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GROWTH OF PELAGIC AGE-0 YELLOW PERCH IN RELATION TO HATCH DATES AND WATER TEMPERATURE IN NORTH-CENTRAL MINNESOTA LAKES

by

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GROWTH OF PELAGIC AGE-0 YELLOW PERCH IN RELATION TO HATCH DATES AND WATER TEMPERATURE IN NORTH-CENTRAL MINNESOTA LAKES

Ethan Karppinen

Exposure to consistent water warming rates and access to abundant populations of edible sized zooplankton affects growth and increases the probability of survival for newly hatched Yellow Perch *Perca flavescens*. Seven lakes with varying physical characteristics were selected in north-central Minnesota to study abiotic (water temperature) and biotic (zooplankton community and fish growth) progressions during the spring and early summer (April-June). Mean water temperatures from ice-out to 28 June (11.98-14.62 °C) had significant relationships with mean depth ($P < 0.01$, $R^2 = 0.85$), max depth ($P < 0.01$, $R^2 = 0.73$), and total volume ($P < 0.01$, $R^2 = 0.54$). Hatch periods ranged from 13 to 19 days in 2015 and 13 to 25 days in 2016. Cumulative degree-days (CDD) were used to predict Yellow Perch hatch periods and explain growth. CDD predicted 21-81% of hatch periods in 2015 and 11-50% in 2016. Mean predicted total lengths at 28 June were 19.65-30.41 mm in 2015 and 20.88-28.54 mm in 2016. There was a significant relationship between CDD and predicted total length ($R^2 = 0.62$, $P < 0.01$) to explain differences in Yellow Perch total length while inhabiting the pelagic zone. Observed gape measurements were highly correlated with predicted gapes from the Schael formula ($R^2 = 0.89$, $P < 0.01$) that was used to assess the availability of edible sized zooplankton for age-0 Yellow Perch in each lake. No predator-prey mismatches were found and earlier hatch dates produced age-0 Yellow Perch with greater predicted total lengths in late June on the majority of lakes. This suggests that earlier hatched Yellow perch have an advantage over later hatched Yellow Perch in attaining greater lengths by late June. Our study provides information on a variety of physical and biological progressions in lakes, which may be used for fisheries management practices in the future.

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INTRODUCTION

Yellow Perch *Perca flavescens* are an important food source for many species and a popular game fish for anglers in temperate lake ecosystems. Studying early stages of life, particularly the first two months, provides information about the upcoming cohort of age-0 Yellow Perch. Investigations into diet, growth, and recruitment of age-0 Yellow Perch have been studied throughout North America, especially in the Midwest, (Claramunt and Wahl 2000; Meerbeek et al. 2002; Graeb et al. 2004; Isermann and Willis 2008; Weber et al. 2011; Kaemingk et al. 2011; Kaemingk et al. 2014) but few studies from Minnesota lakes have been published (Pycha and Smith 1955; Ney and Smith 1975; Whiteside et al. 1985).

Previous age-0 Yellow Perch studies of potential biotic and abiotic factors that affect hatch dates and growth in natural settings have provided mixed results (Isermann and Willis 2008; Weber et al. 2011; Kaemingk et al. 2014). Availability of suitable-size prey for fish in early life stages is important for survival (Claramunt and Wahl 2000; Leclerc et al. 2011; Kaemingk et al. 2014). In addition to prey abundance, water-warming rate during the spring is another important factor affecting fish (Power and van den Heuvel 1999). Larval fish survival is thought to be size dependent and lakes with suitable growing conditions (water temperature, zooplankton abundance, etc.) generally experience higher recruitment (Claramunt and Wahl 2000; Irwin et al. 2009). There are many factors affecting age-0 Yellow Perch abundance making it difficult to predict year class strength (Irwin et al. 2009; Weber et al. 2011), but investigating Yellow Perch populations during the period between 10 and 60 days after hatching can provide information about hatching periods and growth during early stages of life.

Recruitment of Yellow Perch year classes is variable among lakes and years with cohorts classified as strong, weak, or missing (Isermann et al. 2007). Age-0 Yellow Perch densities in late May and early June were significantly related to juvenile abundance in late summer on South Dakota lakes suggesting that early life stage densities can be an early indicator of subsequent year class strength (Anderson et al. 1998). Yellow Perch prefer to spawn and lay ribbons of eggs in shallow vegetation or rocky substrate near shore habitat (Hokanson 1977; Huff et al. 2004; Weber et al. 2011) where the eggs and larvae are exposed to fluctuating environmental conditions of wind, precipitation, and temperature (Clady and Hutchinson 1975; Clady 1976; Isermann and Willis 2008). At times, wind-generated current may even push larval fish to areas less suitable for survival (Quist et al. 2003). Survival of larval Yellow Perch has been associated with warmer water and lower frequencies of high wind (Clady 1976).

Sizes of age-0 fish are usually dependent on the hatch date with earlier-hatching fish having an advantage over later-hatching fish because of growth to a greater size (Isermann and Willis 2008). Fish that hatched later may be more susceptible to predation due to their smaller size and ease of capture. However, hatching too early increases the likelihood of larval Yellow Perch being exposed to colder water temperatures, more variable spring weather conditions, or low abundance of food sources such as appropriate-sized zooplankton. Negative effects of cold temperatures were found in small wetlands (Longhenry et al. 2010) and Midwest lakes (Clady 1976; Ward et al. 2004). Cold fronts likely affect larval fish movement and delay development making them prone to predation for longer periods (VanDeHay et al. 2013). Broad temporal hatch periods likely increase survival in variable environments by allowing some larval Yellow Perch to encounter proper conditions for growth (Isermann and Willis 2008). Power and van den Heuvel (1999) reported that Yellow Perch 40 days or less in age are more susceptible to fluctuations in growth from prey abundance and water temperature than older fish and the generally short growing seasons in northern Minnesota may amplify the effect of temperature changes compared to lakes further south, with longer growing seasons. Because water temperature has been correlated to age-0 Yellow Perch growth in previous studies it is important to monitor water temperature and growth in each study lake to explain differences in age-0 Yellow Perch sizes after the spring warming period (Power and van den Heuvel 1999; Weber et al. 2011; Kaemingk et al. 2014). However, water temperature is not the only variable known to affect age-0 Yellow Perch growth. Additional variables and growth should to be measured to monitor for lake specific relationships.

Yellow Perch spawning usually occurs when the water temperature is between 7-11 °C and hatching typically occurs within 10-20 days (Clady 1976). Although the length of time for Yellow Perch to hatch (hatch period) has ranged from as few as five days (Isermann and Willis 2008) to as long as nine weeks (Fitzgerald et al. 2001). The wide range of incubation and hatch periods likely resulted from differences lake size and geographic location. After hatching, Yellow Perch immediately migrate to the limnetic zone to avoid predation and begin to forage on appropriate-sized zooplankton species after their yolk sac is depleted (Greab et al. 2004). According to Whiteside et al. (1985), Yellow Perch <25 mm in total length have a 30 to 40 day pelagic phase on smaller lakes, while in the Great Lakes this phase is reported to be >60 days (Dettmers et al. 2005; Fulford et al. 2006; Beletsky et al. 2007). After foraging in the limnetic zone, Yellow Perch with total lengths ranging from 40 to 60 mm begin to switch their diets to benthic invertebrates, and eventually to fish once a total length of 80 mm is reached (Greab et al. 2006).

Many fisheries throughout North America are supported by Yellow Perch because they provide an essential prey source to gamefish such as Walleye *Sander vitreus* and are themselves a targeted species by anglers (Isermann and Willis 2008). Investigating the lake basin-scale factors that influence spring and early summer water temperatures, zooplankton availability, and subsequent growth of age-0 Yellow Perch will help managers understand potential Yellow Perch recruitment and consequences for other fish species. Thus, the objectives of this study were to 1) describe Yellow Perch hatch periods in north-central Minnesota, 2) predict hatch periods of age-0 Yellow Perch using spring water temperatures, 3) describe growth rates for age-0 Yellow Perch in north-central Minnesota lakes, 4) use temperature specific growth rates to predict age-0 Yellow Perch total length, 5) determine if age-0 Yellow Perch were food limited in the study lakes during spring and early summer, and 6) establish relationships between lake warming rates and lake morphology.

METHODS

Site description

Sample lakes are located in north-central Minnesota within a 65 km radius of Bemidji, MN. This area of north-central Minnesota straddles two major watersheds, the Red River Basin and Mississippi River Basin. The seven lakes selected for the study were

Big Lake (Division of Waters (DOW) #04-0049-00), Pike Bay (DOW #11-0415-00), Big Turtle Lake (DOW #04-0159-00), Lake Julia (DOW #04-0166-00), Blackduck Lake (DOW #04-0069-00), Kabekona Lake, (DOW #29-0075-00) and Steamboat Lake (DOW #11-0504-00). All but two study lakes (Julia and Blackduck) are located in Mississippi River Basin. Trophic status of the study lakes range from mesotrophic to oligotrophic and the sample lakes presented a large range of morphometrics (Table 1). These lakes have ice cover four to six months during the annual cycle (Jensen et al. 2007). Sample lakes (Big, Big Turtle, Pike Bay, Steamboat, and Kabekona) have flowing water inputs and outputs creating a higher connectivity. All of the lakes are managed for Walleye and stocked with Walleye fry or fingerlings. Lakes stocked with fry are stocked annually (Pike Bay and Big), every other year (Big Turtle), two out of three years (Julia and Blackduck), or alternated with fry and fingerlings every year (Steamboat). Kabekona Lake was the only lake stocked exclusively with fingerlings and this occurred on an every other year basis. Fingerling stocking into Kabekona and Steamboat is the result of poor success of past fry stocking events. Age-0 Yellow Perch recruitment and growth rates were unknown for all of the lakes.

