the farthest up stream that sampling occurred on the Black River. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this thesis.

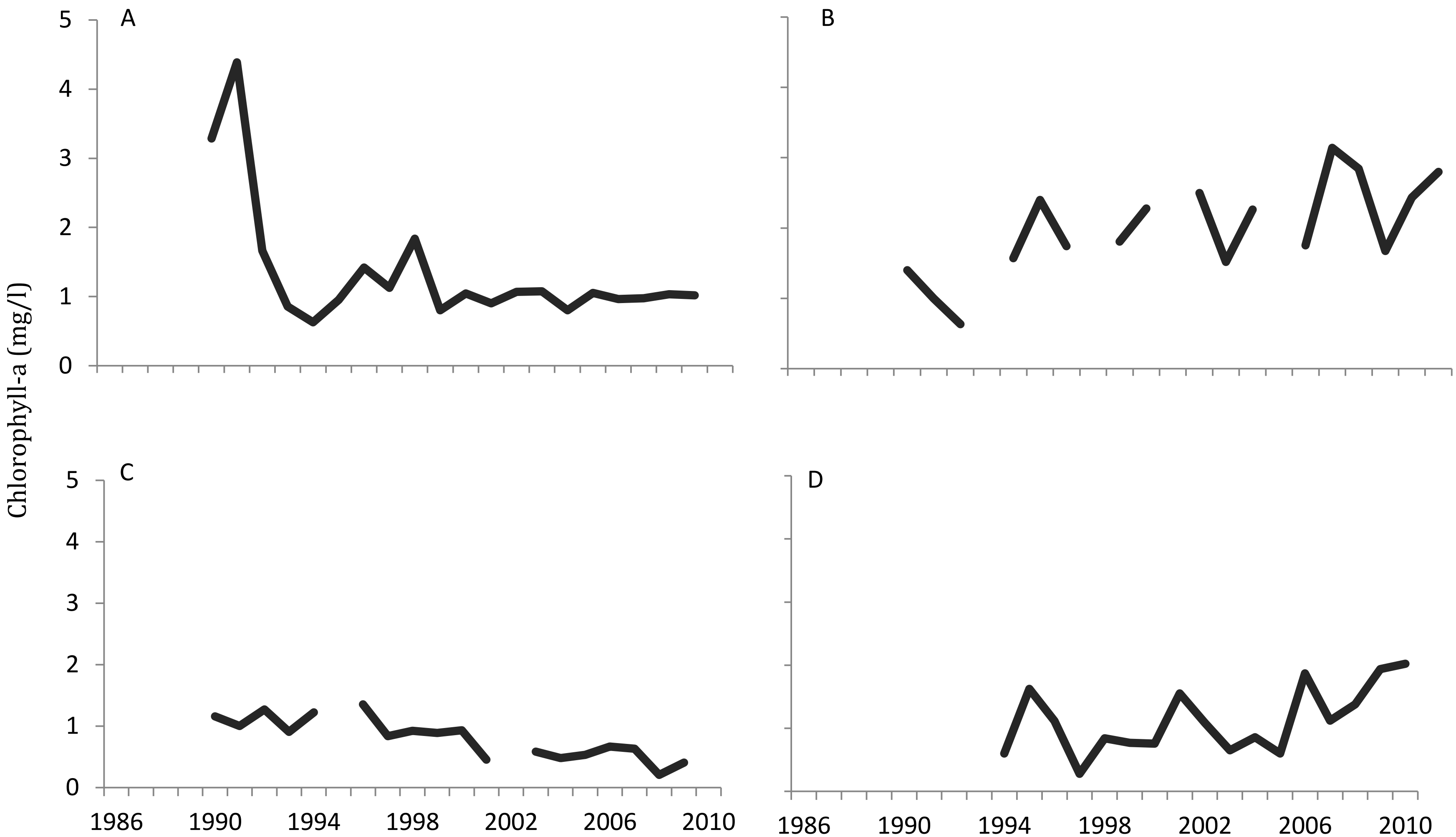

Figure 2: Mean Secchi (m, grey) and Chlorophyll-a (mg/L, black) in Burt Lake (A), Crooked Lake (B), Mullett Lake (C), and Pickerel Lake (D), from 1986-2010. (Tip of The Mitt Watershed Council, unpublished data)

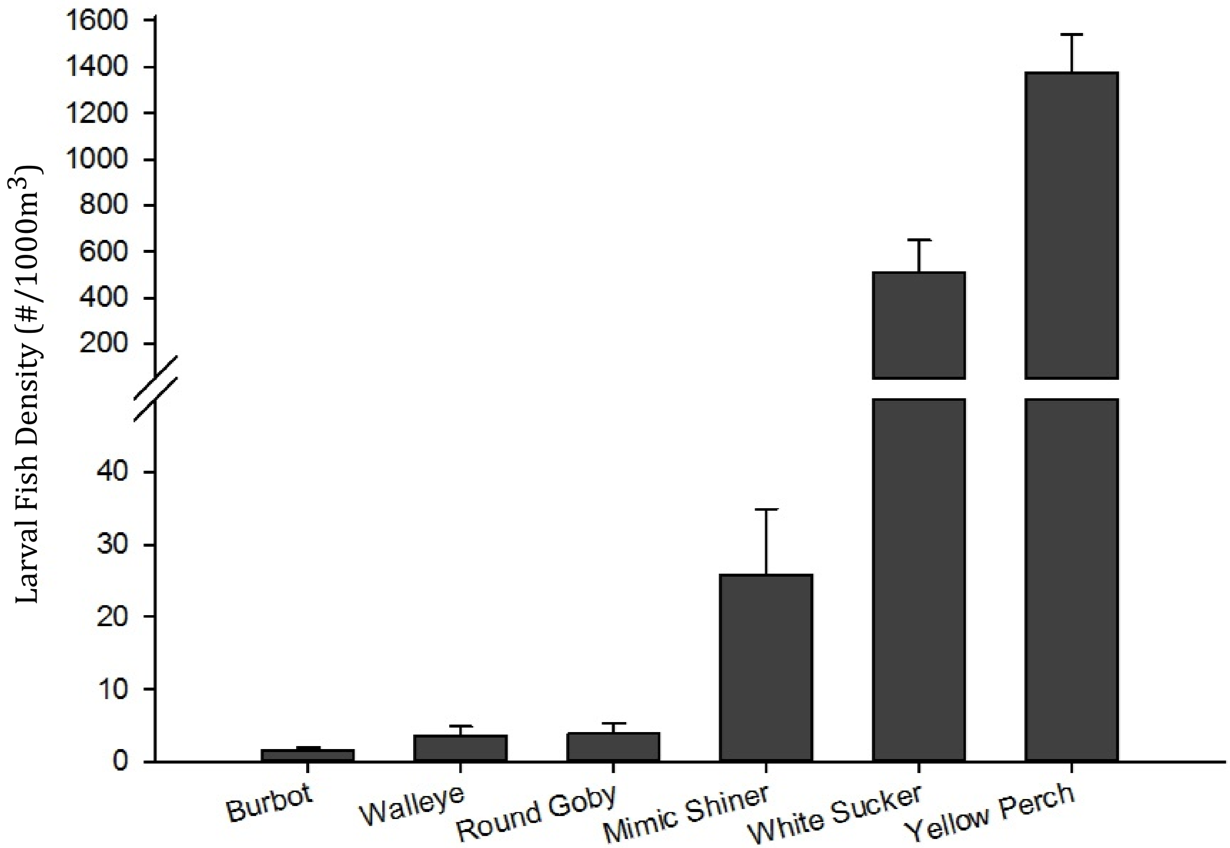

Figure 3: Mean density of commonly observed age-0 ichthyoplankton species over all waterbodies and sampling dates, 2011-2012. Standard error of the mean (SE) represented by error bars.

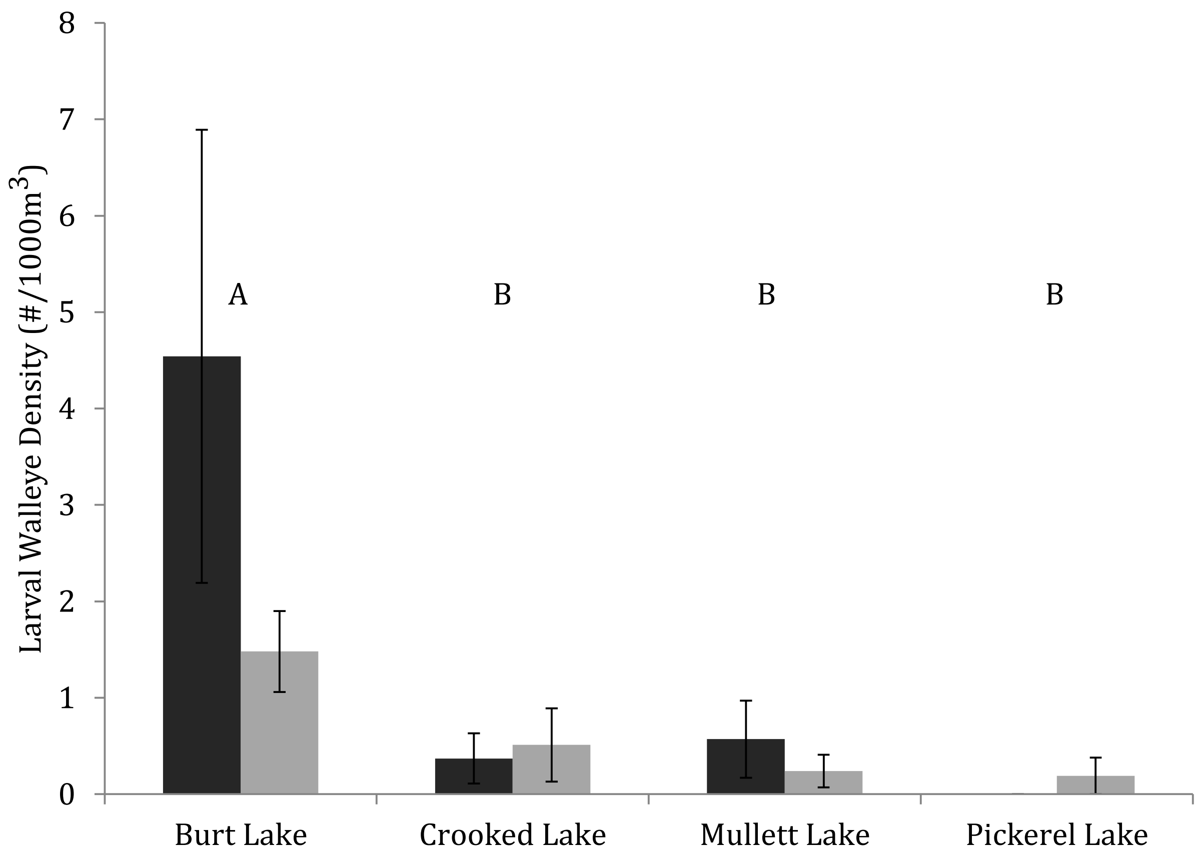

Figure 4: Observed mean larval walleye densities during spring 2011 (black) and 2012 (grey) ichthyoplankton sampling effort. Waterbodies with unique letters designate a significant difference in larval walleye density over all sampling dates across 2011-2012 (Tukey HSD, p= <0.05). Standard error of the mean (SE) represented by error bars.

