Age-0 Walleye Growth Rates Following Spiny Water Flea *Bythotrephes longimanus* Invasion

Joseph Amundson
Aquatic Biology Program
Bemidji State University

Within Voyageurs National Park, spiny water flea *Bythotrephes longimanus* has reduced Lake Kabetogama and Rainy Lake native zooplankton biomass during summer peak by 40-60%. Subsequently, planktivorous age-0 Yellow Perch *Perca flavescens* growth has decreased. A possible trophic cascade may influence predatory fish growth rates like that of age-0 Walleye *Sander vitreus*. Using seine net and electrofishing data, age-0 Walleye growth rates were modeled as a linear function of growing degree days (GDD) and the slope was compared between pre- and post-spiny water flea establishment. Nearby Lake Vermilion, assumed to have been unaffected by spiny water flea until 2015 and found to have no changes in Yellow Perch growth, was used as a reference for natural variation in age-0 Walleye growth in the region. At 1050 GDD, the two infected lakes showed either no change (Lake Kabetogama) or a decline in mean growth rate (Rainy Lake) of 5% related to GDD, whereas the uninfected lake (Lake Vermilion) showed an increase in mean growth rate of 9% during the same time period. The effects spiny water fleas have on age-0 Walleye growth varied from lake to lake and its broader implications are not completely clear. A lakes limnological characteristics and management plans for Walleye may contribute to changes in growth rates of age-0 Walleye just as much as the presence of spiny water flea. Further monitoring and analysis of now infested Lake Vermilion (this studies refence lake) may help determine the effects spiny water fleas have on age-0 Walleye growth.

Faculty Sponsor: Dr. Andrew W. Hafs

Introduction

Spiny water flea *Bythotrephes longimanus* is a predatory cladoceran native to the Ponto-Caspian region of Eurasia. It was first detected in Lake Ontario in 1982 (Johannsson and O'Gorman 1991) and quickly spread to all of the Laurentian Great Lakes. As of 2006, more than 90 inland lakes and reservoirs in Ontario, Minnesota, Michigan, and Ohio have been invaded (Strecker et al. 2006). Invasions of spiny water flea have been observed to shift the species composition, relative abundance, biomass, and size structure of zooplankton communities (Barbiero and Tuchman 2004; Strecker et al. 2006; Kerfoot et al. 2016). The shift in zooplankton communities can negatively affect the growth and survival of age-0 planktivorous fish (Staples et al. 2017).

By 2007 spiny water flea became established in all of the large inter-connected lakes of Voyageurs National Park (VNP) located in northern Minnesota. Samples taken during 2009-2010 by Kerfoot et al. (2016) showed that Lake Kabetogama (located in VNP) had the highest mean density of spiny water flea at 33 individuals/m³ dramatically changing the overall seasonal density patterns of native zooplankton. Most notably, the summer biomass of native zooplankton decreased 40–60%. Staples et al. (2017) found that planktivorous age-0 Yellow Perch *Perca flavescens* mean length decreased approximately 10% relative to growing degree days (GDD). At the same abundance, shorter age-0 length correlates to 25% decrease in biomass available to support higher level predators at the end of the summer.

Yellow Perch are a primary forage species for Minnesota's most sought-after fish, the Walleye *Sander vitreus* (MNDNR 2018a). This predator-prey relationship starts as early as late June for age-0 Walleye in Lake Kabetogama while undergoing ontogenetic shifts in their diet at each life stage where they consume the most profitable prey items available (Galarowicz et al. 2006). Walleye generally transition from eating zooplankton to macroinvertebrates to fish during their first year of life (Graeb et al. 2005; Galarowicz et al. 2006).

The decrease in native zooplankton and Yellow Perch growth post-spiny water flea have raised questions on the effects this may have on predatory fish growth rates like that of age-0 Walleye in Lake Kabetogama. With a long-standing history of strong natural Walleye production, Lake Kabetogama has had only one extremely strong year-class produced (2015) since the invasion of spiny water flea (Vondra 2012). The objective of this study is to determine whether age-0 Walleye length relationship to GDD has changed in Lake Kabetogama after the invasion of spiny water flea.

Methods

Study Sites

This study analyzed age-0 Walleye length data collected from three large lakes in northern Minnesota: Kabetogama, Rainy and Vermilion. Lake Kabetogama was infected by spiny water flea in 2007 and Rainy Lake, which is downstream of Lake Kabetogama and used to verify results of infected lakes in the region, was infected by spiny water flea in 2006. Nearby Lake Vermilion assumed to have been unaffected by spiny water flea until 2015, was used as a reference for natural variation in age-0 walleye growth in the region.

