IDENTIFYING RECRUITMENT BOTTLENECKS FOR AGE-0 WALLEYE *SANDER VITREUS* IN NORTHERN WISCONSIN LAKES

By

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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

June 2016

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ABSTRACT

Walleye *Sander vitreus* recruitment (measured as age-0 catch-per-effort in fall electrofishing) has declined in many northern Wisconsin lakes and the reasons for these declines are not known. Recruitment declines are a significant management concern for the Wisconsin Department of Natural Resources, as many of these walleye populations previously supported popular recreational fisheries. Understanding mechanisms and timing associated with walleye recruitment bottlenecks during the first year of life is important in developing management solutions, as changes to harvest regulations or stocking strategies may be warranted depending on when and where bottlenecks occur. Therefore, the objectives of my research were to: 1) develop sampling protocols for collecting larval and age-0 post-larval walleyes; 2) identify timing of recruitment bottlenecks for age-0 walleyes in two northern Wisconsin walleye lakes with a declining recruitment history (D-NR) relative to trends observed in two lakes with sustained recruitment histories (S-NR); and 3) evaluate differences in abiotic and biotic variables between lakes with the two different recruitment histories.

In 2014 and 2015, I sampled Kawaguesaga and Sawyer lakes (D-NR) and Escanaba and Big Arbor Vitae lakes (S-NR). Adult walleyes were captured in spring using nighttime electrofishing, egg mats were used to verify spawning, and towed ichthyoplankton nets, quatrefoil light traps, beach seines, micro-mesh gillnets, and electrofishing were used to capture age-0 walleyes throughout their first year of life. Water quality data, zooplankton samples, and panfish (potential predator of larvae) diet information were also collected. I compared biotic and abiotic metrics between recruitment histories using repeated-measures analysis of variance.

My results indicated temporal trends in relative abundance of walleyes during their first year of life can be monitored using a combination of ichthyoplankton nets towed at night during mid to late May (i.e., 1-3 weeks after peak walleye spawning), 0.64-cm mesh gill nets set in mid to late July, and fall electrofishing. Age-0 walleyes were not captured in D-NR lakes after the larval stage, while age-0 walleyes were captured at multiple life stages during both years in S-NR lakes. These results suggest a recruitment bottleneck for age-0 walleyes occurred at or before the larval stage in D-NR lakes. Panfish did not appear to be major predators of larval walleyes on any lake in either year. Temperature and dissolved oxygen metrics were similar for all lakes. Although D-NR lakes were slightly clearer (greater Secchi depth), the observed differences were not statistically significant. Mean total length (TL) of adult walleyes was significantly greater ($P < 0.01$, $f = 213.11$, *d*f = 1) on D-NR lakes than S-NR lakes, which suggests low recruitment. Mean coefficient of variation in May daily water temperature, average density and TL of the most common zooplankton taxa, and walleye egg density did not differ significantly between S-NR and D-NR lakes.

Continued research should focus on longer term collection of abiotic and biotic metrics on these lakes, and include addition of more study lakes to determine if trends in age-0 walleye abundance persist and are similar in other D-NR and S-NR lakes. This expanded sampling might also provide more information on the factors responsible for potential recruitment bottlenecks. Future studies might also include experimental stocking of walleye fry to determine if this strategy can be used to circumvent recruitment bottlenecks that occur at or before the larval stage.

ACKNOWLEDGMENTS

I would like to dedicate this thesis to Tom Schlavensky. Tom's love, willingness to support me in my career, and encouragement during the ups and downs of graduate school made it possible for me to complete this project. Thank you also to my family, who instilled in me an appreciation and respect for the outdoors, and who have always pushed me to do my best.

I would like to thank Dr. Dan Isermann for his time, patience, and all that he has taught me during my time at the University of Wisconsin – Stevens Point (UWSP). Dan is an excellent mentor who challenges his students, encourages them to ask good questions, do quality work, and act with integrity. The knowledge and enthusiasm Dan has passed on to me have, and will continue to have, positive impacts during my career in fisheries. Thank you also to my committee members: Dr. Gretchen Hansen, Dr. Justin VanDeHey, and Dr. Josh Raabe for their mentorship, guidance and feedback throughout the stages of my research.

This project was a truly collaborative effort made possible by the cooperation of many people with the Wisconsin Cooperative Fisheries Research Unit (WICFRU) and the Wisconsin Department of Natural Resources (WDNR). In particular, I would like to thank Steve Gilbert (WDNR), John Kubisiak (WDNR), Greg Sass (WDNR), Dave Seibel (WDNR), and Jon Hansen (WDNR) for their mentorship, help with project planning, data sharing, and coordination of field sampling. Thank you to Andrea Musch (WICFRU) for excellent logistical support, Janice Kerns (WICFRU) and Dan Dembkowski (WICFRU) for help in the field, and Keith Turnquist (WICFRU) for designing the qPCR genetic testing technique for use in this project.

Because of the intensity of field sampling and laboratory work, this project would not have been possible without the help of many undergraduate technicians and fellow graduate students. Thank you to all the undergraduate technicians – Brandon Maahs, Erik Carlson, Tim Dobbins, Justin Howard, Taylor Beaman, Aaron Schiller, Drew Wallace, Zach Witzel, Matt Kraus, Logan Sikora, Garrett Johnson, and Adam Garlie – for their hard work, flexibility, and patience putting in many long hours in the field and laboratory. Thank you also to fellow graduate students Mike Vaske, Zach Snobl, Josh Schulze, Nick Rydell, Doug Zentner, Kaitlin Schnell, Matthew Belnap, Zeb Woiak, and Jake Richter, for their assistance and friendship. Lastly, I would like to thank the WDNR for funding this project.

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INTRODUCTION

Understanding recruitment variation is important to the management of exploited fish populations (Ricker 1975; Madenjian et al. 1996; Dubuc and DeVries 2002). Fishery managers use estimates of recruitment along with estimates of growth, mortality, and abundance to evaluate the effects of different management strategies on fisheries sustainability (Ricker 1975; Beverton and Holt 1993; Nate et. al. 2000). Recruitment is influenced by many abiotic and biotic factors (Ricker 1954; Hansen et al. 1998; Beard et al. 2003), and interactions among these factors can be complex (Werner and Gilliam 1984; Dubuc and DeVries 2002; Quist et al. 2004; Hoxmeier et al. 2006). Long-term evaluations of year-class strength are needed to fully understand this complexity (Forney 1971; Myers 1998; Houde 2008). Consequently, the recruitment process remains poorly understood for many fish populations (Houde 1987, 2008; Dubuc and DeVries 2002).

Year-class strength of many fish species is fixed during the first year of life (Hjort 1914; Houde 1987), including walleye *Sander vitreus* (Busch et al. 1975; Forney 1976; Mathias and Li 1982), and indices of age-0 abundance are frequently used to monitor recruitment (Forney 1974; Kallemeyn 1987; Anderson et al. 1998; Zweifel 2006; Isermann and Willis 2008). Abiotic factors that could affect first-year survival include temperature and water level regimes (Johnson 1961; Serns 1982; Quist et al. 2003; Raabe 2006) that can influence hatch timing (Serns 1982; Raabe 2006), prey and habitat availability (Hoxmeier et al. 2004; Jolley et al. 2010; Raabe and Bozek 2012), and growth rates (Serns 1982; Winemiller and Rose 1992; Uphoff et al. 2013). Density of fish within an age-0 cohort can influence growth and survival (Ricker 1975; Graeb et al. 2004), as can prey availability (Bremigan and Stein 1994; Welker et al. 1994), abundance of other age-0 fish (Welker et al. 1994; Roseman et al. 1996; Sanderson et al. 1999), and predator density (Forney 1976; Sanderson et al. 1999; Quist et al. 2003). Fluctuations in year-class strength often regulate abundance of fish available to fishers (Ricker 1954; Beverton and Holt 1993), and periods of low or failed recruitment can result in poor fishing that triggers management actions such as stocking or more restrictive harvest regulations (Fielder 1992; Isermann and Parsons 2011).

Walleyes support important recreational, commercial, and subsistence fisheries across North America (Schmalz et al. 2011). Walleyes are native throughout central North America, and have been stocked extensively both within and outside of their native range to increase catch rates in recreational fisheries or to create new fisheries (Kerr 2011; Schmalz et al. 2011). In Wisconsin, walleyes were originally found in rivers and large lake systems, but extensive stocking has expanded their range to include small inland lakes (Becker 1983). Stocked walleyes established naturally-reproducing populations in many of these lakes (Becker 1983; Nate et al. 2000). Walleye recruitment is highly variable (Forney 1976; Isermann 2007; Bozek et al. 2011) and age-0 walleye density in northern Wisconsin varies substantially among lakes (Beard et al. 2003). Walleye recruitment is influenced by factors such as abundance of adult walleyes and yellow perch *Perca flavescens*, water temperature, water level fluctuations, and prey size and availability (Serns 1982; Hansen et al. 1998; Quist et al. 2003; Hoxmeier et al. 2006).

The walleye fishery in Wisconsin consists of recreational angling that occurs throughout the state combined with tribal spearing that occurs in the Ceded Territory. The Ceded Territory covers 22,400 square miles in northern Wisconsin that was ceded to the United States by the Lake Superior Chippewa Tribes, who retain fishing rights to spear walleye. In the most recent U.S. Fish and Wildlife Service Hunting and Fishing Survey, 45% of 1.1 million Wisconsin anglers reported fishing for walleye (USDOI et al. 2011). More than 200 Wisconsin waters are categorized as supporting naturally reproducing (NR) walleye populations and many other waters are stocked with walleye. In the Ceded Territory, where both angling and spearing of walleye occur, harvest quotas are set using a limit reference point of 35% total annual exploitation (both fisheries combined) for the adult walleye population (Hansen et al. 1991). Density of adult walleye fluctuates in part in relation to variation in year class strength, and declines in walleye recruitment would likely lead to reductions in total allowable harvest.

Over the past decade, walleye recruitment, as indexed by fall electrofishing catch-per-effort (CPE) of age-0 walleyes, has severely declined in some NR walleye populations in northern Wisconsin (Hansen et. al. 2015b). Changes in adult walleye abundance and demographics can lead to declines in recruitment (Ricker 1975; Hansen et al. 1998; Beard et al. 2003). However, based on current and historic walleye recruitment patterns in northern Wisconsin, some walleye populations experiencing recruitment declines should support higher recruitment based on adult abundance (Hansen et al. 1998).