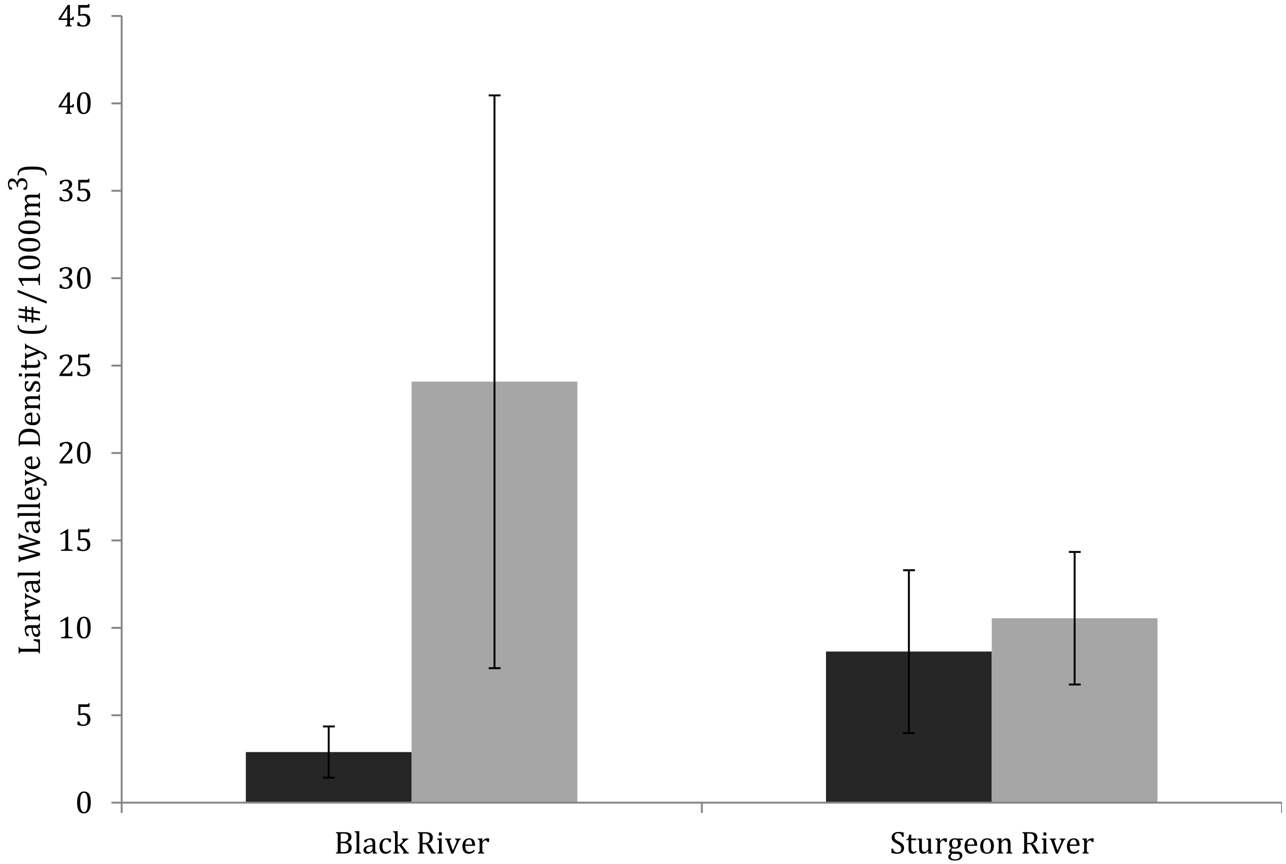

Figure 5: Observed mean larval walleye densities during spring 2011 (black) and 2012 (grey) ichthyoplankton sampling effort. Standard error of the mean (SE) represented by error bars.

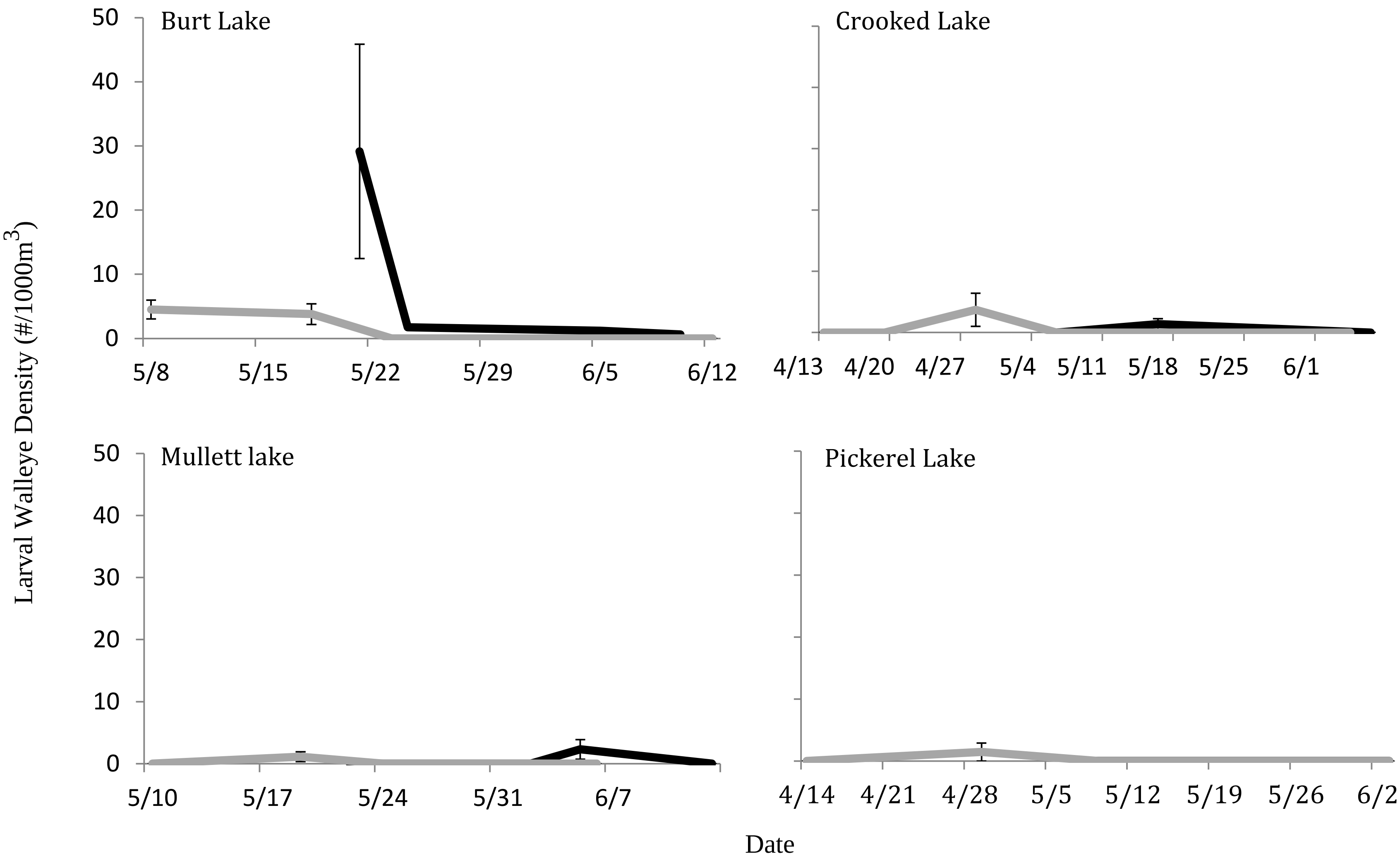

Figure 6: Observed spring larval walleye density (#/1000m^3) in Burt Lake, Crooked Lake, Mullett Lake, and Pickerel Lake per sampling event during 2011 (black) and 2012 (grey) sampling efforts. Bars represent standard error.

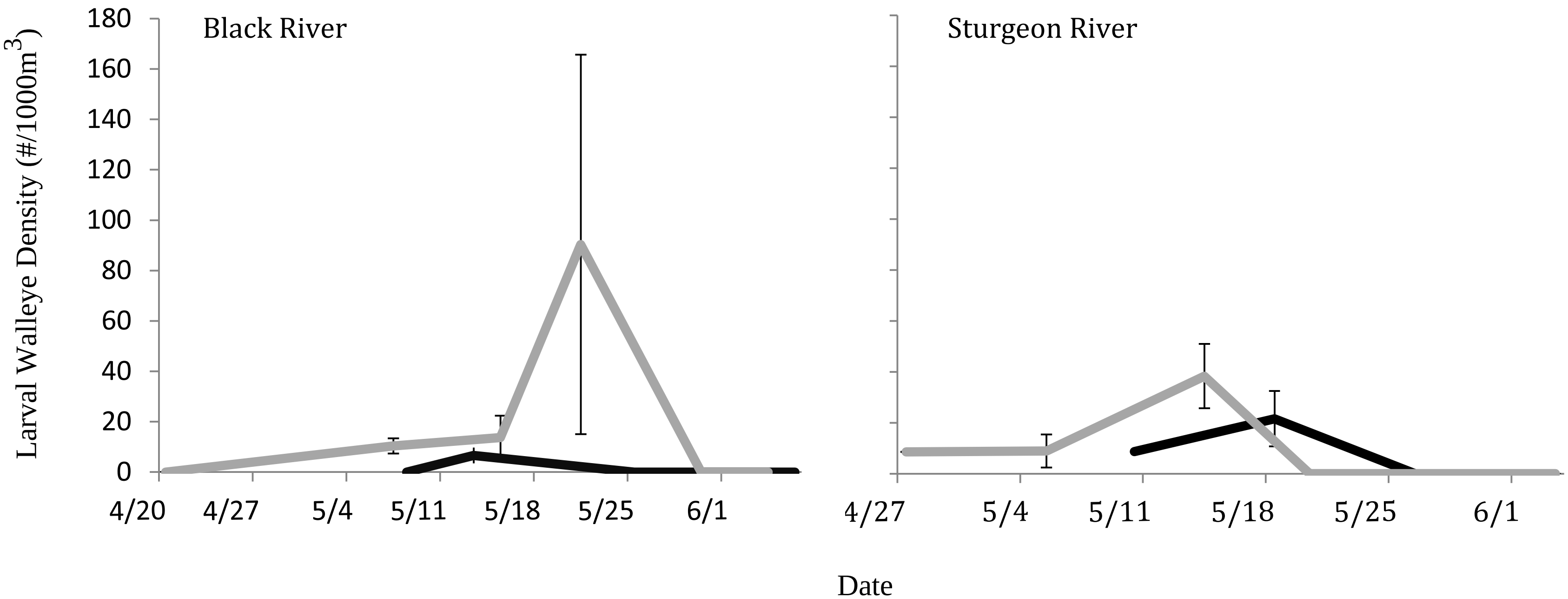

Figure 7: Observed spring larval walleye density (#/1000m^3) in the Black River and the Sturgeon River per sampling event during 2011 (black) and 2012 (grey) sampling efforts. Standard error of the mean (SE) represented by error bars.

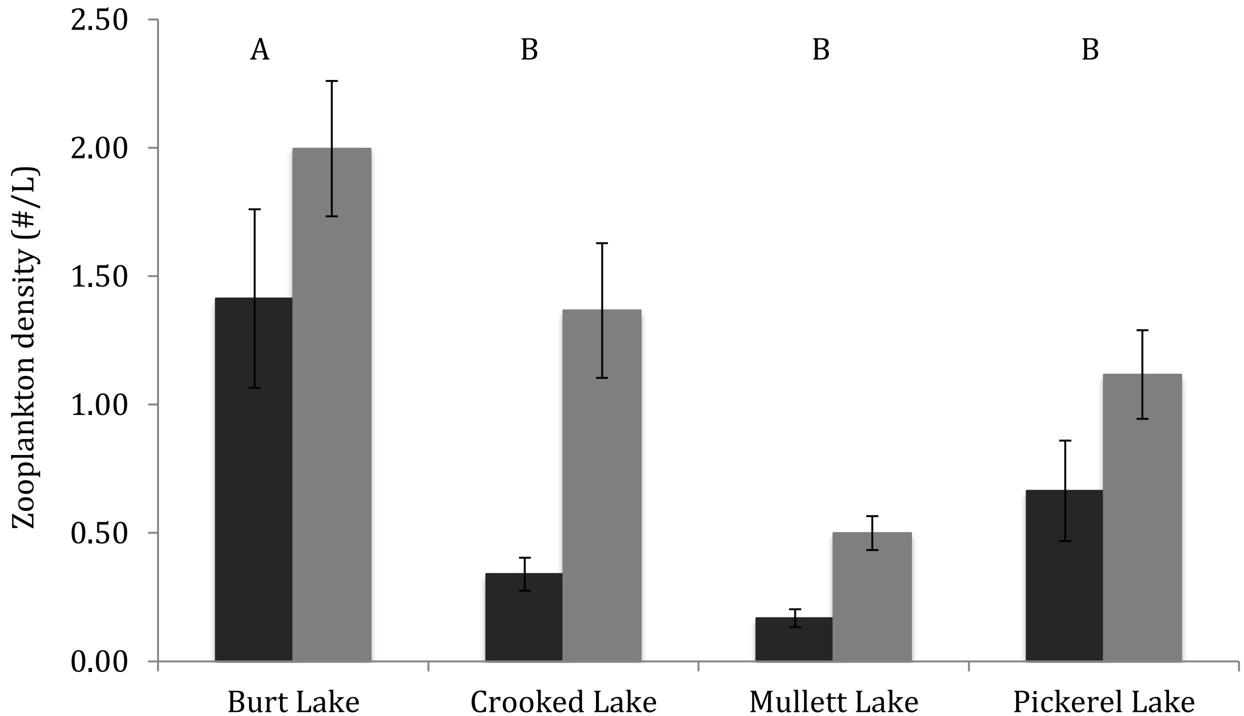

Figure 8: Mean density of large-bodied taxa (Calanoid copepods, *Daphnia*) in the waterway. Waterbodies with unique letters designate a significant difference in density over all sampling dates across 2011 (black) and 2012 (grey) (Tukey HSD, $p<0.05$). Standard error of the mean (SE) represented by error bars.