TABLE 1: Study lakes characteristics

Lake	Area (km^2)	Max Depth (m)	Littoral Habitat %
Kabetogama	104	24	31
Rainy	850	49	8
Vermilion	159	25	39

Data Description

The Minnesota Department of Natural Resources (MNDNR) collected age-0 Walleye length data from 1998-2016 for both Lake Kabetogama (7,597 age-0 measured), Rainy Lake (5,751 age-0 measured) and from 1998-2014 for Lake Vermilion (5,621 age-0 measured) during shoreline seining and electrofishing completed as part of the Minnesota large lakes sampling program (Figure 1).

Fish growth from year to year can be related to the length and characteristics of each growing season. GDD accounts for differences in fish length due to variation in growing season temperature regimes among study years (Neuheimer and Taggart 2007). GDD is a collective total of daily degree days and was used to account for differences in fish length due to variation in growing season temperatures. GDD is calculated as:

$$\text{GDD} = \left(\frac{T_{max} - T_{min}}{2}\right) - T_{base}$$

where T_{max} and T_{min} are the maximum and minimum daily ambient temperatures and T_{base} is the temperature below which growth or development is nonlinear and effectively zero (Chezik et al. 2014). Using air temperature data from International Falls, Minnesota airport weather station (NOAA 2018) to calculate the collective GDD for each sampling date using a T_{base} of 5 °C (Chezik et al. 2014). Starting the day after ice-off through sampling date, all GDD with a negative value are disregarded (Uphoff et al. 2013).

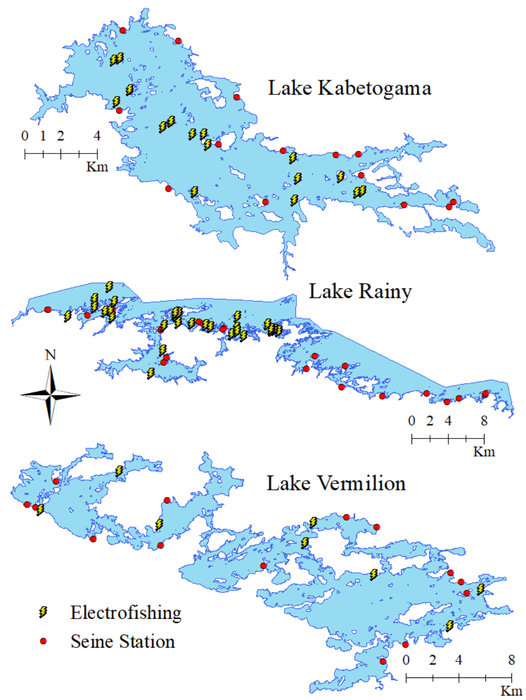

FIGURE 1: Electrofishing and seine netting sites used during data collection for the 3 study lakes.

Data Analysis

This study tested for changes in age-0 Walleye growth after the establishment of spiny water flea in lakes Kabetogama and Rainy effected 2007 and 2006, respectively. For growth comparison purposes, Lake Kabetogama pre-spiny water flea was denoted as the years 1998-2006 and post-spiny water flea was denoted years 2007-2016. Rainy Lake pre-spiny water flea was denoted as the years 1998-2005 and post-spiny water flea was denoted years 2006-2016. Lake Vermilion was used as a regional reference for normal variation in age-0 Walleye growth.

A linear regression base model for each lake was analyzed with age-0 walleye length as a function of GDD accumulated. As described by Staples et al. (2017), a random year effect on the intercept was included to allow for the line to be higher or lower, but with the same slope, to accommodate random differences in mean length among years due to factors other than GDD accumulation. For easier interpretation, a centered GDD variable was used for model fitting by subtracting 276 from each GDD observation. This essentially makes the model intercept values represent estimated age-0 Walleye length at the beginning of the sampling season (approximately mid-June in most years). All analyses were performed in the statistical program R (R Core Team 2014) using the lme4 package (Bates et al. 2015).