Many factors have been proposed as potential causes of walleye recruitment declines, including changes in habitat, prey availability, and predator abundance (Inskip and Magnuson 1983; Fayram et al. 2005, 2014; Kelling et al. 2016). Low water degree-days was found to be an important predictor of successful walleye recruitment in Wisconsin lakes (Hansen et al. 2015a). Predation of naturally reproduced age-0 walleyes by largemouth bass *Micropterus salmoides* was hypothesized to be a potential contributor to recruitment declines in northern Wisconsin lakes (Hansen et al. 2015c). However, a recent assessment conducted on four northern Wisconsin lakes found very low predation rates on walleyes by largemouth bass (Kelling et al. 2016). Consequently, potential bottlenecks regulating survival of age-0 walleyes in northern Wisconsin lakes remain unknown. These bottlenecks could be temporally well defined in terms of ontogeny and could be caused by a variety of factors including weather, predation, prey availability, and competition (Forney 1976; Serns 1982; Madenjian et al. 1996; Hansen et al. 1998). Conversely, walleye recruitment may be a gradual process that occurs over many life history stages and is affected by many of the same factors.

Prey availability for age-0 walleyes may be a key factor regulating their first year survival. As walleyes grow, they undergo ontogenetic diet shifts and transition from a diet of zooplankton to benthic invertebrates, and eventually to fish (Jackson et al. 1992; Hoxmeier et al. 2006). Previous research has suggested that availability and composition of zooplankton and other prey can affect age-0 walleye growth (Hoxmeier et al. 2004). Zooplankton density is related to walleye recruitment (Mathias and Li 1982; Graham and Sprules 1992). For example, Fielder (1992) found low abundance of *Daphnia* related to poor walleye recruitment in Lake Oahe, South Dakota. Walleye and yellow perch are usually closely linked in predator-prey interactions, and yellow perch exhibit wide fluctuations in recruitment (Sanderson et al. 1999). Meerbeek et al. (2002) found walleye condition factor and growth rate increased with abundance of age-0 yellow perch in South Dakota lakes, and Forney (1976) found that yellow perch abundance regulated cannibalism in walleye in Oneida Lake, New York. Zweifel (2006) suggested that timing of yellow perch hatch was very important to larval walleye survival in South Dakota lakes.

Predation on age-0 walleyes by other fishes could also control walleye year class strength (Forney 1976; Hoxmeier et al. 2006; Ivan et al. 2010). Adult yellow perch explained significant variation in abundance of age-0 walleyes in Escanaba Lake, Wisconsin (Hansen et al. 1998). Hoxmeier et al. (2006) found a negative relationship between small centrarchids and larval walleye abundance, suggesting predation was affecting survival and recruitment. Similarly, Quist et al. (2003) found evidence of larval walleye predation by white crappies *Pomoxis annularis* in a mesocosm experiment, and that white crappie abundance was negatively related to walleye recruitment in ponds. Though a small percentage of total mortality, cannibalism by larger walleyes in late summer was responsible for much of the year-class variability in Oneida Lake (Forney 1976). However, the intensity of walleye cannibalism was closely and inversely related to age-0 yellow perch density (Forney 1974).

Changes and annual fluctuations in the physical environment could also affect age-0 walleye survival. For instance, walleye select for gravel and cobble spawning substrates (Raabe and Bozek 2012), and water level decreases can reduce walleye recruitment by decreasing available spawning habitat (Johnson 1961). Spring warming rate and temperature are related to walleye recruitment (Madenjian et al. 1996; Hansen et al. 1998), and wind-wave action along with lake size have been shown to influence survival of age-0 walleyes (Johnson 1961; Nate et al. 2003). Low dissolved oxygen (DO) may limit the success of walleye reproduction, and DO below 3 mg/L may severely reduce hatching success and larval survival (Colby and Smith 1967). Decreases in available thermal optical habitat may also negatively affect walleye survival and production (Lester et al. 2004).

Declines in walleye recruitment in northern Wisconsin lakes represent a significant management concern for the WDNR, as many of these populations historically supported walleye fisheries. At a minimum, anglers had the opportunity to catch walleyes from these lakes and WDNR did not have to support the fishery with stocking. Therefore, understanding the mechanisms and timing associated with potential recruitment bottlenecks during the first year of life is important in developing potential management solutions for these declines, as changes to harvest regulations or stocking strategies may or may not be warranted depending on when and why these bottlenecks occur.

Determining bottlenecks in walleye recruitment is challenging because of possible interactions among many potential regulatory factors at early life history stages, and difficulties in capturing age-0 walleye prior to fall electrofishing (Quist et al. 2004; Zweifel 2006; Uphoff et al. 2013). Comparing biotic and abiotic differences between lakes that currently support sustained NR (S-NR) and those where NR has declined (D-NR), coupled with intensive sampling of age-0 walleyes at early life history stages may enable identification of timing of recruitment bottlenecks and narrow down the list of potential causes. Consequently, the objectives of my research were to: 1) develop sampling protocols for collecting larval and age-0 walleyes during their first summer; 2) identify timing of recruitment bottlenecks for age-0 walleyes in two northern Wisconsin walleye lakes with a D-NR recruitment history relative to trends observed in two lakes with S-NR recruitment histories; and 3) evaluate differences in abiotic and biotic variables between lakes with the two different recruitment histories.

METHODS

Study Sites

My study occurred on four lakes in northern Wisconsin with two different walleye recruitment histories (S-NR and D-NR, as described previously) and sampling was repeated on each lake during two consecutive years (2014 and 2015). I consulted with WDNR biologists to select lakes based on recent estimates of adult walleye density (adults/acre) and fall electrofishing CPE of age-0 walleyes (age-0 walleyes/mile). The WDNR currently categorizes the walleye populations in all four lakes as NR, and all have sufficient adult densities (≥ 7.4 adults/ha; Table 1) to support natural reproduction and have supported natural reproduction in the past.

Escanaba and Big Arbor Vitae lakes were selected as walleye populations with S-NR recruitment histories, as indexed by CPE of age-0 walleyes in WDNR fall electrofishing samples (long-term mean CPE ≥ 30 age-0 walleyes/mile; Figure 1). Escanaba Lake (46.06413, -89.58597) is a 123-ha mesotrophic drainage lake located in Vilas County within the Northern Highland Fisheries Research Area, and is part of a long-term ecological research study dating back to the 1940s. Escanaba Lake has not been stocked with walleyes since the 1950s. Escanaba Lake has a mean depth of 4 m, a maximum depth of 8 m, and bottom substrates primarily consisting of rock (40%) and gravel (30%). Big Arbor Vitae Lake (45.93027, -89.64974) is a 433-ha mesotrophic drainage lake also located in Vilas County, and has not been stocked with walleyes since

1995. Big Arbor Vitae Lake has a mean depth of 5 m, a maximum depth of 12 m, and bottom substrates primarily consisting of sand (40%) and gravel (35%).

Kawaguesaga and Sawyer lakes were selected as walleye populations with D-NR recruitment histories because they have exhibited recruitment declines over the last decade (i.e., recent age-0 walleye CPEs < 6 age-0 fish/mile; Figure 1). Kawaguesaga Lake (45.86752, -89.73823) is a 283-ha mesotrophic drainage lake that is part of the Minocqua Chain of Lakes in Oneida County. Kawaguesaga Lake has a mean depth of 5 m, a maximum depth of 13 m, and bottom substrates primarily consisting of sand (50%) and gravel (32%). Kawaguesaga Lake was stocked with spring fingerling walleyes in 2012, and since 2013, the lake has been stocked with large fingerling walleyes every other year (J. Kubisiak, WDNR, personal communication). Sawyer Lake (45.24754, -88.75906) is a 73-ha mesotrophic seepage lake in Langlade County with a mean depth of 3 m, maximum depth of 9 m, and bottom substrates primarily consisting of sand (35%) and gravel (35%). Sawyer Lake was intermittently stocked with small fingerling walleyes between the 1960s and 1980s, after which a naturally-reproducing population was established. Beginning again in 2014, Sawyer Lake has been stocked with large fingerling walleyes every other year (D. Seibel, WDNR, personal communication). Walleye recruitment declines began in Kawaguesaga and Sawyer lakes in the early 2000s.

Sampling

Lake Characteristics

Measurements were collected weekly during April-June when walleye larvae were likely to be present in the water column, once every two weeks during July, and once in August. Dissolved oxygen (mg/L) and temperature (°C) profiles were recorded using a YSI™ 556 MPS (Multi-Probe System) deployed at the deepest location in each lake. Water clarity was measured using a Secchi disk at the deepest point of each lake on each sampling date.

One temperature logger (Onset® HOBO models Water Temperature Pro U22-001 or TidbiT UTBI-001) was deployed in shallow water (0.5-1.5 m) near the shore in each lake, immediately after ice-out to record water temperatures. Temperature loggers were removed in September of each year.

Adult Walleyes

Within 10 d after ice-out, adult walleyes were collected by nighttime AC electrofishing using WDNR electrofishing boats equipped with a Wisconsin-style electrofishing box and dropper array. Electrofishing was conducted by WDNR or Wisconsin Cooperative Fishery Research Unit (WCFRU) personnel at multiple 20-min shoreline transects or along the entire shoreline. Walleyes were measured to the nearest mm and sex was determined by extrusion of gametes when possible. Number of minutes of pedal time (i.e. electricity on) was recorded for each transect or shoreline run. Catch-per-effort was calculated as number of adult walleyes (≥ 380 mm total length; TL) collected per h of pedal time.

Walleye Eggs

Egg mats were deployed to sample walleye eggs immediately after ice out in water depths of 30-75 cm (Johnson 1961). Egg mats consisted of 40 x 10 x 4 cm cement blocks wrapped in furnace filter on which eggs could be deposited or transported onto (similar to Ivan et al. 2010). Furnace filter material was held in place with rubber bungee cords. Depending on lake size, egg mats were placed at four to six sites per lake. At each site, two egg mats were deployed 2-4 m apart and parallel to shoreline. Half of the egg mat locations were sites where WDNR places fyke nets during spring surveys to capture spawning adult walleyes (i.e., known spawning locations); remaining mats were placed at randomly-selected locations with appropriate gravel-cobble substrates used for spawning. Egg mats were deployed for five consecutive nights, removed, and egg counts were conducted. After counting, egg mats were flipped over and allowed to soak for five additional nights, except on Big Arbor Vitae Lake in 2014 where egg mats were deployed for a single five night set. After each 5-d sampling window, eggs were enumerated within three randomly positioned 7.62-cm diameter (45.6 cm^2) metal rings placed on the surface of each egg mat. Egg density (eggs/cm^2) was averaged across both mats at each sample site (N = 6 counts per site) to account for variability in relative egg density. Relative egg density was standardized to eggs/m^2 for analyses. A novel molecular technique using quantitative polymerase chain reaction (qPCR) was used on a subsample of eggs to verify species of origin (K. Turnquist, UWSP-Molecular Genetics Conservation Laboratory, personal communication).

