# EXPANDED ASSESSMENT OF RECRUITMENT BOTTLENECKS FOR AGE-0 WALLEYE SANDER VITREUS IN NORTHERN WISCONSIN 

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A Thesis
Submitted in partial fulfillment of the requirements of the degree
MASTER OF SCIENCE
IN
NATURAL RESOURCES (FISHERIES)
College of Natural Resources
UNIVERSITY OF WISCONSIN
Stevens Point, Wisconsin

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## Executive Summary

Many northern Wisconsin lakes that historically supported naturally-recruiting walleye Sander vitreus populations have shown declines in recruitment over the last 1015 years. Previous research conducted on four northern Wisconsin lakes suggested a recruitment bottleneck was occurring before mid-July in lakes with declining walleye natural recruitment. Effective management of walleye populations involves understanding these recruitment bottlenecks, as potential management solutions may vary in relation to when and why this recruitment failure is occurring. To further assess these recruitment bottlenecks, I expanded on the previous assessment to determine if: 1) timing of a recruitment bottleneck for age-0 walleyes was consistent among lakes with declining recruitment; 2) abiotic and biotic metrics differed between lakes with declining (D-NR) and sustained (S-NR) walleye recruitment, with a specific focus on the abundance of edible zooplankton and 3 ) catch-per-effort (CPE) of larval and post-larval walleyes can be used to predict the presence, absence, and relative strength of walleye year-classes indexed by standard fall electrofishing conducted by the Wisconsin Department of Natural Resources and the Great Lakes Indian Fish and Wildlife Commission.

In 2016 and 2017, I sampled six D-NR lakes and seven S-NR lakes distributed across northern Wisconsin. I used ichthyoplankton nets in spring, micro-mesh gill nets in summer, and nighttime electrofishing in fall to collect age-0 walleye at multiple stages during their first year of life. In addition, adult walleye were collected in spring to verify that adult abundance was sufficient to support natural recruitment. Limnological data and zooplankton samples were also collected during spring. I used repeated-measures analysis of variance or $t$-tests to compare a suite of metrics describing lake characteristics
(e.g., water temperature and Secchi depth), adult walleye populations (e.g., relative abundance and mean total length), interspecific competition (e.g., larval yellow perch Perca flavescens relative abundance), and zooplankton (e.g., relative abundance, ediblesize relative abundance and mean total length) between lakes with different recruitment histories.

Age-0 walleye were collected during larval and post-larval stages in most S-NR lakes. Larval walleye were collected in four of six D-NR lakes, but lack of age-0 walleye in five of the D-NR lakes after the larval stage supported the conclusion that a recruitment bottleneck was occurring before mid-July. One D-NR lake (Bony Lake) supported a limited level of natural recruitment because age-0 walleye were collected during fall electrofishing in both years. In addition, age-0 walleye were never collected at any stage in one S-NR lake (Windfall Lake), suggesting a lack of natural recruitment.

Statistical analyses indicated that only the mean total length of Daphnia spp. was significantly different between recruitment histories, but this difference was largely a result of the relatively large size of Daphnia spp. in Escanaba Lake (an S-NR lake). Removal of Escanaba Lake from the analysis resulted in no significant difference in mean total length of Daphnia spp. between recruitment histories. Significant interactions between recruitment history and year were also detected when comparing relative abundance of Daphnia spp. and relative abundance of edible Daphnia spp. between lakes with different recruitment histories, but pairwise comparisons indicated that these metrics did not differ between recruitment histories in either year of sampling.

Relative abundance of larval walleye during spring and relative abundance of post-larval walleye during summer were not significantly correlated with relative
abundance of age- 0 walleye in fall electrofishing. Across all lakes, if larval walleye were collected, there was only a $40 \%$ probability that age- 0 walleye would be collected in fall electrofishing at a rate above the threshold for eventual recruitment to the fishery (CPE $\geq$ 15 walleye/h). However, when I examined only S-NR lakes, there was a $75 \%$ probability that age-0 electrofishing CPE would be $\geq 15$ walleye/h if larval walleye were present in spring ichthyoplankton tows. If post-larval walleye were encountered in July gill nets, there was an $80 \%$ probability that age- 0 walleye would be collected in age-0 electrofishing at a rate $\geq 15$ walleye $/ \mathrm{h}$; this probability was the same when examining only S-NR lakes. My results indicate that larval towing and mid-summer micro-mesh gill nets could provide useful tools for allocating walleye fingerlings for stocking, as lakes where age- 0 walleyes were not captured in one of these gears could be prioritized for stocking over lakes where age-0 walleyes were collected.

The presence of larval walleye in some D-NR lakes followed by lack of age- 0 walleye in micro-mesh gill nets and fall electrofishing surveys suggests a recruitment bottleneck is occurring at some point before mid-July and this could be before, during, or immediately after the larval stage. However, the possible causes of this bottleneck remain unclear because I detected only one difference in abiotic and biotic metrics between recruitment histories. Possibly, difference in average size of Daphnia spp., which may reflect differences in species composition, could influence larval walleye survival, but this difference was largely a reflection of the relatively large Daphnia spp. present in Escanaba Lake. Moreover, edible zooplankton were available in similar abundances between lakes with different recruitment histories.

Difficulties with understand the mechanisms regulating these bottlenecks makes it challenging to prescribe management actions that might alleviate walleye recruitment problems. Possibly, increasing the abundance of larval walleye by maintaining higher adult walleye densities or through fry stocking may circumvent this bottleneck. However, higher larval abundance may not result in eventual recruitment. For instance, larval walleye abundance in Sawyer Lake (D-NR) during 2017, exceeded abundance in all but one S-NR lake, yet no age-0 walleyes were collected from Sawyer Lake in micromesh gill nets during July or in fall electrofishing. Currently, stocking fingerling walleye represents one method that might maintain walleye fisheries in these lakes. Ongoing WDNR evaluations of fingerling stocking and changes in walleye harvest regulations will help to determine if these management actions can be used to maintain these fisheries and possibly re-establish natural recruitment in some lakes.

## Acknowledgments

I would like to dedicate this thesis to my mom and dad. They expressed their belief in me and kept me focused during the two years I required to complete this project. I also would like to thank Captain Paul for starting my career and transforming a quiet 18-year old kid into a confident young man, eager to learn and manage fisheries resources.

Thank you also to Dr. Daniel Isermann for providing me with an opportunity to earn my master's degree at the University of Wisconsin-Stevens Point (UWSP). Dan has been an excellent mentor, professor, and advisor. He has pushed me to make sure my thesis is a strong, well-put together product. I have also gained knowledge sitting in his class that will be beneficial as I pursue a career in fisheries management.

I would also like to thank my graduate committee: Dr. Wesley Larson, Dr. Joshua Raabe, Dr. Daniel Dembkowski, and Joseph Hennessy from the Wisconsin Department of Natural Resources (WDNR). This group has provided me with constructive criticism and useful feedback throughout this process and their comments have helped me create a strong thesis document.

Sampling in the field as well as processing larval and zooplankton samples would not have been completed in two years without the help from multiple UWSP staff and technicians. I specifically would like to thank Andrea Musch, Chris Sullivan, Drew Wallace, Jake Steckmesser, Katie Duhm, Taylor Beaman, Matt Kraus, Brad Erdman, Alex Catalano, Kate Carpenter, Zach Mohr, Nic Brown, Taylor Morlan, Ryan Eastman, Boyd Delebreau, Andrew Wieland, and Brandon Braun. I would also like to thank current and previous graduate students for their help including Mike Vaske and Nick

Rydell. Thank you also to Keith Turnquist for completing the genetic analysis portion of my research. I also would like to thank Max Wolter, Steve Gilbert, Hadley Boehm, Zach Lawson, Gretchen Hansen, Greg Sass, John Kubisiak, Scott Toshner, Skip Sommerfeldt, and Dave Seibel with either the Wisconsin or Minnesota Department of Natural Resources for ideas pertaining to this project in addition to assisting with the data collection. Lastly, I would like to thank the WDNR for funding my research.

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## Introduction

Understanding population dynamics is critical to effectively managing fish populations. Specifically, recruitment may represent the most influential dynamic rate affecting abundance and demographics (Ricker 1975; Carline et al. 1984; Sissenwine et al. 1988; Hansen and Nate 2014) because most fish species exhibit high variation in recruitment (Sissenwine 1984; Houde 2009). Recruitment (also referred to as year-class strength) is defined as the number of individuals that survive to a specific age or size and is often indexed at the point when fish become vulnerable to harvest (Fogarty et al. 1991). Many abiotic and biotic factors may regulate annual recruitment (Sissenwine 1984; Fogarty et al. 1991; Baccante and Colby 1996; Bozek et al. 2011a). Moreover, many studies suggest factors operating in the first year of life are important in regulating year-class strength in fish populations (e.g., Hjort 1914; Maloney and Johnson 1957; Kempinger and Churchill 1972; Chevalier 1973; Forney 1976; Mathias and Li 1982; Hoxmeier et al. 2006).

Walleye Sander vitreus are native to north-central North America and have been stocked within and outside their native range for over 100 years (Kerr 2011; Schmalz et al. 2011). Currently, walleye support important recreational, commercial, and tribal subsistence fisheries across their range (Schmalz et al. 2011). Walleye populations exhibit substantial variation in annual recruitment (Isermann 2007; Bozek et al. 2011a), and these fluctuations can directly influence fisheries in terms of the numbers and size of fish available to fishers (Isermann and Paukert 2010; Hansen and Nate 2014). Walleye recruitment is often indexed in the first or second year of life (i.e., age-0 or age-1) using
sampling techniques such as trawling, seining, gillnetting, and electrofishing (Wingate and Schupp 1984; Madenjian et al. 1996; Hansen et al. 2004).

Abiotic factors such as changing water levels (Johnson 1961), wind and waveaction (Raabe and Bozek 2015) and dissolved oxygen (Oseid and Smith Jr. 1971; Siefert and Spoor 1974) can cause variability in hatching success leading to variability in walleye year-class strength (Bozek et al. 2011a). Additional abiotic factors that influence walleye recruitment include water temperature and variation in spring warming rate (Madenjian et al. 1996; Hansen et al. 1998) and habitat availability (Raabe and Bozek 2012). Walleye eggs are deposited close to shore over coarse (e.g., gravel or cobble) substrate (Raabe and Bozek 2012) or on offshore reefs (Roseman et al. 2001). A decrease in water level can reduce the amount of spawning area available to adult walleye and subsequently reduce hatching success (Johnson 1961). Wind and wave-action can destroy walleye eggs or transport them to areas that are unsuitable for incubation (Raabe and Bozek 2015). Dissolved oxygen (DO) levels in and around spawning areas are also important for hatching and larval survival. Oseid and Smith Jr. (1971) determined DO levels below $5 \mathrm{mg} / \mathrm{L}$ led to reduced hatching success and Siefert and Spoor (1974) showed only $40 \%$ survival of larvae at DO levels of $3.4 \mathrm{mg} / \mathrm{L}$. Egg deposition and incubation are determined by spring water temperatures (Busch et al. 1975) and larval walleye which hatch sooner are able to feed on zooplankton earlier in the spring.