To evaluate for post-invasion changes in growth, a two-level categorical variable for spiny water flea establishment epoch (pre-spiny water flea and post-spiny water flea) was included as an interaction term with GDD in the regression. This allowed for unique regression lines for the two epochs, while still modeling annual variation in mean length with the random year effect. To test for changes in age-0 growth rate between the two epochs, we compared four linear regression models of age-0 length relative to GDD in each study lake (Table 2): the same average intercept and slope in both epochs (denoted as Model 1), different intercepts but same slope (Model 2), different slopes but same intercept (Model 3), and different slopes and intercepts (Model 4). Choice of Model 1 would indicate age-0 Walleye are the same average size in each epoch at the start of the summer sampling season and grow at the same rate relative to GDD (i.e., spiny water flea had no effect on growth), whereas Model 4 would indicate a different size in early summer and different growth rates during the sampling season. Model 2 would indicate that the age-0 Walleye are a different size in early summer but grow at the same rate; Model 3 would indicate similar size at the beginning of summer, but different growth rates among epochs throughout the sampling period.

TABLE 2: Linear Regression Models. Total Length (TL) is the length of each fish in mm at time of capture, Growing Degree Days (GDD) is the total GDD for each fish at time of capture, Epoch is a two-level categorical variable for spiny water flea establishment pre- and post-spiny water flea and a random year effect on the intercept is represented by Year.

Model	Equation
1	TL ~ GDD + Year
2	TL ~ GDD + Epoch + Year
3	TL ~ GDD + GDD · Epoch + Year
4	TL ~ Epoch + GDD · Epoch + Year

Models were compared using Bayesian information criterion (BIC) scores (Schwarz 1978). To analyze the BIC scores, Raftery (1995) explains the model with the lowest BIC score was assumed to fit the best. The best fit BIC score was subtracted from all models' BIC score (denoted ∆BIC) and were used to judge its relative fit compared to the best fitted model. ∆BIC greater than 10 indicated very strong support, ∆BIC 6-10 indicated strong support for the model with the lower score compared to the higher score, ∆BIC < 2 indicated weak support and have similar levels of fit. If models had similar fit the simplest model was chosen.

Results

In Lake Kabetogama the lowest BIC score was associated with Model 1 (Table 3), with BIC comparisons indicating no evidence for a change in age-0 Walleye growth rates following spiny water flea invasion. In Rainy Lake the lowest BIC score was associated with Model 3 (Table 3), with BIC comparisons indicating strong evidence for a change in age-0 Walleye growth rates following spiny water flea invasion. In Lake Vermilion the lowest BIC score was associated with Model 3 (Table 3), with BIC comparisons indicating strong evidence for a change in age-0 Walleye growth rates between year groups 1998-2006 and 2007-2014.

Predicted average growth regression lines for the pre- and post-spiny water flea epochs for Lake Kabetogama using Model 1 show no change in slope between epochs (Figure 2). Rainy Lake using Model 3 shows a negative change in slope post-spiny water flea epoch (Figure 2). Lake Vermilion using Model 3 shows a positive change in slope during study period (Figure 2).

Predicted average growth at 1050 GDD throughout the study period was highly variable using individual year specific growth regression lines to estimate mean growth (only years with seine and electrofishing data used) (Figure 3). Despite this, the overall trends depicted in Figure 2 can be seen in each study lake. Using the best fitting BIC models from Table 3 for each lake, predictions were made for age-0 Walleye average length at 1050 GDD. Lake Kabetogama pre and post-spiny water flea was 127 mm. Rainy Lake pre-spiny water flea was 109 mm and post-spiny water flea was 104 mm, growth decrease of 5%. Lake Vermilion 1998-2006 was 124 mm and 2007-2014 was 136 mm, growth increase of 9%.

Discussion

Kabetogama and Rainy lakes have very different limnological characteristics (Kabetogama

TABLE 3: Walleye age-0 length model BIC scores and coefficient estimates for lakes Kabetogama, Rainy and Vermilion. Intercepts represent mean age-0 Walleye length at the beginning of the sampling season GDD is the slope of length versus GDD, Post-spiny water flea is the change in intercept value following establishment and GDD · Post-spiny water flea is the change in slope after establishment; values in parentheses are standard errors of the estimates. A centered GDD variable was used for model fitting by subtracting 276 from each GDD observation; thus, model intercept represents estimated Walleye length at 276 GDD (approximately mid-June in most years).