Larval Walleyes

Sampling for larval walleyes began within 1 week of egg mat removal and continued on each lake at 7-10 d intervals until early to mid-June when age-0 walleyes were expected to become demersal (Faber 1967; Houde and Forney 1970).

In 2014, larvae were collected using both ichthyoplankton nets and quatrefoil light traps. A 1,000-µm mesh conical ichthyoplankton net was towed for five minutes immediately below the lake surface during daylight hours at multiple sampling locations on each lake (Isermann and Willis 2008). Each lake was divided into four quadrats and tow sites were established at a randomly-selected inshore (within 100 m of shore) and an offshore (≥100 m from shore) location in each quadrat for a total of eight tows per lake on each sampling date. Once selected, tow locations remained fixed throughout the study. Volume of water filtered during each tow was estimated using a General Oceanics© model 2030R flowmeter mounted in the center of the net frame (Isermann and Willis 2008).

Previous studies have suggested that daytime sampling can be effective for capturing larval walleyes (Forney 1980), however, in 2014 both day and night tows were conducted on the same dates and at the same locations on Escanaba Lake to determine if larval walleye catch differed between time periods. Outcomes of this comparison resulted in a switch to nighttime surface tows on all lakes in 2015. In 2015, I also completed larval tows during daylight hours at shallow (1.0-1.5 m) and deep (2.0-2.5 m) depths by suspending the ichthyoplankton net from a multi-strand wire cable attached to a custom-made boom extending over the side of the boat as shown in Figure 2. Downrigger balls (approximately 4 kg) were attached to the frame of the net, and the cable was released until the net reached desired depth. Daytime tows at depth were only conducted at offshore tow locations, and two deep and two shallow depth tows were conducted on each sampling date. Towing at depth occurred either the day before or the day after night surface tows were completed. Tow duration and locations remained the same in 2015 as in 2014.

In 2014, quatrefoil light traps (similar to those described by Zweifel [2006] and Pierce et al. [2007]) were also used to sample larval walleyes. Light traps were deployed during the same time period larval tows were conducted. Light traps were fished at locations near the tow sites to allow for comparisons. Plexiglas quatrefoil light traps were illuminated by a battery powered LED light and had four 4-mm slots through which larvae entered the trap (Figure 3). Traps were anchored using a small concrete anchor (approximately 2.5 kg), and Styrofoam floats were fixed to the top to ensure the traps floated just below the surface. A 1,000-µm mesh conical net was attached to the bottom of the light trap where larval fishes were entrapped. Light traps were deployed for approximately 4 h beginning at sunset. Light traps were not used in 2015.

All larval samples were immediately preserved in 80-95% ethanol and then brought to the Fisheries Analysis Center laboratory at UWSP. In the laboratory, larvae were removed from samples and identified to family, and percid larvae were identified to species using the key provided by Auer (1982). Total walleye and yellow perch larvae per sample were determined and a subsample of ≤30 individuals of each species from each sample was measured to the nearest mm. In 2014, larvae >15 mm were measured with a ruler under a dissecting microscope, and larvae ≤15 mm were photographed and measured digitally using ImagePro^{TM} software. Because obtaining digital measurements required less time, all larvae collected in 2015 were measured using Image Pro^{TM}. For each sample, larval walleyes and yellow perch densities were standardized to number of fish per 100 L of filtered water.

A subsample of up to 300 individual larvae were selected to undergo genetic testing each year. Most larvae selected for genetic testing were percids, but some non-percids were included to verify visual identification to family. The qPCR genetic analysis was performed by the UWSP Molecular Conservation Genetics Laboratory to verify visual identifications assigned to the subsample of larvae (K. Turnquist, UWSP-MCGL, personal communication). Because species identification of larval percids is very difficult at smaller sizes, a greater number of small fish (≤ 15 mm) underwent qPCR testing.

Post-Larval Walleyes

Larval walleyes reportedly move from the pelagic zone to the littoral zone sometime between mid- to late-June (Eschmeyer 1950). Therefore, in mid-June, post-larval walleye sampling began in the near-shore littoral zone (<1.2 m deep) of each lake using 5.24-m long beach seines with 0.64-cm mesh. Eight seining sites were selected on each lake. Sites were chosen to represent a variety of habitat types and based on ability to effectively use the seine. Seining sites remained fixed for the duration of the study. Seines were used weekly during daylight hours on each lake. In 2014, seining was also conducted at night on Big Arbor Vitae Lake at 2-week intervals to determine if there was a difference in seine CPE of age-0 walleyes between day and night time periods. In 2015, all seining occurred during daylight hours. All age-0 walleyes and yellow perch collected in seines were counted, all age-0 walleyes were measured to the nearest mm, and in 2015 age-0 yellow perch were also measured to the nearest mm.

In 2015, micromesh gill nets were used as an experimental gear to assess their effectiveness in capturing age-0 walleyes in mid-summer. Between mid-June and early July, 46-m x 1.2-m gillnets with 0.95-cm bar mesh were used. Based on the size of an age-0 walleye captured while seining in early July, nets of the same dimensions with 0.64-cm bar mesh were used for the last half of the month. Two to five gill nets were set at night weekly in various habitat types and at depths ranging from 0-7.5 m. Set times varied from dusk to after dark. Set duration ranged from approximately 1-3 hours to minimize by catch, so catches were standardized to number of age-0 walleyes collected per 10 hours of soak time.

When water temperatures decreased below 21°C in September of 2014 and 2015, age-0 walleyes were sampled using nighttime electrofishing. All electrofishing was conducted by WDNR or WICFRU personnel for either multiple 20-minute transects or the entire shoreline. All electrofishing was conducted before walleye fingerling stocking occurred on Kawaguesaga and Sawyer lakes. Catch per effort was calculated as number of age-0 walleyes/h of pedal time (i.e., electricity on). All age-0 walleyes were measured to the nearest mm (TL).

Zooplankton

Zooplankton samples were collected weekly during May and June, and once every two weeks during July and August. On each sampling date, zooplankton were collected at offshore larval sampling locations using a conical plankton net with 80-µm nylon mesh. The net was lowered to 1 m above the lake bottom and towed vertically at approximately 0.33 m/s to the surface (Dodson et al. 2008). Samples were put into jars and preserved in 80-95% ethanol. Serial dilutions were used to facilitate zooplankton enumeration. Zooplankton were identified as nauplii, calanoid or cyclopoid copepods, and to genus for cladocerans, and counted. Up to 10 individuals of the three most frequent taxa per sample were measured using an optical micrometer.

Panfish Predation

During the period when peak larval abundance of percids was observed in each year, daytime shoreline electrofishing was used to collect panfish (i.e., yellow perch, rock bass *Ambloplites rupestris,* black crappie *Pomoxis nigromaculatus,* bluegill *Lepomis macrochirus*) and other small (≤ 200 mm TL) fishes (e.g., largemouth bass and northern pike *Esox lucius*) to determine if these fish preyed on larval walleyes. Electrofishing continued until at least 30 individuals of each panfish species were collected, or until the entire shoreline was sampled. Total length of each fish was recorded and stomach contents were removed using a gastric lavage consisting of a syringe fitted with a small plastic tube of 0.16-cm diameter (Figure 4). The syringe was filled with water and the tube inserted through the mouth and into the stomach. The fish was turned up-side-down over a mesh-lined funnel as diet contents were washed out, after which it was released. Fish too small for gastric lavage were sacrificed and stomach contents removed in the laboratory. Stomach contents containing larvae were preserved in 80-95% ethanol. Whole or partially digested fish larvae were removed from each diet sample, and the same molecular qPCA technique described above was used to determine if these larvae were walleye.

Analyses

To address objective 1, I used experimentation through trial and error to determine how and when to fish light traps, ichthyoplankton nets, seines, and gill nets to most effectively capture age-0 walleyes. Presence/absence and CPE of age-0 walleyes at each early life history stage in different sampling gears were used to address objective 2. Specifically, observed trends in relative egg density, larval walleye density, seine CPE, gill net CPE, and fall electrofishing CPE of age-0 walleyes were used to determine timing of potential recruitment bottlenecks.

To address objective 3, twelve repeated-measures analyses of variance (ANOVAs) were conducted to compare: mean Secchi depth (m), mean TL of adult walleyes (mm), adult walleye CPE, relative walleye egg density, variation in May water temperature, and densities and mean lengths of the most abundant zooplankton taxa. Timing of ice-out on all lakes differed between 2014 and 2015 by nearly a month, so Julian Day did not account for differences in thermal regimes between years. Therefore, day post ice out was used instead of Julian Day, and values of mean Secchi depth, larval yellow perch TL, and length and density of zooplankton used for comparisons were calculated for the 40-d window after ice out. Coefficient of variation of May water temperature was compared because this metric has been shown to influence age-0 walleye growth and recruitment (Hansen et al. 1998). All metrics were compared between recruitment histories (S-NR and D-NR) and years, and the interaction between recruitment history and year was tested. Lakes served as experimental units and recruitment histories as treatment effects. Alpha (α) was set at 0.05 for all analyses and was not adjusted for the increased risk of committing a Type I error associated with running multiple tests.

Because larval towing techniques (day vs. night) differed between years, I only compared $\log_e$ transformed values of larval yellow perch and walleye CPE + 1 between D-NR and S-NR lakes in 2015 using a *t*-test ($\alpha = 0.05$).

RESULTS

Water Temperatures and Clarity

Seasonal patterns in average daily water temperature were similar among lakes during 2014 and 2015 (Figure 5), and mean CV of May daily water temperature did not differ significantly between D-NR and S-NR lakes ($P = 0.64$, $f = 0.29$, $df = 1$; Figure 6). On average, D-NR lakes were clearer than S-NR lakes, however, the difference was not statistically significant ($P = 0.34$, $f = 1.53$, $df = 1$; Figure 7). Dissolved oxygen levels were similar between lakes and years and did not reach < 3 mg/L until a depth of 5.5 m or greater during the larval stage.

Adult Walleyes

Catch per effort of adult walleyes was higher in both years in S-NR lakes, though the difference was not significant ($P = 0.06$, $f = 13.95$, $df = 1$; Figure 8). Mean TL of adult walleyes was significantly higher in D-NR lakes than in S-NR lakes ($P < 0.01$, $f = 213.11$, $df = 1$; Figure 9).