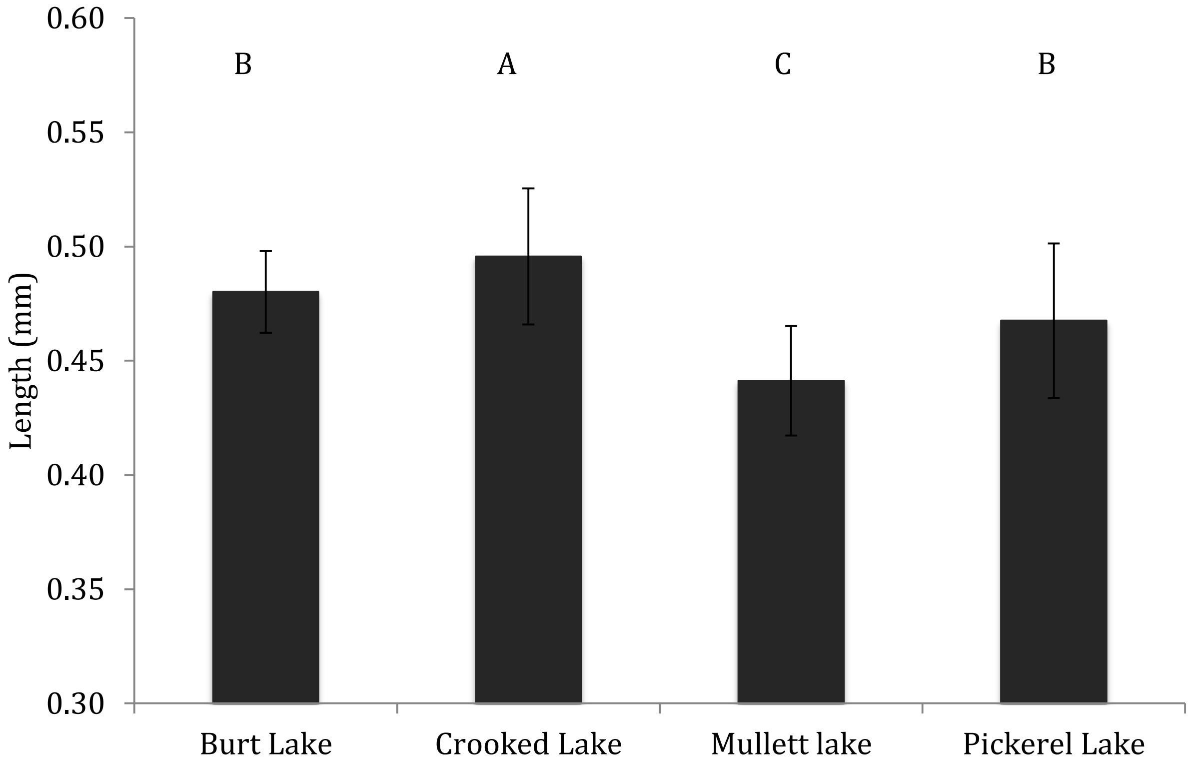

Figure 9: Mean length of zooplankton community over all sampling dates, 2011-2012. Waterbodies with unique letters designate a significant difference in zooplankton length (Tukey HSD, $p<0.05$). Standard error of the mean (SE) represented by error bars.

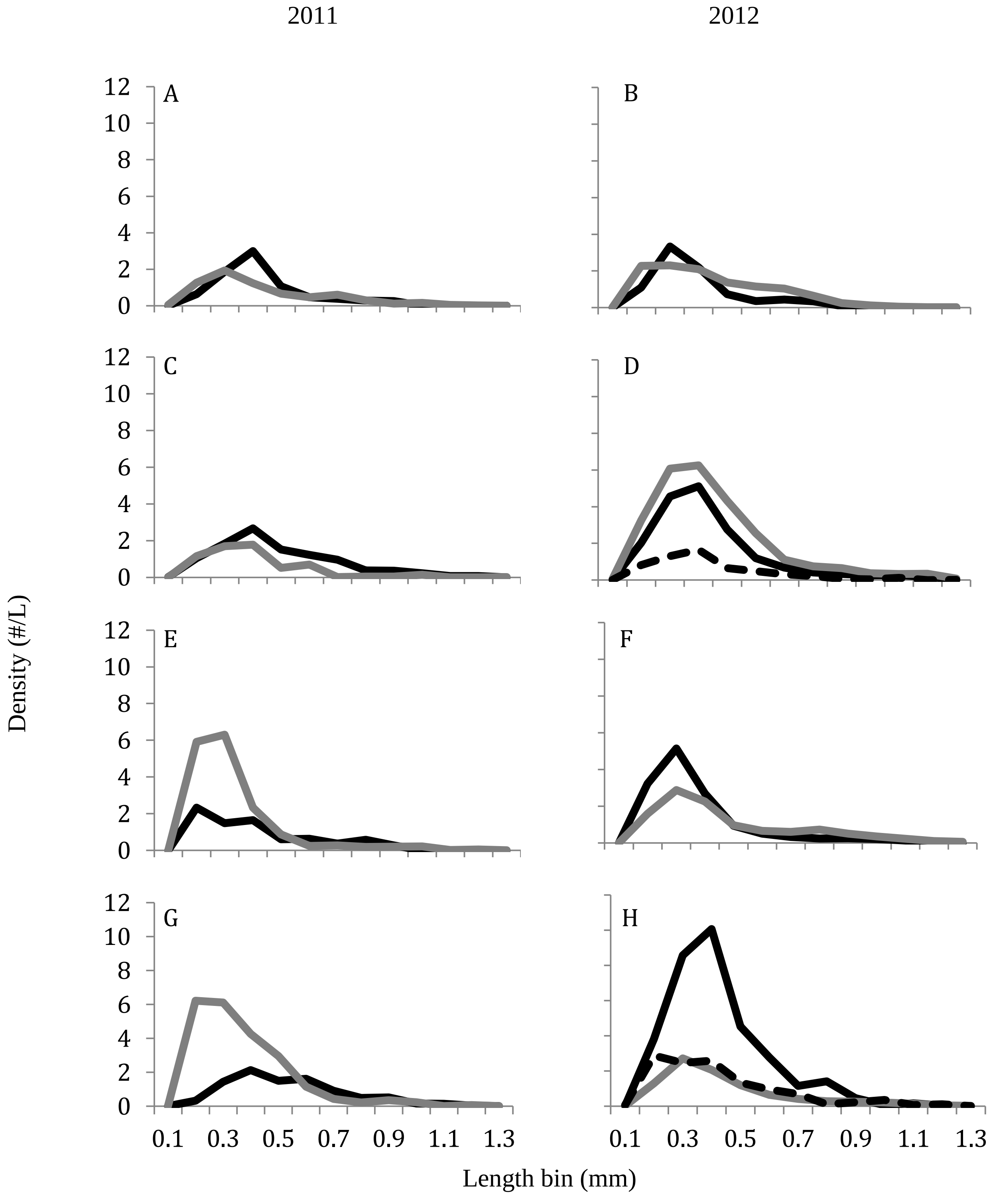

Figure 10: Length frequency of zooplankton in Burt Lake (A-B), Crooked Lake (C-D), Mullett Lake (E-F), and Pickerel Lake (G-H) in April (dashed black), May (solid black), and June (solid grey) in 2011 and 2012 (first and second columns, respectively). Error bars represent standard error of the mean.

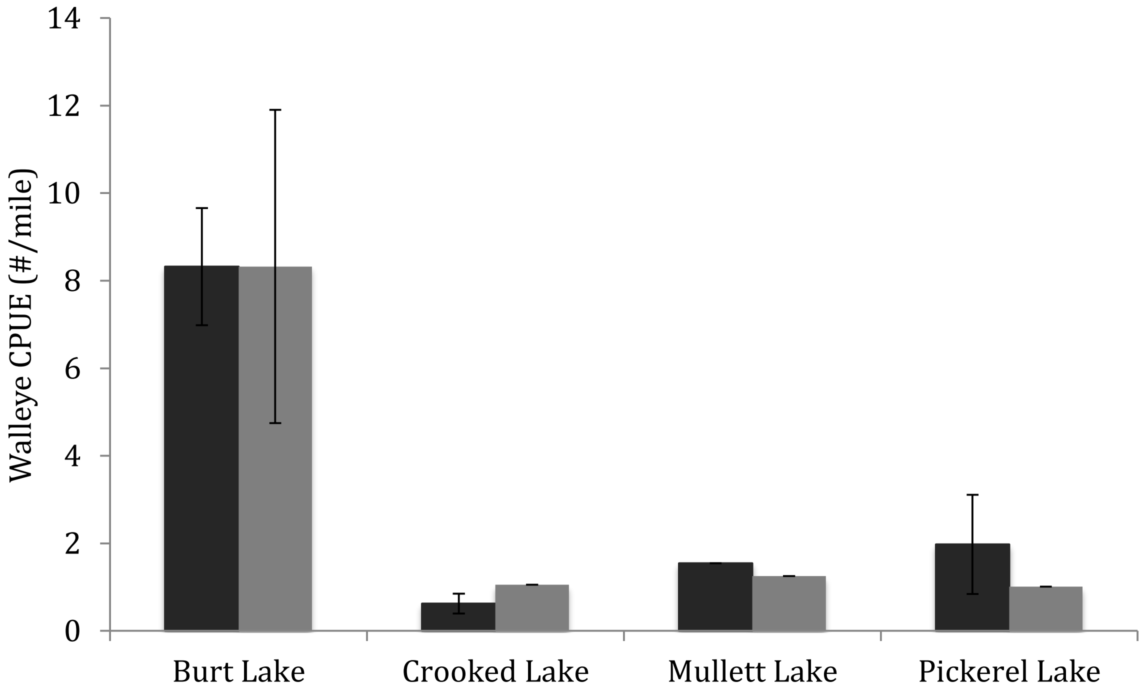

Figure 11:Fall walleye CPUE in the Inland Waterway in 2011 (black) and 2012 (grey). Error bars represent standard error of the mean.

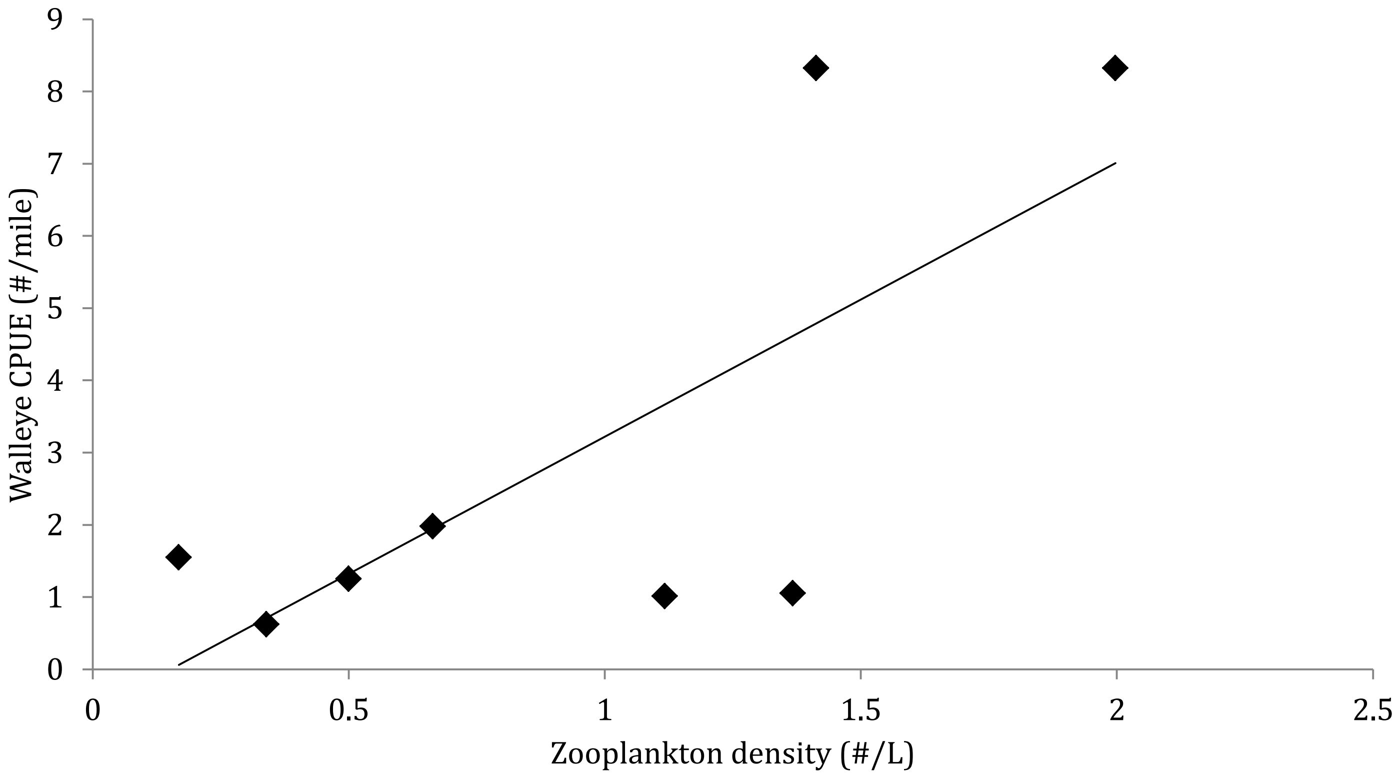

Figure 12: Regression of large-bodied zooplankton density and fall age-0 walleye catch per mile by lake and year (r^2=0.53, p=0.042).

