PREY UTILIZATION AND SOMATIC GROWTH OF WALLEYE *SANDER VITREUS* IN THE MUSKEGON RIVER AND MUSKEGON LAKE, MICHIGAN

by

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Abstract

Walleye *Sander vitreus* is a far-ranging species that makes long-range movements between spawning and foraging habitats. Walleye inhabiting the eastern portion of the Lake Michigan watershed move into the Muskegon River in spring to spawn. After spawning, some walleye immediately leave the Muskegon River, while some may suspend their downstream movement to exploit prey availability and temperatures optimal for consumption and growth. The purpose of this study was to determine if prey availability and temperature affect growth, and, therefore, movement of walleye between the Muskegon River and Muskegon Lake during spring and summer.

The optimal temperature range for walleye consumption and growth is 18 to 22^{o}C, and temperature in 2004 in the Muskegon system remained in this range for nearly one month. During this time, walleye ingested large prey items such as rainbow trout *Oncorhynchus mykiss* in the Muskegon River, and alewife *Alosa pseudoharengus* in Muskegon Lake. These optimal conditions had a positive effect on short-term walleye growth, demonstrated by the increase in the relative weight of walleye between spring and summer. The mean total length and mean length-at-age of walleye inhabiting the Muskegon system also increased from 2004 to 2005, signifying that favorable temperature and forage conditions in 2004 resulted in increased walleye growth over the course of the year.

This study established that growth of walleye was strongly related to forage availability and temperature. The similarity of forage and temperature

conditions in the Muskegon River and Muskegon Lake facilitated movement between the two systems and led to comparable length-at-age and relative weight values for walleye in each system. Therefore, significant yearly variations in prey abundance and temperature in the Muskegon system should more strongly affect walleye feeding and growth than slight differences in these conditions between the Muskegon River and Muskegon Lake within a year.

Introduction

Walleye *Sander vitreus* make long-range movements between habitats associated with spawning, foraging, and over-wintering in the Great Lakes, inland lakes, and rivers (DePhilip et al. 2005). Although walleye are regarded as a far-ranging species, tagging studies conducted in Michigan have shown walleye annually return to the same spawning site (Crowe 1962). In spring, walleye from the eastern portion of the Lake Michigan watershed and all parts of the Muskegon watershed move into the Muskegon River to spawn below Croton Dam (Crowe 1954; Schneider and Leach 1979; Schneider et al. 1991; O'Neal 1997).

After spawning in the Muskegon River, some walleye immediately return to their pre-spawning location, while some remain in the river indefinitely. This delayed downstream movement of post-spawning walleye has been demonstrated in several studies (Rawson 1956; Paragamian 1989; DePhilip et al. 2005). While several factors affect walleye movement, prey availability and temperature are potentially the most important factors influencing the amount of time walleye inhabit the Muskegon River after spawning. Walleye may suspend their downstream movement to exploit prey availability and temperatures optimal for consumption and growth.

Walleye are opportunistic predators, and the relative amount of various invertebrate and fish species eaten by walleye depends on prey availability (Scott and Crossman 1973; Smith 1985). The Muskegon River is thermally diverse, supporting cold, cool, and warm water fishes, with the most common families being Salmonidae, Cyprinidae, Catostomidae, and Cottidae (O'Neal 1997). Every spring, the Michigan Department of Natural Resources (MDNR) stocks the Muskegon River with potential prey for walleye, including rainbow trout *Oncorhynchus mykiss* (mean length = 181 mm), brown trout *Salmo trutta* (mean length = 169 mm), and Chinook salmon *Oncorhynchus tshawytscha* (mean length = 82 mm). During spring, post-spawning walleye have high energy demands, and stocked trout and salmon are particularly vulnerable to predation by walleye (DePhilip et al. 2005).