Walleye Eggs

Genetic qPCR testing verified my identification of walleye eggs, confirming that walleye spawning occurred in all lakes in both years. Eggs from Iowa darter (*Etheostoma exile*), muskellunge (*Esox masquinongy*), and yellow perch were also encountered on the egg mats. Relative walleye egg density was higher in S-NR lakes than in D-NR lakes, however, the observed difference was not statistically significant (P = 0.25, f = 2.56, df = 1; Figure 10).

Larval Sampling

Light traps

No larval walleyes were collected in light traps in 2014 and I did not use them in 2015.

Ichthyoplankton tows

No larval walleyes were collected in day surface tows in 2014, and only 9 walleyes were collected in night surface tows on Escanaba Lake between 27 May and 17 June (Table 2).

In 2015, larval walleyes were caught in night surface tows in both S-NR lakes between 13 May and 31 May, and in deep and shallow depth tows conducted during the day on Escanaba Lake between 13 May and 20 May. Larval walleyes were caught in night surface tows between 14 May and 20 May in Sawyer Lake (D-NR; Table 2), but were not collected in subsequent towing conducted on 30 May. No larval walleyes were collected from Kawaguesaga Lake. Changes in larval sampling methods precluded my ability to compare larval CPE between years and lake types using ANOVA. However, in 2015, $\log_e$ CPE of larval yellow perch in night tows conducted during the 40-d after ice out was significantly greater ($t = 4.84$; $df = 1, 61$; $P < 0.001$) in D-NR lakes (mean = 0.050 larvae/100 L; SE = 0.013) than in S-NR lakes (mean = 0.005 larvae/100 L; SE = 0.002).

Larval Identification

Quantitative PCR verified correct visual identification of all walleyes (N = 9) collected from Escanaba Lake in night tows during 2014. Two larvae from Sawyer Lake were visually identified as walleyes in 2014 (4 June), but qPCR identified them as yellow perch. These larvae were captured 30 days post ice-out, were less than 15 mm TL, and difficult to identify. In 2014, 171 visually identified yellow perch larvae were verified by genetic testing. Of these, 11 samples failed qPCR testing, leaving 160 genetic identifications, 93% (149 of 160) of which I correctly identified as yellow perch. Incorrectly identified larvae were white sucker (N = 10) and black crappie (N = 1).

Quick PCR verified visual identifications of all larval walleyes (N = 31) submitted for genetic testing in 2015. Some of these fish were collected during the early larval stage, but the majority were collected during the late larval stage (> 40 days post ice out). In 2015, 8 of 246 larvae (3%) visually identified as yellow perch were actually walleyes, and all but one incorrectly identified larvae were collected during the early larval stage (captured 13 to 30 May; mean TL ≤ 11 mm).

Post-Larval Sampling

Seines

In general, seining was not effective for capturing age-0 walleyes during this study. In 2014, only a single age-0 walleye was collected by seine; the single walleye was collected at night on Big Arbor Vitae Lake in late August. Because night seining did not appear to dramatically improve catch of age-0 walleyes, only day seining was conducted in 2015.

In 2015, no age-0 walleyes were collected by seine in either D-NR lake. One 48-mm age-0 walleye was collected by seine from Escanaba Lake on 10 July and only seven age-0 walleyes were collected in late July and August from Big Arbor Vitae (N = 1) and Escanaba lakes (N = 6). Consequently, we did not use seine CPE in assessing timing of walleye recruitment bottlenecks.

Micro-mesh gill nets

No age-0 walleyes were collected in 0.95-cm bar mesh gill nets in 2015. However, after the first 48-mm TL walleye was collected by seine in mid-July, 0.64-cm mesh gill nets were set on all lakes during the last two weeks in July. The 0.64-cm mesh gillnets were effective in collecting age-0 walleyes from both S-NR lakes (Table 2; Figure 11), but no age-0 walleyes were collected in D-NR lakes. Age-0 walleyes collected in gill nets in Big Arbor Vitae (N = 6) ranged from 76-130 mm and had a mean TL of 96 mm. Age-0 walleyes collected in gill nets in Escanaba Lake (N = 9) ranged from 70-116 mm and had an average TL of 92 mm.

Fall electrofishing

Age-0 walleyes were collected from both S-NR lakes in both years during fall night electrofishing (Table 2). However, no age-0 walleyes were captured during fall electrofishing from D-NR lakes in either year (Table 2).

Zooplankton

Zooplankton taxa collected from all lakes included *Bosmina*, *Ceriodaphnia*, *Daphnia*, *Diaphanosoma*, *Holopedium*, *Leptidora*, and calanoid and cyclopoid copepods (adults and nauplii). Most abundant taxa were *Daphnia* spp., and calanoid and cyclopoid copepods, including nauplii. Total lengths of *Daphnia*, and calanoid and cyclopoid copepods within 40 days of ice out did not differ significantly between D-NR and S-NR lakes (Figure 12). Densities of *Daphnia*, calanoid and cyclopoid copepods, and nauplii within 40 days of ice out also did not differ significantly between D-NR and S-NR lakes (Figure 13).

Larval Predation

Over both years, I examined diets of 847 small panfish and other small predators collected during the time that percid larvae (primarily yellow perch) were present in peak numbers based on larval tows (Table 3). Larval fish or remnants were found in the diets of two black crappies, one bluegill, two largemouth bass, and one pumpkinseed. Based on qPCR analysis, these larvae were yellow perch or white suckers.

DISCUSSION

Objective 1: Age-0 Sampling

My work with various sampling gears for collecting age-0 walleyes provided initial insights regarding what gears might allow biologists to track relative abundance of age-0 walleyes through their first summer of life. While my experimental design did not allow for full comparisons of sampling gears among lakes and between years, my work suggests biologists can monitor temporal trends in relative abundance of age-0 walleyes using a combination of ichthyoplankton nets towed at night during mid to late May (i.e., 1-3 weeks after peak walleye spawning), 0.64-cm mesh gill nets set in mid to late July, and fall electrofishing. This sampling protocol has been adopted for the next phase of this project. If research goals are to verify walleye spawning and track relative egg density, egg mats may also be used.

Although previous research suggested surface ichthyoplankton tows during the day (Forney 1980) and quatrefoil light traps (Zweifel 2006) were effective for collecting larval walleyes, this was not the case in my study. Additional assessment of these two sampling approaches may be warranted, as low CPE of age-0 walleyes in Big Arbor Vitae and Escanaba lakes and CPE of age-0 walleyes in WDNR fall electrofishing indicated that walleye recruitment may have been relatively poor throughout the region in 2014 (J. Hansen, WDNR, unpublished data). However, capture of some larval walleyes on Escanaba Lake during 2014 suggested night towing of ichthyoplankton nets was effective for collecting some larval walleyes, even when relatively few larvae may have been available for capture. While light traps may capture larval walleyes in some lakes at certain times (Zweifel 2006), in the context of my experimental design they cost more on a per-lake basis ($475 x 8 per lake) than an ichthyoplankton net with flowmeter ($1,030) and required more overall time for collecting samples (i.e., deployed 4 h before retrieval). Because ichthyoplankton nets cost less and required less sampling time, I would recommend their use over light traps to agency personnel interested in tracking age-0 walleye at early life history stages in northern Wisconsin.

I did collect a few larval walleyes by towing at depth during the day on Escanaba Lake in 2015, but this approach was not as effective (i.e., lower CPE) as surface tows conducted at night. Walleyes are not reported to be negatively phototaxic until approximately eight weeks of age (Bulkowiski and Meade 1983), but my work suggests larval walleyes may move vertically within the water column either in response to light conditions or the diel migration of zooplankton prey. Walleye larvae within 17 days post-hatch were observed to move to sides of fry tanks in hatchery raceways in clearer water compared to turbid water (Rieger and Summerfelt 1997), suggesting differences in behavior depending on water clarity. These behavioral differences may be related to light sensitivity at an earlier age than found in previous studies. Similar behavior in a lake setting might include migration within the water column or movement to areas with cover such as vegetation, and could explain low CPE of larval walleye during daytime tows.

While shoreline seining has been used to sample age-0 walleyes in previous studies (Maloney and Johnson 1957; Kempinger and Churchill 1972), I collected few fish using this method even during a year with relatively strong recruitment. Conversely, 0.64-cm mesh gill nets set in mid-July were effective in collecting age-0 walleyes and I suspect these nets would have caught fish earlier in the year if I had used them. During this time frame, age-0 walleyes were too small to be caught in 0.95-cm mesh gill nets. Future sampling is needed to determine when age-0 walleyes become susceptible to 0.64-cm mesh gill nets. I suggest deploying 0.64-cm mesh gill nets in the third week in June to begin collecting age-0 walleyes in northern Wisconsin lakes. Gill nets set approximately 30 minutes before sunset on sand flats at depths of 0.25-1.5 m and lifted 30 minutes later generally provided highest catches. By-catch of small (5-12 cm) yellow perch, *Notropis* spp. or other small species may be high for nets set in vegetated areas of some lakes. My relatively short set times were designed to help reduce by-catch, but longer set times or additional sets per lake may be needed to capture larger samples of walleyes.

Objective 2: Timing of Recruitment Bottleneck

Although previous research suggests year-class strength is established after age-0 (Forney 19760), my research suggests a recruitment bottleneck is occurring at or before the larval stage in D-NR lakes. Spawning was verified by the presence of walleye eggs in all four study lakes, but no age-0 walleyes were captured in Kawaguesaga Lake after the egg stage. Few larval walleyes were collected within 40 days of ice out in Sawyer Lake (D-NR) and no age-0 walleye were collected thereafter. In 2015, age-0 walleyes were collected from S-NR lakes in all sampling gears, suggesting that gear effectiveness was not the reason for the lack of age-0 walleyes in D-NR lakes. It is possible that larvae hatch rates were lower on D-NR lakes or that newly hatched larvae were not able to successfully feed due to increased water clarity or lack of prey.

Determining presence and abundance of larval walleyes immediately after hatching can be difficult because species identification of larval percids ≤ 15 mm is challenging. Identification guides (e.g., Auer 1982) provide identification guidance based on myomere counts, pigmentation, eye, and larvae size, but there is variability within and among walleye and yellow perch larvae. In northern Wisconsin, yellow perch generally hatch later than walleye, however, many factors influence spawn duration and hatch timing of both species (Clady 1976; Forney 1976; Isermann and Willis 2008). Moreover, both species were collected simultaneously in my larval tows. For percid larvae ≤ 15 mm TL, qPCR provides more reliable method for species identification than visual assessment (i.e., correctly distinguishes larval yellow perch from walleyes greater than 90% of the time; K. Turnquist, UWSP Molecular Conservation Genetics Laboratory, personal communication), especially when multiple personnel are used for visual identification of larvae. Failure to use qPCR would have resulted in some errors in my assessment. Thus, my larval walleye densities reported at the early larval stage may have underestimated actual density of larval walleyes present at the time because visual identification may have been incorrect for some larvae not subjected to qPCR. At a minimum, future research involving larval percid identification should use qPCR or some other method to validate visual species identification of percid larvae ≤ 15 mm TL.