Lake	Model	Δ BIC	Intercept	GDD	Post-spiny water flea	GDD · spiny water flea
Kabetogama	1	0.0	19.2 (1.5)	0.1024 (0.0004)	NA	NA
	2	7.5	20.8 (1.9)	0.1024 (0.0004)	3.3 (2.8)	NA
	3	7.0	19.1 (1.4)	0.1030 (0.0006)	NA	-0.0011 (0.0006)
	4	34.9	20.4 (2.1)	0.1030 (0.0006)	2.7 (3.0)	0.0009 (0.0005)
Rainy	1	8.9	22.3 (1.1)	0.0847 (0.0006)	NA	NA
	2	17.4	22.0 (1.4)	0.0848 (0.0006)	0.8 (2.1)	NA
	3	0.0	22.7 (1.1)	0.0819 (0.0009)	NA	-0.0046 (0.0011)
	4	27.8	23.3 (1.5)	0.0866 (0.0007)	1.4 (2.3)	-0.0048 (0.0009)
Vermilion	1	59.8	29.9 (1.7)	0.0836 (0.0007)	NA	NA
	2	63.1	33.4 (2.1)	0.0836 (0.0007)	6.7 (2.7)	NA
	3	0.0	28.7 (1.7)	0.0908 (0.0011)	NA	0.0110 (0.0013)
	4	22.1	25.1 (2.5)	0.0793 (0.0009)	6.5 (3.3)	1.239 (0.0012)

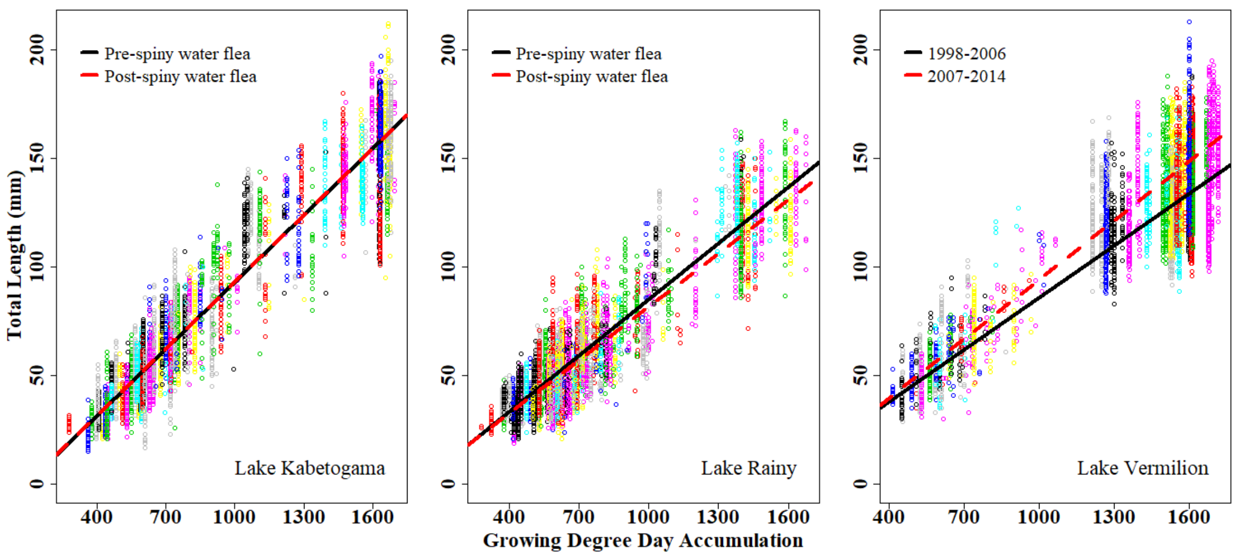

FIGURE 2: Predicted mean relationship between age-0 Walleye and growing degree days (GDD) for the 3 study lakes during the time periods of 1998-2016, representing 8-9 years before and 10-11 years after spiny water flea establishment in Lake Kabetogama and Rainy Lake. Circles are individual age-0 length measurements data shaded by year.

is eutrophic and Rainy is oligotrophic). The higher nutrient levels in Lake Kabetogama historically has produced faster growing walleyes than Rainy Lake. This study indicates this trend is still true although Lake Kabetgama age-0 Walleye growth has remained relatively the same and Rainy Lake age-0 Walleye growth has decreased following the establishment of spiny water fleas while the nearby reference lake age-0 Walleye growth has increased during the same time period. This provides evidence, although circumstantial, that spiny water flea can cause trophic cascades to higher levels of the food web. The statistical analysis shows that age-0 Walleye growth rates changed in spiny water flea lakes relative to the reference lake. This study is limited by the number of lakes used, two invaded