Objective 1: Yellow Perch hatch periods

Neuston net tows were used to sample larval and juvenile Yellow Perch during their pelagic phase. Tows were conducted twice on each lake with 10-day intervals separating sampling periods. Sampling occurred between 12 June and 27 June in 2015 and 2016. Sample dates were based on weekly lake temperature profiles that indicated when first spawning temperatures were observed (7 $^{\circ}$C; Clady 1976), followed by the minimum time needed for eggs to develop (10 days; Clady 1976), and an additional 20-

40 days to allow Yellow Perch to grow to the preferred size of 15-25 mm (Whiteside et al. 1985). At this size age-0 Yellow Perch are catchable in pelagic habitats, near the maximum size before migrating to littoral habitats, daily growth rings on otoliths were still legible, and key physical characteristics have developed for easy identification.

The neuston net (500 μm, 1.0 x 1.5m) was towed during daylight hours following the methods of Kaemingk et al. (2014). Each lake was divided into quadrants and a minimum of four random tows was conducted in the limnetic zone (one per quadrant). Additional tows were made when less than 30 fish were captured in the initial four tows to meet minimum sample size requirements. Tow duration ranged from two to five minutes and varied to reduce back flushing resulting from high concentrations of zooplankton and algae. The volume of water towed was estimated using the time fished in combination with average tow speed (1.75 m/s), and volumes towed were used to calculate age-0 Yellow Perch densities. Differences in Yellow Perch densities between lakes and years were determined using multifactor ANOVA.

After temporary storage in 90% alcohol for three to six months, sampled Yellow Perch total lengths were recorded and sagittal otoliths were extracted from 300 to 350 fish each year. A maximum of 30 fish were aged per lake per sampling period, with a maximum of 60 fish aged from a single lake each year. Both otoliths from individual fish were mounted on a glass slide using a small amount of a cyanoacrylate adhesive. Otoliths were sanded with 2000-grit wet/dry sandpaper and viewed at 200x magnification. Immersion oil was added to the surface of the otoliths prior to viewing to improve clarity. Otoliths were projected on a computer screen and daily rings were counted to assign ages. Daily rings were counted three times by one reader and the mean of the three counts was used to determine the daily age (DA). Hatch dates (HD) and date captured (DC) were reported as day of year and one day was added to the age determination for each fish, because initial growth increments become visible one day following hatch (Isermann and Willis 2008). Thus, hatch dates were estimated using the following formula:

$$HD = DC - DA + 1.$$

The hatch period was identified as the observed range of hatch dates and the median hatch date for each lake was also reported.

Total length at capture in relation to age was modeled using linear regression analysis. Linear regression models were compared using Akaike's information criterion (AIC_c; Akaike 1978; Burnham and Anderson 2002). Three candidate models were selected to test whether or not the age-length relationship differed by lake (Age = TL; Age = TL + Lake; Age = TL· Lake).

Objective 2: Prediction of Yellow Perch hatch periods using water temperature

Past literature indicated that spawning occurs from 7 to 11 °C in northern Minnesota lakes systems (Clady 1976) and that Yellow Perch eggs require 95-108 Cumulative Degree-Days (CDD; °C days) to fully develop and hatch (Hinshaw 2006). Based on those criteria, I estimated the earliest and latest potential hatch dates for age-0 Yellow Perch by summing the non-negative Degree-Days (DD; °C days) values using the following equation from (Chezik et al. 2014a):

$$DD = (T_{max} + T_{min}) / 2 - T_0$$

where DD was calculated from temperatures measured by an Ibutton temperature logger (DS1921Z-F5, Maxim Integrated, San Jose, CA) located one meter deep in the water column in close proximity to the deepest location in each lake. I assumed this location accurately reflected temperature fluctuations occurring at near-shore habitats where Yellow Perch eggs were deposited. T_{max} and T_{min} represented maximum daily temperature and minimum daily temperature, respectfully, measured in degree Celsius. Mean water temperature was then subtracted by the base temperature (T_0) needed for Yellow Perch egg development (5 °C; Hinshaw 2006). CDD calculations for the start of hatch and end of hatch were initiated when water temperature first reached 7 and 11 °C, respectively. The predicted date of the start and end of hatch periods were defined as when 95 and 108 CDD were achieved, respectively. Linear regression analysis was used to test for a relationship between observed median hatch date and the midpoint of the predicted hatch periods. The percentage of the observed hatch period included in the predicted hatch period was also reported.

Objective 3: Age-0 Yellow Perch daily growth rates

Daily growth rates were calculated for each fish that was aged using the following equation by Isermann and Willis (2008):

$$GR = (TL_{capture} - 4.7) / DA$$

where specimen shrinkage from preservation was accounted for by adding 1.25 mm to total length at capture (Fisher et al. 1998). Average total length at hatch (4.7 mm; Kaemingk et al. 2014) and total length at capture ($TL_{capture}$) were expressed in mm, while age of the fish (DA) was in days. Differences in growth rates were analyzed using a multifactor ANOVA and pairwise comparisons to test for significance between lakes and years. The mean and range of growth rates were compared among lakes in the study and to other Yellow Perch studies in the region.

Objective 4: Explaining predicted total length using cumulative degree-days

For this objective, CDD was calculated using temperature logger data collected at one, three, and five meters deep in the water column in close proximity of the deepest location of each lake. The top five meters were chosen because age-0 Yellow Perch likely inhabit this portion of the water column during their pelagic phase (Whiteside et al. 1985). The CDD equation from objective 2 was also used to predict total length, however, (T_0) was changed to 6 °C, the lowest temperature needed to initiate Yellow Perch growth (Hokanson 1977). Total CDDs were calculated for each individual fish from the observed hatch to 28 June, which was the latest date fish were captured in 2015 and 2016. Total CDD was averaged from the three depths (1, 3, and 5 m) and compared to predicted total length for each fish.

Predicted total length on 28 June was calculated using the following equation:

$$TL_{predicted} = (DOY_{end} - DOY_{capture}) \cdot GR + TL_{capture}$$

where Yellow Perch predicted total length ($TL_{predicted}$) and total length at capture ($TL_{capture}$) are in mm; the end date (DOY_{end}: 28 June) and capture date ($DOY_{capture}$) are in day of year (DOY); and growth rates (GR) are represented as millimeters per day (mm/day). This method allowed for TL to be determined by date and compared between lakes. To test for differences in predicted total length among lakes and years, a multifactor ANOVA, and pairwise comparison was used. Regression analysis was used to test for a relationship between CDD and predicted total length at 28 June.

Objective 5: Age-0 Yellow Perch food availability

Zooplankton tows were conducted at the deepest point on each lake. One vertical zooplankton tow was conducted every five to ten days beginning in late April/early May in 2015 and 2016. Zooplankton tow intervals were every five days until hatching was estimated to be complete for Yellow Perch then sampling intervals were ten days following the estimated hatching period. Vertical tows were made from just above the lake bottom to the surface near the deepest point in the lake basin. The simple zooplankton net had an 80-µm mesh with a 30-cm diameter opening. The net was lowered to within 0.5 m of the bottom and withdrawn at a rate of approximately 0.5 m per a second. If bottom sediments were observed in the plankton net following a tow, the sample was discarded and a new sample was taken. Contents were rinsed into a sample bottles and preserved with 90% alcohol. Minnesota Department of Natural Resources (MN DNR) personnel analyzed the samples.

Food availability was based on zooplankton mean total body length, species composition, and total biomass present for each emerging daily cohort of Yellow Perch. To estimate the prey sizes Yellow Perch could possibly consume, gape size (G) was calculated using the formula from Schael et al. (1991):

$$G = -0.597 + 0.159 \cdot \mathrm{TL}$$

where total length (TL) and gape (G) are in mm. Yellow Perch total length and gapes were predicted for each day from hatch to 28 June and compared to the zooplankton community. Zooplankton species with a total body length smaller than the predicted gape were considered potential prey items (Schael et al. 1991). For each zooplankton tow the smallest predicted Yellow Perch gape was compared to the smallest zooplankton species. This conservative approach predicted when Yellow Perch gapes were too small to consume the smallest zooplankton species available, indicating a potential predator-prey mismatch (Schael et al. 1991). Gape was measured with a digital caliper for every fish aged, and measured gapes were compared to the predicted gapes form the Schael formula using linear regression.

Species composition from the plankton tows was used to represent different prey opportunities for Yellow Perch, and plankton total biomass was used to compare of available zooplankton for each lake and year. Yellow Perch predicted gapes and zooplankton species size comparisons were done for each lake for each of the zooplankton sampling intervals to determine the presence or absence of edible sized zooplankton. In addition, gapes of Yellow Perch ranging from 4.7 (newly emerged) to 15 mm (gape is no longer limiting zooplankton consumption) in total length were compared to observed zooplankton species.

Objective 6: Relationships between lake warming rates and lake morphology

Prior to ice off in early April, temperature loggers were deployed in each lake suspended near the deepest location. The ice-out dates were determined from observations by residents on sample lakes and from readings from temperature loggers deployed near the surface of the water column (one meter) following the methods of Cahill et al. (2005). Temperatures (°C) were recorded every three hours until the middle of July in each year. Observed water temperatures were used to describe warming and cooling periods between lakes and years from ice-out to 28 June. Mean water temperatures from ice-out to 28 June were regressed with lake morphology predictor variables (surface area, mean depth, max depth, total volume, and littoral area) to test for significant relationships.