Biotic factors, such as adult walleye density (Madenjian et al. 1996; Hansen et al. 1998), cannibalism (Craig 2000), predation by other species (Hoxmeier et al. 2006), and growth rate (Serns 1982; Uphoff et al. 2013) can also influence walleye year-class strength. Abundance of spawners explained $20 \%$ of the variation in walleye recruitment
in Lake Erie; however, peak recruit abundance was estimated to occur below the highest estimates of adult abundance, suggesting density-dependent mortality was occurring (Madenjian et al. 1996). Similarly, Hansen et al. (1998) determined abundance of age-5 and older walleye explained $32 \%$ of recruitment variability in Escanaba Lake, Wisconsin, and that high numbers of recruits resulted from low numbers of spawners. Cannibalism of age-0 walleye can also contribute to total mortality (Chevalier 1973; Forney 1976). Cannibalism by adult walleye in Oneida Lake, New York was determined to account for a large portion of age-0 walleye total mortality from August through December (Chevalier 1973). However, the level of cannibalism by adult walleye is influenced by availability of other prey items and was proportional to age-0 walleye abundance (Chevalier 1973). Predation on larval walleye by other species has also been studied and Quist et al. (2003) and Hoxmeier et al. (2006) reported negative relationships between small centrarchids and larval walleye abundance, but Boehm (2016) found no larval walleye in 847 diets of centrarchids and other small predators in northern Wisconsin lakes. After hatching, larval walleye and yellow perch Perca flavescnes are both pelagic and are frequently collected in the same locations (Staggs and Otis 1996; Zweifel 2006; Boehm 2016), suggesting that interspecific interactions could occur. High abundance of larval yellow perch may provide a predation buffer for larval walleye (Forney 1974; 1977) or provide an important source of prey for age-0 walleyes when they transition to piscivory at 20-30 mm total length (TL; Mathias and Li 1982; Galarowicz and Wahl 2005; Galarowicz et al. 2006). For example, Meerbeek et al. (2002) determined age-0 walleye growth rates increased with abundance of age-0 yellow perch in two South Dakota lakes.

Prey availability and composition can also influence growth, survival, and subsequent recruitment of larval walleye (Johnston and Mathias 1994; Galarowicz and Wahl 2005; Hoxmeier et al. 2006). Larval walleye have limited energy reserves at hatching and will begin exogenous feeding before their yolk sac is completely absorbed (Engel et al. 2000). Houde (1967) identified prey items of age-0 walleye during their first six weeks of life and determined their diet predominately consisted of copepods, but also identified cladocera, fish, chironomids, ostracods and rotifers at lower frequencies. Other studies have also observed cladocerans and copepods in the gut of larval walleyes (e.g., Smith Jr. and Moyle 1945; Bulkley et al. 1976; Johnston and Mathias 1994). Mathias and Li (1982) fed larval walleye crustacean zooplankton and suggested that rotifers and copepod nauplii are too small for larval walleye to see and would not actively be chosen but consumed during respiration. Roswell et al. (2013) suggested larval yellow perch will consume copepods and Daphnia and Bremigan et al. (2003) determined the primary prey of larval yellow perch was copepods. These results suggest larval walleye may compete with larval yellow perch for prey resources. In contrast, Bulkley et al. (1976) suggested pelagic larval walleye and yellow perch in Clear Lake, Iowa selected for different prey items, which would limit competition between species.

Walleye represent one of the most economically- and culturally-important fish species in the state of Wisconsin, where the native range of walleye was limited to large lakes and river systems, but stocking has resulted in range expansion (Becker 1983). The recreational fishery for walleye occurs across Wisconsin and is closed from March to May in most inland waters, while the tribal fishery occurs during early spring and is limited to Ceded Territory waters in northern Wisconsin. Walleye harvest in Wisconsin
is determined by a quota system with a maximum risk level of harvest exceeding $35 \%$ of a population occurring only one out of forty times (Hewett and Simonson 1998). This quota is then divided between recreational and tribal harvest. McClanahan and Hansen (2005) found that among recreational anglers reporting a preference, walleye were the most targeted species in Wisconsin. Consequently, both the Wisconsin Department of Natural Resources (WDNR) and the Great Lakes Indian Fish and Wildlife Commission (GLIFWC) expend substantial effort monitoring and managing walleye populations within the state.

Some lakes in northern Wisconsin that previously exhibited varying degrees of natural recruitment have failed to produce measurable year-classes of walleye in recent years as indexed in fall electrofishing samples (Hansen et al. 2015a; Boehm 2016). These declines in natural recruitment have occurred even though unpublished WDNR data indicated adult walleye densities in some lakes were sufficient ( $\geq 3$ adults/ac; Luehring and Rose 2015) to produce fall electrofishing catch rates of age-0 walleye above $0 / \mathrm{mi}$. Biologists understand abiotic and biotic factors are important in regulating walleye recruitment in Wisconsin lakes, but questions remain (e.g., Hansen et al. 1998; Fayram et al. 2014, Hansen et al. 2015a). Furthermore, Hansen et al. (2015b) developed a model that correctly predicted walleye recruitment success (> 10 age- 0 walleye/mi) or failure ( $<10$ age- 0 walleye $/ \mathrm{mi}$ ) with $81 \%$ accuracy based on lake surface area, water temperature degree-days, shoreline development factor, and conductivity, which suggests year-class strength is regulated by a combination of factors. However, the factors limiting recruitment, and when and how these factors are operating in lakes exhibiting recruitment failure, are not fully known at this time.

The lack of age- 0 walleyes captured in fall electrofishing suggests potential walleye recruitment bottlenecks are occurring in the first year of life, but lack of targeted sampling for age- 0 walleye before fall electrofishing surveys has prevented managers from determining when and how recruitment failure occurs. Expansion of largemouth bass Micropterus salmoides populations in Wisconsin (Hansen et al. 2015) led to initial concerns that adult bass predation on age- 0 walleyes might be at least partially responsible for walleye recruitment declines. Subsequent assessment of largemouth bass diets in four Wisconsin lakes indicated adult bass predation on age- 0 walleye was unlikely (Kelling et al. 2016) and further assessment of trends in age-0 walleye abundance were warranted.

To better evaluate when recruitment failure was occurring, Boehm (2016) developed a protocol for sampling age-0 walleye on four northern Wisconsin lakes with different recruitment histories, two with declining natural recruitment (D-NR) and two with sustained natural recruitment (S-NR). Egg mats, ichthyoplankton nets towed during day and night, beach seines, short term sets of $0.64-\mathrm{cm}$ bar and $0.95-\mathrm{cm}$ bar micro-mesh gill nets (at night) and standard fall electrofishing were used to sample walleye at different stages during their first year of life. Boehm (2016) determined ichthyoplankton tows conducted at night during May and early June and $0.64-\mathrm{cm}$ bar micro-mesh gill nets set in mid-summer could be used to detect the presence of age-0 walleye before fall electrofishing.

Boehm (2016) also suggested that a recruitment bottleneck was occurring at or before the larval stage in her two D-NR lakes. These conclusions were based on collection of walleye eggs from both D-NR lakes and newly hatched larvae from one
lake, but no age- 0 walleyes were collected in fall electrofishing on either lake. Conversely, Boehm (2016) collected walleye at all life history stages on S-NR lakes. Boehm (2016) compared a variety of abiotic (e.g., temperature variation, Secchi depth, dissolved oxygen levels) and biotic variables (e.g., adult walleye population structure, zooplankton size and abundance) between lakes with differing recruitment histories and only detected differences in mean total length of adult walleyes and age-0 yellow perch abundance in one of the two years of sampling. On average, adult walleyes in the two D NR lakes were significantly longer than in the two S-NR lakes because of fewer individuals present at younger year-classes in D-NR lakes, a trend that is consistent with recruitment failure. In addition, age-0 yellow perch abundance was higher in D-NR lakes, suggesting that factors affecting larval walleye survival were not having the same effect on larval yellow perch (Boehm 2016). However, these initial analyses were limited by small sample size (two lakes within each recruitment history) and analysis of zooplankton data that did not incorporate a temporal component or account for which zooplankton were actually preyed upon by larval walleye.

Walleye populations exhibiting prolonged periods of poor natural recruitment remain an important management concern for the WDNR and GLIFWC and have prompted changes in stocking regimes and harvest regulations in an attempt to maintain these fisheries. Verifying the timing of potential recruitment bottlenecks identified by Boehm (2016) across a larger number of lakes and identifying the factors that may contribute to this bottleneck will help the WDNR and GLIFWC determine management actions which might be effective in circumventing the loss of natural recruitment. Furthermore, developing a method for determining walleye year-class strength before
age-0 electrofishing occurs in fall might allow for better allocation of the limited number of fish available for stocking. However, catches of larval walleyes in previous studies have been low (Quist et al. 2004; Zweifel 2006; Uphoff et al. 2013; Boehm 2016), making it difficult to understand the relationship between larval density and recruitment to later life stages.

The objectives of my study were to determine if: 1) timing of a recruitment bottleneck for age-0 walleyes was consistent among lakes with declining recruitment; 2) abiotic and biotic metrics differed between D-NR and S-NR lakes, with a specific focus on the abundance of edible zooplankton and 3) catch-per-effort (CPE) of larval and postlarval walleyes can be used to predict presence, absence, and relative strength of walleye year-classes indexed by fall electrofishing conducted by WDNR and GLIFWC.