Temperature is one of the most significant abiotic factors affecting individual fish and fish populations, influencing spawning, metabolism, consumption, conversion efficiency, growth, and behavior (Rawson 1956; Kelso 1972; Huh et al. 1976; Kershner et al. 1999; Kocovsky and Carline 2001; Diana 2004). Studies have shown the thermal optimum for walleye growth and consumption is 22^{o}C (Kelso 1972; Huh et al. 1976; Koenst and Smith 1976; Nickum 1978; Hartman 1989), with the desirable temperature range being 18 to 22^{o}C (Christie and Regier 1988). At temperatures above 22^{o}C, walleye stop active foraging and seek thermal refuge (Kelso 1972; Hokanson 1977; Kocovsky and Carline 2001). During spring and summer, temperatures in the Muskegon River are often in the optimal range for walleye consumption and growth, potentially influencing walleye to remain in the river until temperature exceeds the optimum.

Prey availability, fish assemblage structure, temperature, and length of the growing season influence walleye growth and overall body condition (Quist et al.

2003). Condition indices such as relative weight are indicators of the relationship between body condition and prey availability (Porath and Peters 1997). The relative weight index developed by Wege and Anderson (1978) is a ratio between the weight of an individual fish and the standard weight for that length and species. Using a length-specific standard weight equation developed to calculate the relative weight of walleye (Murphy et al. 1990), evaluations of body condition can be compared among walleye populations in North America. Using the relative weight index for walleye collected in the Muskegon River and Muskegon Lake, growth due to prey availability and temperature can be evaluated across sites. Relative weight values for walleye in the Muskegon system can also be compared to other walleye populations in the Midwest region to determine the overall health of the Muskegon walleye population.

The purpose of this study was to determine if prey availability and temperature affect growth, and, therefore, movement of walleye between the Muskegon River and Muskegon Lake during spring and summer. Population characteristics from walleye inhabiting the Muskegon system were examined during spring and summer over a two-year period to determine differences in walleye growth due to forage abundance and temperature. It was hypothesized that walleye would remain in the Muskegon River after spawning until prey availability and/or temperature became less than optimal in terms of growth. At this time, walleye would leave the Muskegon River and return to Muskegon Lake or Lake Michigan in search of better growth conditions.

Study Sites

The Muskegon River and Muskegon Lake are located on the western side of Michigan's Lower Peninsula (Figure 1). The Muskegon River is the second largest watershed in Michigan, with a drainage area of 6,822 km^2 and a total length of 370 km. This study examined 80 km of the Muskegon River between Croton Dam and the river mouth, which flows into Muskegon Lake. Walleye were sampled at six sites on the Muskegon River (Figure 1). The four farthest upstream sites were similar in habitat, including cobble substrate, woody debris, overhanging branches along the shore, and combinations of deep pools (2 m) and shallow riffles (< 0.2 m) throughout the reach. The two downstream sites had elevated sediment levels, sandy substrate, limited woody debris, and shallow runs (0.5 to 1 m). Accessibility to each of the six sites and the movement of walleye throughout the study area dictated where sampling occurred in the Muskegon River. In all analyses, data from these six sites were combined to attain a comprehensive view of the Muskegon River downstream of Croton Dam. The land use surrounding the 80-km reach of the Muskegon River is mostly forest, with some agriculture and residential areas.

Muskegon Lake is a 17-km^2 inland coastal lake connected to Lake Michigan by a man-made channel created in the 1880s. Sampling occurred at water depths of 1.8 to 2.4 m along the northeast shore, where the North Branch of the Muskegon River flows into the lake (Figure 1). This area contains sandy substrate with small cobbles and large amounts of aquatic vegetation. The area immediately surrounding Muskegon Lake is primarily residential and industrial, including chemical and petro-chemical companies, foundries, and a paper mill, and has been identified by the Environmental Protection Agency (EPA) as an Area of Concern (EPA 2004).

Methods

Walleye in the Muskegon River and Muskegon Lake were captured weekly from May through August 2004 and April through August 2005 using boom-electroshocking equipment. The 6-m long electroshocking boat (model SR-18H; Smith-Root, Inc.) ran on DC current and emitted approximately 170 volts. Since walleye feed mainly at night (Forney 1980), sampling occurred immediately after sunrise on the Muskegon River and several hours after sunset on Muskegon Lake, with a total shocking time of one hour per sample. Walleye were captured and placed in a live-well until the end of that sampling period. In August 2004, the Michigan Walleye Tour State Championship occurred on Muskegon Lake, and data were obtained from walleye caught by anglers who participated in that event. In April 2005, data were collected from walleye captured by the MDNR for egg and sperm collection.