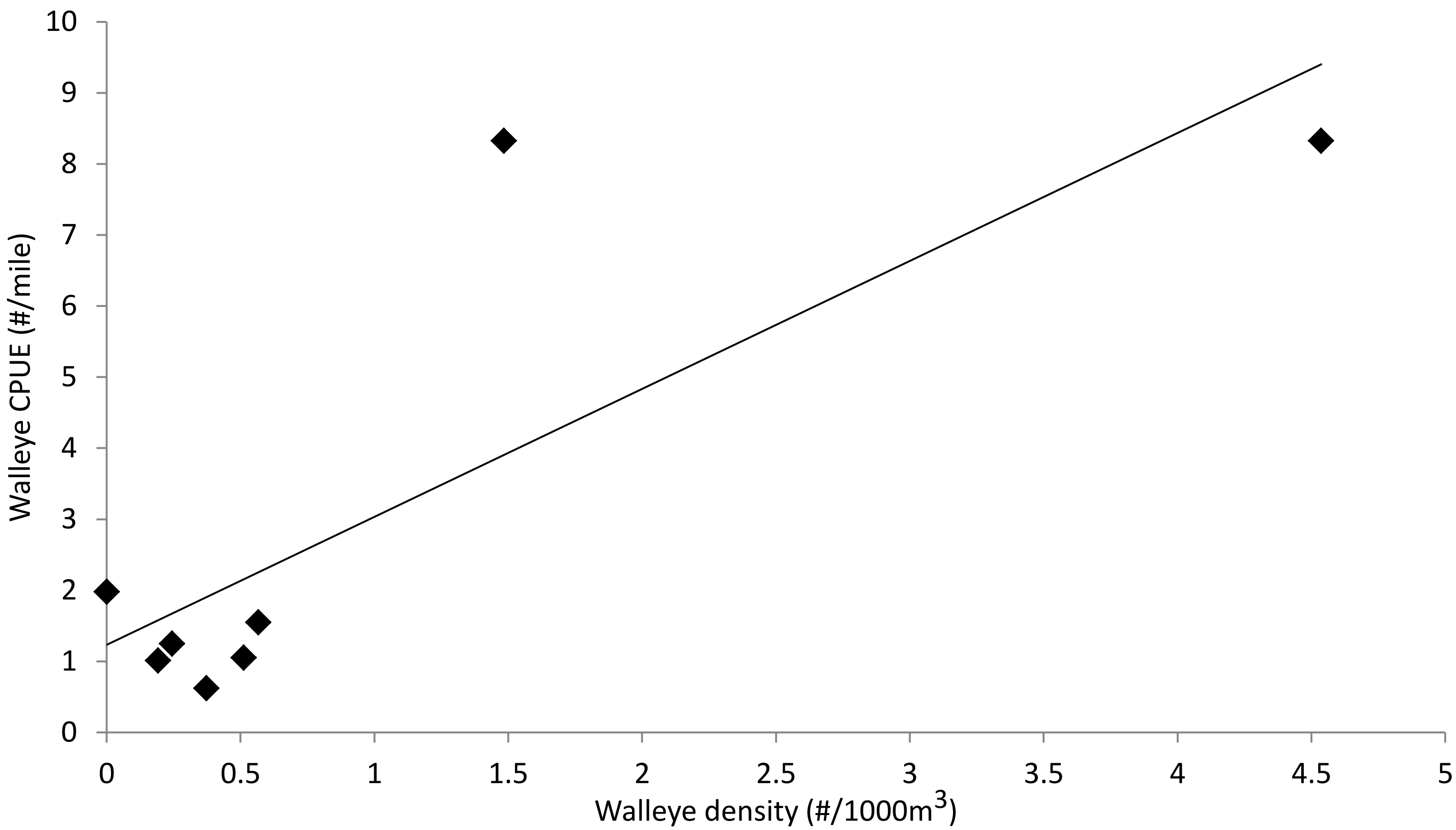

Figure 13: Regression of spring age-0 walleye density and fall age-0 walleye catch per mile by lake and year (r^2=0.67, p=0.01)

Table 1: Summary of physical characteristics of the lakes of the Inland Waterway. Secchi and Chl-a provided by 2008 water quality survey conducted by the Tipp Of The Mitt Watershed Council.

	Area (km^2)	Mean Depth (m)	Max Depth (m)	Secchi (m)	Chl-a (ppb)
Burt Lake	69.3	22.3	22.3	4.9	1.0
Mullett Lake	67.6	11.3	44	5.2	0.2
Crooked Lake	9.5		15.2	3.5	1.7
Pickerel Lake	4.4		22.9	3.0	1.4

Table 2: Recent walleye stocking history of the Inland Waterway. Repeated years indicate multiple size groups stocked.

	Burt Lake			Crooked Lake			Mullett Lake			Pickerel Lake		
Year	Number stocked	Density stocked (#/km^2)	Size (cm)	Number stocked	Density stocked (#/km^2)	Size (cm)	Number stocked	Density stocked (#/km^2)	Size (cm)	Number stocked	Density stocked (#/km^2)	Size (cm)
1985				5,500	578.9	3.8				5,500	1,250.0	3.8
1986				4,000	421.1	3.8						
1987												
1988				500	52.6	4.3						
1989	20,350	293.7	3.5	750	78.9	3.8				750	170.5	3.8
1990	18,346	264.7	4.6	50	5.3	2.5						
1991	17,000	245.3	4.6	75,000	7,894.7	5.1						
1992	17,000	245.3	3.6									
1993	16,280	234.9	3.6									
1994				160,750	16,921.1	3.0				50,000	11,363.6	4.8
1995												
1996				108,500	11,421.1	3.3				25,000	5,681.8	3.0
1997												
1998				80,500	8,473.7	3.0				28,000	6,363.6	3.0
1999				2,700	284.2	3.8	100,000	1,479.3	3.0			
2000				52,500	5,526.3	2.8	100,000	1,479.3	2.3	12,500	2,840.9	3.0
2001							100,000	1,479.3	2.8			
2002							13,870	205.2	3.0			
2003							100,000	1,479.3	2.8			
2010							101,000	1,494.1	4.6			
2010							4,000	59.2	17.8			
2011							97,951	1,449.0	4.6			
2011							7,500	110.9	17.8			
2012							7,500	110.9	17.8			

Table 3: Mean zooplankton community density over both sampling years, including the four most common taxa.

	Bosmina		Calanoid		Cyclopoid		Daphnia	
	Mean density (#/L)	SE	Mean density (#/L)	SE	Mean density (#/L)	SE	Mean density (#/L)	SE
Burt Lake	3.52	0.28	3.03	0.34	1.79	0.12	0.61	0.22
Crooked Lake	5.18	0.72	1.67	0.31	9.25	0.98	0.32	0.11
Mullett Lake	9.87	0.98	0.62	0.08	3.34	0.28	0.19	0.05
Pickerel Lake	4.08	0.56	1.96	0.23	6.90	0.86	0.02	0.00

APPENDIX B: Supplemental figures and tables

Table 4: Ichthyoplankton trawl and drift effort for May-June 2011 in study lakes. Effort is measured as the number of trawls and drifts performed.

	Lake				
Week	Burt Lake	Crooked Lake	Mullett Lake	Pickerel Lake	Total
1	-	30	-	12	42
2	-	-	-	-	0
3	8	13	-	8	29
4	8	-	4	9	21
5	12	-	12	9	33
6	36	4	13	-	53
7	-	-	24	-	24
Total	64	47	53	38	202

Table 5: Ichthyoplankton trawl and drift effort for May-June 2011 in study rivers. Effort is measured as the number of trawls and drifts performed.

Week	River						Total
	Black River	Crooked River	Crooked-Pickerel Narrows	Cheboygan River	Indian River	Sturgeon River	
1	-	-	3	-	-	-	3
2	17	12	-	1	10	18	58
3	-	-	2	5	-	9	16
4	12	5	-	-	5	-	22
5	-	-	2	5	-	-	7
6	5	-	-	5	-	-	10
Total	34	17	7	16	15	27	116

Table 6: Ichthyoplankton trawl and drift effort for April-June 2012 in study lakes. Effort is measured as the number of trawls performed

Week	Lake				Total
	Burt Lake	Crooked Lake	Mullett Lake	Pickerel Lake	
1	-	12	-	-	12
2	-	7	-	10	17
3	-	12	-	-	12
4	-	-	-	12	12
5	25	12	24	12	73
6	24	12	24	12	72
7	24	12	24	16	76
8	24	12	24	12	72
9	24	12	12	12	60
10	24	-	12	-	36
Total	145	91	120	86	442

Table 7: Ichthyoplankton drift effort for April-June 2012 in study rivers. Effort is measured as the number of transects and drifts performed.

Week	River		Total
	Black River	Sturgeon River	
1	-	12	12
2	-	-	0
3	9	12	21
4	-	12	12
5	12	-	12
6	12	10	22
7	12	9	21
8	12	12	24
9	12	12	24
10	-	-	-
Total	69	79	148

Table 8: Number of young of year walleyes captured in study lakes during May-June 2011 trawl effort.

Week	Lake				Total
	Burt Lake	Crooked Lake	Mullett Lake	Pickerel Lake	
1	-	-	-	-	0
2	-	-	-	-	0
3	16	2	-	-	18
4	1	-	-	-	1
5	2	-	-	-	2
6	1	-	2	-	3
7	-	-	-	-	0
Total	20	2	2	0	24

Table 9: Number of young of year walleyes captured in study rivers during May-June 2011 trawl and drift effort.

	River						
Week	Black River	Cheboygan River	Crooked-Pickerel Narrows	Crooked River	Indian River	Sturgeon River	Total
1	-	-	-	-	-	-	0
2	-	-	-	-	-	1	1
3	15	-	-	-	-	13	28
4	-	-	-	-	-	-	0
5	-	2	-	-	-	-	2
6	-	-	-	-	-	-	0
Total	15	2	0	0	0	14	31

Table 10: Number of young of year walleyes captured in study lakes during April-June 2012 trawl effort.

	Lakes				
Week	Burt Lake	Crooked Lake	Mullett Lake	Pickerel Lake	Total
1	-	-	-	-	0
2	-	-	-	-	0
3	-	3	-	-	3
4	-	-	-	1	1
5	8	-	-	-	8
6	6	-	2	-	8
7	-	-	-	-	0
8	-	-	-	-	0
9	-	-	-	-	0
10	-	-	-	-	0
Total	14	3	2	1	20

Table 11: Number of young of year Walleyes captured in study rivers during the April-June 2012 drift effort.

	River		
Week	Black River	Sturgeon River	Total
1	-	-	0
2	-	-	0
3	-	2	2
4	13	3	16
5	4	43	47
6	2	-	2
7	-	-	0
8	-	-	0
9	-	-	0
10	-	-	0
Total	19	48	67

Table 12: Observed mean density of common species captured in Burt Lake during spring 2011-2012 ichthyoplankton sampling efforts

	Burbot		White Sucker		Mottled Sculpin		Round Goby			Walleye	Yellow Perch	
Date	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr
5/21/2011	26.29	22.08	1.77	1.77	0	0	0	0	29.16	16.71	755.75	357.23
5/24/2011	3.25	2.14	11.13	11.13	1.75	1.75	0	0	1.74	1.74	820.07	426.27
6/05/2011	0	0	257.55	89.78	6.15	2.94	0	0	1.2	1.2	1271.6	368.77
6/10/2011	0	0	19.58	5.72	1.71	1.71	0	0	0.6	0.6	634.41	138.71
5/08/2012	28.71	7.94	2.3	1.37	0	0	0	0	4.51	1.47	957.24	214.11
5/18/2012	1.72	0.95	50.43	21.21	0	0	0	0	3.78	1.6	1446.2	344.67
5/23/2012	1.8	1.25	243.05	82.81	0	0	0	0	0	0	1430.1	281.09
6/01/2012	0	0	30.68	12.6	2.57	2.57	0	0	0	0	363.05	63.67
6/06/2012	0	0	12.18	6.13	0	0	0	0	0	0	359.31	81.76
6/12/2012	0	0	15.51	7.05	0	0	26.48	17.55	0	0	154.07	46.07

Table 13: Observed mean density of common species captured in Crooked Lake during spring 2011-2012 ichthyoplankton sampling efforts.