## Methods

## Study Sites

My study occurred on 13 lakes (Figure 1) across northern Wisconsin and all lakes previously supported or currently support some level of natural walleye recruitment (Table 1). All sampling occurred during 2016 and 2017. Lakes were chosen through consultation with WDNR biologists such that the most recent estimates of adult walleye density were considered sufficient ( $\geq$ three adults/acre) to support natural recruitment. Each lake was categorized as S-NR or D-NR based on trends in age-0 CPE in standardized fall electrofishing surveys conducted by WDNR or GLIFWC (Table 2). Lakes in the S-NR category had a long-term mean CPE for young-of-year (YOY) walleye $\geq 45$ fish $/ \mathrm{h}$, while lakes in the D-NR category had recent age- 0 CPEs $<9$ fish $/ \mathrm{h}$. A threshold of 10 age- 0 walleye/mile was suggested to be the minimum CPE that would
result in eventual recruitment to the fishery (Hansen et al. 2015b). This minimum threshold was converted to catch-per-hour by multiplying catch-per-mile estimates by 1.5 (Serns 1982), such that a year class with $\mathrm{CPE} \geq 15$ age- 0 walleye/h was expected to eventually recruit to the fishery.

Sampling

## Limnology

Secchi depth was recorded at the deepest part of each lake at weekly intervals during May and June when larval walleye should have been present in the water column. Temperature loggers (Onset ${ }^{\circledR}$ HOBO models Water Temperature Pro U22-001 or TidbiT UTBI-001) were deployed at eight lakes in 2016 and eleven lakes in 2017 immediately after ice out and loggers were retrieved in fall. Temperature loggers were placed in shallow water (< 1 m ) and recorded hourly water temperatures. Temperature logger malfunction in 2016 limited water temperature analysis to only data collected in 2017. Temperature loggers were not deployed in two D-NR lakes in 2017 because of limited access (Bony Lake) and unsafe travel conditions cancelling the deployment trip (Lac Vieux Desert).

## Adult Walleye

Adult walleye were collected 7-10 d after ice out by nighttime AC electrofishing in 2016 or 2017. Electrofishing boats, paired with a Wisconsin-style MBS-2DH-40 electrofishing box and dropper array were used by WDNR, GLIFWC, or Wisconsin Cooperative Fishery Research Unit (WCFRU) personnel to collect fish at randomly chosen 20-min transects along the shoreline. Time for each transect was measured as
number of minutes of pedal time (i.e., electricity on). All walleye were measured to the nearest mm (total length; TL) and sex was determined when possible based on extrusion of gametes. Adult CPE was calculated as the number of walleye $\geq 381 \mathrm{~mm}$ TL caught per h of electrofishing for each transect. The average of all transects was used to estimate adult CPE for each lake. Adult walleye relative abundance and mean adult walleye TL were estimated once for each lake over the two-year study.

## Larval Walleye

Larval walleye sampling started in mid-May of each year when water surface temperatures were $11-16^{\circ} \mathrm{C}$ and continued at $7-10 \mathrm{~d}$ intervals until early June. Each lake was sampled three times and sampling periods were grouped by sampling date (Table 3). In 2016, sampling period 1 occurred from 12 May-17 May, sampling period 2 was 19 May-24 May, and sampling period 3 was 28 May-3 June. Similarly, in 2017 sampling period 1 was during 15 May-21 May, sampling period 2 was 23 May- 27 May, and sampling period 3 was 31 May- 5 June. Sampling was conducted at this time in order to estimate temporal overlap between larval walleye and zooplankton. A $1,000-\mu \mathrm{m}$ mesh conical ichthyoplankton net was towed at the surface for five-min at both nearshore and offshore locations on each lake (Isermann and Willis 2008). All towing was conducted at night (Boehm 2016). Lakes were divided into three to six approximately equal zones based on surface area with two tows conducted in each zone on each sampling date (Table 4). Inshore (within $100-\mathrm{m}$ of shore) and offshore ( $\geq 100-\mathrm{m}$ from shore) sites were randomly selected within each zone for the first sample and then remained fixed throughout the study. A General Oceanics ${ }^{\ominus}$ Model 2030R flowmeter was attached in the
mouth of the net to estimate volume of water sampled. Larval samples were preserved in $95 \%$ ethanol. Larval fish were identified to family and percid larvae identified to species. For each sample, all yellow perch and walleye larvae were counted. All walleye larvae and a subsample of up to 120 yellow perch were measured to the nearest 0.1 mm TL for each lake during both years. All larvae visually identified as walleye and a subsample of larvae visually identified as yellow perch were randomly selected to undergo quantitative polymerase chain reaction (qPCR; Kelling et al. 2016) to verify visual species identification. The Molecular Conservation Genetics Laboratory (MCGL) at UWSP conducted qPCR analysis. Most individuals for genetic analysis were small fish ( $\leq 15$ mm ) visually identified as yellow perch because of the difficulty in correctly identifying percid larvae to species at small sizes using morphometric and meristic characteristics.

The gut from all larval walleye collected during ichthyoplankton tows were removed to identify and measure prey items. Zooplankton diet items were removed from the gut, classified to order for adult copepods and genus for cladocerans, and carapace length ( $\mu \mathrm{m}$ ) was measured. Larval fish encountered in diets were submitted to the MGCL for species identification.

## Post-larval Walleye

Multiple $0.64-\mathrm{cm}$ mesh, $30-\mathrm{m}$ long x $1-\mathrm{m}$ tall gill nets ( 0.10 diameter monofilament twine; referred to as micro-mesh gill nets herein) were used to collect age0 (i.e., post-larval) walleye in mid-July. Micro-mesh gill nets were set perpendicular to shore in water less than five $m$ deep. Between four to eight nets were set on a single night at randomly-selected locations; number of sets varied with lake surface area (Table
4). Nets were set during the hour before sunset and allowed to soak for a minimum of one h in the dark (mean total set time $=2.0 \mathrm{~h} ; \mathrm{SE}=0.05$ ). In 2016, nets were set at each location one time. In 2017, a subsample of locations were selected for a second round of net sets during the same night. Post-larval walleye relative abundance was estimated using all gill net data for 2016 and only data from the first gill net set in 2017. All walleye were counted and measured to the nearest mm TL . Catch rates were estimated as number of age- 0 walleye $/ \mathrm{h}$ for each net and standardized to 10 net sets for each lake.

Age-0 walleye were collected in late September or early October via nighttime electrofishing conducted by WDNR, GLIFWC, or WCFRU personnel except for Spillerberg Lake (S-NR), which was not sampled by electrofishing in 2017. Fall sampling occurred before advanced fingerlings were stocked in D-NR lakes.

Electrofishing occurred at multiple 20-min transects and time for each transect was measured as minutes of pedal time (i.e., electricity on). All walleye collected were measured to the nearest mm TL. Breaks in length-frequencies and WDNR age estimates from scales were used to determine the maximum TL of age- 0 walleye and minimum TL of age-1 walleye each year. These length criteria were used to assign ages to fish of unknown age (i.e., no scales collected) to calculate CPE of age-0 walleye, which was reported as catch/h.

## Zooplankton

Zooplankton were collected in conjunction with larval tows at offshore sites. Samples were collected using a Wisconsin plankton net ( $30-\mathrm{cm}$ opening, three to one length to diameter ratio, $80-\mu \mathrm{m}$ mesh, $63-\mu \mathrm{m}$ mesh collection bucket). The net was
lowered to one m above bottom and slowly ( $\approx 0.3 \mathrm{~m} / \mathrm{s}$ ) retrieved vertically (Dodson et al. 2008). Each sample was washed into collection jars and preserved with $95 \%$ ethanol. Samples were diluted to the nearest $25-\mathrm{mL}$. One one-mL subsample per $25-\mathrm{mL}$ of total sample volume were randomly taken using a Hensen-Stempel pipette and placed into a zooplankton counting wheel to identify and enumerate individual zooplankton.

Individuals were classified to order for adult copepods (e.g., calanoid or cyclopoid) and to genus for cladocerans (e.g., Diaphanosoma, Daphnia, Leptidora, Bosmina). A Nikon ${ }^{\text {TM }}$ DS-Fi2 camera mounted to a Nikon ${ }^{\text {TM }}$ SMZ1500 microscope and Nikon ${ }^{\text {TM }}$ Elements software were used to measure total length (top of head to end of caudal spine) and carapace length (total length not including caudal spine) to the nearest $\mu \mathrm{m}$ for up to ten individuals from the three most frequent taxa in each sample.

Diet information from larval walleye were used to calculate the relative abundance of edible zooplankton (based on taxonomic group and size) consumed during the period larval walleyes were pelagic. The gut was removed from larval fish visually identified as walleye but only data for larval fish confirmed as walleye were used for analysis. Relative abundance of edible zooplankton was determined using carapace lengths of zooplankton items removed from the gut. Minimum and maximum carapace lengths of zooplankton diet items determined the length of edible zooplankton for each taxa. Relative abundance of edible individuals for each taxa was estimated as the number of zooplankton in the subsample within the edible size range and scaled to whole sample.

## Analyses

To address objective 1, patterns of presence and absence in CPE of age- 0 walleye at different life stages (i.e., larval, post-larval during summer, and age-0 during fall) were used to determine the timing of potential walleye recruitment bottlenecks. For example, when no age- 0 walleyes were collected in a lake during fall electrofishing, mid-summer gill net sampling, or during larval sampling, I concluded a recruitment bottleneck was occurring at or before the larval stage. Alternatively, I concluded a recruitment bottleneck occurred before mid-summer if larval walleye were collected on a lake, but no age-0 walleyes were observed during mid-summer gill net sampling or during fall electrofishing.

To address objective 2, abiotic and biotic metrics were compared between recruitment histories treating individual lakes within each recruitment history as experimental units or subjects. Because adult walleye relative abundance and adult walleye TL were estimated only once for each lake over the two-year study, $t$-tests were used to compare means of those two metrics between recruitment histories. Variance associated with adult walleye CPE was not equal between recruitment histories, so a Satterthwaite approximation for degrees of freedom was used. A $t$-test was also used to compare coefficient of variation ([SD/mean] x 100; CV) in daily mean May surface water temperatures because the comparison between recruitment histories was made using only one year of data. Alpha ( $\alpha$ ) was set at 0.05 for all analyses.