Temperature loggers (Onset Computer Corp. 1998) were placed in the Muskegon River and Muskegon Lake throughout the entire sampling period, and surface temperature was taken during each sampling day using a thermometer. Temperature data were evaluated as the percent of days a given temperature was exceeded (percent exceedence). Unfortunately, most of the temperature loggers were moved or stolen. Daily surface temperature from either the loggers or the thermometer was used for analyses, and temperature data were linearly extrapolated for days surface temperature was not measured.

After capture, total length (mm) and round weight (g) were measured. Sex was also determined during spring when walleye were expressing gonadal material. For aging purposes, the first three dorsal fin spines were clipped with surgical utility shears and placed flat in scale envelopes to dry. Walleye stomach contents were collected using gastric lavage. The hose from a garden sprayer was cut off at the spraying end and filed to a smooth edge. The hose was carefully inserted through the esophagus of each walleye, and pressurized water was pumped into the stomach, flushing the stomach contents out of the mouth into a 76.2 x 127-mm fine-mesh (1.6 mm) aquarium net. The walleye's abdomen was rubbed during this process to facilitate water flow (Waters et al. 2004). Diet items were placed in plastic jars with 95% ethanol for later identification.

In the laboratory, starting at the base of the dorsal fin spines, several transverse cross sections were made from each walleye spine using a MultiPro variable speed Dremel Tool with a 22.2 x 0.1-mm Damascus Separating Disc (from MDNR in Charlevoix). Each section was cleaned with water, set on a glass slide, and, using a dissecting microscope with an image analysis system (Media Cybernetics, L. P. 1999), an image was taken of the spine with the best defined annuli. The second spine was used for all aging, and the magnification was set at 80X. Using this image, a radius was drawn horizontally along the compressed portion of the section from the focus to the outer edge. Annuli were identified along this axis and an age was assigned to each walleye. I aged all walleye spines three times, and spines without two common ages were discarded. To ensure precision, several walleye spines were also aged by another scientist experienced with this technique (C. Schelb; MDNR in Charlevoix), and 93% of his ages agreed with my readings.

Walleye stomach contents were identified in the laboratory to the lowest possible taxonomic group. For each walleye stomach, diet items were separated into similar species, and total length (mm) measurements were taken. When total length could not be measured due to digestion of the diet item, standard lengths (mm) or vertebral lengths (mm) were measured. Standard and vertebral lengths were converted into total lengths using percentages calculated from specimens collected in the Muskegon system.

Relative weight was evaluated as an index of walleye body condition (Wege and Anderson 1978). Relative weight (W_r) relates individual weight to a species-specific standard weight (W_s):

$$W_r = (\text{weight}/W_s) \times 100 \qquad (1)$$

Murphy et al. (1990) generated a length-specific standard weight (W_s) equation for walleye in North America:

$$\log_{10} W_s = -5.453 + 3.180 \log_{10} TL \qquad (2)$$

To accurately detect changes in body condition, relative weight values were determined within each season (spring and summer). To determine somatic body condition not including gonadal material during spawning, spring data only included walleye captured after spawning occurred, as well as walleye captured by the MDNR after egg and sperm collection in April 2005. Summer data included walleye captured from June, July, and August. For walleye larger than 200 mm, seasonal relative weight values were calculated for each 50-mm length interval with a sample size of 10 or more. For each length interval, a three-way analysis of variance (ANOVA; SPSS 2003) was conducted to evaluate differences in relative weight between years, sites, and seasons.

Data collected throughout the entire study were categorized by year (2004 and 2005), site (Muskegon River and Muskegon Lake), and season (spring: April and May; and summer: June, July, and August). Walleye catch-per-effort (CPE) within each site was evaluated by year and season using a two-way ANOVA (SPSS 2003). Length, weight, and age data were compared independently between years, sites, and seasons using a three-way ANOVA (SPSS 2003). Walleye length-at-age data were evaluated for 50-mm length intervals between years, sites, and seasons using a three-way ANOVA (SPSS 2003). The number of walleye diet items was compared within each site between months using a Chi-square analysis (x^2), where equal proportions of each diet item were expected every month. The total length of walleye prey items was correlated with walleye total length using linear regression (SPSS 2003). For all analyses, significance level was set at $\alpha = 0.05$.