Objective 3: Abiotic and Biotic Differences

Evaluating differences in selected abiotic and biotic metrics between S-NR and D-NR lakes was an exploratory exercise designed to provide initial insights regarding underlying mechanisms causing walleye recruitment bottlenecks in D-NR lakes. However, D-NR and S-NR lakes were generally similar in terms of all metrics, except for mean TL of adult walleyes and larval yellow perch density in 2015. In general, the use of two lakes within each recruitment history is not sufficient to fully determine whether these abiotic and biotic variables vary between lakes with each history. Expanding this research to more lakes should help determine whether differences in the metrics I compared exist between other D-NR and S-NR lakes.

Although I did not observe a significant difference in water clarity between recruitment histories, D-NR lakes were slightly clearer than S-NR lakes. It is possible that if I had a historical record of water clarity over the last 10-15 years I may have observed a significant difference between recruitment histories. Water turbidity has been shown to be positively related to earlier larval walleye feeding, increased growth rate, greater average swimming speeds, and improved gas bladder inflation in hatcheries (Bristow and Summerfelt 1994; Rieger and Summerfelt 1997). In Lake Erie, larval walleye density was negatively associated with water clarity, though also with water depth (Roseman et al. 2005). These findings suggest walleye larvae may face more challenges to survival in clearer water conditions.

Though I did not observe a significant difference in zooplankton size or abundance between D-NR and S-NR lakes, continued zooplankton sampling of my study lakes and addition of more lakes within each recruitment history is warranted. Larval walleye feeding success, and hence survival, may be limited by both zooplankton abundance and size (Johnston and Mathias 1994). In previous studies, zooplankton density has not been found to consistently affect selectivity for certain prey taxa or size, but the number of larvae with empty guts decreased with increased prey density (Mayer and Wahl 1997). Small larvae (8-10 mm TL) fed cladocerans were also found to experience greater survival than those fed copepods in the laboratory (Mayer and Wahl 1997).

I did not observe a significant difference in adult walleye CPE between D-NR and S-NR lakes. However, S-NR lakes did have slightly higher adult CPE and significantly greater adult walleye mean TL. Both declining adult walleye CPE and higher mean TL of adult walleyes in D-NR lakes is consistent with a lack of recruitment and adult mortality due to angling pressure.

The higher CPE of larval yellow perch observed in D-NR lakes suggests that natural reproduction of yellow perch and survival to the larval stage is not being adversely affected as was apparent for walleye. Furthermore, the differences in larval perch CPE between lake types may also indicate that predation by age-0 walleyes affects larval perch abundance in S-NR lakes, which is consistent with previous research (Forney 1974). Sampling of larval yellow perch should be continued to determine if the same trend is observed in future years and on additional lakes.

My initial diet assessment suggested that panfish eat few larval fish during the period of time that percid larvae (primarily yellow perch) are abundant in the water column. My cursory analysis also suggested that many of these fish were actively feeding before capture, as the majority of fish we collected contained numerous diet items that were largely zooplankton or aquatic insect larvae. A possible explanation for lack of larvae in panfish diets may be that panfish occupy littoral areas during spring while larvae are in deeper water, so that panfish encounter of larval percids is low. If panfish are not major predators of larval yellow perch, which were far more abundant than walleyes in my larval samples, it would seem unlikely they are major predators of larval walleyes. Larvae present in panfish diets were in varying stages of digestion, and it is possible diets were sampled that contained larvae digested beyond recognition. However, despite the rapid digestion of larvae, if panfish were frequent predators of larval percids, a large number of diets would still be expected to contain larvae or at least partially digested larvae, unless this predation is episodic in nature.

Management Implications

Mechanisms responsible for the apparent recruitment bottleneck at or before the larval stage have not yet been identified. While adult walleye populations in D-NR lakes exhibited densities historically capable of supporting NR, environmental changes may now require higher adult walleye densities to provide sustained NR. If this is the case, more restrictive walleye length or bag limits or fishery closures may be needed to sustain or increase adult walleye abundance in D-NR lakes. Supplemental stocking of walleye fingerlings has been effective in increasing year-class strength in some northern Wisconsin lakes (Jennings et al. 2005), and it may be required to replace or supplement natural reproduction until sufficient adult densities are reached in D-NR lakes. This proposed solution presumes stocked fish will reach adulthood, but additional recruitment bottlenecks could occur after age-0 electrofishing occurs during fall.

Environmental factors that may be operating to reduce walleye recruitment in D-NR lakes include changes to water clarity and temperature. Although not significantly different, D-NR lakes were clearer than S-NR lakes during the two years of my project. Unfortunately, historical records of water clarity do not exist for my D-NR study lakes, but it is possible that changes in water clarity have occurred. It is also possible that climatic changes have altered thermal environments in D-NR lakes. If optimal thermal-optical habitat for walleyes (Lester et al. 2004) has decreased in D-NR lakes, they may no longer be able to support the walleye populations they once did, and management goals and actions may need to be revised (Hansen et al. 2015b). For example, a 5-year walleye harvest moratorium (spearing and angling) was implemented in 2015 on the Minocqua Chain of Lakes (including Kawaguesaga Lake) and consistent stocking of fingerling walleyes has commenced in both Kawaguesaga, Sawyer, and many other D-NR lakes.

Future Research

Predicting walleye recruitment is important for management of walleye (Hansen et al. 2015a). Although my research suggests a recruitment bottleneck is occurring at or before the larval stage in at least some D-NR populations, continued sampling is needed to determine if a similar bottleneck is occurring at a broader scale (i.e., more than two lakes). More intensive sampling at the early larval stages including increases in frequency and number of tows may help better determine the timing of this bottleneck. If funding allows, genetic identification of larval percids ≤ 15 mm would be preferable over visual identification, but at a minimum some technique should be used to determine accuracy of visual identifications. I recommend continued sampling on the four lakes I studied using the age-0 sampling protocols I have provided with the addition of more lakes within each recruitment history. Furthermore, Sawyer and Kawaguesaga lakes have exhibited low recruitment for the past 10-15 years. Addition of lakes exhibiting recent declines in recruitment (i.e., last 5-7 years) might provide additional insights into mechanisms or factors responsible for these declines.

Identifying differences in abiotic and biotic metrics between D-NR and S-NR lakes requires increased sample size in terms of both lakes and years, and could involve comparisons of more metrics. I did not compare zooplankton sizes with larval walleye sizes or examine overall zooplankton community composition between D-NR and S-NR lakes, but additional research might include such comparisons to test for gape limitations and differences in percent composition of taxa and overall diversity between recruitment histories. Additional research might also calculate larval walleye hatch date compared with zooplankton size and density to test the match-mismatch hypothesis (Cushing 1982) by identifying if sufficient prey are available to larvae at hatch. Previous research has identified some species of panfish as walleye egg predators (Roseman et al. 2006), so further panfish predation studies could be conducted during the walleye egg phase. Future studies on D-NR lakes might also include experimental fry stocking to determine if these fish survive and if this strategy successfully circumvents the apparent recruitment bottleneck I observed.

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TABLE 1 – Density (number per hectare) of adult walleyes (≥ 380 mm total length) calculated from the most recent adult walleye population estimate completed by the Wisconsin Department of Natural Resources (WDNR) for Big Arbor Vitae, Escanaba, Kawaguesaga, and Sawyer lakes. All four lakes were categorized by WDNR as naturally reproducing. Sustained natural reproduction (S-NR) lakes continue to support variable levels of natural walleye recruitment, while walleye recruitment has declined dramatically over the last 15 years in D-NR lakes (Figure 1).

Recruitment History	**Lake**	**Adults/ha**	**Year**
S-NR	Big Arbor Vitae	20	2011
	Escanaba	19	2013
D-NR	Kawaguesaga	8	2009
	Sawyer	7	2008

TABLE 2 – Summary of sampling for age-0 walleye during early life history stages in 2014 and 2015. Sustained natural reproduction (S-NR) lakes continue to support variable levels of natural walleye recruitment, while walleye recruitment has declined dramatically over the last 15 years in D-NR lakes (Figure 1).Walleye eggs were collected using egg mats for a period of 10-d after ice out. The larval sampling period occurred within 40 d of ice out on each lake. Larvae were collected in surface ichthyoplankton tows conducted during daylight in 2014, tows were conducted at night during 2015. Post-larval walleye were captured in July using micromesh gill nets in 2015. Juvenile walleye were captured in September of both years by night electrofishing.

Recruitment History	**Lake**	**Egg (eggs/m^2)**	**Larvae (fish/100 L)**	**Post-Larvae (fish/10 h set)**	**Juvenile (fish/h)**
			2014		
S-NR	Big Arbor Vitae	362.42	0	-	11.3
	Escanaba	21.32	0.000249	-	61.45
D-NR	Kawaguesaga	9.14	0	-	0
	Sawyer	39.59	0	-	0
			2015		
S-NR	Big Arbor Vitae	155.32	4.62×10^{-5}	3.18	165.97
	Escanaba	307.60	2.76×10^{-4}	4.19	46.53
D-NR	Kawaguesaga	1.83	0	0	0
	Sawyer	73.09	1.35×10^{-4}	0	0

Table 3 – Panfish and other small potential larval predator fish species collected for diet analysis. Fish were collected using daytime electrofishing when percid larval abundance was at its peak in 2014 and 2015. Gastric lavage was used to remove diet contents. Black crappie (*Pomoxis nigromaculatus*), bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), rock bass (*Ambloplites rupestris*), smallmouth bass (*M. dolomieu*), walleye (*Sander vitreus*), yellow perch (*Perca flavescens*), pumpkinseed (*L. gibbosus*).