Repeated-measures analysis of variance (ANOVA) was used to test for differences in Secchi depth and mean larval yellow perch relative abundance between
recruitment history, year, and the interaction between these two main effects. Repeatedmeasures ANOVA was also used for comparing all other metrics: relative abundance and total length for the three most abundant zooplankton taxa, relative abundance of edible individuals for the three most abundant zooplankton taxa, and relative abundance of total edible individuals combined for the three most abundant zooplankton taxa. These ANOVAs included recruitment history, year, and sampling period as main effects and the three-way interaction among these main effects as well as two-way interactions between recruitment history and year and recruitment history and sampling period. A significant interaction between year and sampling period was not tested because differences in these metrics were expected among sampling periods between years and this interaction did not include the main factor of interest, which was recruitment history. Lake was included as a random effect in the ANOVAs, recognizing that observations represented repeated measurements on the same lakes. Calanoid copepod relative abundance in D-NR lakes during 2016 and cyclopoid copepod relative abundance in S-NR lakes during 2017 were not normally distributed and this was not remedied by $\log _{e}$ transformation. However, ANOVA is robust to violations of the normality assumption (Glass et al. 1972) and there is not a clear consensus on appropriate nonparametric procedures for repeated measures data (Zimmerman and Zumbo 1993). Consequently, I used repeated measures ANOVA to make these comparisons. All repeated measures ANOVA analyses were conducted in SAS and a Tukey (HSD) post hoc test was used for pairwise comparisons if ANOVA indicated differences between factors or among treatments.

To address objective 3, Pearson correlations were used to determine if CPE of larval and post-larval walleye were correlated with relative strength of age- 0 walleye
year-classes indexed by fall electrofishing. Correlations were fit using all lakes and using only S-NR lakes. I also calculated the probabilities that age-0 walleye electrofishing CPE would be $\geq$ the minimum threshold likely to contribute to the fishery ( 15 age- 0 walleye $/ \mathrm{h}$ ) if larval or post-larval walleye were captured in ichthyoplankton tows or micro-mesh gill nets. Probabilities were calculated for all lakes and for S-NR lakes only.

## Results

## Objective 1: Timing of Recruitment Bottleneck

In 2016, 33 larval fish collected from nine study lakes (four of seven S-NR lakes, two of six D-NR lakes; Table 5) were visually identified as walleye. Genetic analyses confirmed visual identifications for 29 of these 33 fish (mean TL = 11.3 mm ); the remaining four fish were yellow perch based on genetic assignments. In addition, genetic analyses assigned eight small (< 15 mm TL ) larval fish, which were visually identified as yellow perch, as walleye (total $\mathrm{N}=37$ ). Larval walleyes were collected during all three sampling periods, which occurred between 12 May and 3 June 2016. Relative abundance of larval walleye in S-NR lakes ranged from 0 to $5.12 \mathrm{fish} / 1,000 \mathrm{~m}^{3}$ ( mean $=1.77$ fish $/ 1,000 \mathrm{~m}^{3} ; \mathrm{SE}=0.87$ ). Larval walleye were collected in five of seven S-NR lakes (Escanaba, Little John, Sand, Spillerberg, and Turtle Flambeau Flowage). Larval walleye were collected in three of six D-NR lakes (Big Sissabagama Lake, Lac Vieux Desert, and Sawyer Lake) and relative abundance of larval walleye in D-NR lakes ranged from 0 to 2.14 fish $/ 1,000 \mathrm{~m}^{3}\left(\right.$ mean $=0.66$ fish $\left./ 1,000 \mathrm{~m}^{3} ; \mathrm{SE}=0.39\right)$.

In 2017, 66 larval fish collected from seven study lakes (four of seven S-NR lakes, three of six D-NR lakes; Table 5) were visually identified as walleye. Genetic analyses confirmed correct visual identification of all walleye (mean $\mathrm{TL}=13.9 \mathrm{~mm}$ ).

Additionally, 16 small ( $<15 \mathrm{~mm}$ TL) larval fish, originally identified as yellow perch through visual identification, were identified as walleye (total $\mathrm{N}=82$ ). Larval walleye were present in ichthyoplankton tows during all three sampling periods from 15 May to 5 June 2017. Relative abundance of larval walleye in S-NR lakes ranged from 0 to 9.60 fish $/ 1000 \mathrm{~m}^{3}\left(\right.$ mean $=2.91$ fish $\left./ 1,000 \mathrm{~m}^{3} ; \mathrm{SE}=1.39\right)$. Larval walleye were collected in five of seven S-NR lakes (Big Arbor Vitae, Escanaba, Sand, Spillerberg, and Turtle Flambeau Flowage). Larval walleye were collected in four of six D-NR lakes (Big Sissabagama Lake, Durphee Lake, Lac Vieux Desert, and Sawyer Lake). Relative abundance of larval walleye in D-NR lakes ranged from 0 to 9.54 fish $/ 1000 \mathrm{~m}^{3}$ (mean $=$ $\left.1.87 \mathrm{fish} / 1,000 \mathrm{~m}^{3} ; \mathrm{SE}=1.54\right)$.

In 2016, no age-0 walleye were collected in July micro-mesh gillnets from D-NR lakes, but age-0 walleye were collected in five of seven S-NR lakes. Little John and Windfall lakes were the two S-NR lakes where no age-0 walleye were collected. In 2017, age-0 walleye were collected in micro-mesh gill nets from one D-NR lake (Bony Lake) and in all S-NR lakes with the exception of Windfall Lake. Mean TL of age-0 walleyes captured in micro-mesh gill nets was $80 \mathrm{~mm}(\mathrm{SE}=1.3)$ in 2016 and $81 \mathrm{~mm}(\mathrm{SE}$ $=1.7)$ in 2017. Re-setting the gill nets in 2017 for a second time in the same night did not provide many additional walleye $(n=4)$ compared to the first set $(n=80)$. In addition, there were no occasions where the second set of nets caught post-larval walleye when the first set did not.

With the exception of Windfall Lake, age-0 walleye were collected during fall electrofishing from all S-NR lakes (Table 5). Conversely, age-0 walleye were collected in only one D-NR lake (Bony Lake) in both years. In 2017, CPE of age-0 walleyes in

Bony Lake exceeded the minimum threshold of 15 fish $/ \mathrm{h}$, indicating that eventual recruitment to the fishery was likely to occur. Age-0 walleye CPE in S-NR lakes during fall electrofishing ranged from 0 to 101 fish $/ \mathrm{h}$ (mean $=45$ fish $/ \mathrm{h} ; \mathrm{SE}=14.6$ ) in 2016 and 0 to 171 fish $/ \mathrm{h}($ mean $=59 \mathrm{fish} / \mathrm{h} ; \mathrm{SE}=45.9)$ in 2017. In 2016, five $S-N R$ lakes had age0 CPEs above the minimum threshold for recruitment and four S-NR lakes were above the threshold in 2017.

In summary, age- 0 walleye were present during spring, summer, and fall in most S-NR lakes but were only collected after the larval stage in one D-NR lake over the twoyear study. Larval walleye were present in some D-NR lakes during spring but a pattern of low catch-rates of age- 0 walleye in most D-NR lakes started during gill net sampling in July and continued during fall electrofishing (i.e., 0 fish/net in summer and 0 fish $/ \mathrm{h}$ in fall). Furthermore, age-0 walleye were consistently collected at higher rates during summer and fall in S-NR lakes. Larval walleye presence in some D-NR lakes followed by a lack of age- 0 walleye in summer and fall suggests a recruitment bottleneck is occurring in D-NR lakes before mid-July and this could be happening before, during or immediately after the larval stage.

## Objective 2: Comparison of Abiotic and Biotic Metrics between Recruitment Histories

Mean daily surface water temperatures were similar between D-NR lakes (Figure 2) and S-NR lakes (Figure 3) in 2017, and mean CV of May surface water temperature did not differ significantly between recruitment histories (Figure 4). Furthermore, mean Secchi depth was not significantly different between recruitment histories (Table 6;

Figure 5), but Secchi depth was significantly higher among all lakes in 2016 (mean $=3.6$ $\mathrm{m} ; \mathrm{SE}=0.369)$ when compared to $2017($ mean $=3.1 \mathrm{~m} ; \mathrm{SE}=0.391)$.

Mean adult walleye relative abundance (Figure 6) and adult walleye TL (Figure 7) were not significantly different between recruitment histories. Additionally, mean relative abundance of larval yellow perch was not significantly different between recruitment histories (Table 6; Figure 8).

Daphnia spp., calanoid copepods, and cyclopoid copepods were the most abundant zooplankton taxa collected in my study lakes. There was a significant interaction between recruitment history and year when comparing relative abundance of Daphnia spp. between lakes of different recruitment histories (Table 6). Mean Daphnia spp. relative abundance was significantly lower in D-NR lakes in 2016 than D-NR lakes in 2017, but Daphnia spp. abundance did not differ between recruitment histories during either year (Figure 9). Mean relative abundance of calanoid copepods was not significantly different between lakes with different recruitment histories, but abundance differed between years (Table 6). Regardless of recruitment history, abundance of calanoid copepods was significantly lower in 2016 than 2017 (Figure 10). Mean relative abundance of cyclopoid copepods was not significantly different between recruitment histories (Table 6; Figure 11).

Mean Daphnia spp. total length was significantly higher in S-NR lakes than in DNR lakes (Table 6; Figure 12). Mean total lengths for calanoid and cyclopoid copepods were not significantly different between recruitment histories (Table 6), but mean calanoid copepod total length was significantly lower in 2016 than 2017 across all lakes (Figure 13). In addition, mean cyclopoid copepod total length was not significantly
different between recruitment histories but was significantly lower in 2016 than 2017 and significantly lower during sampling period 3 for all lakes than the other two sampling periods (Figure 14).

Guts were removed from 94 larval walleye over the course of the study and 37 of these fish had no prey present (Table 7). The majority of larval walleye diets ( $n=42$ of 57) contained larval fish (Table 7); zooplankton were encountered in 15 larval walleye (Table 7). Genetic analysis indicated five larval fish were walleye and 11 were yellow perch. Most larval fish in the diets were too deteriorated for visual identification and were not verified as walleye or yellow perch from genetic analysis, but were assumed to be yellow perch based on composition of ichthyoplankton tows at time of collection.

Daphnia spp., calanoid copepods, and cyclopoid copepods comprised 51\%, 19\%, and $30 \%$, respectively, of the 67 zooplankton items observed in larval walleye diets (Table 8). Carapace lengths of zooplankton in larval walleye diets ranged from 272-1816 $\mu \mathrm{m}$ for Daphnia spp., from 318-1200 $\mu \mathrm{m}$ for calanoid copepods, and from 125-930 $\mu \mathrm{m}$ for cyclopoid copepods (Table 8). Over $90 \%$ of Daphnia spp., calanoid copepods, and cyclopoid copepods collected in the water column were within the size range consumed by larval walleye during all three sampling periods (Table 8).