Results

A total of 388 walleye were captured in the Muskegon River, and 158 were captured in Muskegon Lake. In the Muskegon River, there was a significant difference in the CPE of walleye collected between years ($p = 0.046$) and seasons ($p = 0.007$; Figure 2). On average, there was a higher CPE of walleye captured in 2005 (mean ± SE = 14.1 ± 2.5) than 2004 (4.8 ± 3.8). In 2004 and 2005, CPE was higher in spring (mean ± SE = 7.2 ± 1.7 and 24.5 ± 5.2, respectively) than summer (2.4 ± 0.9 and 3.8 ± 3.6, respectively). In Muskegon Lake, there was no significant difference in the number of walleye collected between years ($p = 0.087$) or seasons ($p = 0.295$).

In the Muskegon River, walleye captured in 2005 had the highest mean total length, while the mean weight of walleye was similar between years, sites, and seasons. There was a significant difference in the mean length of walleye captured between years ($p = 0.003$) and sites ($p < 0.001$), but not between seasons ($p = 0.533$). Walleye captured in 2004 were smaller on average (481 ± 8.9 mm) than those captured in 2005 (517 ± 7.7 mm; Figure 3). In 2004, there was no significant difference in the mean length of walleye captured at either site ($p = 0.061$), while in 2005, walleye captured in the Muskegon River (576 ± 6.2 mm) were longer on average when compared to Muskegon Lake (483 ± 14.6 mm; $p < 0.001$). There was no significant difference in the mean weight of walleye captured between years ($p = 0.245$), sites ($p = 0.513$), or seasons ($p = 0.058$).

Walleye captured during spring in the Muskegon River had the highest mean age, indicating movement of older walleye into the river to spawn. There was a significant difference in the mean age of walleye captured between sites ($p < 0.001$) and seasons ($p = 0.004$), but not between years ($p = 0.856$). Walleye captured in the Muskegon River were significantly older on average (mean ± SE = 5.2 ± 0.1 years) than those captured in Muskegon Lake (4.3 ± 0.2 years). In Muskegon Lake, there was no significant difference in the mean age of walleye captured in either season ($p = 0.272$), while in the Muskegon River, walleye captured in spring were significantly older on average (mean ± SE = 6.0 ± 0.1 years) than those captured in summer (4.5 ± 0.1 years).

Length-at-age, an indicator of growth rate, was generally similar among sites and seasons but was greater for walleye collected in 2005 compared to 2004. There was no significant difference in the mean length-at-age between sites or seasons for walleye ages 2 through 8 (Table 1). For every age except ages 7 ($p = 0.346$) and 8 ($p = 0.466$), there was a significant difference in walleye mean length-at-age between years. Except for age 2, all ages of walleye captured in 2005 had longer mean lengths-at-age compared to 2004.

The relative weight of walleye in the Muskegon system was similar between years and sites, but was higher among walleye captured in summer compared to spring. The mean relative weight (± SE) of walleye captured over the entire study was 88.5 ± 0.6, and values ranged from 39 to 142. Relative weight was examined within each 50-mm length interval ($N \geq 10$) for walleye larger than 200 mm (Table 2). For every 50-mm length interval within each season, there was no significant difference in walleye relative weight between years or sites. While there was a slight increase in relative weight of walleye between spring and summer for all size intervals, for walleye 551 to 650 mm there was a significant difference between seasons, where walleye captured in summer had higher relative weight values compared to spring (Table 2).

Walleye diet composition was similar between years, with a shift in composition occurring between spring and summer. In 2004 and 2005, the diet composition of walleye captured in the Muskegon River consisted mainly of Chinook salmon (67.7% and 62.3%, respectively), rainbow trout (10.9% and 17.3%), and cyprinids (7.3% and 2.9%; Table 3). Between spring and summer, the diet items from walleye captured in the Muskegon River shifted from primarily Chinook salmon and rainbow trout to mostly cyprinids ($x^2 = 227.4$, df = 2, $p < 0.001$). In 2004 and 2005, the diet composition of walleye captured in Muskegon Lake consisted mainly of alewife *Alosa pseudoharengus* (25.4% and 34.0%, respectively) and cyprinids (9.0% and 14.9%; Table 4). Between spring and summer, the diet items from walleye captured in Muskegon Lake shifted from primarily invertebrates and cyprinids to mostly alewife ($x^2 = 22.8$, df = 3, $p < 0.001$).