	Burbot		White Sucker		Mottled Sculpin		Round Goby		Walleye		Yellow Perch	
Date	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr
5/06/2011	0	0	0	0	0	0	0	0	0	0	531.69	152.62
5/16/2011	0	0	0	0	0	0	0	0	1.35	0.92	1765.6	385.3
6/06/2011	0	0	11.5	11.5	0	0	0	0	0	0	594	256.54
4/13/2012	0.63	0.63	0	0	0	0	0	0	0	0	231.36	68.35
4/19/2012	0	0	0	0	0	0	0	0	0	0	1379.3	697.48
4/28/2012	0	0	0	0	0	0	0	0	3.71	2.69	900.71	141.41
5/06/2012	0	0	0	0	0	0	0	0	0	0	672.63	140.94
5/14/2012	0	0	1.22	1.22	1.26	1.26	0	0	0	0	666.6	122.64
5/22/2012	0	0	5.25	3.03	0	0	0	0	0	0	2869.5	499.36
5/30/2012	0	0	2.22	2.22	0	0	0	0	0	0	2862.1	730.34
6/04/2012	0	0	3.59	2.41	0	0	0	0	0	0	1677.1	411.38

Table 14: Observed mean density of common species captured in Mullett Lake during spring 2011-2012 ichthyoplankton sampling efforts

	Burbot		White Sucker		Mottled Sculpin		Round Goby			Walleye	Yellow Perch	
Date	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr
5/22/2011	3.87	3.87	0	0	0	0	0	0	0	0	99.13	29.58
6/02/2011	0	0	690.78	440.18	0	0	0	0	0	0	4273.8	1105.4
6/05/2011	0	0	121.81	63.84	1.02	1.02	0	0	2.31	1.57	1721.2	501.33
6/13/2011	0	0	118.18	48.03	0	0	0	0	0	0	1231.3	330.16
5/10/2012	1.63	1.12	5.95	3.14	0	0	0	0	0	0	350.26	162.18
5/19/2012	0	0	1644.1	1017.4	0	0	0	0	1.14	0.79	2973.1	585.27
5/24/2012	0	0	167.17	61.57	0	0	0	0	0	0	4249.1	912.5
6/01/2012	0	0	93.83	74.45	0	0	0	0	0	0	1116	252.42
6/06/2012	0	0	89.35	52.11	0	0	0	0	0	0	759.47	108.02

Table 15: Observed mean density of common species captured in Pickerel Lake during spring 2011-2012 ichthyoplankton sampling efforts

	Burbot		White Sucker		Mottled Sculpin		Round Goby		Walleye		Yellow Perch	
Date	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr
5/07/2011	0	0	0	0	0	0	0	0	0	0	456.55	163.5
5/17/2011	0	0	0	0	0	0	0	0	0	0	319.6	150.39
6/03/2011	0	0	0	0	0	0	0	0	0	0	895.26	415.01
4/14/2012	0	0	0	0	0	0	0	0	0	0	225.34	64.83
4/29/2012	0	0	0	0	0	0	0	0	1.46	1.46	684.5	131.72
5/09/2012	0	0	0	0	0	0	0	0	0	0	232.72	67.23
5/16/2012	0	0	2.56	1.73	0	0	0	0	0	0	454.75	73.74
5/21/2012	0	0	0	0	0	0	0	0	0	0	947.07	322.83
5/29/2012	0	0	5.62	3.89	0	0	0	0	0	0	731.95	265.82
6/03/2012	0	0	0	0	0	0	0	0	0	0	176.22	25.14

Table 16: Observed mean density of common species captured in the Black River during spring 2011-2012 ichthyoplankton sampling efforts

	Burbot		White Sucker		Mottled Sculpin		Round Goby		Walleye		Yellow Perch	
Date	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr
5/08/2011	1.41	0	0	0	0	0	0	0	0	0	0	0
5/13/2011	0	0	0	0	0	0	0	0	6.61	3.15	291.39	168.01
5/25/2011	0	0	278.33	75.55	0	0	0	0	0	0	437.33	106.31
6/06/2011	0	0	557.43	477.97	2.6	2.6	0	0	0	0	178.47	121.72
4/20/2012	12.09	12.09	0	0	0	0	0	0	0	0	15.94	9.2
5/07/2012	0	0	0	0	0	0	0	0	10.37	3.05	25.66	4.27
5/15/2012	0	0	2310.4	340.49	0	0	0	0	13.67	8.68	4284.2	1316.4
5/21/2012	0	0	13831	6713.1	0	0	15.14	15.14	90.35	75.35	19951	7925.9
5/30/2012	0	0	128.36	97.19	0	0	0	0	0	0	1437.5	526.21
6/04/2012	0	0	8.21	6.37	0	0	141.13	51.57	0	0	78.57	45.12

Table 17: Observed mean density of common species captured in the Sturgeon River during spring 2011-2012 ichthyoplankton sampling efforts

	Burbot		White Sucker		Mottled Sculpin		Round Goby			Walleye	Yellow Perch	
Date	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr	Mean	StdErr
5/10/2011	0	0	0	0	0	0	0	0	8.65	0	0	0
5/18/2011	0	0	1.43	1.43	0	0	0	0	21.6	10.85	2.92	1.85
5/26/2011	0	0	485.1	109.69	0	0	0	0	0	0	15.61	5.04
4/27/2012	0	0	0	0	0	0	0	0	8.56	0.02	0	0
5/05/2012	0	0	8.54	3.96	0	0	0	0	8.91	6.47	12.26	9.68
5/14/2012	0	0	1560.8	279.53	0	0	0	0	38.33	12.63	93.84	58.33
5/20/2012	0	0	10612	4003.8	2.82	2.82	0	0	0	0	70.3	30.56
5/29/2012	2.32	2.32	195.66	47.68	4.45	2.95	1.98	1.98	0	0	101.94	41.61
6/03/2012	3.48	3.48	29.58	17.78	1.74	1.74	0	0	0	0	65.51	19.19

Table 18: Observed mean density of spring larval walleyes during spring 2011-2012 sampling efforts

Density (#/1000m3)				
Waterbody	2011	SE	2012	SE
Burt Lake	4.54	2.35	1.48	0.42
Crooked Lake	0.37	0.26	0.51	0.38
Mullett Lake	0.57	0.4	0.24	0.17
Pickerel Lake	0	0	0.19	0.19
Black River	2.89	1.47	24.08	16.39
Sturgeon River	8.64	4.66	10.55	3.8

Table 19: Tukey Post-Hoc HSD output for mean spring age-0 walleye density comparisons by lake over the 2011-2012 sampling effort. Comparisons significant at the 0.05 level are indicated by ***.

Waterbody Comparison	Δ	95% Confidence Limits		
Burt Lake – Crooked Lake	2.01	0.03	3.99	***
Burt Lake – Mullett Lake	2.12	0.26	3.99	***
Burt Lake – Pickerel Lake	2.33	0.18	4.48	***
Crooked Lake – Burt Lake	-2.01	-3.99	-0.03	***
Crooked Lake – Mullett Lake	0.12	-1.94	2.17	
Crooked Lake – Pickerel Lake	0.32	-2.00	2.64	
Mullett Lake – Burt Lake	-2.12	-3.99	-0.26	***
Mullett Lake – Crooked Lake	-0.12	-2.17	1.94	
Mullett Lake – Pickerel Lake	0.21	-2.02	2.43	
Pickerel Lake – Burt Lake	-2.33	-4.48	-0.18	***
Pickerel Lake – Crooked Lake	-0.32	-2.64	2.00	
Pickerel Lake – Mullett Lake	-0.21	-2.43	2.02	

Table 20: Tukey Post-Hoc HSD output for mean spring age-0 walleye density comparisons by river over the 2011-2012 sampling effort. Means with the same letter are not significantly different at the 0.05 level.

Tukey Grouping	Mean	N	Waterbody
A	16.38	88	Black River
A	10.04	59	Sturgeon River

Table 21: Tukey Post-Hoc HSD output for mean spring zooplankton density (all taxa) comparisons by lake over the 2011-2012 sampling effort. Comparisons significant at the 0.05 level are indicated by ***.

Waterbody Comparison	Δ	95% Confidence Limits		
Crooked Lake – Mullett Lake	0.26	-0.08	0.61	
Crooked Lake – Pickerel Lake	0.33	-0.05	0.71	
Crooked Lake – Burt Lake	0.67	0.35	0.99	***
Mullett Lake – Crooked Lake	-0.26	-0.61	0.08	
Mullett Lake – Pickerel Lake	0.07	-0.30	0.44	
Mullett Lake – Burt Lake	0.41	0.10	0.71	***
Pickerel Lake – Crooked Lake	-0.33	-0.71	0.05	
Pickerel Lake – Mullett Lake	-0.07	-0.44	0.30	
Pickerel Lake – Burt Lake	0.34	0.00	0.68	***
Burt Lake – Crooked Lake	-0.67	-0.99	-0.35	***
Burt Lake – Mullett Lake	-0.41	-0.71	-0.10	***
Burt Lake – Pickerel Lake	-0.34	-0.68	0.00	***

Table 22: Tukey Post-Hoc HSD output for mean large-bodied spring zooplankton density comparisons by lake over the 2011-2012 sampling effort. Comparisons significant at the 0.05 level are indicated by ***.

Waterbody Comparison	Δ	Simultaneous 95% Confidence Limits		
Burt Lake – Crooked Lake	0.82	0.21	1.44	***
Burt Lake – Pickerel Lake	0.83	0.16	1.50	***
Burt Lake – Mullett Lake	1.41	0.81	2.02	***
Crooked Lake – Burt Lake	-0.82	-1.44	-0.21	***
Crooked Lake – Pickerel Lake	0.00	-0.73	0.74	
Crooked Lake – Mullett Lake	0.59	-0.09	1.27	
Pickerel Lake – Burt Lake	-0.83	-1.50	-0.16	***
Pickerel Lake – Crooked Lake	0.00	-0.74	0.73	
Pickerel Lake - Mullett Lake	0.59	-0.14	1.31	
Mullett Lake – Burt Lake	-1.41	-2.02	-0.81	***
Mullett Lake – Crooked Lake	-0.59	-1.27	0.09	
Mullett Lake – Pickerel Lake	-0.59	-1.31	0.14	

Table 23: Results of Tukey HSD Post-Hoc test comparing mean zooplankter length by waterbody. Comparisons significant at the 0.05 level are indicated by ***.

Waterbody Comparison	Δ	Simultaneous 95% Confidence Limits		
Crooked Lake-Burt Lake	0.02	0.00	0.03	***
Crooked Lake-Pickerel Lake	0.03	0.02	0.04	***
Crooked Lake-Mullett Lake	0.05	0.04	0.07	***
Burt Lake-Crooked lake	-0.02	-0.03	0.00	***
Burt Lake-Pickerel Lake	0.01	0.00	0.03	
Burt Lake- Mullett Lake	0.04	0.02	0.05	***
Pickerel Lake- Crooked Lake	-0.03	-0.04	-0.02	***
Pickerel Lake-Burt Lake	-0.01	-0.03	0.00	
Pickerel Lake-Mullett Lake	0.03	0.01	0.04	***
Mullett Lake-Crooked Lake	-0.05	-0.07	-0.04	***
Mullett Lake-Burt Lake	-0.04	-0.05	-0.02	***
Mullett Lake-Pickerel Lake	-0.03	-0.04	-0.01	***

Table 24: Observed mean density (#/L) of large-bodied zooplankton taxa by waterbody and year.

Density (#/L)				
Waterbody	2011	SE	2012	SE
Burt Lake	1.41	0.35	2.00	0.26
Crooked Lake	0.34	0.06	1.37	0.26
Mullett Lake	0.17	0.04	0.50	0.07
Pickerel Lake	0.66	0.20	1.12	0.17

Table 25: Observed mean length (mm) of zooplankton community by waterbody, averaged over the 2011-2012 sampling effort

Length (mm)		
Lake	Mean	SE
Burt Lake	0.48	0.02
Crooked Lake	0.50	0.03
Mullett lake	0.44	0.02
Pickerel Lake	0.47	0.03

Table 26: Secchi and Chlorophyll-a trends in the waterway from 1986-2010. Data from The Tip of the Mitt Watershed Council.