RESULTS

Objective 1: Yellow Perch hatch periods

During the two years of sampling, 126 neuston tows were completed on seven lakes. Mean tow duration was 276.20 sec (SD = 93.33), mean tow speed was 1.11 m/s (SD = 0.03), and mean volume filtered was 531.45 m^3 (SD = 181.21). Two sampling periods (mid-late June) were used at all lakes except Steamboat where no Yellow Perch were captured in 2016 despite extensive additional effort. Yellow Perch were captured in 109 tows with >10 fish captured in 69 of the tows. Yellow Perch densities ranged from 0.00 to 476.40 ind/100 m^3 in 2015 and 2016. Densities varied significantly between lakes (ANOVA: $F_{6,118} = 8.5262$, $P < 0.01$) but lakes did not vary significantly by years (ANOVA: $F_{1,118} = 0.1486$, $P = 0.70$). Yellow Perch density in Blackduck Lake was greater than in Big, Julia, Kabekona, and Steamboat lakes and density in Steamboat Lake was significantly lower than Big Turtle, Blackduck, and Pike Bay in 2015 and 2016 (Figure 1).

A total of 679 age-0 Yellow Perch were aged from the two years of sampling with ages ranging from 11 to 61 days. Based on counts of daily rings in otoliths, Yellow Perch hatched from late April to early June in both years. The hatch period for all lakes started later and lasted longer in 2015, while hatch periods started earlier and were shorter in duration in 2016 (Figure 2). In 2015, observed hatch dates ranged from 30 April to 5 June with Steamboat having the earliest hatch dates (median = 9 May) and Kabekona having the latest (median = 26 May; Figure 2). Hatch periods were as long as 19 days (Kabekona) and as short as 13 days (Big; Figure 2). In 2016, observed hatch dates ranged from 24 April to 26 May with Julia having the earliest hatching fish and Kabekona having the latest (Figure 2). Median hatch dates ranged from 4 May (Big) to 18 May (Kabekona) with hatch periods lasting up to 25 days (Julia) but were as short as 13 days (Blackduck;

Figure 2). Age-0 Yellow Perch total length distributions were unimodal in all lakes both years suggesting Yellow Perch hatched as one cohort on all lakes. Yellow perch age and total lengths were significantly related and lake specific (R^2 = 0.73, P < 0.01, RMSE = 4.62; Table 2; Figure 3). Coefficients of the best-supported model are found in Table 3. Predictive models allow for future predictions of hatch dates from total length rather than aging otolith structures.

Objective 2: Prediction of Yellow Perch hatch periods using water temperature

No significant relationship was observed between ice-out date and median hatch date (R^2 = 0.01, P = 0.70) or observed date of mid-spawning period temperature (9 ˚C) and median hatch date (R^2 = 0.009, P = 0.75). Predicted hatch periods based on CDD ranged from 8 May to 3 June in 2015 and 10 May to 1 June in 2016. Predicted lake-specific hatch periods overlapped with 21-81% and 11-50% of observed hatch periods in 2015 and 2016, respectively (Figure 2). The relationship between observed median hatch date and the midpoint of predicted hatch periods from CDD (R^2 = 0.39, P = 0.02; Predicted Median Hatch Date = 60.8622 + 0.5741 · Observed Median Hatch Date) was significant but had low predictive capability (Figure 4).

Objective 3: Age-0 Yellow Perch daily growth rates

Growth rates were significantly different between years (ANOVA: $F_{1,671}$ = 133.633, P < 0.01) and lakes (ANOVA: $F_{6,671}$ = 19.262, P < 0.01). Growth rates for individual Yellow Perch ranged from 0.31 (Big Turtle) to 0.64 mm/day (Pike Bay) in 2015 and ranged from 0.23 (Julia) to 0.59 mm/day (Julia) in 2016 (Figure 5). Mean growth rates for all of the lakes except for Big Turtle and Steamboat (no fish sampled in 2016) were slower in 2015 than 2016. Big had the fastest mean growth rate in 2015 (0.52

mm/day, SD = 0.05) and Blackduck had the fastest in 2016 (0.45 mm/day, SD = 0.05; Figure 5). Big Turtle had the slowest mean growth rate in 2015 (0.40 mm/day, SD = 0.05) and Pike Bay had the slowest mean growth rate in 2016 (0.39 mm/day, SD = 0.05; Figure 5).

Objective 4: Explaining predicted total length using cumulative degree-days

The average CDD from depths of 1, 3, and 5 meters ranged from 366.42 (SD = 27.72; Kabekona) to 649.05 (SD = 17.86; Big) during 2015 and 417.34 (SD = 19.19; Kabekona) to 572.88 (SD = 21.33; Big) during 2016. Mean CDD increased on all lakes, except for Big Lake in 2016. The relationship between average CDD and predicted total length for 28 June in 2015 and 2016 was significant ($R^2 = 0.62$, $P < 0.01$; TL = 10.36344 + 0.02862 · Mean CDD; Figure 6).

Predicted total lengths showed no significant differences between years (ANOVA: $F_{1,671} = 0.8739$, $P = 0.35$) but a significant difference was observed among lakes (ANOVA: $F_{6,671} = 107.7318$, $P < 0.01$). Mean predicted total lengths among lakes ranged from 19.65 to 30.41 mm in 2015 and 20.88 to 28.54 mm in 2016 (Figure 7). Kabekona had the shortest predicted total length in both 2015 (Mean = 19.66 mm, SD = 0.66) and 2016 (Mean = 20.88 mm, SD = 0.40), whereas the longest predicted lengths were from Steamboat in 2015 (Mean = 30.41 mm, SD = 1.26) and Blackduck in 2016 (Mean = 28.54 mm, SD = 0.55; Figure 7).

Objective 5: Age-0 Yellow Perch food availability

Predicted gape sizes and observed gape sizes for Yellow Perch were closely related ($R^2 = 0.89$, $P < 0.01$), however, predicted gapes averaged 0.25 mm greater than observed gapes (Figure 8). Predicted gapes were used to assess the presence or absence of appropriate-sized zooplankton. Zooplankton composition indicated that there was zooplankton in relation to Yellow Perch gape size from hatch to capture in all of the study lakes. Edible sized zooplankton species/developmental stages were present from the time of Yellow Perch hatch to their capture during both years. Zooplankton species assemblages ranged from 4 to 13 species in 2015 and 5 to 13 species in 2016. In deeper lakes, copepods were the largest component of zooplankton biomass across all sample dates in 2015 (58-94% from Kabekona and Pike Bay) and 2016 (57-98% from Steamboat, Kabekona, and Pike Bay). Cladocerans were important in Julia in 2015 (88-98%) of biomass and 2016 (54-93%) through late June with peaks of copepods varying between years. Copepod percent biomass varied in the other lakes during late April to mid-May 2015 (1-92%; Big Turtle, Blackduck, Big, and Steamboat) and 2016 (57-92%; Big Turtle, Blackduck, and Big), while cladoceran biomass peaked in late May to early June each year (Figure 9). Copepod nauplii were present in all tows and were one of two species/developmental stages sampled (*Chydorus sphaericus*) with a mean total length small enough for emerging Yellow Perch to consume. The number of appropriate-sized zooplankton species increased in tandem with comparisons of Yellow Perch greater in total length.

Objective 6: Relationships between lake warming rates and lake morphology

In 2015, water temperatures increased during 25 April to 5 May (0.44 to 0.61 $^{\circ}$C/day), decreased during 8-14 May (–0.30 to –0.48 $^{\circ}$C/day), increased 19-27 May (0.40 to 0.74 $^{\circ}$C/day), and decreased 28-31 May (–0.22 to –0.61 $^{\circ}$C/day; Figure 10). In 2016, water temperatures gradually increased following ice-out until late April when water temperatures increased (0.34 to 0.52 $^{\circ}$C/day). Water temperatures decreased during 9-15

May (–0.15 to –0.64 °C/day), and warmed during 16-24 May (0.55 to 0.71 °C/day; Figure 10). Mean water temperature from ice-out to 28 June was greater in 2016 than 2015 in five of the seven lakes (Big Turtle: 0.38 °C, Blackduck: 0.35 °C, Big: 0.24 °C, Steamboat: 0.23 °C, and Pike Bay: 0.32 °C). Mean water temperatures among lakes and years ranged 11.98 to 14.62 °C, with Kabekona Lake, the only oligotrophic lake in this study, markedly cooler than the other sample lakes (Figure 10).

The study lakes differed in morphology (surface area, max depth, mean depth, littoral zone, and volume), which affected how individual lakes warmed from ice-out to late June. Lake characteristics that were significant in explaining warming rates in 2015 and 2016 were maximum depth (R^2 = 0.73, P < 0.01; Mean Water Temperature = 14.6754 – 0.05391 · Maximum Depth) and total volume (R^2 = 0.54, P < 0.01; Mean Water Temperature = $1.432e^{01} - 1.026e^{-08}$ · Total Volume; Figure 11). Surface area (R^2 = 0.002, P = 0.88) and littoral area (R^2 = 0.08, P = 0.33) did not explain differences in water warming rates. Mean depth (the ratio of volume to surface area) had the strongest relationship to mean temperature (R^2 = 0.85, P < 0.01; Mean Water Temperature = 14.74 – 0.1615 · Mean Depth; Figure 11), as lakes with a greater mean depth required additional energy to warm water. For example, deeper lakes (Steamboat, Pike Bay, and Kabekona) required additional days from ice-out to reach a water temperature of 15 °C in comparison to shallower lakes (Big Turtle, Julia, Blackduck, and Big) for 2015 (Mean = 7.67 days) and 2016 (Mean = 2.17 days).