Year	Lake	Predator	N	Mean TL (SE)	Larvae
2014	Big Arbor Vitae	Black Crappie	18	232 (6)	0
		Bluegill	74	106 (4)	0
		Largemouth Bass	9	157 (21)	1
		Yellow Perch	49	85 (6)	0
		Pumpkinseed	52	128 (4)	0
		Rock Bass	19	198 (9)	0
	Escanaba	Bluegill	8	121 (17)	0
		Northern Pike	1	267 (NA)	0
		Yellow Perch	18	91 (7)	0
		Pumpkinseed	54	97 (3)	0
		Rock Bass	3	181 (18)	0
	Kawaguesaga	Black Crappie	4	174 (29)	0
		Bluegill	56	93 (4)	0
		Largemouth Bass	11	233 (25)	0
		Northern Pike	4	270 (16)	0
		Yellow Perch	17	125 (7)	0
		Pumpkinseed	17	152 (4)	0
		Rock Bass	15	178 (16)	0
		Smallmouth Bass	6	149 (27)	0
		Walleye	1	219 (NA)	0
	Sawyer	Black Crappie	19	184 (3)	2
		Bluegill	55	118 (9)	0
		Largemouth Bass	21	186 (2)	0
		Yellow Perch	6	161 (1)	0
		Pumpkinseed	8	159 (2)	1
		Rock Bass	27	147 (5)	0
2015	Big Arbor Vitae	Black Crappie	19	244 (5)	0
		Bluegill	22	123 (5)	0
		Yellow Perch	9	82 (14)	0
		Pumpkinseed	37	118 (5)	0
		Rock Bass	3	216 (13)	0
		Smallmouth Bass	1	272 (NA)	0
	Escanaba	Bluegill	8	103 (8)	0
		Yellow Perch	12	102 (12)	0
		Pumpkinseed	34	117 (2)	0
		Rock Bass	2	128 (6)	0
	Kawaguesaga	Black Crappie	10	236 (12)	0
		Bluegill	18	144 (12)	0
		Largemouth Bass	8	206 (16)	0
		Yellow Perch	17	160 (11)	0
		Pumpkinseed	11	142 (12)	0
		Rock Bass	2	197 (12)	0

TABLE 3 (Continued)

2015	Sawyer	Bluegill	25	128 (7)	1
		Largemouth Bass	11	143 (34)	1
		Pumpkinseed	9	123 (6)	0
		Rock Bass	16	171 (6)	0
		Smallmouth Bass	1	308 (NA)	0

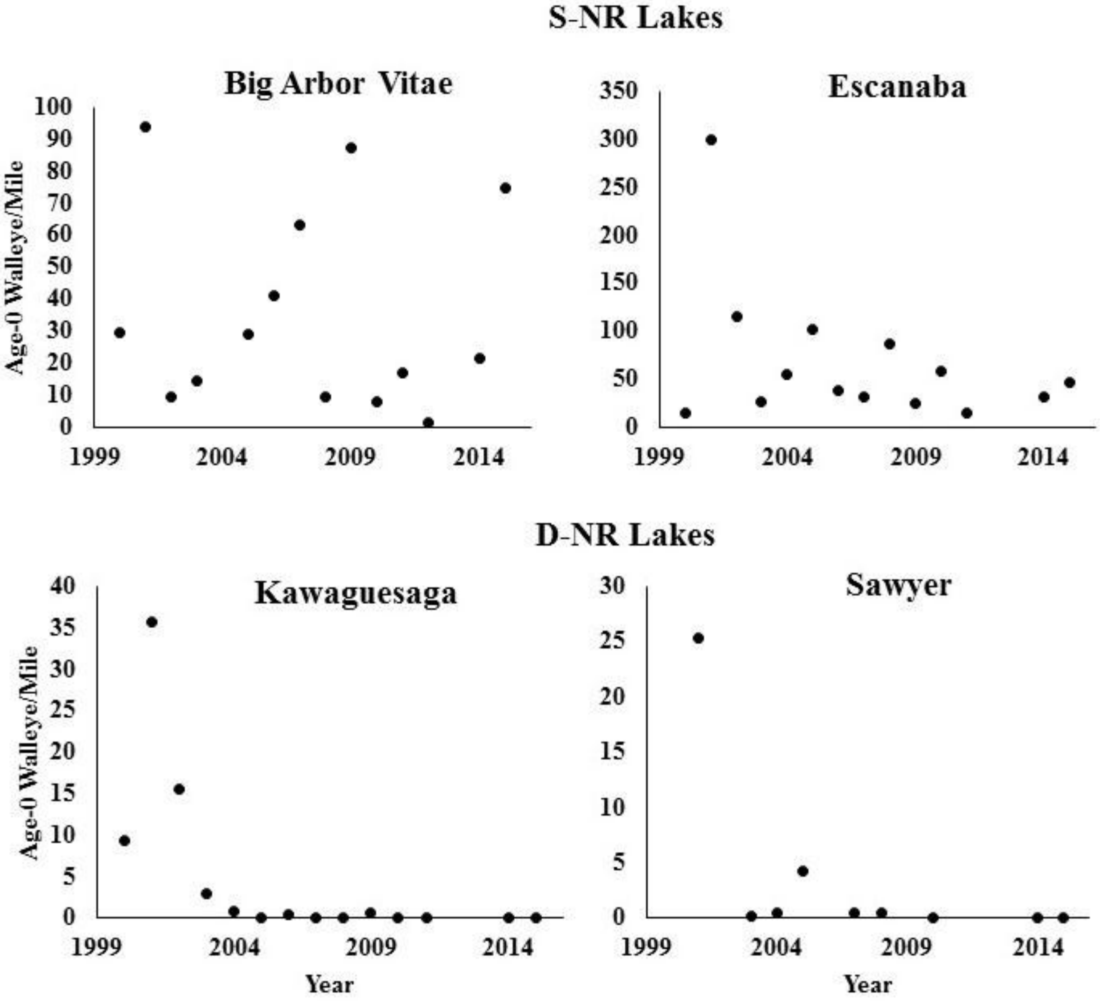

FIGURE 1 – Catch-per-effort (number/mile) of age-0 walleyes collected in fall electrofishing surveys conducted by the Wisconsin Department of Natural Resources (WDNR) on Big Arbor Vitae, Escanaba, Kawaguesaga, and Sawyer lakes. Scale of y-axis differs among graphs. All lakes were categorized by WDNR as naturally reproducing walleye populations and have supported natural reproduction (NR) in the past. Kawaguesaga and Sawyer lakes have experienced a decline in walleye recruitment over the past 15 years and were categorized as declining NR (D-NR) lakes for the purposes of this study. Big Arbor Vitae and Escanaba lakes continue to sustain variable levels of NR and were categorized as S-NR lakes.

FIGURE 2 – Custom-made boom used to tow ichthyoplankton nets at shallow (1.0-1.5 m) and deep (2.0-2.5 m) depth ranges. The boom extended perpendicularly over the hull of the boat. A steel cable extended from the reel on the boom and was clipped to the bridle of the net. Downrigger balls (approximately 4 kg) were attached to the frame of the net, and the cable was extended until the net reached desired depth range.

FIGURE 3 – Plexiglas quatrefoil light trap used to sample larval fish in 2014. Light traps were illuminated by a battery powered LED light, with four 4-mm slots at points of the cloverleaf configuration through which larvae enter. Traps were anchored using a small concrete anchor, and Styrofoam floats fixed to the top of the traps ensured the traps floated just below the water surface. A 1,000-µm mesh conical net was attached to the bottom of the light trap where larvae were entrapped.

FIGURE 4 – Small gastric lavage used to remove diet contents of panfish and other small (> 200 mm TL) fish that might prey upon larval walleyes. The gastric lavage consisted of a livestock syringe fitted with small plastic tubing (0.16-cm diameter). The syringe was filled with water and the tube inserted through the mouth and into the esophagus. Fish were turned upside down over a mesh-lined funnel as diet contents were flushed out. Fish were released and diet items preserved for further analysis.

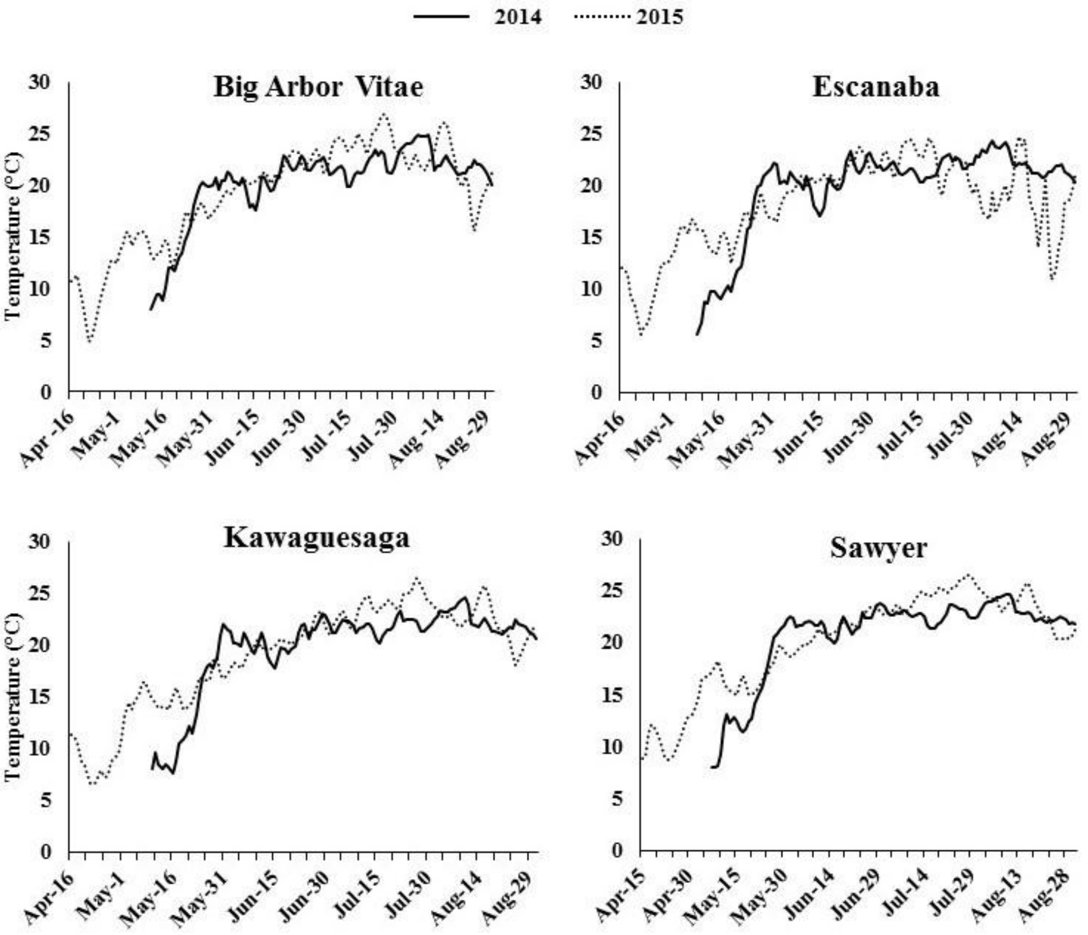

FIGURE 5 – Mean daily water temperature (°C) recorded from spring to fall during 2014 and 2015 in Big Arbor Vitae Lake, Escanaba Lake, Kawaguesaga Lake, and Sawyer lakes. April temperatures are not included for 2014, because ice did not go off from the lakes until early May.