	Burt Lake		Crooked Lake		Mullett Lake		Pickerel Lake	
Year	Secchi (m)	Chl-Avg (PPB)	Secchi (m)	Chl-Avg (PPB)	Secchi (m)	Chl-Avg (PPB)	Secchi (m)	Chl-Avg (PPB)
1986			2.28				2.43	
1987			2.65		3.79		2.12	
1988			2.32		3.58		2.42	
1989	3.24				3.88		2.87	
1990	2.86	3.29	4.10	1.40	3.87	1.16	2.67	2.29
1991	3.11	4.39	3.05	1.00	3.54	1.00	2.26	
1992	3.28	1.66	4.11	0.63	3.17	1.27	2.61	0.70
1993	6.42	0.86	2.20		4.15	0.91	2.05	
1994	3.77	0.63	3.44	1.57	3.46	1.22	2.39	0.60
1995	4.85	0.96	2.21	2.40			2.44	1.63
1996	4.50	1.42	3.96	1.74	2.90	1.35	2.53	1.12
1997	4.60	1.13	3.11		3.52	0.84	3.13	0.28
1998	3.98	1.84	3.27	1.81	4.15	0.92	2.63	0.84
1999	4.78	0.80	3.28	2.28	5.23	0.89	2.82	0.77
2000	4.57	1.05	3.00		4.43	0.93	3.14	0.76
2001	5.18	0.90	2.69	2.50	5.33	0.45	2.91	1.55
2002	6.34	1.07	3.35	1.52	5.06		3.16	1.09
2003	5.79	1.08	3.08	2.26	5.40	0.58	3.20	0.65
2004	6.10	0.80	3.35		5.33	0.48	3.14	0.86
2005	5.12	1.05	3.49	1.75	5.08	0.53	2.49	0.60
2006	5.33	0.96	2.66	3.14	5.12	0.67	3.44	1.87
2007	5.60	0.98	3.23	2.84	5.13	0.63	3.92	1.12
2008	4.92	1.03	3.54	1.67	5.17	0.21	3.04	1.38
2009	5.44	1.02		2.43	4.72	0.41	3.09	1.94
2010	5.00		2.90	2.80			2.73	2.02

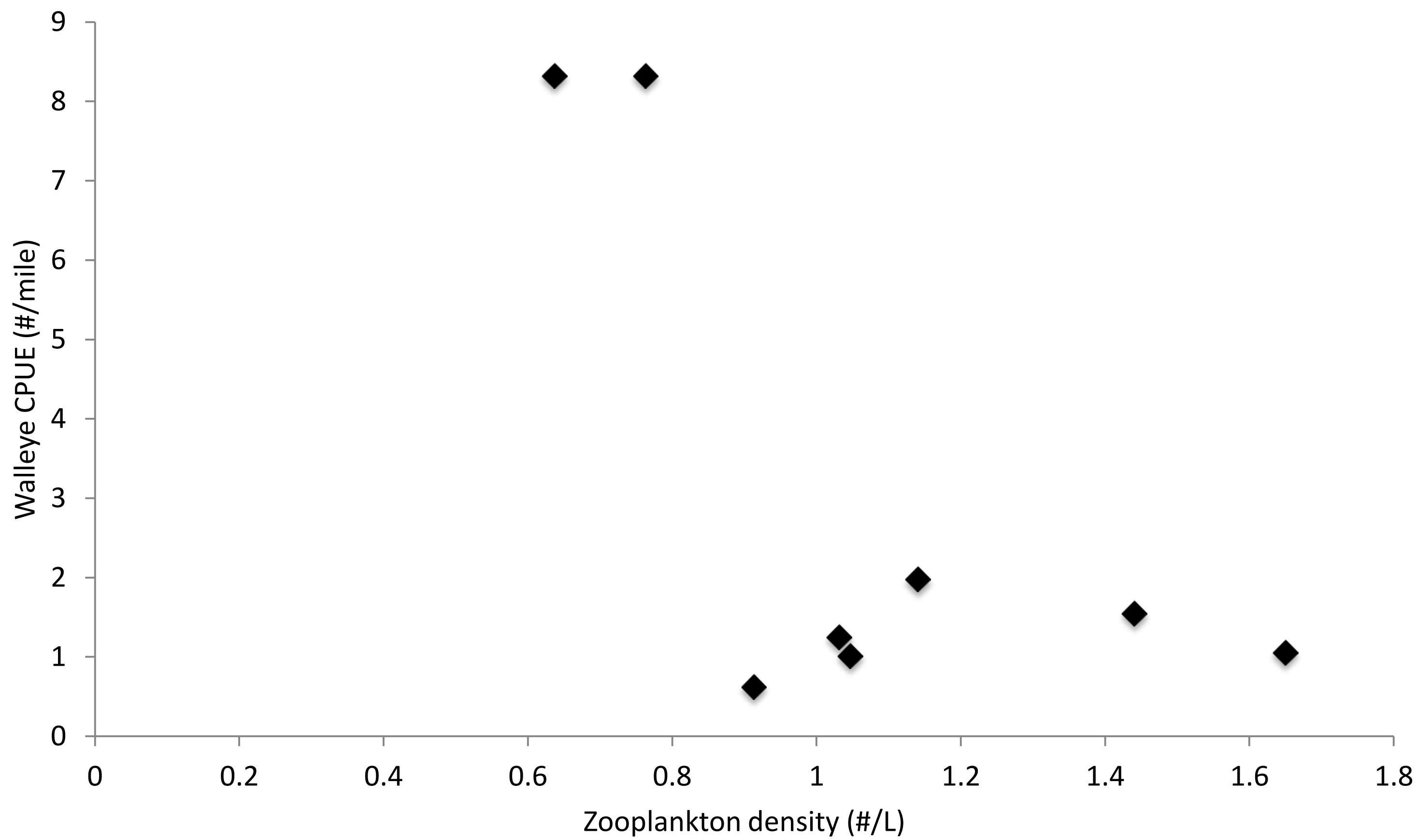

Figure 14: Regression of mean spring mixed-zooplankton community density and fall age-0 walleye catch per mile by lake and year (r^2=0.45, p>0.05).

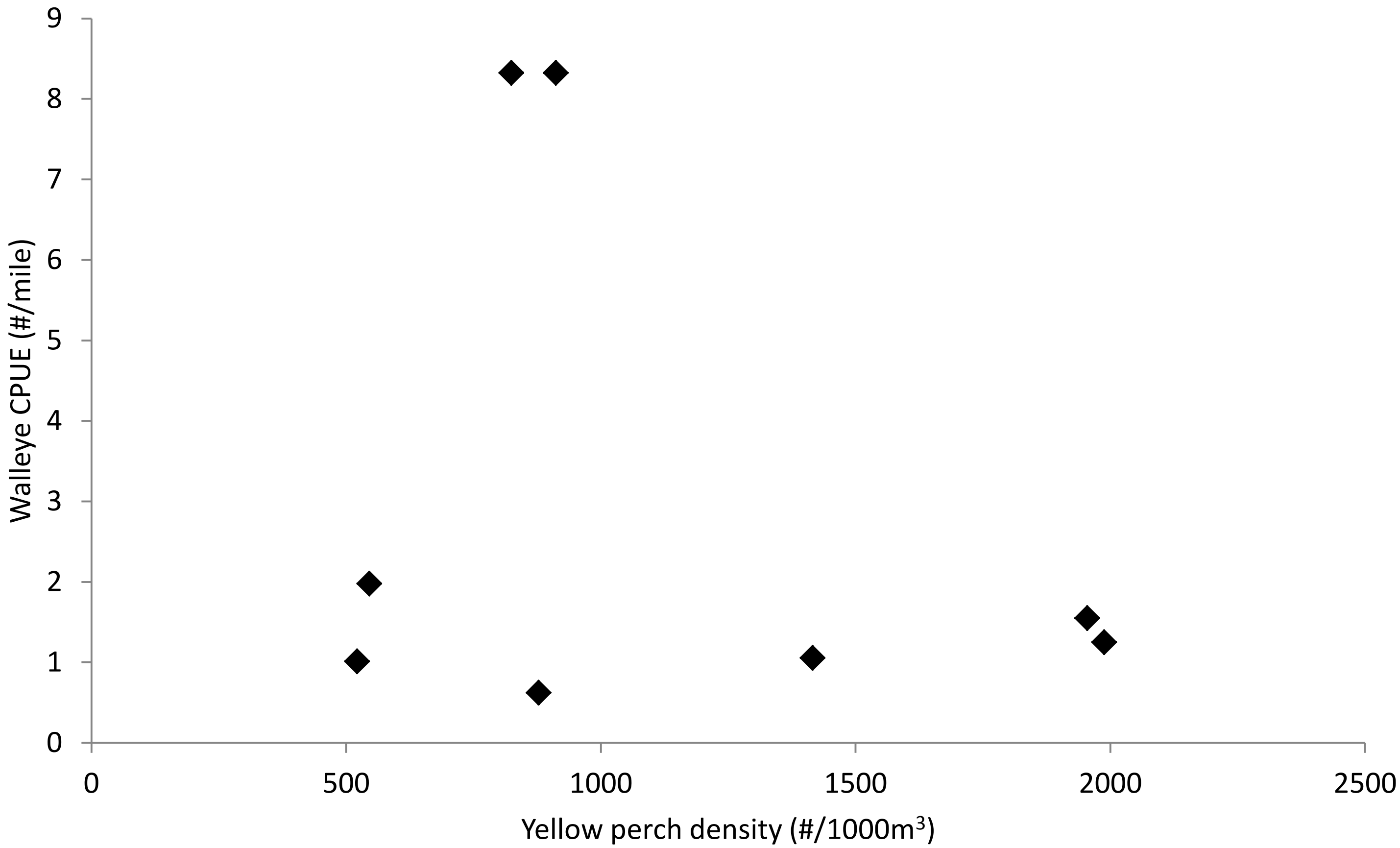

Figure 15: A regression of spring age-0 yellow perch density and fall age-0 walleye catch per mile by lake and year (r^2=0.07, $p>0.05$).

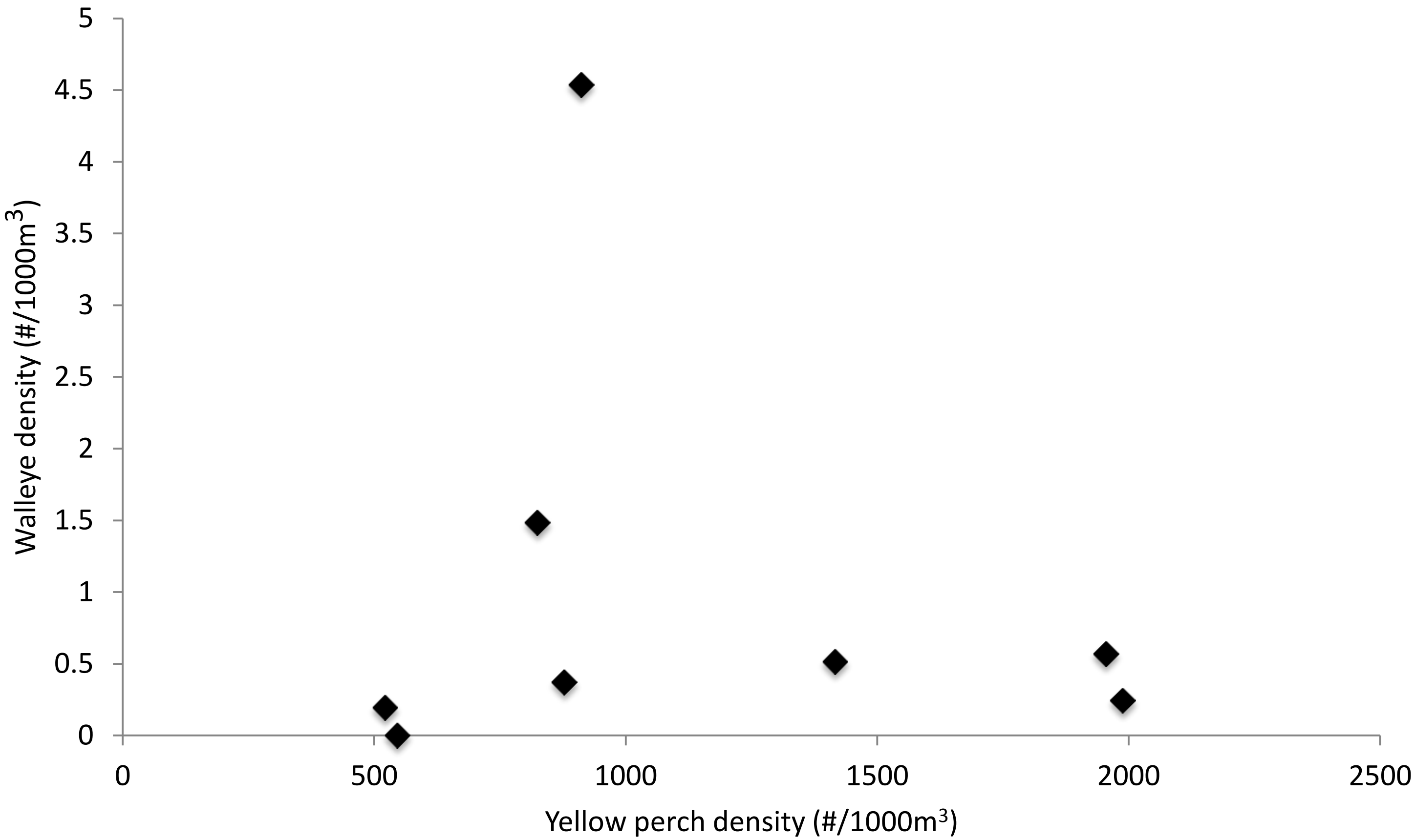

Figure 16: Regression of spring age-0 yellow perch and spring age-0 walleye density by lake and year (r^2=0.02, p>0.05).