DISCUSSION

Hatch dates derived from otolith ages indicated age-0 Yellow Perch emerged as one cohort in north-central Minnesota lakes during 2015 and 2016. Lakes in this study did not produce more than one cohort each year, in contrast to much larger lakes like the Great Lakes. The Great Lakes can produce multiple cohorts due to different habitats and water temperature conditions (Fitzgerald et al. 2001). Hatch periods had durations of 13 to 25 days for both years. This study had similar hatch periods (6-22 days) to other age-0 Yellow Perch studies (Clady 1976; Weber and Les 1982; Powles and Warlen 1988; Post et al. 1995; Fisher 1996; Isermann and Willis 2008; Kaemingk et al. 2011; Kaemingk et al. 2014). The timing of ice-out and warming trends were similar for both years of this study, but years with more sporadic weather could substantially change spawning, incubation, and hatch durations (Weber and Les 1982). Steamboat Lake in 2016 was the only instance when Yellow Perch were not captured in a given year. This was likely due to a year class failure, as neuston netting was effective in all other lakes. Moreover, Yellow Perch were captured in Steamboat in 2015. Water temperatures and zooplankton availability did not appear to be reasons for the year class failure. One possible explanation for the year class failure was daily wind speeds. High winds (>25.74 kmph) were orientated east to west in the Bemidji area for 8 consecutive days during 22-30 April in 2016 (Weather Underground 2018). Due to the east-west orientation of Steamboat Lake, high winds may have created less favorable conditions for age-0 Yellow Perch survival.

Hatch periods and median hatch dates of age-0 Yellow Perch were not well predicted from lake water temperatures. According to temperature measurement recommendations by Hinshaw (2006), thresholds for the minimum temperature (5 °C) required for egg growth and total CDD (95 and 108) needed for egg development predicted at least a portion of the observed hatch periods in all lakes in both years.

Hinshaw’s temperature recommendations were developed in a controlled setting and were not expected to predict exact hatch periods in natural settings. According to Hinshaw’s criteria, start times for hatch periods were earlier in most of the lakes than predicted and the duration of hatch periods were underestimated in all comparisons. Predicting median hatch times for both years by using the midpoint of the CDD hatch period predictions accounted for only 39% of the variation. Possible sources of error included the choice of indicator temperatures for the start and end of spawning, and spatial differences in water temperature within each lake. Adjusting indicator temperatures and collecting water temperature measurements from multiple areas could alter hatch period predictions and increase the accuracy of predicted hatch periods and median hatch dates. Using the hatch period and median hatch date predictions from CDD provided only a very general estimate of hatch dates, that may not be useful when more accurate predictions are needed.

Total lengths of age-0 Yellow Perch <37.3 mm were related to their daily ages. The total length and age relationship was significant, linear, and capable of predicting Yellow Perch age ± 4.6 days. This reinforces the findings of Post and Prankevicius (1987), where growth was considered linear during the first 40 days of life. Length-based age predictions were more accurate with the addition of lake name to the analysis, indicating growth rates were lake specific. Length-age relationships differed between lakes in a similar geographic location, likely due to differences in environmental conditions in each lake, which may be due to differences in lake morphology. Lake morphology, specifically mean depth, indicated study lakes with greater average depths produced colder average water temperatures. These water temperatures likely affected age-0 Yellow Perch hatch dates and growth rates, which resulted in lake specific length-age relationships. Although, age-0 Yellow Perch may have hatched earlier of later in a given year, similar total lengths were reached in each lake by the beginning of July in 2015 and 2016. Prior to this study, differences in age-length relationships between lakes for age-0 Yellow Perch have not been investigated in this geographic location (north-central Minnesota). However, variation in age-0 fish growth has been observed in studies sampling multiple habitats in Lake Michigan and between lakes in study areas ranging from local to regional geographic areas (Fisher and Willis 1997; Power and van den Heuvel 1999; Claramunt and Wahl 2000; Weber et al. 2011). An important finding of my study is that total length can be used to predict Yellow Perch ages, thus avoiding the extensive work of extracting otolith structures and counting daily growth rings. However, aging otolith structures are necessary to establish lake specific relationships for more precise measurements of age.

Age-0 Yellow Perch growth rates were similar to rates reported by previous literature. Literature values of growth rates range from 0.09-0.52 mm/day for age-0 Yellow Perch inhabiting pelagic habitat compared to 0.23-0.64 mm/day observed in my study (Weber et al. 2011; Kaemingk et al. 2014). Age-0 Yellow Perch in my study were captured at greater total lengths (>25 mm) and ages (>40 days) than previously documented for small lakes (Whiteside et al. 1985), indicating the fish may inhabit the limnetic zone and have linear growth for longer periods.

According to the literature, growth of age-0 Yellow Perch is primarily regulated by hatch dates, water temperature, and zooplankton availability (Greab et al. 2004; Fulford et al. 2006; Greab et al. 2006; Isermann and Willis 2008; Kaemingk et al. 2014).

Hatch dates seemed to have the biggest influence on growth rates in the Bemidji area. Hatching began earlier (3-10 days) in 2016 on all lakes, which exposed age-0 Yellow Perch to less favorable daily water temperatures causing slower initial growth. Median growth rates were consistently low for Big Turtle and high for Blackduck between years. Interestingly, hatching began at similar times between years (3-4 days) on both lakes. Yellow Perch hatch periods were later in 2015, providing newly hatched age-0 Yellow Perch warmer water temperatures during early growth. In contrast, mean water temperatures from hatch to capture were higher on 71% of the lakes in 2016, whereas growth rates were slower in 2016, and all lakes contained appropriate sized zooplankton species throughout the study.

Similar total lengths were predicted at 28 June in each lake in 2015 and 2016 despite differences in water temperature between years. Predicted total lengths from each lake were used to compare year class total lengths prior to the age-0 Yellow Perch moving to littoral habitat. Previous studies have suggested and reviewed temperature thresholds to use when calculating CDD for age-0 Yellow Perch (Chezik et al. 2014a; 2014b). Temperatures from 0 to 13.5 °C were used in some other studies for the minimum temperature for physiological growth of Yellow Perch or European Perch (Mills et al. 1989; Tardif et al. 2005). In my study a temperature threshold of 6 °C was used, which is the minimum temperature required for Yellow Perch growth, according to Hokanson (1977). By including hatch dates and mean daily water temperatures in calculating CDD, it was a strong metric to explain the influence of water temperature on age-0 Yellow Perch growth. In three instances (Julia, Big, and Pike Bay) CDD was greater and predicted total length was shorter between years, suggesting other variables (abiotic and biotic) would be necessary to explain predicted total lengths. Four of the lakes (Big Turtle, Julia, Blackduck, and Kabekona) demonstrated Yellow Perch were capable of surviving earlier hatch dates and reached longer total lengths. This reinforces previous findings where hatch dates are an important variable influencing age-0 Yellow Perch total length (Isermann and Willis 2008). Assessing total length at this point in time is an indicator of which age-0 Yellow Perch populations are most fit to transition to littoral habitats and benthic invertebrates. The age-0 Yellow Perch with the greatest average total lengths to transition to littoral habitat were captured in Steamboat (2015) and Blackduck (2016) with average total lengths of 30.41 and 28.54, respectfully. Differences in growth between lakes were much greater than differences in growth between 2015 and 2016, even though the lakes experienced earlier hatch dates in 2016. However, age-0 Yellow Perch were able to achieve similar predicted total lengths at 28 June despite differences in water temperature and hatch dates. Predicted total lengths were not significantly different between years making age-0 Yellow Perch total lengths comparable between lakes. It could be argued age-0 Yellow Perch experienced favorable conditions in 2015 by achieving similar total lengths at 28 June with less exposure to adverse weather conditions and predation due to later hatch dates.

Based on measures of zooplankton mean total body length, species assemblage, and total biomass it is unlikely a predator-prey mismatch occurred in any lake during the study. In addition to the zooplankton measures, age-0 Yellow Perch survived through late June in all of the lakes, except Steamboat Lake in 2016. Suggesting the zooplankton composition was appropriate for age-0 Yellow Perch to survive. Edible sized zooplankton species were present from hatch to capture on all lakes in both years of this study. Small sized copepod nauplii were present in all tows on all lakes and a potential food source for newly hatched Yellow Perch (Whiteside et al. 1985; Greab et al. 2004; Greab et al. 2006). Medium to large-bodied copepods and cladocerans were present in all tows with increases in biomass occurring in most lakes in late May through the end of June providing larval and juvenile Yellow Perch a potential food sources in pelagic habitats. Vertical net tows ensured all available zooplankton were sampled, but due to the differences in water depths, zooplankton measurements could not be compared among lakes.

Lake morphology measurements such as mean depth explained much of the differences in water temperatures between study lakes. According to previous literature, the variation in mean water temperature may have affected age-0 Yellow Perch growth and recruitment in these systems (Clady 1976; Ward et al. 2004; Kaemingk et al. 2014). Kabekona has the greatest max depth (40.54 m), mean depth (15.32 m), and volume (150,839,704 m^3) of all the study lakes. Kabekona experienced the lowest mean water temperatures, latest hatch periods, and lowest predicted total lengths for 2015 and 2016. Previous studies have investigated max depth (Kettle et al. 2004; Becker and Daw 2005), mean depth (Shulter et al. 1983; Snucins and Gunn 2000), and total volume (Gorham 1964; Wetzel 2001) influence on water temperature with mixed results. In this study, lakes greater in max depth, mean depth, and total volume needed more thermal energy to warm compared to smaller/shallower lakes. By accounting for differences in water temperature due to lake morphology biologists may anticipate differences in warming processes based on lake characteristics.