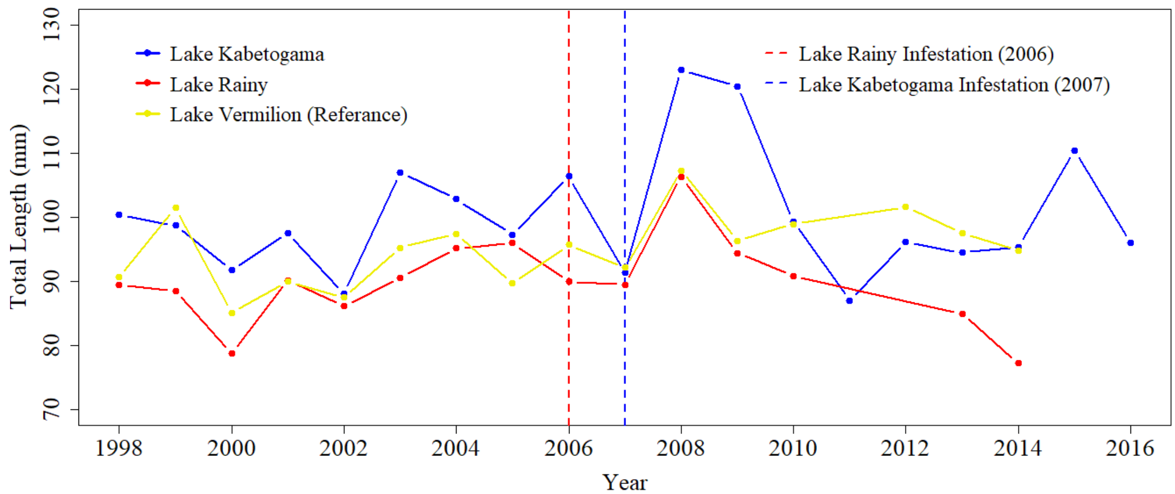

FIGURE 3: Annual predictions of mean age-0 Walleye length at 1050 GDD for the 3 study lakes.

and one reference making this its broader implications are less clear.

In both invaded lakes (Kabetogama and Rainy) the models show that age-0 Walleye mean length typically reach at least 20 mm by July pre and post-spiny water flea invasion. Spiny water flea densities in both invaded lakes increase rapidly from June to August with the subsequent decrease of native zooplankton during those months (Kerfoot et al. 2016). Spiny water flea may not directly influence age-0 walleye growth. According to Galarowicz et al. (2006) laboratory trials of juvenile Walleye of 20 mm in length started their ontogenetic diet shifts to macroinvertebrates and fish when zooplankton densities decreased. Once juvenile Walleye consume fish, they were less likely to consume zooplankton or macroinvertebrates after capturing the energetically more valuable fish prey. According to Einfalt and Wahl (1997) the capture efficiency by age-0 Walleyes are higher when prey fish, like Yellow Perch, are smaller. The decreased Yellow Perch length maybe contributing to a higher capture rate but the caloric intake per fish captured has also decreased. Therefore, it is likely post-spiny water flea age-0 Walleye must expel more energy to consume the same biomass of Yellow Perch showing a trophic level cascade.

Density dependence could be another factor that is influencing the growth of age-0 Walleye in Lake Kabetogama. Since the change in slot limit for Walleyes in 2006 female spawner biomass generally has increased with 2016 estimated female spawner biomass setting a record exceeding three pounds per acre for the first time in the lake's history (MNDNR 2018b). An increase in larger fish in the system maybe a limiting factor for age-0 Walleye growth by creating competition for food sources and higher predation rates contributing to the lack of year class success post 2006.

The invasion of spiny water flea has decreased the growth of Yellow Perch in both infected lakes (Kabetogama and Rainy). The trophic cascade to age-0 Walleye is evident by the decrease in growth in Rainy Lake and the static growth in Lake Kabetogama in comparison to the increased growth of age-0 Walleye in uninfected Lake Vermilion. It would be unrealistic to think there are no other abiotic or even biotic factors contributing to the changes of growth of age-0 Walleye. Therefore, future monitoring of both invaded lakes (Kabetogama and Rainy) and Lake Vermilion age-0 Walleye growth will be beneficial to assess the heath of the population and help with management plans. Lake Vermilion age-0 Walleye growth changes post-spiny water flea (2015) could shed some light on the effect spiny water flea have on age-0 Walleye growth, since the lake has shown an increase in growth 2007-2014 compared to 1998-2006.