Similar to mean Daphnia spp. relative abundance, there was a significant interaction between recruitment history and year when comparing mean relative abundance of edible-size Daphnia spp. (Table 6). Mean abundance of edible-size Daphnia spp. was significantly lower in D-NR lakes during 2016 than in D-NR lakes during 2017, but abundance of edible-size Daphnia spp. did not differ between recruitment histories during either year (Figure 15). There was no significant difference
in mean abundance of edible-size calanoid copepods between recruitment histories; however, relative abundance of edible-size calanoid copepods did significantly differ between years (Table 6; Figure 16). Additionally, there was no significant difference in mean abundance of edible-size cyclopoid copepods between recruitment histories or years (Table 6; Figure 17). Furthermore, mean $\log _{e}$ relative abundance of edible-size individuals for all three zooplankton taxa combined was not significantly different between recruitment histories or years, but was significantly higher in all lakes during sampling period 1 compared to sampling period 3 (Table 6; Figure 18).

## Objective 3: Year-class Strength Correlations

Larval walleye CPE and post-larval walleye CPE in micro-mesh gill nets were not significantly correlated with age-0 walleye CPE during fall electrofishing when all lakes were included in the analysis (Figure 19). In 6 of 15 cases (40\%) where larval walleye were captured, age-0 CPE in fall electrofishing was at or above the minimum threshold where eventual recruitment to the fishery is likely to occur ( $\geq 15$ age- 0 walleye/h). In 9 of 11 cases $(80 \%)$ where post-larval walleye were present in micro-mesh gill nets, age- 0 CPE was at or above the minimum threshold where eventual recruitment to the fishery is likely to occur.

Larval walleye CPE and post-larval walleye CPE in micro-mesh gill nets were not significantly correlated with age-0 walleye CPE during fall electrofishing when only SNR lakes were included in correlations (Figure 20). In six of eight cases (75\%) where larval walleye were captured in S-NR lakes, CPE of fish in fall electrofishing was at or above the minimum threshold where eventual recruitment to the fishery is likely to occur.

In eight of ten cases ( $80 \%$ ) where post-larval walleye were present in micro-mesh gill nets, age- 0 CPE was at or above the minimum threshold where eventual recruitment to the fishery is likely to occur.

## Discussion

Similar to Boehm (2016), my results suggest that a walleye recruitment bottleneck is operating at or before mid-July in D-NR lakes. All D-NR lakes had estimated adult walleye populations sufficient for natural recruitment to occur ( $\geq 3$ adult walleye/ac), but larval walleyes were never collected in some D-NR lakes and age-0 walleye were not collected after the larval stage in five of six D-NR lakes. Conversely, except for Windfall Lake, age-0 walleyes were always collected in fall electrofishing conducted on S-NR lakes and were typically collected in July micro-mesh gill nets.

Windfall Lake (S-NR) and Bony Lake (D-NR) did not exhibit patterns that were similar to other lakes within their respective recruitment categories. Windfall Lake was classified as an S-NR lake, but age-0 walleye were never collected in any gear during 2016 or 2017. In contrast, Bony Lake was categorized as a D-NR lake, but post-larval walleyes were collected in micro-mesh gill nets in 2017 and during electrofishing in both years. This data suggests that conditions in Bony Lake are still conducive to walleye recruitment during at least some years. In addition, Lac Vieux Desert (D-NR) was stocked with walleye fry in 2016 ( $n=850,000$ fry) and 2017 ( $n=1,060,000$ fry) before ichthyoplankton tows were conducted. However, age-0 walleye were only collected in ichthyoplankton tows during the first sampling period during both years and not in micromesh gill nets or fall electrofishing, suggesting fry stocking did not circumvent the recruitment bottleneck in this lake.

Boehm (2016) compared similar metrics between lakes with different walleye recruitment histories and found significant differences in mean TL of adult walleyes and relative abundance of larval yellow perch between recruitment histories, despite having only two lakes within each recruitment category. Results from my study provide a more comprehensive comparison of these metrics between recruitment histories given the increased number of lakes and more in-depth assessment of zooplankton metrics. The lack of differences in metrics observed between recruitment histories suggests that mechanisms regulating survival beyond the larval stage are likely complex, involving interactions among several variables or variables that were not included in my assessment, such as thermal-optical habitat area or planktivore relative abundance.

In general, relative abundance of adult walleye in D-NR lakes appears to be sufficient to produce year-classes based on historic data and mean adult abundance did not differ between recruitment histories. However, detecting differences in this metric may be difficult given the large amount of variation in adult relative abundance for S-NR lakes. Adult relative abundance was consistently low across D-NR lakes, which is indicative of poor recruitment. But the role of adult abundance in regulating walleye recruitment may be limited, as this metric only explained $10 \%$ of the variation in age- 0 walleye abundance for 162 lakes in northern Wisconsin, whereas year and yellow perch density accounted for over $30 \%$ of the residual variation (Beard et al. 2003). Moreover, Hansen et al. (1998) reported the strongest year-class estimated for Escanaba Lake, Wisconsin between 1958 and 1996 was produced by low numbers of spawners (< 1000 individuals) while the largest number of spawners ( $\approx 3,000$ individuals) produced the fewest recruits. More recently, Haglund et al. (2016) determined $\log _{e}$ density of age-0
walleye did not significantly change while $\log _{e}$ density of adult female walleye did increase after strict regulations eliminated walleye harvest on Escanaba Lake, Wisconsin.

Larval walleyes were collected in three to four D-NR lakes each year. Possibly, D-NR lakes have changed to the point that they need more larvae and therefore more adult walleye to produce larvae to result in capture of age-0 walleye in fall electrofishing. However, in 2017, larval walleye catch in Sawyer Lake (D-NR) exceeded catches observed in all but one S-NR lake, yet no age-0 walleyes were collected in micro-mesh gill nets during July or in fall electrofishing. This suggests at least some D-NR lakes are capable of producing larval walleye densities that should result in capture of age-0 walleyes in fall electrofishing in S-NR lakes, but this rarely occurs. Consequently, management actions that are designed to increase or maintain adult abundance and size structure, such as implementing more restrictive harvest regulations or stocking, may not necessarily result in increased numbers of naturally produced age-0 walleye in fall electrofishing, if walleye fry do not survive.

Except for Daphnia spp. total length, which was higher in S-NR lakes than D-NR lakes, abiotic and biotic metrics were similar between lakes with different walleye recruitment histories. However, the difference in mean total length of Daphnia spp. between recruitment histories was largely a product of the relatively large Daphnia spp. encountered in Escanaba Lake. Removal of Escanaba Lake from this analysis resulted in no significant difference in mean total length of Daphnia spp. between recruitment histories. Moreover, abundance of edible zooplankton prey available to larval walleye does not appear to be limiting in D-NR lakes as there were no differences in edible zooplankton abundance between recruitment histories. Zooplankton prey type and size
identified in larval walleye diets were similar to previous studies focused on larval walleye diets (e.g., Houde 1967; Johnston and Mathias 1994; Hoxmeier et al. 2004). In addition, mean cyclopoid copepod relative abundance for both recruitment histories during all three sampling events was above the minimum maintenance threshold for larval walleye reported in previous research (Johnston and Mathias 1996).

Factors preventing age-0 walleye from surviving beyond the larval stage in most D-NR lakes remain unclear. Possibly, zooplankton prey resources in June and early July (i.e., after my sampling was completed) might differ between lakes with different recruitment histories. For example, if the relative abundance of other zooplanktivorous fish at all life stages (e.g., yellow perch, bluegill Lepomis macrochirus, black crappie Pomoxis nigromaculatus) is higher in D-NR lakes, demand for zooplankton prey may be greater, reducing prey availability to larval walleye. This assertion assumes that zooplankton remain an important prey item for walleyes after the larval stage, but my diet assessment suggested that piscivory is more common in larval walleye.

The presence of larval fish in the diet of larval walleye (10-20 mm) collected from lakes within both recruitment histories suggests this prey source may be more important to survival at these small sizes than previously suggested (Houde 1967; Priegel 1970; Galarowicz et al. 2006). Although some of the larval fish in walleye diets were genetically assigned as walleye, these assignments were likely an artifact of crosscontamination resulting from removal of ingested larvae from the guts of walleye (K. Turnquist, personal communication). Consequently, I assumed that the majority of the larval fish found in larval walleye diets were larval yellow perch, as these were the predominant fish collected in ichthyoplankton tows. Larval yellow perch abundance was
not significantly different between recruitment histories, suggesting this source of prey was not a limiting factor in D-NR lakes.

Previous research by Boehm (2016) examined diet contents of 847 centrarchids and other small predators. Limited numbers of larval fish were present in diets and no larval fish were identified as walleye. However, larval fish in the gut may be difficult to discern due to rapid digestion, but genetic barcoding of these items can reduce the number of unidentified fish (Kelling et al. 2016). Furthermore, selective predation of centrarchids on larval walleye is unlikely given the high abundance of larval yellow perch that are available. Currently, a centrarchid removal project is addressing this issue and will help determine if lower abundances of centrarchids will result in higher natural walleye recruitment.

The effects of incremental environmental and biological changes over a long period may not be captured over two years of data collection. Furthermore, studies have suggested water temperature and clarity have been increasing across Wisconsin (Lester et al. 2004; Hansen et al. 2017a; Hansen et al. 2017b). Larval walleye utilize sight to feed but increased light intensity may have negative effects on larval walleye survival because of their sensitivity to light (Ryder 1977). Although CV in May water surface temperature and mean Secchi depth were not significantly different between recruitment histories, lakes may experience declines in natural recruitment if they are already on the margins for successful walleye recruitment and small environmental changes drive them further away from optimal thermal and optical habitat (Lester 2004).

The lack of correlation between larval or post-larval walleye CPE with age-0 walleye CPE from fall electrofishing suggests recruitment strength is not fixed before
fall, although this assessment is likely affected by various sampling errors. Nighttime ichthyoplankton tows were suggested as an effective gear for collecting larval walleye (Boehm 2016); however, I only collected 119 larval walleye during two years of sampling and 636 ichthyoplankton tows. Determining associations between CPEs among multiple sampling gears is challenging when larval CPEs are low regardless of recruitment history; although, low larval walleye catch rates are consistent with catches reported in previous research (Quist et al. 2004; Zweifel 2006; Uphoff et al. 2013; Boehm 2016). Additionally, catch rates of age-0 walleye in micro-mesh gill nets did not offer a good index of eventual year class strength indexed by fall electrofishing. Conversely, my results indicate the presence of age- 0 walleyes in ichthyoplankton tows or micro-mesh gill nets in S-NR lakes provide useful indicators that age-0 electrofishing CPE of age-0 walleye will be $\geq 15 \mathrm{fish} / \mathrm{h}$.