Hatching was successful and resulted in age-0 Yellow Perch recruitment through their pelagic phase in all but one lake in one year, confirming the presence of age-0 Yellow Perch populations inhabiting these aquatic systems. Acquiring daily ages from otolith structures was a labor-intensive method that provided accurate age measurements of age-0 Yellow Perch across a variety of lakes. Using CDD was inaccurate to predict hatch periods and median hatch dates but aided in the explanation of total lengths at 28 June and determined when to conduct sampling. Lake specific age and total length relationships can be used to provide a less labor-intensive option to age juvenile Yellow Perch and determine hatch dates. Water temperature, specifically CDD, explained 62% of the variation in total lengths by the end of June, indicating the importance of this variable to age-0 Yellow Perch growth. However, the remaining unexplained variation suggests other factors such as weather conditions and hatch dates need to be considered when explaining age-0 Yellow Perch growth. Structural indices of zooplankton and fish gape size were successfully used to assess food availability. In this study, comparing predicted gape measurements to zooplankton body lengths, species assemblages, and biomass provided evidence adequate-sized prey species were available for age-0 Yellow Perch. Measurements of spring temperatures following ice-out in subsequent years and measurements of lake morphology revealed warming patterns of lakes. Kabekona was the only oligotrophic lake in this study and was consistently behind the other area lakes in water temperature, hatch dates, and predicted total lengths for Yellow Perch.

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Table 1. Morphometric characteristics collected from north-central Minnesota lakes sampled for age-0 Yellow Perch, 2015-2016.

Lake	Surface Area (ha)	Littoral Area (ha)	Maximum Depth (m)	Total Volume (m^3)	Mean Depth (m)	Trophic Status
Big Turtle	650.0	290.6	13.7	24,980,529	3.8	Mesotrophic
Julia	206.9	67.6	13.1	9,974,745	4.8	Mesotrophic
Blackduck	1,087.1	556.0	8.5	48,360,932	4.5	Mesotrophic
Big	1,453.6	852.3	10.7	60,801,880	4.2	Mesotrophic
Kabekona	984.7	215.3	40.5	150,839,704	15.3	Oligotrophic
Steamboat	710.5	215.3	28.4	77,842,474	11.0	Mesotrophic
Pike Bay	1,922.7	905.7	29.0	142,125,688	7.4	Mesotrophic

Table 2. Rankings of linear models to explain variation in daily age predictions of age-0 Yellow Perch in north-central Minnesota. Model ranks were determined using the Akaike information criterion (AIC_i) where the smallest value indicated the most supported model.

Model	K	AIC_i	Δ_i	R^2	RMSE
TL • Lake	3	4019.88	0.00	0.73	4.62
TL + Lake	3	4125.59	105.71	0.68	5.01
TL	2	4165.96	146.08	0.66	5.19

Table 3. Coefficients of the best supported model for predicting age-0 Yellow Perch daily age in north-central Minnesota based on AIC values ($R^2 = 0.73$, $P < 0.01$, RMSE = 4.62; Age = TL · Lake).

Coefficients	Estimate
Intercept	20.92
TL	0.95
Big Turtle	-22.24
Blackduck	-28.80
Julia	-11.86
Kabekona	-40.05
Pike Bay	-23.70
Steamboat	-5.42
TL:Big Turtle	1.03
TL:Blackduck	1.12
TL:Julia	0.47
TL:Kabekona	1.97
TL:Pike Bay	0.99
TL:Steamboat	0.18

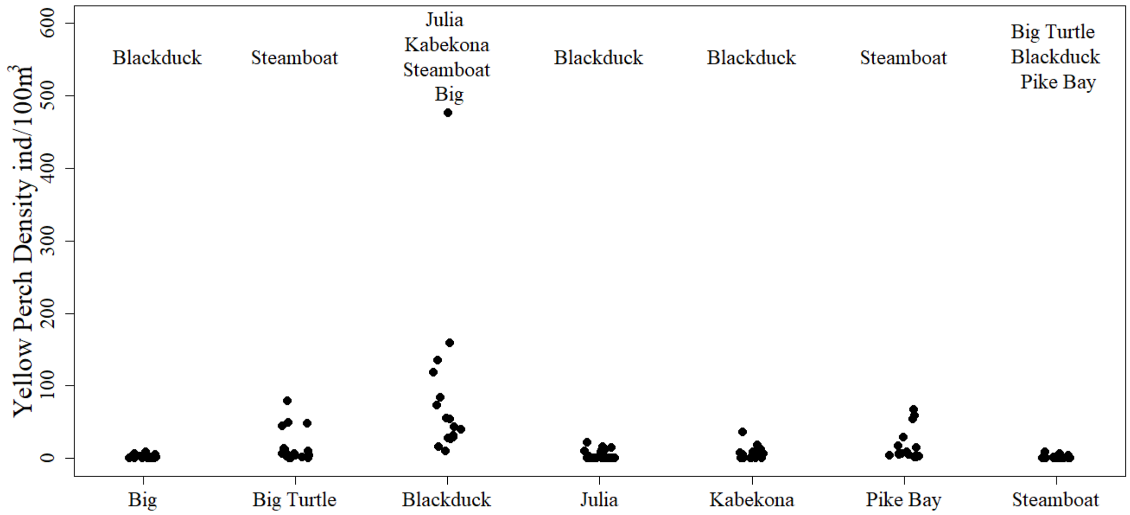

Figure 1. Dot plot of Yellow Perch densities in relation to lake and year captured by neuston netting. Both sampling rounds occurred in mid to late June for 2015 and 2016 in the limnetic zone. Densities are displayed in ind/100m^3 on the y axis and individual lakes on the x axis. Pairwise comparisons of significant difference among lakes on the x axis are labeled with lake names in the upper portion of the figure.

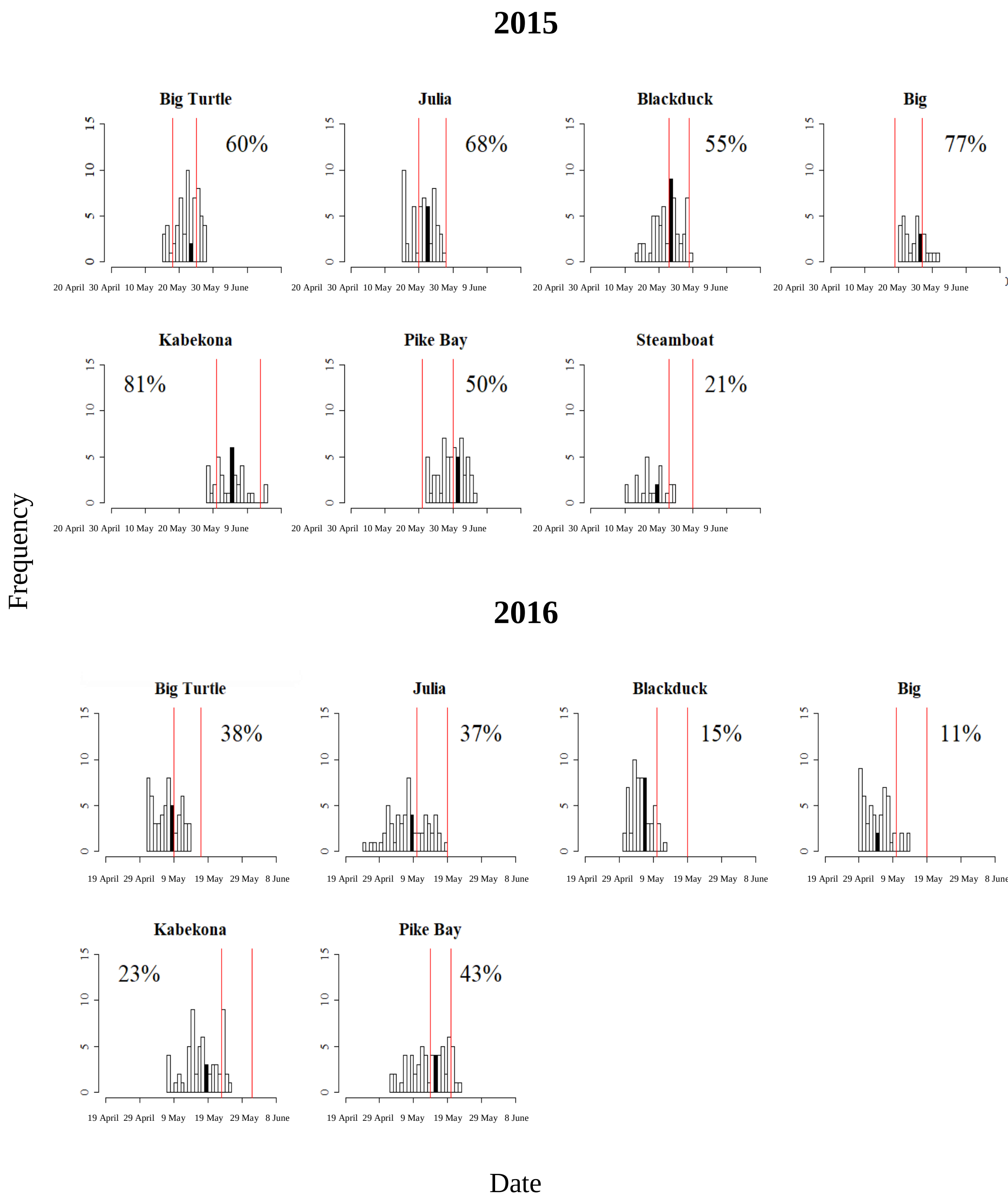

Figure 2. Observed hatch dates for 2015 and 2016 for north-central Minnesota. The y axis shows the frequency of fish hatched on a specific day and x axis indicates the specific day hatch was observed based on otolith structures. Median hatch dates are indicated by a black bar in each barplot. Predicted hatch period in 2015 and 2016 were calculated using cumulative degree-days (CDD) for a temperature unit. The red lines show the predicted start and end of hatching based on the CDD calculation. Percentages are based on the number of Yellow Perch hatched in the predicted hatch period.