Acknowledgements

I would like to thank Benjamin Vondra (Large Lake Specialist) of the International Falls, MN Fisheries Office and Matthew Hennen (Large Lake Specialist) of the Tower, MN Fisheries Office for supplying the data and their willingness to answer any questions I had throughout this study.

References

Barbiero, R. P. and M. L. Tuchman. 2004. Changes in the crustacean communities of Lakes Michigan, Huron, and Erie following the invasion of the predatory cladoceran *Bythotrephes longimanus*. Canadian Journal of Fisheries and Aquatic Sciences 61:2111-2125.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software 67:1-48

Chezik, K. A., N. P. Lester, P. A. Venturelli, and K. Tierney. 2014. Fish growth and degree-days I: selecting a base temperature for a within-population study. Canadian Journal of Fisheries and Aquatic Sciences 71:47-55.

Einfalt, L. M. and D. H. Wahl. 1997. Prey selection by juvenile walleye as influenced by prey morphology and behavior. Canadian Journal of Fisheries and Aquatic Sciences 54:2618-2626.

Galarowicz, T. L., J. A. Adams, and D. H. Wahl. 2006. The influence of prey availability on onto-genetic diet shifts of a juvenile piscivore. Canadian Journal of Fisheries and Aquatic Sciences 63:1722-1733.

Graeb, B. D. S., T. Galarowicz, D. H. Wahl, J. M. Dettmers, and M. J. Simpson. 2005. Foraging behavior, morphology, and life history variation determine the ontogeny of piscivory in two closely related predators. Canadian Journal of Fisheries and Aquatic Sciences 62:2010-2020.

Johannsson, O. E. and R. O'Gorman. 1991. Roles of predation, food, and temperature in structuring the epilimnetic zooplankton populations in Lake Ontario, 1981–1986. Transactions of the American Fisheries Society 120:193-208.

Kerfoot, W. C., M. M. Hobmeier, F. Yousef, B. M. Lafrancois, R. P. Maki, and J. K. Hirsch. 2016. A plague of waterfleas *Bythotrephes*: impacts on microcrustacean community structure, seasonal biomass, and secondary production in a large inland-lake complex. Biological Invasions 18:1121-1145.

MNDNR (Minnesota Department of Natural Resources). 2018a. Walleye and Saugers. Accessed 12 October 2018. https://www.dnr.state.mn.us/fish/walleye/index.html.

MNDNR (Minnesota Department of Natural Resources). 2018b. Fisheries Management Lake Survey Report, Lake Kabetogama. Large Lake Survey DOW:69-0845-00.

NOAA (National Oceanic and Atmospheric Administration). 2018. Generated on 13 September 2018. National Environmental Satellite, Data, and Information Service. Station: International Falls, Minnesota International Airport. USUSW00014918

Neuheimer, A. B. and C. T. Taggart. 2007. The growing degree-day and fish size-at-age: the overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences 64:375-385.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Raftery, A. E. 1995. Bayesian model selection in social research. Sociological Methodology 25:111-163.

Schwarz, G. 1978. Estimating the dimension of a Model. The Annals of Statistics 6:461-464.

Staples, D. F., R. P. Maki, J. K. Hirsch, W. C. Kerfoot, J. F. LeDuc, T. Burri, B. M. Lafrancois, and J. Glase. 2017. Decrease in young-of-the-year Yellow Perch growth rates following *Bythotrephes longimanus* invasion. Biological Invasions 19:2197-2205.

Strecker, A. L., S. E. Arnott, N. D. Yan, and R. Girard. 2006. Variation in the response of crustacean zooplankton species richness and composition to the invertebrate predator *Bythotrephes longimanus*. Canadian Journal of Fisheries and Aquatic Sciences 63.9:2126-2136.

Uphoff, C. S., C. W. Schoenebeck, W. W. Hoback, K. D. Koupal, and K. L. Pope. 2013. Degree-day accumulation influences annual variability in growth of age-0 Walleye. Fisheries Research 147:394-398.

Vondra, B. A. 2012. Investigation of Natural Reproduction of Walleye in Lake Kabetogama. Completion Report. Minnesota DNR (Department of Natural Resources) Fish and Wildlife. F 29 R(P) 30(1). Area F217. Study 4. Job 867.