## Management Implications

Stocking, harvest regulations, and habitat improvements are three tools that managers typically use in efforts to enhance recruitment. Walleye stocking is widely used in the upper Midwestern USA to supplement fisheries in lakes with little natural recruitment (Jennings et al. 2005), or to maintain fisheries where no recruitment occurs (Laarman 1978). If a greater number of walleye fry are required to ensure some walleye survive to their first fall, stocking fry offers one management option. However, the success of walleye fry stocking in supplementing recruitment varies widely (Carlander et al. 1960; Willis and Stephen 1987; Fielder 1992; Lucchesi 2002; Kerr 2007). Lake Mendota, Wisconsin was stocked with 60 million walleye fry from 1987-1992, but fry
survival to summer was estimated to be $<1 \%$ and did not significantly affect the age- 0 walleye population in fall (Johnson et al. 1996). Moreover, throughout the duration of my study, walleye fry stocking in 2016 and 2017 was unsuccessful in creating a walleye year-class in Lac Vieux Desert based on age-0 electrofishing CPE.

Similar to fry stocking, stocking walleye fingerlings and advanced fingerlings have also had mixed results in supplementing or maintaining walleye populations (Li et al. 1996b; Parsons and Pereira 2001; Mitzner 2002). Walleye fingerlings stocked in Escanaba Lake, Wisconsin did not significantly increase the walleye population and yield was $<1 \%$ of the number stocked in three of four stocked year-classes (Kempinger and Churchill 1972). Conversely, survival to age-1 of walleye fingerlings stocked in June and advanced fingerlings stocked in September were detected in 7 of 12 and 11 of 12 stocking events, respectively, in Wisconsin lakes (Kampa and Hatzenbeler 2009). Moreover, fingerling stocking in Minnesota lakes with little or no natural reproduction significantly increased walleye population abundance after the initial stocking event; however, there was not a linear relationship between CPE and stocking frequency (Li et al. 1996a). All six of the D-NR lakes in my study have been stocked with advanced fingerlings in fall since the recent decline in natural recruitment; however, these lakes have not re-established walleye populations sustained by natural recruitment. Stocking small fingerlings earlier in the year may provide another option for increasing walleye abundance in D-NR lakes (Reed and Staples 2017). Walleye stocked as small fingerlings were larger than walleye stocked as large fingerlings in their third year in Illinois lakes (Brooks et al. 2002). Additionally, Olson et al. (2000) reported success of small and large fingerlings is variable among lakes but the cost to raise large fingerlings is higher
and stocking advanced fingerlings may not result in a higher frequency of successful year-classes.

Length-based harvest regulations have had mixed success in increasing walleye abundance and recruitment (Serns 1978; 1981; Sullivan 2003). A partial-year minimum length limit and reduced bag limit was implemented on a Missouri River impoundment to reduce harvest of walleyes during April-June, however, no significant change in recruitment occurred during the nine-year post-regulation period (Stone and Lott 2002). Furthermore, Munger and Kraal (1997) reported no significant increase in average recruitment but an increase in recruitment variability, total abundance, and abundance of legal-size walleye after a minimum length limit and bag limit was implemented in Meredith Reservoir, Texas. Furthermore, increasing adult walleye abundance may result in declines in recruitment (Ricker 1975; Hansen et al. 1998). Variability in successfully reducing harvest and increasing abundance of walleye after imposing a minimum length limit suggests many factors influence the results from regulation changes and shifts in harvest to larger walleye may limit increases in walleye abundance (Larscheid and Hawkins 2005).

Fisheries managers have also used habitat modifications, such as constructing artificial spawning reefs, to increase the amount of suitable spawning habitat and attempt to increase natural walleye recruitment (Bozek et al. 2011b). This approach relies on the assumption that egg survival and recruitment is limited by the availability of spawning habitat (Johnson 1961; Geiling et al. 1996). Many habitat improvement projects have used artificial reefs to increase recruitment and adult abundance, but long-term success has not occurred (Weber and Imler 1974; McKnight 1975; Newburg 1975; Wagner
1990). Suitable spawning habitat has not been quantified for the D-NR lakes in my study although some lakes had larval walleye abundances similar to S-NR lakes, suggesting successful spawning is occurring and larval survival is high enough to produce a yearclass. Furthermore, Richter (2015) reported that walleye spawning habitat did not differ between Wisconsin lakes with high and low levels of walleye recruitment. This finding suggests that availability of spawning habitat does not directly limit walleye recruitment, although there is likely some threshold level of habitat that must be available for recruitment to occur. Lack of success reported in previous research, in addition to high costs associated with habitat improvement projects, suggests that artificially increasing the amount of suitable spawning habitat is not a viable option to improve recruitment and re-establish a naturally-recruiting walleye population in D-NR lakes.

## Future Research

The mechanisms causing recruitment failure in Wisconsin lakes where natural recruitment previously occurred remains unknown. Possibly, more intensive sampling of the zooplankton community over a longer duration may reveal subtle differences that I did not detect. Additionally, adequate thermal-optical habitat area (TOHA) is important for walleye production (Lester et al. 2004) and estimating TOHA may determine differences exist in available habitat for walleyes between recruitment histories.

It remains possible that relative abundance of other small fish present during the time larval walleye are present influences walleye recruitment. Although previous research by Boehm (2016) suggested predation by panfish on larval walleye was not occurring, interspecific competition for prey may be limiting walleye survival in D-NR
lakes rather than predation. Relative abundance estimates of small planktivores are another metric that could be compared between recruitment histories. A centrarchid removal project is ongoing in lakes where walleye recruitment previously occurred and will determine if reducing the abundance of centrarchids increases walleye year-class strength.

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Table 1. Characteristics for 13 study lakes located in northern Wisconsin including recruitment history ( $\mathrm{S}-\mathrm{NR}=$ sustained natural recruitment, D-NR = declining natural recruitment), area (ha), maximum depth (m), average depth ( m ), hydrology, trophic status (based on Wisconsin Department of Natural Resources classification), and average conductivity ( $\mu \mathrm{S} / \mathrm{cm}$ ).

| Rec. Hist. | Lake | County | Area (ha) | Max. Depth (m) | Avg. Depth (m) | Hydrology | Trophic Status | Avg. Cond. <br> ( $\mu \mathrm{S} / \mathrm{cm}$ ) |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| D-NR | Big Sissabagama | Sawyer | 326 | 15 | 3 | Drainage | Eutrophic | 68 |
| D-NR | Bony | Bayfield | 77 | 17 | 7 | Drainage | Oligotrophic | 130 |
| D-NR | Durphee | Sawyer | 80 | 5 | 3 | Seepage | Eutrophic | 22 |
| D-NR | Kawaguesaga | Oneida | 283 | 13 | 5 | Drainage | Mesotrophic | 128 |
| D-NR | Lac Vieux Desert | Vilas | 1626 | 12 | 3 | Drainage | Mesotrophic | 82 |
| D-NR | Sawyer | Langlade | 73 | 9 | 3 | Seepage | Mesotrophic | 186 |
| S-NR | Big Arbor Vitae | Vilas | 433 | 12 | 5 | Drainage | Mesotrophic | 109 |
| S-NR | Escanaba | Vilas | 123 | 8 | 4 | Drainage | Mesotrophic | 45 |
| S-NR | Little John | Vilas | 61 | 6 | 3 | Drainage | Mesotrophic | 95 |
| S-NR | Sand | Sawyer | 384 | 15 | 6 | Drainage | Eutrophic | 82 |
| S-NR | Spillerberg | Ashland | 30 | 7 | 3 | Drainage | Mesotrophic | 50 |
| S-NR | Turtle Flambeau | Iron | 5237 | 50 | 5 | Flowage | Eutrophic | 60 |
| S-NR | Windfall | Sawyer | 42 | 5 | 4 | Seepage | Mesotrophic | 34 |

Table 2. Catch-per-effort (fish/h) for age-0 walleye from fall electrofishing conducted by Wisconsin Department of Natural Resources or Great Lakes Indian Fish and Wildlife Commission personnel on 13 study lakes from 2000 to 2015.

| Rec. Hist. | Lake | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| D-NR | Big Sissabagama | 2.93 | 1.10 | 0.18 | 0.18 | 18.84 | 4.94 | 7.32 | 4.75 | 0.73 | 0.37 | 0.55 | 0.37 | 0 | 0 | 0 | 0 |
| D-NR | Bony |  |  |  |  | 163.33 |  |  | 29.40 |  |  | 15.00 |  |  | 2.22 | 1.11 | 7.22 |
| D-NR | Durphee | 92.78 |  |  | 43.89 | 25.00 |  |  |  | 0 | 0 |  |  | 0 |  | 0 | 0.56 |
| D-NR | Kawaguesaga | 14.09 | 53.66 | 23.24 | 4.29 | 1.27 | 0 | 0.71 | 0 | 0 | 0.97 | 0 | 0.14 |  |  | 0 | 0 |
| D-NR | Lac Vieux Desert | 22.09 | 63.51 | 82.50 | 8.45 | 18.04 | 23.87 | 0.47 | 0 | 0 | 0 | 0.09 | 4.89 | 0.09 | 0.46 | 2.52 | 2.39 |
| D-NR | Sawyer |  | 37.94 |  | 0.29 | 0.75 | 6.35 |  | 0.58 | 0.58 |  | 0 |  |  | 0 | 0 | 0 |
| S-NR | Big Arbor Vitae | 44.03 | 140.58 | 14.27 | 21.29 |  | 43.46 | 61.15 | 94.62 | 14.23 | 130.58 | 12.12 | 25.58 | 1.73 | 53.46 | 8.46 | 173.27 |
| S-NR | Escanaba | 21.33 | 448.76 | 172.13 | 38.03 | 82.19 | 151.34 | 55.94 | 45.92 | 129.60 | 36.49 | 86.49 | 21.06 |  | 58.62 | 56.87 | 68.37 |
| S-NR | Little John |  |  | 243.21 |  | 209.55 |  |  | 17.73 | 200.00 | 54.55 |  | 317.50 | 59.55 | 250.91 |  |  |
| S-NR | Sand | 0 | 50.29 | 31.47 | 33.53 | 90.59 | 99.41 | 63.24 | 17.06 | 71.76 | 104.41 | 10.88 | 114.86 | 45.59 | 43.53 | 102.65 | 47.06 |
| S-NR | Spillerberg |  | 1.00 |  | 54.00 | 68.00 | 66.00 |  | 176.00 | 68.00 | 33.00 | 121.00 | 90.00 | 9.00 | 59.00 | 6.56 | 62.00 |
| S-NR | Turtle Flambeau | 71.70 | 228.45 | 251.10 | 88.62 | 30.86 | 159.84 | 101.25 | 89.59 | 36.27 | 278.84 | 62.66 | 190.96 | 163.24 | 37.80 | 4.35 | 57.14 |
| S-NR | Windfall |  | 99.38 | 78.75 | 30.94 | 161.25 | 165.00 | 198.75 |  |  |  | 75.94 | 56.25 | 78.75 | 200.63 |  |  |