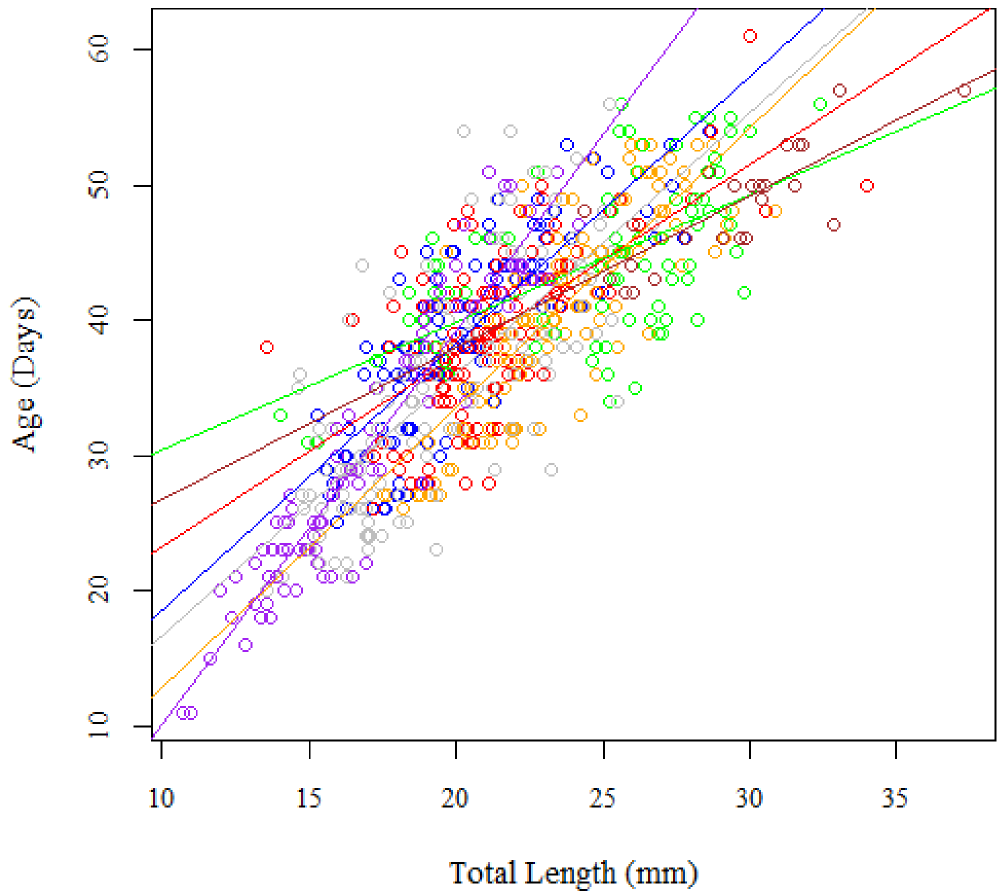

Figure 3. Daily ages of age-0 Yellow Perch in relation to total length measurements for 2015 and 2016. The y axis is age (days) and the x axis is total length (mm) of age-0 Yellow Perch at capture. Each lake and linear relationship is illustrated with a different color (Big Turtle, blue; Julia, red; Blackduck, orange; Big, green; Kabekona, purple; Steamboat, brown; and Pike Bay, grey).

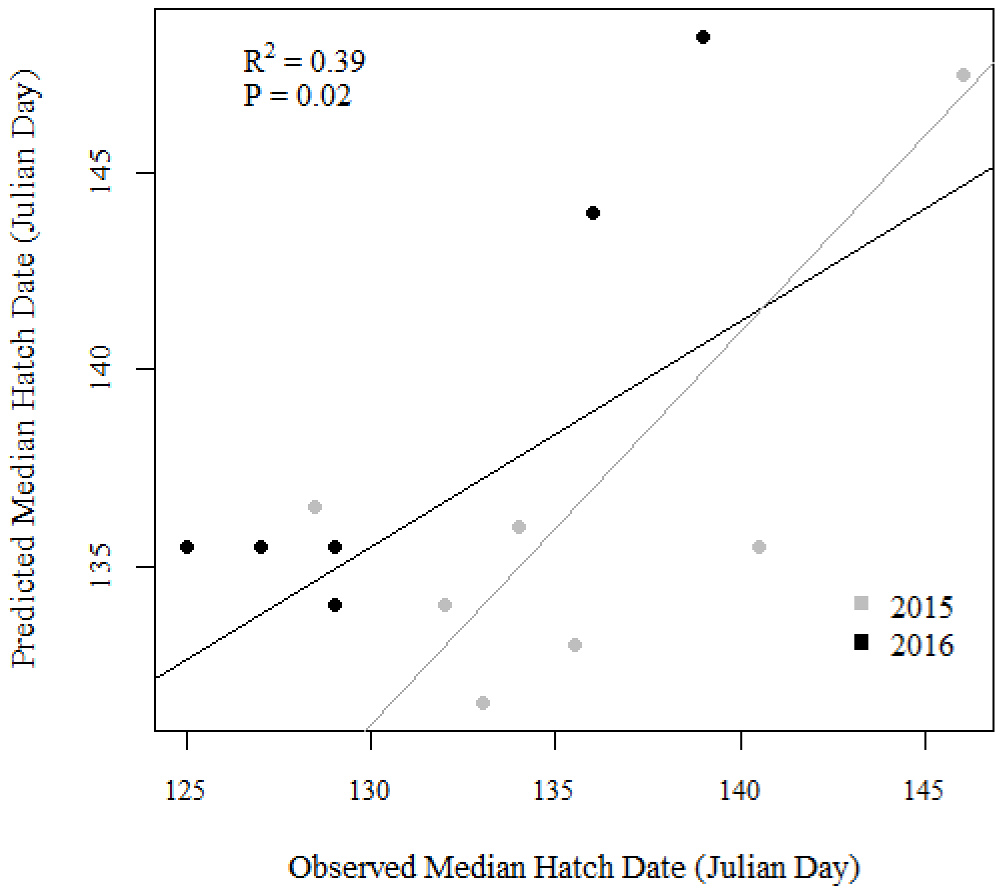

Figure 4. Predicted median hatch dates are located on the y axis and compared to observed hatch dates located on the x axis. Median hatch dates were predicted from the midpoint of the hatch period prediction using cumulative degree-days (CDD). The linear regression line [black; Predicted Median Hatch Date = 60.8622 + 0.5741 · Observed Hatch Date] and 1:1 line (grey) are displayed to illustrate the relationship.

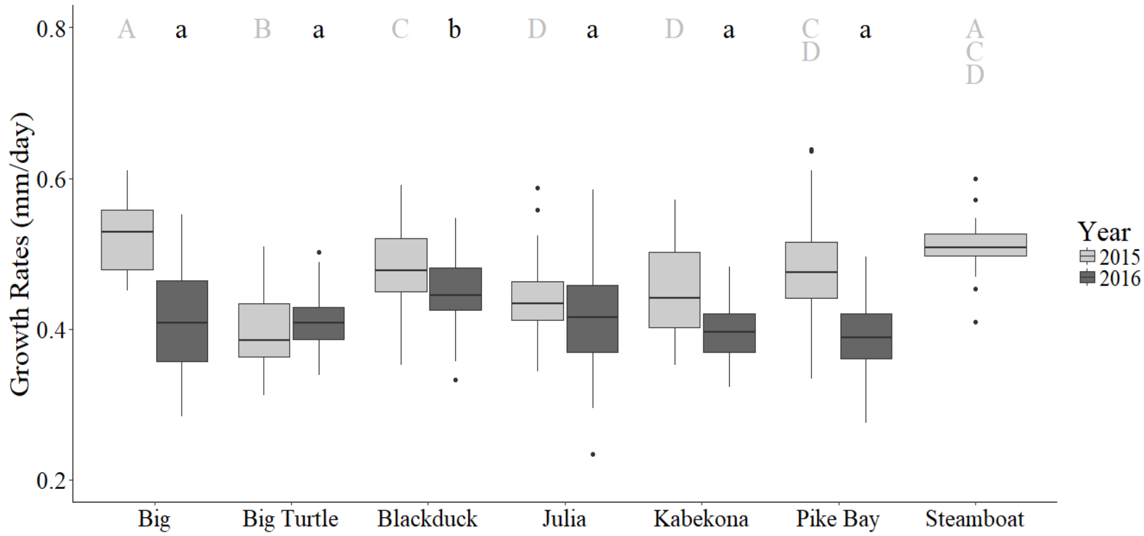

Figure 5. Box and whisker plot displaying age-0 Yellow Perch growth rates from all sample lakes for 2015 and 2016. Growth rates are grouped by lake and separated by year with light grey (2015) and dark grey is (2016). Pairwise comparisons of significant difference groups are labeled with grey uppercase (2015) and black lowercase (2016) letters in the upper portion of the figure. Lakes with different letters are considered significantly different.