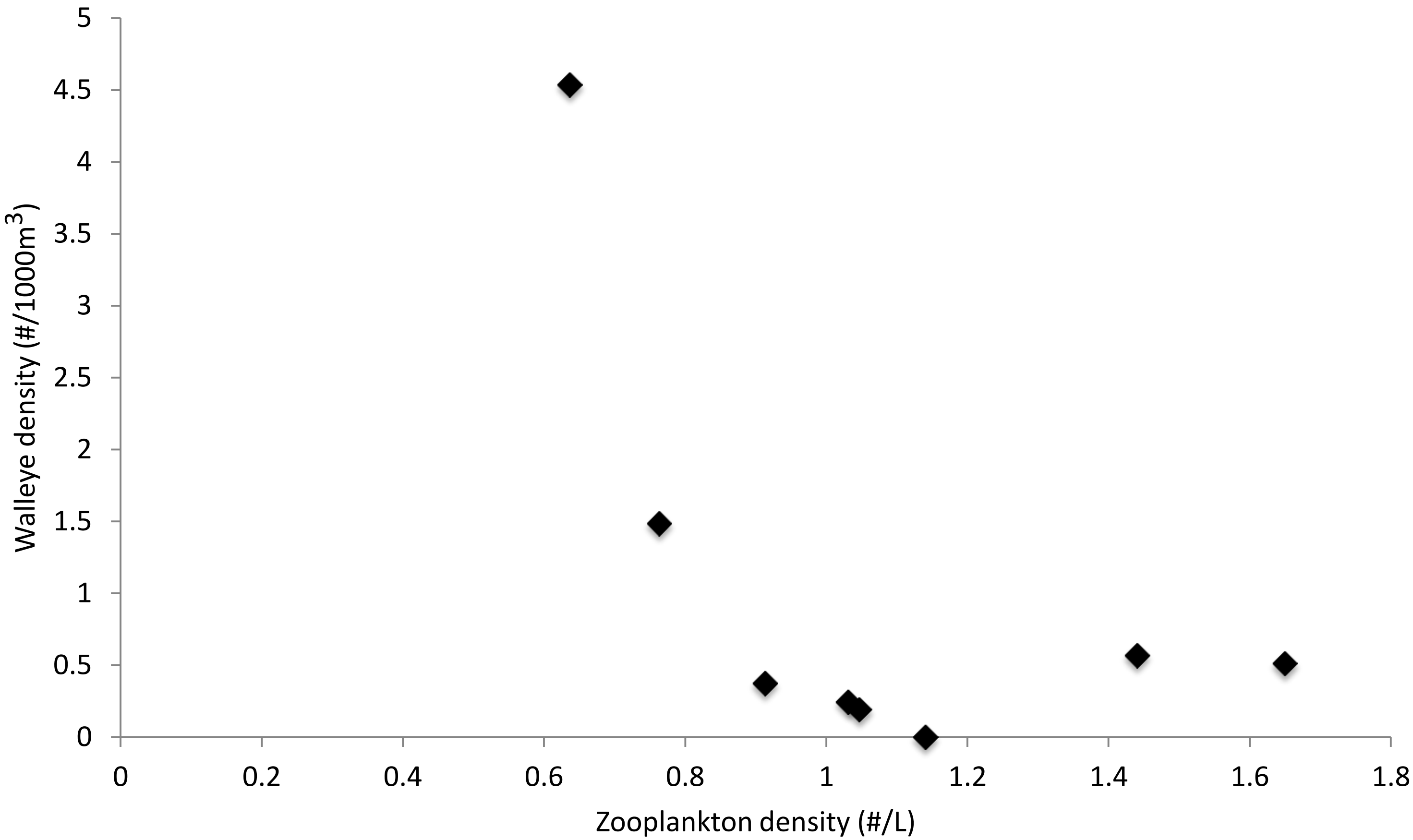

Figure 17: Regression of spring mixed-zooplankton community density and spring age-0 walleye density by lake and year (r^2=0.34, p>0.05).

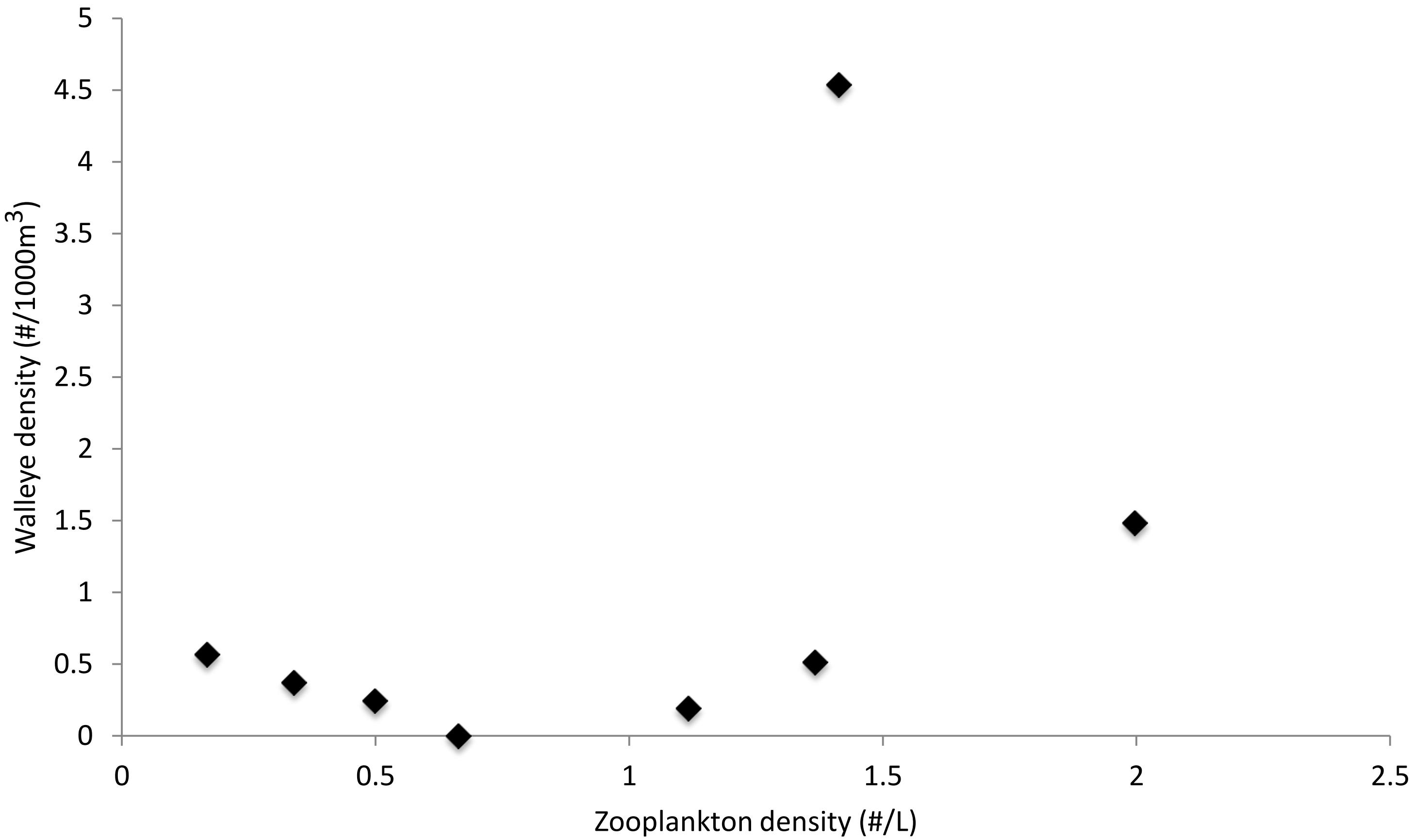

Figure 18: Regression of spring large-bodied zooplankton density and spring age-0 walleye density by lake and year (r^2=0.23, p>0.05).

REFERENCES

REFERENCES

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

Barton, B. A., editor. 2011. Biology, management, and culture of walleye and sauger. American Fisheries Society, Bethesda, Maryland.

Beisner, B. E., A. R. Ives, and S. R. Carpenter. 2003. The effects of an exotic fish Invasion on the prey communities of two lakes. J. Animal Ecology 72(2): 331-342.

Blaxter, J. H. S. 1986. Development of sense organs and behaviour of teleost larvae with special reference to feeding and predator avoidance. Trans. Am. Fish. Soc. 115: 98–114.

Bogue, M. B. 2000. Fishing the Great Lakes: an environmental history. 1783-1933. University of Wisconsin Press, Madison.

Brandt, S. B., D. M. Mason, D. B. MacNeill, T. Coates, and J. E. Gannon. 1987. Predation by alewives on larvae of Yellow Perch in Lake Ontario. Trans. Am. Fish. Soc. 116: 641– 645.

Brazner, J. C., S. E. Campana, D. K. Tanner, and S. T. Schram. 2004. Reconstructing habitat use and wetland nursery origin of yellow perch from Lake Superior using otolith elemental analysis. J. Great Lakes Res. 30(4): 492–507.

Bronte, C. R. , R. J. Hesselberg, J. A. Shoesmith, and M. H. Hoff. 1996. Discrimination among spawning concentrations of Lake Superior lake herring based on trace element profiles in sagittae. Trans. Am. Fish. Soc. 125(6): 852–859.

Brooking, T. E., L. G. Rudstam, M. H. Olson, and A. J. VanDeValk. 1998. Size-dependent Alewife predation on larval walleye in laboratory experiments. N. Am. J. Fish Mgmt. 18: 960-965.

Brooks, J. L., and S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science 150: 28-35.

Brothers, E., and R. Thresher. 2004. Statolith chemical analysis as a means of identifying stream origins of lampreys in Lake Huron. Trans. Am. Fish. Soc. 133(5): 1107–1116.

Bulkley, R. V., V. L. Spykermann, and L. E. Inmon. 1976. Food of the pelagic young of walleyes and five cohabiting fish species in Clear Lake, Iowa. Trans. Am. Fish. Soc. 105(1): 77-83.

Chalupnicki, M. A., J. H. Johnson, J. E. McKenna Jr. and D. E. Dittman. 2010. Habitat selection and spawning success of walleyes in a tributary to Owasco Lake, New York. N. Am. J. Fish Mgmt. 30(1): 170-178.

Chevalier, J.R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. Trans. Am. Fish. Soc. 4: 739–744.

Claramunt, R. M., and D. H. Wahl. 2000. The effects of abiotic and biotic factors in determining larval fish growth rates: a comparison across species and reservoirs. Trans. Am. Fish. Soc. 129:835–851.

Colby, P. J., R. E. McNicol, and R. A. Ryder. 1979. Synopsis of biological data on the walleye (*Stizostedion vitreum vitreum* Mitchill 1818). Food and Ag. Org. of the United Nations Fisheries Synopsis 119.

Confer J. L., and L. M. O'Bryan. 1989. Changes in prey rank and preference by young planktivores for short-term and long-term ingestion periods. Can. J. Fish. Aquat. Sci. 46: 1026-1032.

Corbett, B. W. and P. M. Powles. 1986. Spawning and larval drift of sympatric walleye and white suckers in an Ontario stream. Trans. Am. Fish. Soc. 115: 41-46.

Crowder, L. B., M. E. McDonald, and J. A. Rice. 1987. Understanding recruitment of Lake Michigan fishes: the importance of size-based interactions between fish and zooplankton. Can. J. Fish. Aquat. Sci. 44(2): 141-147.

Dettmers, J. M., M. J. Raffenberg, and A. K. Weis. 2003. Exploring zooplankton changes in southern Lake Michigan: implications for yellow perch recruitment. J. Great Lakes Res. 29: 355–364.