Table 3. Range of dates for spring ichthyoplankton tows during 2016 and 2017.

| 2016 |  |
| :--- | :---: |
| Sampling Period 1 | 12 May-17 May |
| Sampling Period 2 | 19 May-24 May |
| Sampling Period 3 | 28 May-3 June |
| 2017 |  |
| Sampling Period 1 | 15 May-21 May |
| Sampling Period 2 | 23 May-27 May |
| Sampling Period 3 | 31 May-5 June |

Table 4. Sampling gear and effort used to collect larval and post larval walleye with recruitment history ( $\mathrm{S}-\mathrm{NR}=$ sustained natural recruitment, $\mathrm{D}-\mathrm{NR}=$ declining natural recruitment; Rec. History), number of ichthyoplankton tows each year, and gill net sets completed for each study lake.

|  |  |  | Gill net sets |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Lake | Rec. History | Area (ha) | Tows | 2016 | 2017 |
| Big Sissabagama | D-NR | 326 | 12 | 8 | 13 |
| Bony | D-NR | 77 | 6 | 4 | 6 |
| Durphee | D-NR | 80 | 6 | 4 | 6 |
| Kawaguesaga | D-NR | 283 | 8 | 6 | 11 |
| Lac Vieux Desert | D-NR | 1626 | 12 | 8 | 12 |
| Sawyer | D-NR | 73 | 8 | 4 | 4 |
| Big Arbor Vitae | S-NR | 433 | 8 | 8 | 14 |
| Escanaba | S-NR | 123 | 8 | 6 | 12 |
| Little John | S-NR | 61 | 6 | 4 | 7 |
| Sand | S-NR | 384 | 12 | 8 | 9 |
| Spillerberg | S-NR | 30 | 6 | 4 | 8 |
| Turtle Flambeau | S-NR | 5237 | 12 | 8 | 14 |
| Windfall | S-NR | 42 | 6 | 4 | 7 |

Table 5. Summary of relative abundance of larval (fish/1000 $\mathrm{m}^{3}$ ), and catch-per-effort of post-larval (fish/net extrapolated to 10 micro-mesh gill net sets), and age-0 walleye (fish/h in fall electrofishing) for declining natural recruitment (D-NR) and sustained natural recruitment (S-NR) lakes during 2016 and 2017. In spring, surface ichthyoplankton tows were used to collect larval walleye. Post-larval walleye were collected in mid to late July with micro-mesh gill nets and age-0 walleye relative abundance was estimated from fall electrofishing. Gears used to collect walleye were consistent across years.

| Lake | Rec. History | Larval WAE <br> (fish/1000m |  |  |
| :--- | :---: | :---: | :---: | :---: |
|  |  |  | Post-larval WAE <br> (fish/10 net sets) | Age-0 WAE <br> (fish/h) |
| Big Sissabagama | D-NR | 0.26 | 2016 |  |
| Bony | D-NR | 0 | 0 | 0 |
| Durphee | D-NR | 0 | 0 | 6 |
| Kawaguesaga | D-NR | 0 | 0 | 0 |
| Lac Vieux Desert | D-NR | 2.14 | 0 | 0 |
| Sawyer | D-NR | 1.58 | 0 | 0 |
| Big Arbor Vitae | S-NR | 0 | 0 | 0 |
| Escanaba | S-NR | 5.12 | 0.40 | 16.46 |
| Little John | S-NR | 0 | 0 | 44 |
| Sand | S-NR | 1.3 | 1.93 | 17 |
| Spillerberg | S-NR | 1.00 | 6.24 | 66 |
| Turtle Flambeau | S-NR | 4.97 | 14.67 | 9 |
| Windfall | S-NR | 0 | 0 | 80 |
|  |  |  | 2017 | 0 |
| Big Sissabagama | D-NR | 0.28 | 0 |  |
| Bony | D-NR | 0 | 2.39 | 0 |
| Durphee | D-NR | 0.49 | 0 | 34 |
| Kawaguesaga | D-NR | 0 | 0 | 0 |
| Lac Vieux Desert | D-NR | 0.92 | 0 | 0 |
| Sawyer | D-NR | 9.54 | 0 | 0 |
| Big Arbor Vitae | S-NR | 0.37 | 0.43 | 0 |
| Escanaba | S-NR | 5.19 | 18.49 | 56 |
| Little John | S-NR | 0 | 3.20 | 10 |
| Sand | S-NR | 4.55 | 10.00 | 171 |
| Spillerberg | S-NR | 0.64 | 4.87 | 50 |
| Turtle Flambeau | S-NR | 9.60 | 6.15 | NA |
| Windfall | S-NR | 0 | 0 | 71 |

Table 6. Results from repeated-measures ANOVA models evaluating recruitment history, year, sampling period, and their interaction for comparisons of Secchi depth (m), larval yellow perch relative abundance (fish/ $1000 \mathrm{~m}^{3}$ ), total length of Daphnia spp. ( $\mu \mathrm{m}$ ), calanoid copepods ( $\mu \mathrm{m}$ ), and cyclopoid copepods ( $\mu \mathrm{m}$ ), $\log _{e}$ relative abundance of Daphnia spp. (number/l), relative abundance of calanoid (number/l) and cyclopoid copepods (number/l), $\log _{e}$ relative abundance of edible-size Daphnia spp. (number/l), relative abundance of edible-size calanoid (number/l) and cyclopoid copepods (number/l), and $\log _{e}$ relative abundance of edible Daphnia spp., calanoid, and cyclopoid copepods combined (number/l). Significant differences at $\alpha=0.05$ highlighted in bold.

| Metric | $d f$ | $F$ | $P$ | Metric | $d f$ | F | P | Metric | $d f$ | F | $P$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Secchi depth |  |  |  | Daphnia spp. total length |  |  |  | Edible calanoid copepod relative abundance |  |  |  |
| Recruitment History | 1,11 | 0.08 | 0.786 | Recruitment History | 1,11 | 5.69 | 0.036 | Recruitment History | 1,11 | 0.84 | 0.378 |
| Year | 1,10 | 5.20 | 0.046 | Year | 1,47 | 2.34 | 0.133 | Year | 1,47 | 12.03 | 0.001 |
| Recruitment History*Year | 1,10 | 0.10 | 0.755 | Sampling Period | 2,47 | 2.02 | 0.144 | Sampling Period | 2, 47 | 1.65 | 0.203 |
| Larval yellow perch relative abundance |  |  |  | Recruitment History*Year | 1,47 | 0.04 | 0.849 | Recruitment History*Year | 1,47 | 0.02 | 0.897 |
| Recruitment History | 1,11 | 0.69 | 0.422 | Recruitment History*Sampling Period | 2,47 | 0.63 | 0.537 | Recruitment History*Sampling Period | 2, 47 | 0.11 | 0.894 |
| Year | 1,11 | 2.39 | 0.151 | Recruitment History*Year*Sampling Period | 4,47 | 0.63 | 0.641 | Recruitment History*Year*Sampling Period | 4, 47 | 0.39 | 0.814 |
| Recruitment History*Year | 1,11 | 1.12 | 0.312 | Calanoid copepod total length |  |  |  | Edible cyclopoid copepod relative abundance |  |  |  |
| $\log _{e}$ Daphnia spp. relative abundance |  |  |  | Recruitment History | 1,11 | 0.15 | 0.704 | Recruitment History | 1,11 | 1.69 | 0.220 |
| Recruitment History | 1,11 | 0.56 | 0.469 | Year | 1,47 | 8.56 | 0.005 | Year | 1,47 | 2.33 | 0.134 |
| Year | 1,47 | 32.54 | <0.001 | Sampling Period | 2, 47 | 2.04 | 0.142 | Sampling Period | 2, 47 | 2.18 | 0.124 |
| Sampling Period | 2,47 | 0.91 | 0.4112 | Recruitment History*Year | 1,47 | 0.02 | 0.878 | Recruitment History*Year | 1,47 | 0.10 | 0.759 |
| Recruitment History*Year | 1,47 | 9.64 | 0.003 | Recruitment History*Sampling Period | 2,47 | 0.96 | 0.39 | Recruitment History*Sampling Period | 2, 47 | 0.30 | 0.742 |
| Recruitment History*Sampling Period | 2,47 | 2.24 | 0.117 | Recruitment History*Year*Sampling Period | 4,47 | 2.13 | 0.092 | Recruitment History*Year*Sampling Period | 4, 47 | 0.66 | 0.624 |
| Recruitment History*Year*Sampling Period | 4,47 | 0.58 | 0.678 | Cyclopoid copepod total length |  |  |  | $\log _{e}$ edible zooplankton relative abundance |  |  |  |
| Calanoid copepod relative abundance |  |  |  | Recruitment History | 1,11 | 3.28 | 0.097 | Recruitment History | 1,11 | 2.25 | 0.159 |
| Recruitment History | 1,11 | 0.92 | 0.360 | Year | 1,47 | 16.91 | <0.001 | Year | 1,47 | 31.44 | <0.001 |
| Year | 1,47 | 10.87 | 0.002 | Sampling Period | 2,47 | 6.00 | 0.005 | Sampling Period | 2,47 | 12.99 | <0.001 |
| Sampling Period | 2,47 | 1.84 | 0.169 | Recruitment History*Year | 1,47 | 0.06 | 0.802 | Recruitment History*Year | 1,47 | 0.02 | 0.880 |
| Recruitment History*Year | 1,47 | 0.03 | 0.863 | Recruitment History*Sampling Period | 2,47 | 0.54 | 0.587 | Recruitment History*Sampling Period | 2, 47 | 0.64 | 0.534 |
| Recruitment History*Sampling Period | 2,47 | 0.07 | 0.936 | Recruitment History*Year*Sampling Period | 4,47 | 2.05 | 0.102 | Recruitment History*Year*Sampling Period | 4,47 | 1.30 | 0.283 |
| Recruitment History*Year*Sampling Period | 4,47 | 0.38 | 0.820 | $\log _{e}$ edible Daphnia spp. relative abundance |  |  |  |  |  |  |  |
| Cyclopoid copepod relative abundance |  |  |  | Recruitment History | 1,11 | 0.25 | 0.628 |  |  |  |  |
| Recruitment History | 1,11 | 1.74 | 0.214 | Year | 1,47 | 28.79 | <0.001 |  |  |  |  |
| Year | 1,47 | 2.41 | 0.127 | Sampling Period | 2, 47 | 0.89 | 0.418 |  |  |  |  |
| Sampling Period | 2,47 | 2.47 | 0.096 | Recruitment History*Year | 1,47 | 8.66 | 0.005 |  |  |  |  |
| Recruitment History*Year | 1,47 | 0.09 | 0.769 | Recruitment History*Sampling Period | 2,47 | 2.32 | 0.109 |  |  |  |  |
| Recruitment History*Sampling Period | 2,47 | 0.24 | 0.785 | Recruitment History*Year*Sampling Period | 4,47 | 0.47 | 0.761 |  |  |  |  |
| Recruitment History*Year*Sampling Period | 4,47 | 0.60 | 0.664 |  |  |  |  |  |  |  |  |