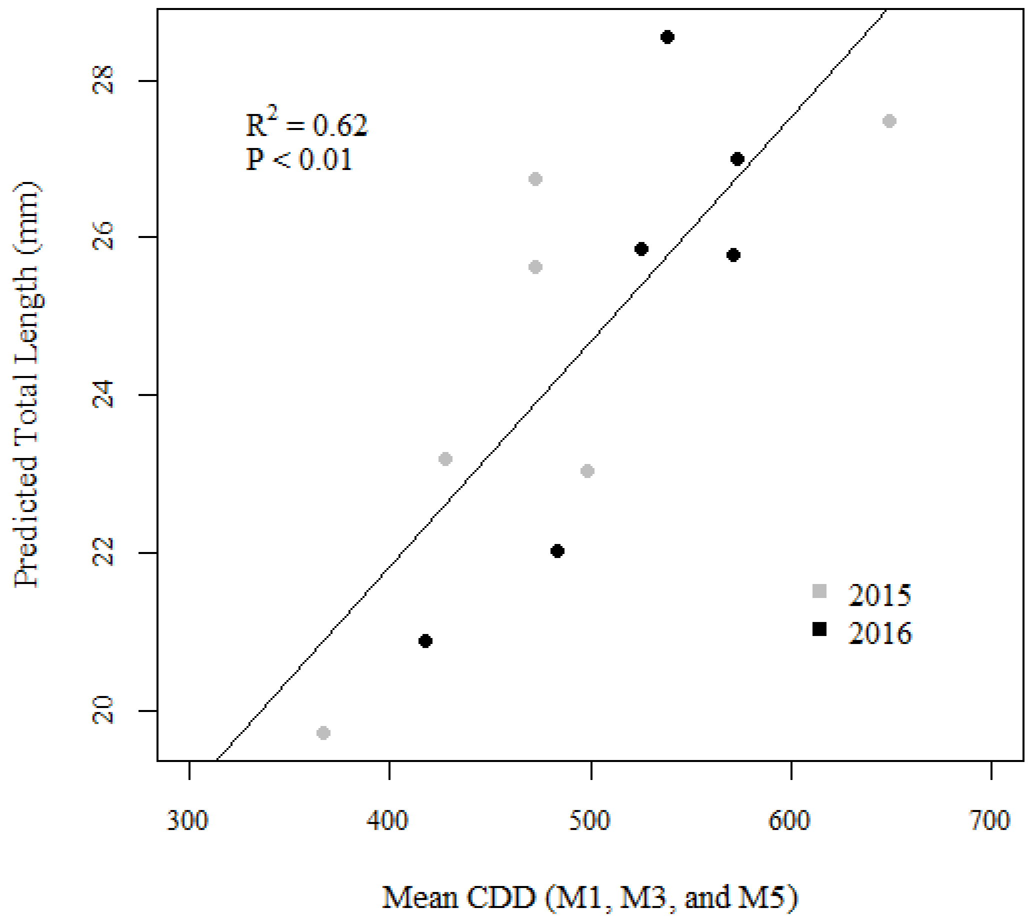

Figure 6. Mean cumulative degree-days (CDD) from depths of one, three, and five meters in relation to predicted total length on 28 June [Predicted Total Length = 8.14048 + 0.02991 · CDD] for 2015 (grey) and 2016 (black).

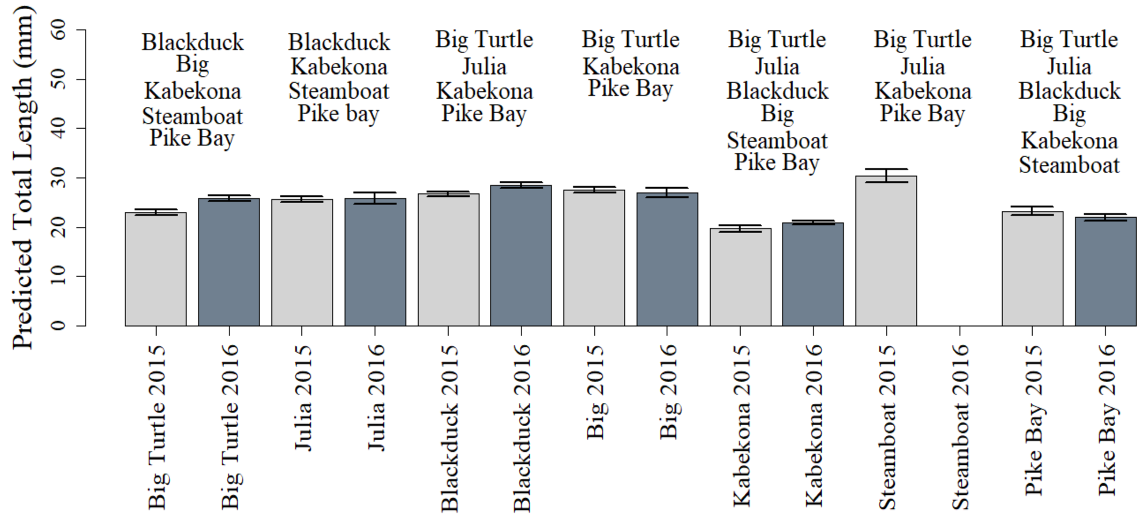

Figure 7. Predicted total length of age-0 Yellow Perch for 2015 and 2016. Total length was predicted for 28 June both years using growth rates and total lengths at capture of the respective lake and year. The y axis is total length (mm) and x axis is lake name with light grey (2015) and dark grey (2016) indicating year. The standard error is displayed on the top of each bar. Pairwise comparisons of significant difference among pooled (2015 and 2016) predicted total lengths for each lake are labeled with lake names in the upper portion of the figure.

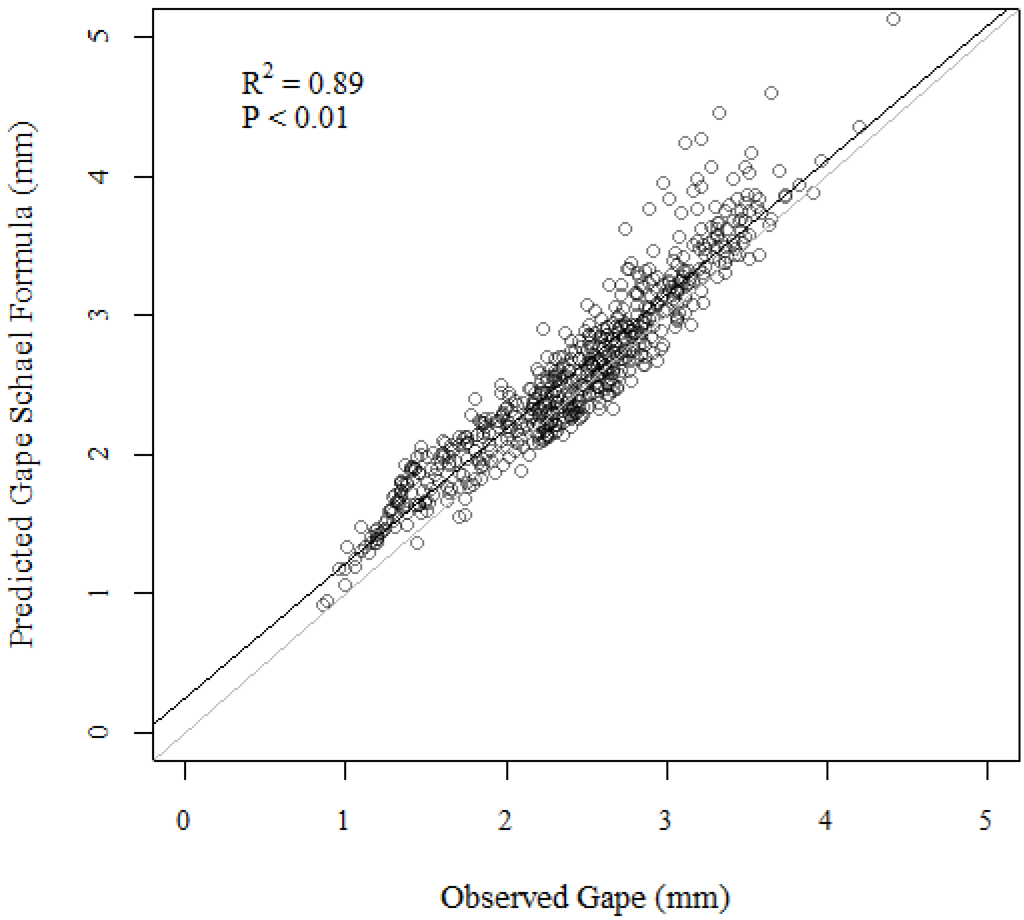

Figure 8. Predicted gape measurements compared to measured gapes of age-0 Yellow Perch captured in 2015 and 2016. The Schael gape formula [$G = -0.597 + 0.159 \cdot \mathrm{TL}$] was used to predict gape (mm) from total length measurements. Observed gapes were measured with a micrometer to the 0.1 mm. The grey line is a 1:1 line illustrating an unbiased relationship.