Dufour, E., T. O. Ho¨o¨k, W. P. Patterson, and E. S. Rutherford. 2008. High-resolution isotope analysis of young Alewife *Alosa pseudoharengus* otoliths: assessment of temporal resolution and reconstruction of habitat occupancy and thermal history. J. Fish Biol. 73(10): 2434–2451.

Dustin, D. L. and P. C. Jacobson. Evaluation of walleye spawning habitat improvement projects in streams. Minnesota Department of Natural Resources, Investigational Reports 502.

Engel, S., M. H. Hoff, and S. P. Newman. 2000. Walleye fry hatching, diet, growth and abundance in Escanaba Lake, Wisconsin, 1985-1992. Wisconsin Department of Natural Resources, Research Report 184, Madison.

Fielder, D. G. 1992. Relationship between walleye fingerling stocking density and recruitment in lower Lake Oahe, South Dakota. N. Am. J. Fish. Mgmt.12: 346-352.

Forney, J. L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Trans. Am. Fish. Soc. 103: 15–24.

Forney, J. L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–73. J. Fish. Res. Board of Canada 33: 783–792.

Fox, M. 1989. Effect of prey density and prey size on growth and survival of juvenile walleye (*Stizostedian vitreum vitreum*). Can. I. Fish. Aquat. Sci. 46: 1323-1328.

Garner, S. R., S. M. Bobrowicz, and C. C. Wilson. 2013. Genetic and ecological assessment of population rehabilitation: walleye in Lake Superior. Ecological Applications 23(3): 594-605.

Geiling, W. D., J. R. M. Kelso, and E. Iwachewski. 1996._Benefits from incremental additions to walleye spawning habitat in the Current River, with reference to habitat modification as a walleye management tool in Ontario. Can. J. Fish. Aquat. Sci. 53(Suppl. 1): 79-87.

Godby, N. A., T. C. Willis, T. A. Cwalinksi, and B. Bury. Cheboygan River Assessment. Michigan Department of Natural Resources, Fisheries Division Draft Report.

Haas, R. C., and M. V. Thomas. 1997. Nutrient levels and plankton populations of five Great Lakes tributaries and their relation to walleye year class strength (spawning success). Michigan Department of Natural Resources, Fisheries Research Report 2022, Ann Arbor.

Hanchin, P. A., R. D. Clark, R. N. Lockwood, and T. Cwalinki. 2005a. The fish community and fishery of Burt Lake, Cheboygan County, Michigan in 2001-02 with emphasis on walleyes and Northern Pike. Michigan Department of Natural Resources, Fisheries Special Report 36, Ann Arbor.

Hanchin, P. A., R. D. Clark, Jr., R. N. Lockwood, and N. A Godby, Jr. 2005b. The fish community and fishery of Crooked and Pickerel lakes, Emmet County, Michigan with emphasis on walleyes and northern pike. Michigan Department of Natural Resources, Fisheries Special Report 34, Ann Arbor.

Hansen, S. P. and J. M. Hennessy. 2006. Wisconsin Department of natural Resources 2003-2004 ceded territory fishery assessment report. Wisconsin Department of natural resources Administrative Report No. 61, Madison.

Houde, E.D. 1967. Food of pelagic young of the walleye, *Stizostedion vitreum vitreum*, in Oneida Lake, New York, Trans. Am. Fish. Soc. 96(1): 17-24.

Houde, E.D. 1987. Fish early life dynamics and recruitment. American Fisheries Society Symposium 2: 17-29.

Hoxmeier, R.J.H., D.H. Wahl, M.L. Hooe and C.L. Pierce. 2004. Growth and survival of larval walleyes in response to prey availability. Trans. Am. Fish. Soc. 133(1): 45-54.

Ivan, L. N., E. S. Rutherford, C. Riseng, and J. A. Tyler. Density, production and survival of walleye (*Sander vitreus*) eggs in the Muskegon River, Michigan. J. Great Lakes Res. 36: 328-337.

Jensen, A.L. 1992. Relation between mortality of young walleye (*Stizostedion vitreum*) and recruitment with different forms of compensation. Environmental Pollution 76: 177-

181.

Johnson, F. H. and J. G. Hale. 1977. Interrelations between walleye (*Stizostedion vitreum vitreum*) and smallmouth bass (*Micropterus dolomieui*) in four northeastern Minnesota Lakes, 1948-69. J. Fish. Res. Board of Canada 34: 1626-1632.

Jonas, J. L., and D. H. Wahl. 1998. Relative importance of direct and indirect effects of starvation for young walleyes. Trans. Am. Fish. Soc. 127: 192–205.

Kelder, B. F. and J. M. Farrell. 2009. A spatially explicit model to predict walleye spawning in an eastern Lake Ontario tributary. No. Am. J. Fish. Mgmt. 29(6): 1686-1697.

Kempinger, J. J., W. S. Churchill, G. R. Priegel, and I. M. Christenson. 1975. Estimates of abundance, harvest, and exploitation of the fish population of Escanaba Lake, Wisconsin. 1946-1969. Wisconsin Department of Natural Resources, Technical Bulletin. 84: 30.

Kempinger, J.J. and W.S. Churchill. 1972. Contribution of native and stocked walleye fingerlings to the anglers' catch, Escanaba Lake, Wisconsin. Trans. Am. Fish. Soc. 101(4): 644-649.

Kinietz, W. V. 1940. The Indians of the western Great Lakes, 1615-1760. University of Michigan Press, Ann Arbor.

Kissman, C. E. H., L. B. Knoll, and O. Sarnelle. 2010. Dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*) reduce microzooplankton and macrozooplankton biomass in thermally stratified lakes. Limnol. Oceanogr. 55(5): 1851-1859.

Kohler, C. C., and Ney. 1980. Piscovority in a lanklocked population of Alewife, *Alosa pseudoharengus*. Canadian Journal of Fisheries and Aquatic Science 37: 1314-1317.

Krueger, J. 2008. Open water spearing in northern Wisconsin by Chippewa Indians during 2007. Administrative Report 2008-02. Great Lakes Indian Fish and Wildlife Commission, Odanah Wisconsin.

Laurence, G. C. 1972. Comparative swimming abilities of fed and starved larval largemouth bass (*Micropterus salmoides*). J. Fish Bio. 4: 73–78.

Lemly, A. D., and J. F. Dimmick. 1982. Growth of young-of-the-year and yearling Centrarchids in relation to zooplankton in the littoral zone of lakes. Copeia 1982:305–321.

Li, K. T., J. K. Wetterer, and N. G. Hairston. 1985. Fish size, visual resolution, and prey selectivity. Ecology 66(6): 1729-1745.

Li, S., and J. A. Mathias. 1982. Causes of high mortality among cultured larval walleyes. Trans. Am. Fish. Soc. 111: 710–721.

Miller, T. J., L. B. Crowder, I. A. Rice, and E. A. Marshall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. 45: 1657-1670.

Mills, E. L., R. Sherman, and D. S. Robson. 1989. Effect of zooplankton abundance and body size on growth of age-0 yellow perch (*Perca flavescens*) in Oneida Lake, New York, 1975–86. Can. J. Fish. Aquat. Sciences 46: 880–886.

Mills, E.L., Confer, J.L., and Ready, R.C. 1984. Prey selection by young yellow perch (*Perca flavescens*): the influence of capture success, visual acuity and prey choice. Trans. Am. Fish. Soc. 113(5): 579–587.

Milroy, N. J. Krueger, and E. Madsen. 2007. Open-water spearing and netting in the 1837 Minnesota ceded territory during the 2005-2006 quota year. Great Lakes Indian Fish and Wildlife Commission, Administrative report 2007-15, Odanah, Wisconsin.

Mion, J. B., R. A. Stein, and E. A. Marschall. 1998. River discharge drives survival of larval walleye. Ecological Applications 8(1): 88-103.

Mitro, M. G., and D. L. Parrish. 1997. Temporal and spatial abundances of larval walleyes in two tributaries of Lake Champlain. Trans. Am. Fish. Soc. 126: 273-287.

Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370-1386.

Murphy, H. M., G. P. Jenkins, P. A. Hamer, and S. E. Swearer. Interannual variation in larval survival of snapper (*Chrysophrys auratus*, Sparidae) is linked to diet breadth and prey availability. Can. J. Fish. Aquat. Sci. 69: 1340–1351.

Nate, N. A., M. A. Bozek, M. J. Hansen, C. W. Ramm, M. T. Bremigan, and S. W. Hewett. 2003. Prediction the occurrence and success of walleye populations from physical and biological features of northern Wisconsin lakes. No. Am. J. Fish. Mgmt. 23(4), 1207-1214.

Nepszy, S. J., D. H. Davies, D. Einhouse, R. W. Hatch, G. Isbell, D. MacLennan, and K. M. Muth. 1991. Walleye in Lake Erie and Lake St. Clair. *In* Status of walleye in the Great Lakes: case studies prepared for the 1989 workshop. *Edited by* P.J. Colby, C.A. Lewis, and R.L. Eshenroder. Great Lakes Fishery Commission, Ann Arbor, Mich. Spec. Publ. 91-1. pp. 145–168.

Noble, R. L. 1972. Mortality rates of walleye fry in a Bay of Oneida Lake, New York. Trans. Am. Fish. Soc. 101(4): 720-723.

Olson, D. E. and W. J. Scidmore. 1962. Homing behavior of spawning walleyes, Trans. Am. Fish. Soc. 91(4): 355-361.

Pangle, K. L., S. A. Ludsin, and B. J. Fryer. Otolith microchemistry as a stock identification tool for freshwater fishes: testing its limits in Lake Erie. Can. J. Fish. Aquat. Sci. 67: 1475–1489.

Partridge, D. G. and D. R. DeVries. 1999. Regulation of growth and mortality in larval bluegills: implications for juvenile recruitment. Trans. Am. Fish. Soc. 128(4): 625-638.

Pelham, M. E., C. L. Pierce, and J. G. Larscheid. 2001. Diet dynamics of the juvenile piscivorous fish community in Spirit Lake, Iowa, USA, 1997–1998. Ecol. of Freshwater Fish 10: 198–211.

Peterson, D. L., J. Peterson and R.F. Carline. 2006. Effects of zooplankton density on survival of stocked walleye fry in five Pennsylvania reservoirs. J. Fresh. Ecology 21(1), 121-129.

Quinn, S. P. 1992. Angler perspectives on walleye management. N. Am. J. Fish. Mgmt. 12: 367-378.

Rice, J. A., L. B. Crowder, and F. P. Binkowski. 1987. Evaluating potential mortality for larval bloater (*Coregonus hoyi*): starvation and vulnerability to predation. Can. J. Fish. Aquat. Sciences 44: 467–472.

Roseman, E.F., Taylor, W.W., Hayes, D.B., Tyson, J.T., and Haas, R.C. 2005. Spatial patterns emphasize the importance of coastal zones as nursery areas for larval walleye in western Lake Erie. J. Great Lakes Res. 31(Suppl. 1): 28–44.

Schael, B. M., L. G, Rudstam, and J. R. Post. 1994. Gape limitation and prey selection in larval yellow perch (*Perca flavescens*), freshwater drum (Aplodinotus grunniens), and black crappie (*Pomoxis nigrormaculatus*). Can. J. Fish. Aquat. Sci. 48: 1919-1 925.

Schneider, J. C. and J. H. Leach. 1977. Walleye (*Stizostedion vitreum vitreum*) fluctuations in the Great Lakes and possible causes, 1800-1975. J. Fish. Res. Bd. Canada 34: 1878-1889.

Spykerman, V.L, 1974. Food habits, growth and distribution of larval walleye, *Stizostedion vitreum vitreum* (Mitchill), in Clear Lake, Iowa. Proc. Iowa Acad. Sci. 81: 143-149.

USDOI (U.S. Department of the Interior), U.S. Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau. 2001. National survey of fishing, hunting and wildlife-associated recreation. Washington, D.C.

USDOI (U.S. Department of the Interior), U.S. Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau. 2008. 2006 national survey of fishing, hunting, and wildlife-associated recreation. Washington, D.C.

Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. Limnol. Oceanog. 15: 556–565.

Whitledge, G. W., B. M. Johnson, P. J. Martinez, and A. M. Martinez. 2007. Sources of nonnative centrarchids in the upper Colorado River revealed by stable isotope and microchemical analyses of otoliths. Trans. Am. Fish. Soc. 136(5): 1263-1275.

Winnebago County University of Wisconsin Extension. 2006. The economic impact of angling on the Lake Winnebago system. Winnebago County University of Wisconsin Extension, Oshkosh.

Zimmerman, M. P. 1999. Food habits of smallmouth bass, walleyes and Northern Pikeminnow in the lower Columbia River basin during out-migration of juvenile anadromous salmonids. Trans. Am. Fish. Soc. 128: 1036-105