Table 7. Contents of larval walleye diets and number of occurrences ( $n$ ) for larval walleye collected from spring ichthyoplankton tows during 2016 and 2017.

| Diet Items | $n$ |
| :--- | :--- |
| Zooplankton | 15 |
| Larval fish | 42 |
| Empty | 37 |
| Total | 94 |

Table 8. Percent-composition-by-count, carapace length, and proportion of edible individuals based on carapace length from larval walleye prey items across the three sampling periods (SP) for the three most abundant zooplankton taxa consumed by larval walleye.

| Zooplankton Taxa | \% Comp. by count Carapace Length $(\mu \mathrm{m})$ | Proportion Edible |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
|  |  | SP 1 | SP 2 | SP 3 |  |
| Daphnia spp. | 51 | $272-1816$ | 0.94 | 0.95 | 0.93 |
| Calanoid copepod | 19 | $318-1200$ | 0.97 | 0.95 | 0.97 |
| Cyclopoid copepod | 30 | $125-930$ | 0.94 | 0.92 | 0.93 |



Figure 1. Study lakes across northern Wisconsin, USA. Black circles represent declining natural recruitment lakes and white circles represent sustained natural recruitment lakes.


Figure 2. May 2017 mean daily water surface temperature $\left({ }^{\circ} \mathrm{C}\right)$ in four declining natural recruitment lakes: Big Sissabagama, Durphee, Kawaguesaga, and Sawyer lakes.


Figure 3. May 2017 mean daily water surface temperature $\left({ }^{\circ} \mathrm{C}\right)$ in seven sustained natural recruitment lakes: Big Arbor Vitae, Escanaba, Little John, Sand, Spillerberg, Turtle Flambeau Flowage, and Windfall lakes.


Figure 4. Mean May surface water temperature coefficients of variation (CV) for declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle) in 2017. A $t$-test indicated no significant difference in CV between recruitment histories. Error bars represent $95 \%$ confidence intervals.


Figure 5. Mean Secchi depth (m) for declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle; top panel) and all lakes in 2016 (black diamond) and 2017 (black triangle; bottom panel). A repeatedmeasures ANOVA indicated no significant difference between recruitment history but a significant difference between years. A Tukey (HSD) post hoc test determined mean Secchi depth during 2016 than 2017. Different letters indicate statistically significant differences between groups. Error bars represent $95 \%$ confidence intervals.


Figure 6. Mean relative abundance of adult walleye for declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle) from spring electrofishing. A $t$-test with a Satterthwaite approximation for degrees of freedom determined no significant difference in adult walleye relative abundance between recruitment histories. Error bars represent 95\% confidence intervals.


Figure 7. Mean adult walleye total length (TL) from spring electrofishing for declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (SNR; white circle). A $t$-test indicated no significant difference in adult walleye TL between recruitment histories. Error bars represent $95 \%$ confident intervals.


Figure 8. Mean relative abundance of larval yellow perch from spring ichthyoplankton tows for declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle) lakes. A repeated-measures ANOVA determined no significant difference between recruitment history, year, or their interaction. Error bars represent $95 \%$ confidence intervals.


Figure 9. Mean Daphnia spp. relative abundance compared between declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle; top panel) and between D-NR lakes and S-NR lakes in 2016 and 2017 (bottom panel). Abundance values were $\log _{e}$ transformed prior to statistical analysis. A repeated-measures ANOVA indicated a significant interaction between recruitment history and year. A Tukey (HSD) post hoc test determined mean Daphnia spp. relative abundance in D-NR lakes during 2016 was lower than D-NR lakes in 2017 but not significantly different from S-NR lakes in either year. Different letters indicate statistically significant differences between groups. Error bars represent $95 \%$ confidence intervals.


Figure 10. Mean calanoid copepod relative abundance compared between declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (SNR; white circle; top panel) between 2016 (black diamond) and 2017 (black triangle; bottom panel). A repeated measures ANOVA indicated no significant difference between recruitment histories or sampling periods, but a significant difference did exist between years. A Tukey (HSD) post hoc test determined mean calanoid copepod relative abundance was significantly lower in 2016 than 2017. Different letters indicate statistically significant differences between years. Error bars represent $95 \%$ confidence intervals.


Figure 11. Mean cyclopoid copepod relative abundance between declining natural recruitment lakes (black circle) and sustained natural recruitment lakes (white circle). A repeated-measures ANOVA determined no significant difference between recruitment history, year, sampling period, or their interaction. Error bars represent $95 \%$ confidence intervals.


Figure 12. Mean Daphnia spp. total length compared between declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle). A repeated-measures ANOVA determined a significant difference between recruitment histories. A Tukey (HSD) post hoc test determined mean Daphnia spp. total length was significantly lower in D-NR lakes than S-NR lakes. Different letters indicate statistically significant differences between recruitment histories. Error bars represent 95\% confidence intervals.


Figure 13. Mean calanoid copepod total length compared between declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle; top panel) and between all lakes in 2016 (black diamond) and all lakes in 2017 (black triangle; bottom panel). A repeated-measures ANOVA determined no significant difference between recruitment histories or sampling periods, however there was a significant difference between years. A Tukey (HSD) post hoc test determined mean calanoid copepod total length was significantly lower in 2016 than 2017. Different letters indicate statistically significant differences between years. Error bars represent 95\% confidence intervals.


Figure 14. Mean cyclopoid copepod total length compared between declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle; top panel) and between sampling period one (white triangle), period two (white diamond), and period three (white square) and 2016 (black diamond) and 2017 (black triangle; bottom panel). A repeated-measures ANOVA determined no significant difference between recruitment histories, but there was a significant difference between sampling periods and years. A Tukey (HSD) post hoc test determined mean cyclopoid copepod total length was significantly lower during sampling period three than the other two periods and significantly lower in 2016 than 2017. Different letters indicate statistically significant differences between sampling period (a, b) and years (y, z). Error bars represent $95 \%$ confidence intervals.


## Recruitment History and Year

Figure 15. Mean edible-size Daphnia spp. relative abundance compared between declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle; top panel) and between D-NR lakes (black circle) and S-NR lakes (white circle) in 2016 and 2017 (bottom panel). Abundance values were $\log _{e}$ transformed prior to statistical analysis. A repeated-measures ANOVA indicated a significant interaction between recruitment history and year. A Tukey (HSD) post hoc test determined mean edible Daphnia spp. relative abundance in D-NR lakes during 2016 was lower than D-NR lakes in 2017 but was not different than S-NR lakes in either year. Different letters indicate statistically significant differences between groups. Error bars represent $95 \%$ confidence intervals.


Figure 16. Mean edible-size calanoid copepod relative abundance compared between declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle; top panel) and between all lakes during 2016 (black triangle) and 2017 (black diamond; bottom panel). A repeated-measures ANOVA indicated no significant difference between recruitment histories or sampling periods, but there was a significant difference between years. A Tukey (HSD) post hoc test determined mean edible-size calanoid copepod relative abundance was significantly lower in 2016 than 2017. Different letters indicate statistically significant differences between years. Error bars represent 95\% confidence intervals.


Figure 17. Mean edible-size cyclopoid copepod relative abundance compared between declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment lakes (S-NR; white circle). A repeated-measures ANOVA determined no significant difference between recruitment history, year, sampling period or their interaction. Error bars represent 95\% confidence intervals.


Figure 18. Mean relative abundance of edible-size zooplankton relative abundance for declining natural recruitment lakes (D-NR; black circle) and sustained natural recruitment history (S-NR; white circle; top panel), and between sampling period one (white triangle), period two (white diamond), and period three (white square) and between 2016 (black diamond) and 2017 (black triangle; bottom panel). Abundance values were $\log _{e}$ transformed prior to analysis. A repeated-measures ANOVA determined no significant difference between recruitment histories, but a there was a significant difference between sampling periods and years. A Tukey (HSD) post hoc test determined edible abundance was significantly higher in sampling period one than period three and significantly higher in 2017 than 2016. Different letters indicate statistically significant differences between sampling period (a, b) and year (y, z). Error bars represent 95\% confidence intervals.


Figure 19. Larval walleye relative abundance and age-0 walleye relative abundance from fall electrofishing for all study lakes (left panel). Post-larval walleye relative abundance and age-0 walleye relative abundance from fall electrofishing for all study lakes (right panel). A Pearson correlation determined no significant association between larval walleye relative abundance and age- 0 walleye relative abundance from fall electrofishing or between post-larval walleye relative abundance and age- 0 walleye relative abundance from fall electrofishing.


Figure 20. Larval walleye relative abundance and age-0 walleye relative abundance from fall electrofishing for sustained natural recruitment lakes (left panel). Post-larval walleye relative abundance and age-0 walleye relative abundance from fall electrofishing for sustained natural recruitment lakes (right panel). A Pearson correlation determined no significant association between larval walleye relative abundance and age- 0 walleye relative abundance from electrofishing or between post-larval walleye relative abundance and age- 0 walleye relative abundance from electrofishing.