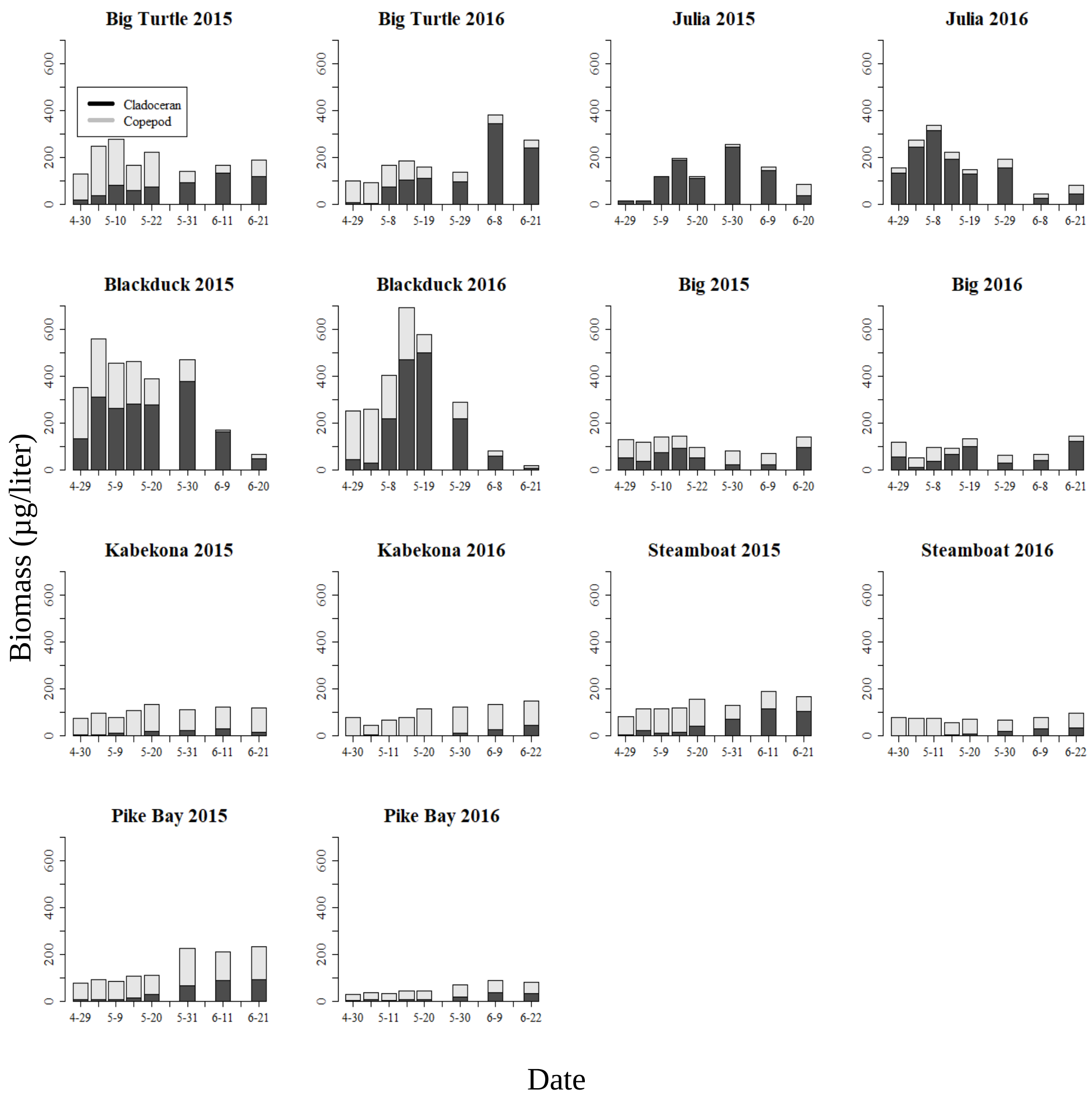

Figure 9. Zooplankton biomass for 2015 and 2016 from late April to late June for cladocerans (black) and copepods (grey). The y axis is zooplankton biomass (µg/liter) and x axis is the sampling date for each year. Each barplot plot was created for individual lakes by year for visual comparison. Sampling intervals were every 5 days (early season sampling) or 10 days (late season sampling).

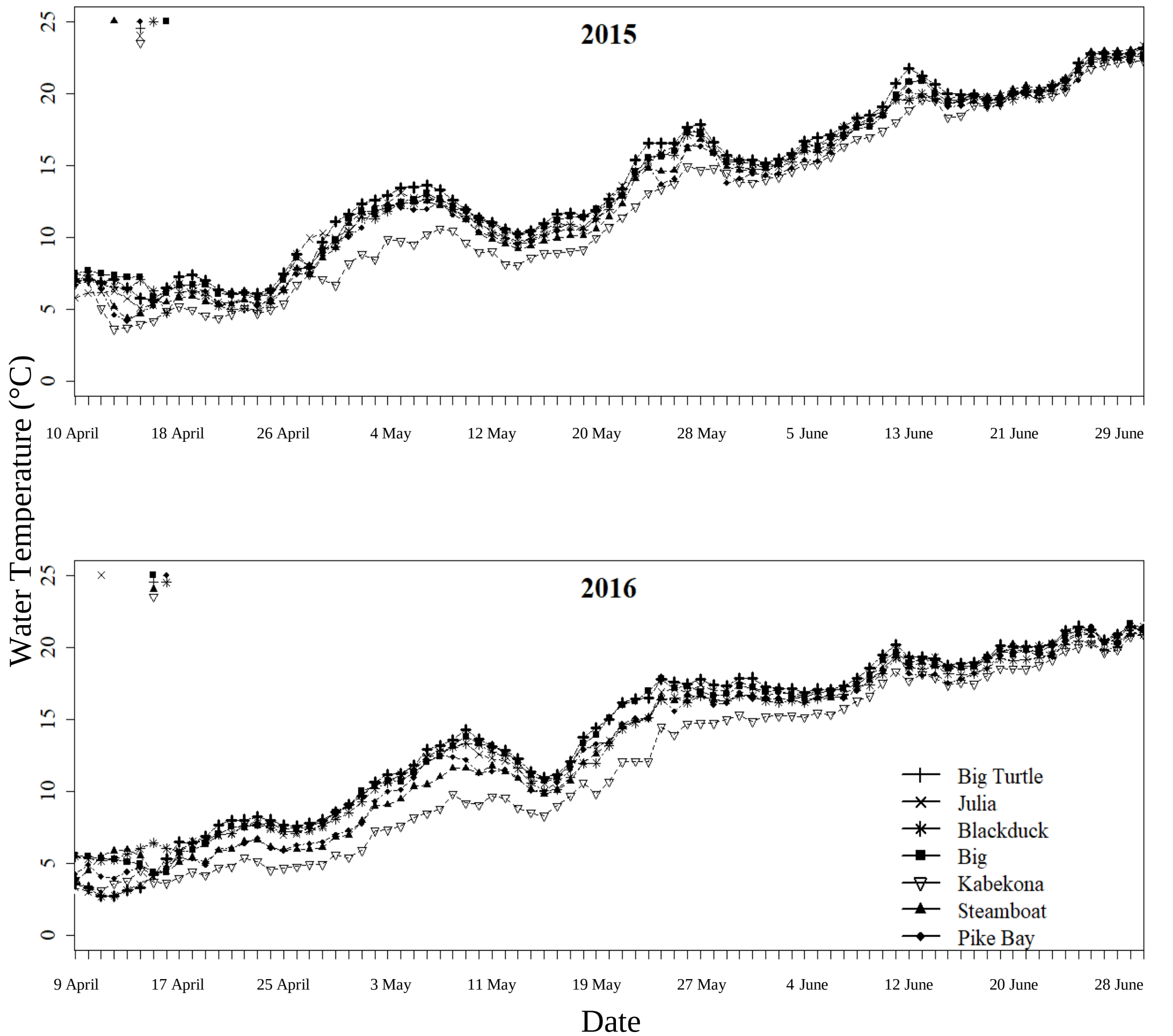

Figure 10. Water temperature (° C) at one meter below the surface for all study lakes from ice-out to 1 July (2015) and 30 June (2016; Leap Year). Each lake is identified with unique symbols for mean water temperatures and has ice-outs indicated in the upper left corner of each figure with the appropriate symbol.

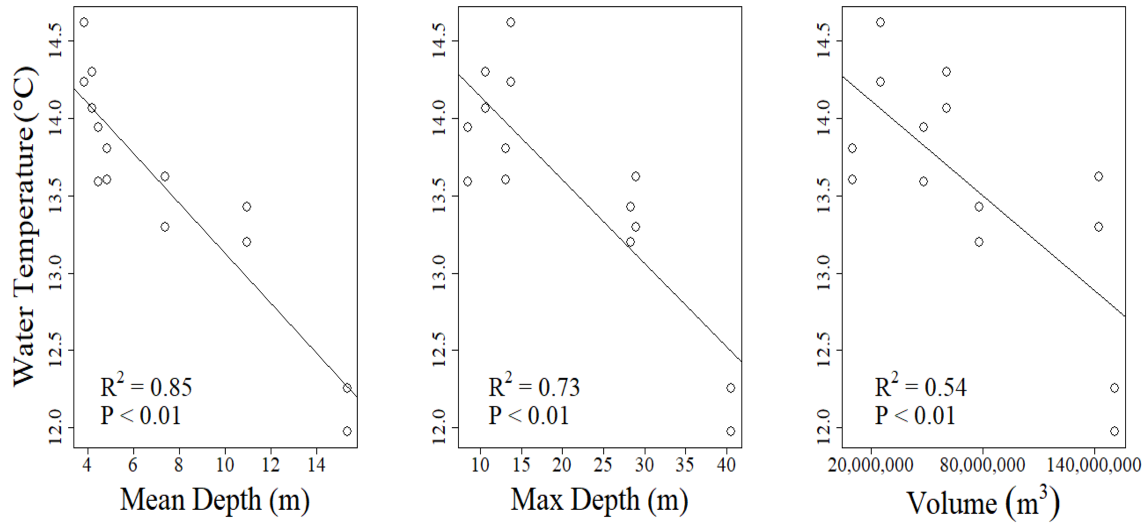

Figure 11. X and Y scatter plots of lake morphology [Mean Depth, Water Temperature = 14.74 – 0.1615 · Mean Depth; Max Depth, Water Temperature = 14.6754 – 0.05391 · Max Depth; and Total Volume, Water Temperature = $1.432e^{01} - 1.026e^{-08}$ · Total Volume] highlighted in individual plots. Meter one mean water temperatures from ice-out to 28 June for 2015 and 2016 is displayed on the y axis in degree Celsius. The x axis is specific for each plot in regards to the morphometric characteristic.