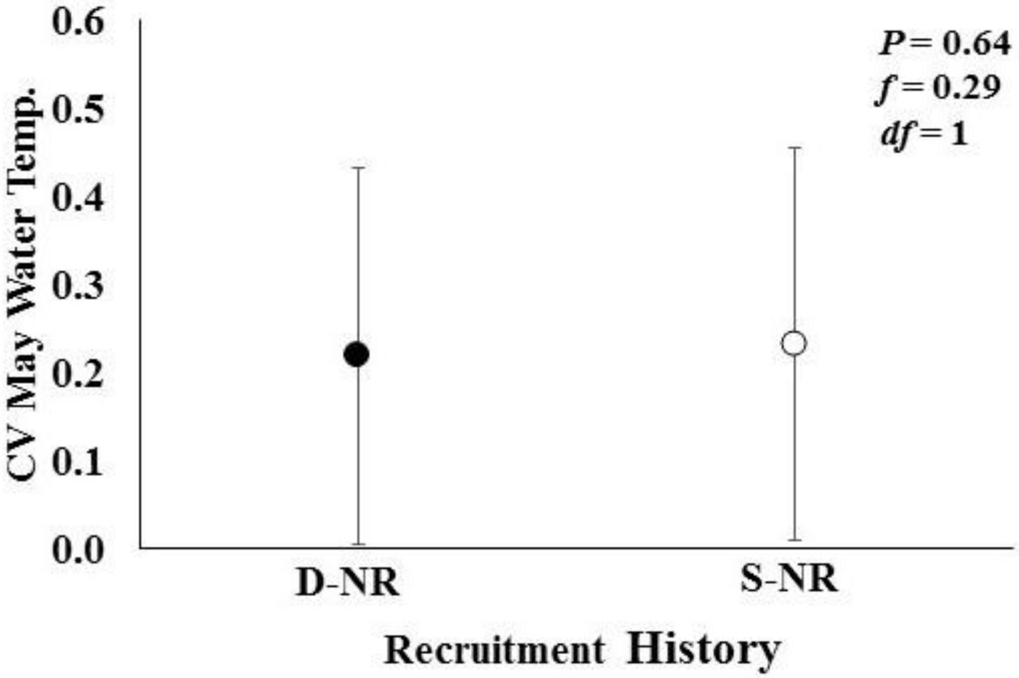

FIGURE 6 – Coefficient of variation of May daily water temperature compared between D-NR (black circle; Kawaguesaga and Sawyer) and S-NR (white circle; Big Arbor Vitae and Escanaba) lakes using data collected in 2014 and 2015. A repeated-measures ANOVA did not indicate a significant difference between D-NR and S-NR lakes. Error bars represent 95% confidence intervals.

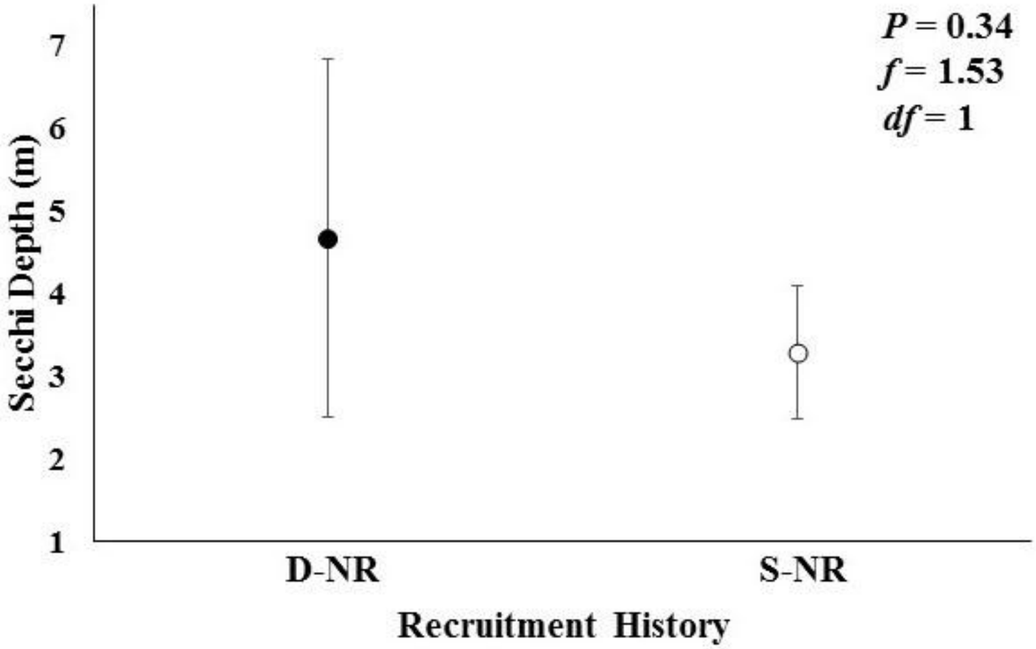

FIGURE 7 – Mean Secchi depth compared between D-NR (black circle; Kawaguesaga and Sawyer) and S-NR (white circle; Big Arbor Vitae and Escanaba) lakes using data collected within 40 days of ice out in 2014 and 2015. A repeated-measures ANOVA indicated no significant difference in water clarity between D-NR and S-NR lakes. Error bars represent 95% confidence intervals.

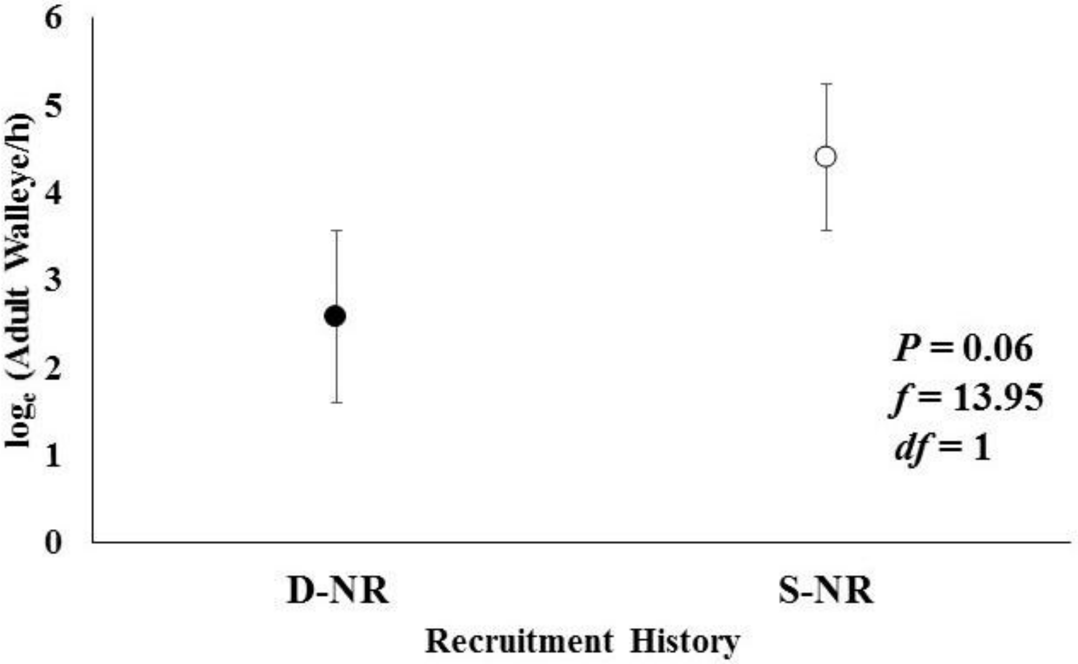

FIGURE 8 – Adult walleye CPE (adults/h) compared between D-NR (black circle; Kawaguesaga and Sawyer) and S-NR (white circle; Big Arbor Vitae and Escanaba) lakes using data collected in 2014 and 2015. Values were log$_e$ transformed prior to analysis. A repeated-measures ANOVA indicated no significant difference in adult CPE between D-NR and S-NR lakes. Error bars represent 95% confidence intervals.

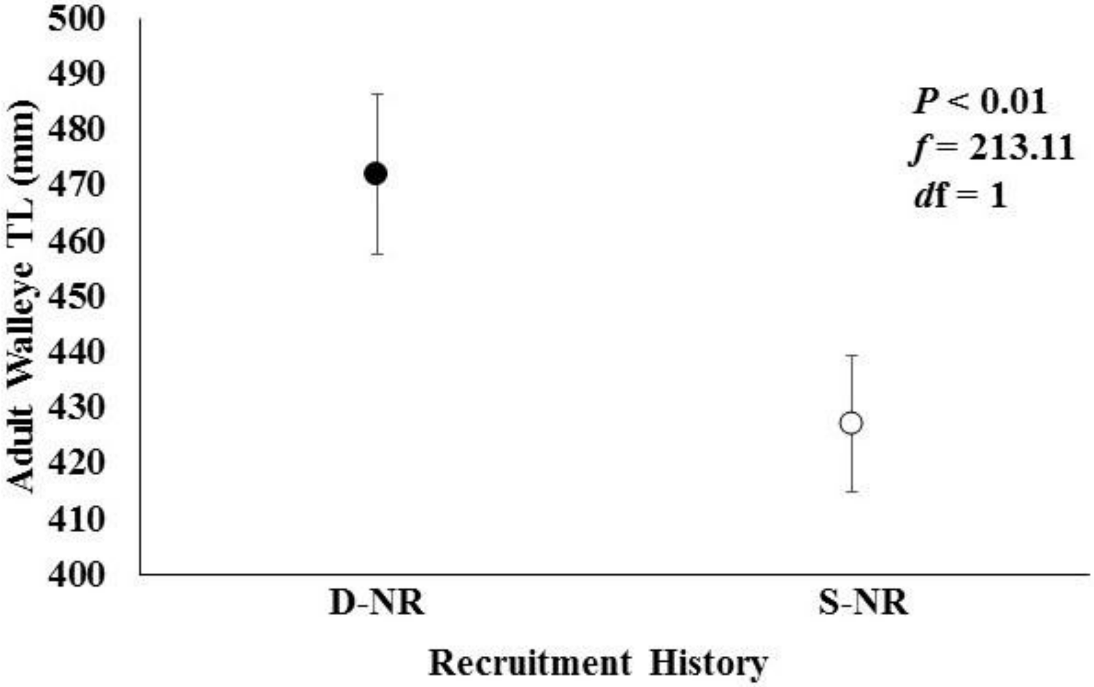

FIGURE 9 – Mean adult walleye TL (mm) compared between D-NR (black circle; Kawaguesaga and Sawyer) and S-NR (white circle; Big Arbor Vitae and Escanaba) lakes using data collected in 2014 and 2015. Adult walleyes were defined as fish ≥ 380 mm TL. A repeated-measures ANOVA indicated adult walleye TL was significantly greater in D-NR lakes than in S-NR lakes. Error bars represent 95% confidence intervals.

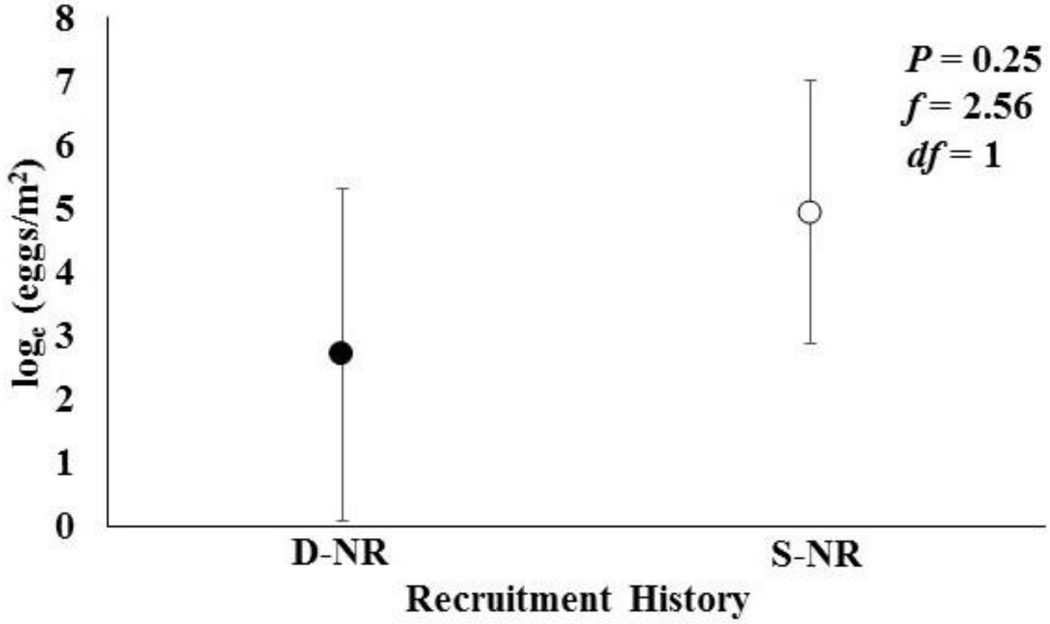

FIGURE 10 – Relative walleye egg density compared between D-NR (black circle; Kawaguesaga and Sawyer) and S-NR (white circle; Big Arbor Vitae and Escanaba) lakes using data collected in 2014 and 2015. Values were $\log_e$ transformed prior to analysis. A repeated-measures ANOVA indicated no significant difference in egg density between D-NR and S-NR lakes. Error bars represent 95% confidence intervals.

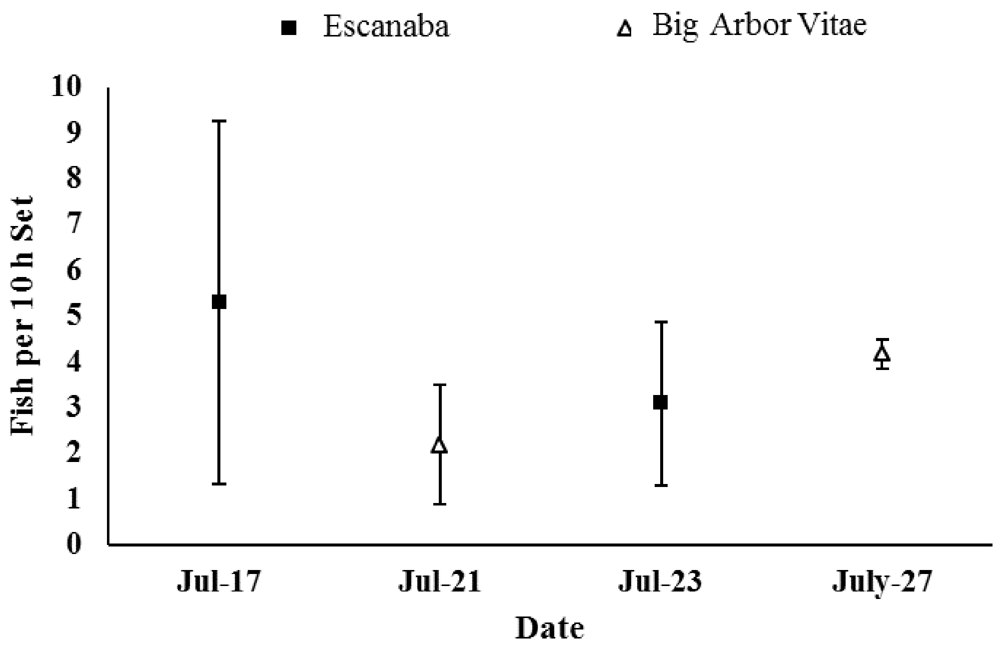

FIGURE 11 – Standardized catch per effort (CPE) for age-0 walleye collected in 0.64-cm mesh gill nets in Escanaba and Big Arbor Vitae lakes. All nets were set near to after dark in July 2015. Gill net soak time varied between approximately 45 minutes and 3 hours, so CPE has been standardized to fish/10 h. Error bars represent standard errors.

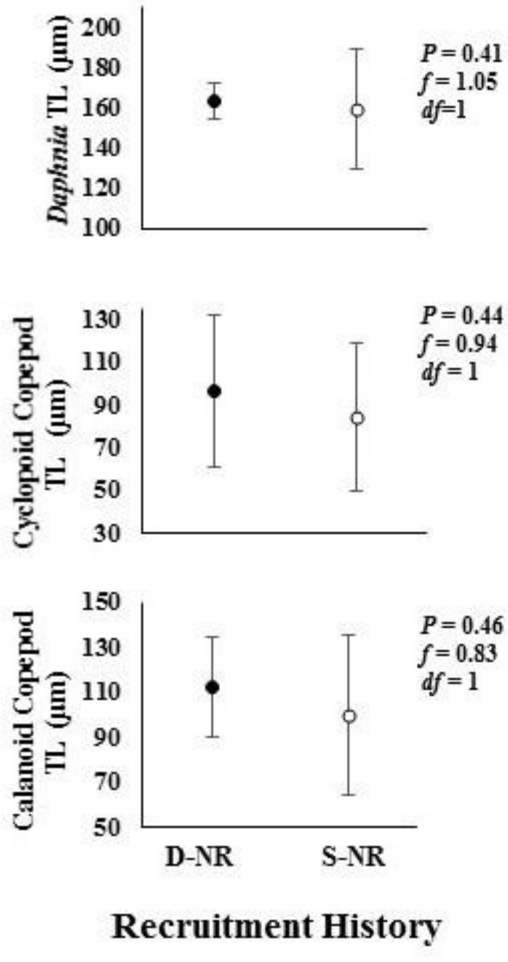

FIGURE 12 – TL (µm) of most abundant zooplankton taxa compared between D-NR (black circles; Kawaguesaga and Sawyer) and S-NR (white circles; Big Arbor Vitae and Escanaba) lakes using data collected within 40 days of ice out in 2014 and 2015. Repeated-measures ANOVAs indicated no significant differences in zooplankton TL between D-NR and S-NR lakes. Error bars represent 95% confidence intervals.

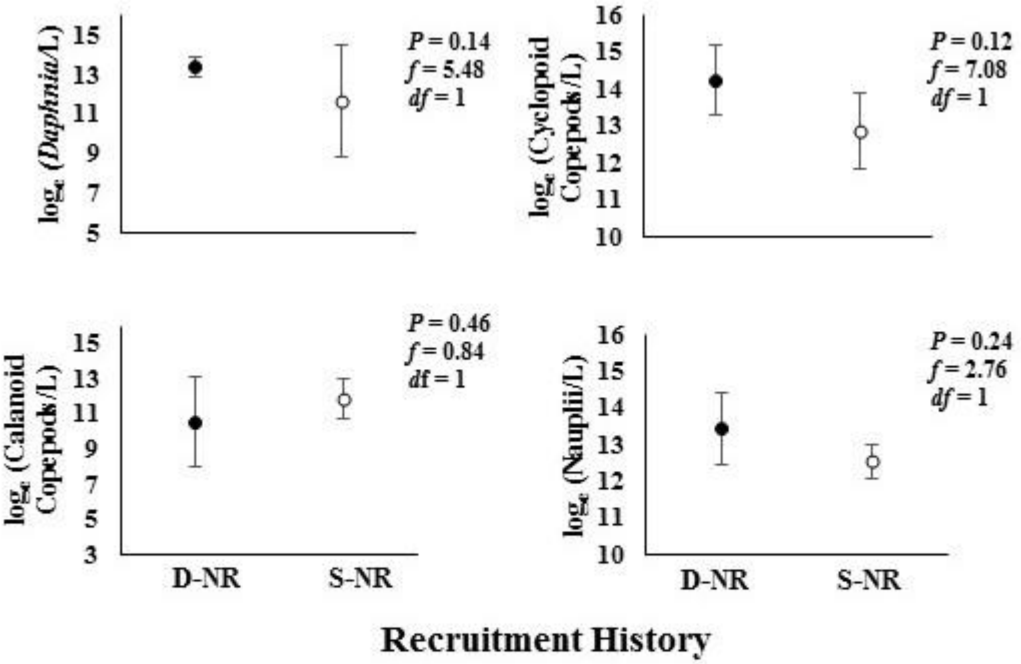

FIGURE 13 – Density of most abundant zooplankton taxa compared between D-NR (black circles; Kawaguesaga and Sawyer) and S-NR (white circles; Big Arbor Vitae and Escanaba) lakes using data collected within 40 days of ice out in 2014 and 2015. Values were log$_e$ transformed prior to analysis. Repeated-measures ANOVAs indicated no significant differences in zooplankton densities between D-NR and S-NR lakes. Error bars represent 95% confidence intervals.