During spring 2005 in the Muskegon River, the total length of ingested Chinook salmon and rainbow trout increased with walleye total length. Since Chinook salmon and rainbow trout were the only prey items with a large enough sample size to adequately compare to total length of walleye, only diets from walleye collected in the Muskegon River were evaluated. While only a small amount of the variation was explained, there was a significant correlation for Chinook salmon ($p = 0.003$) and rainbow trout ($p = 0.019$), where the total length of these prey items increased as walleye total length increased (Figure 4). For rainbow trout, both the slope of the regression line and the mean total length was higher compared to Chinook salmon, indicating potential gape limits for walleye consumption of rainbow trout.

In 2005, temperature in both the Muskegon River and Muskegon Lake increased more rapidly and reached a higher maximum value than 2004. In the Muskegon River, temperature in 2004 reached the optimal range for walleye growth (18 to 22^{o}C) June 24 and remained in this range for a month (until July 26; Figure 5). In 2005, temperature in the Muskegon River reached the optimal range sooner (June 9), and exceeded the optimal temperature after only 11 days (June 20). In Muskegon Lake, temperature in 2004 reached the optimal range June 16, and remained in this range for three weeks (until July 7; Figure 5). In 2005, temperature in Muskegon Lake reached the optimal range earlier (May 26), and exceeded this range in 19 days (June 14).

Discussion

This study documented sizeable differences in availability of large prey and temperature in the Muskegon River and Muskegon Lake on both seasonal and annual time scales, and growth of walleye inhabiting the Muskegon system appeared to be strongly correlated to these conditions. In 2004, optimal temperature and forage conditions had a positive effect on short-term walleye growth, demonstrated by the increase in the relative weight of walleye between spring and summer. The mean total length and mean length-at-age of walleye also increased between 2004 and 2005, indicating that favorable temperature and forage conditions in 2004 resulted in increased walleye growth over the course of the year.

Walleye from the Muskegon River system were longer on average in 2005 compared to 2004, although mean age was similar between years. The age structure of walleye in the Muskegon River system was similar between years, with older walleye entering the Muskegon River in spring to spawn. However, the length distribution of these walleye differed between years, with walleye captured in 2005 having longer mean lengths compared to 2004. The difference in relative weight of walleye between spring and summer indicates increased body condition due to favorable consumption and growth conditions during this time. The increase in mean total length and length-at-age of walleye between years indicates that long-term growth occurred during the 2004 growing season.

In Michigan, adult fish experience seasonally favorable periods with conditions for rapid growth and unfavorable periods with reduced growth

(DePhilip et al. 2005). The majority of walleye growth occurs during fall, when temperatures decline from the warm summer, and prey availability is relatively high (Forney 1966; Kelso and Ward 1972; Carlander 1997; Quist et al. 2002). Since this study examined factors affecting walleye location after spawning and into summer, fall sampling was not conducted. By the end of summer, the Muskegon River was inaccessible due to shallow water and most walleye had moved out of the river. However, fall sampling on Muskegon Lake might give insight into walleye growth influenced by prey availability and temperature during this time.

The mean length-at-age of walleye captured throughout this study demonstrated the rapid growth of walleye inhabiting the Muskegon system. This was expected since historically (1947 to 1987) walleye in the Muskegon system had relatively high mean lengths-at-age (Schneider et al. 1991). Migrating walleye populations tend to grow rapidly since they can take advantage of favorable conditions in each system (Kershner et al. 1999). For example, if temperature in the Muskegon River is outside the optimal range and prey availability is poor, walleye can move into Muskegon Lake or Lake Michigan to encounter better conditions, while walleye inhabiting a land-locked inland lake cannot move away from poor conditions. Compared to another migrating walleye population inhabiting Lake Erie (Thomas and Haas 2000), walleye located in the Muskegon system during spring were actually longer at all ages (Table 5).

Relative weight values calculated for walleye inhabiting the Muskegon system were comparable to other North American walleye populations, especially those in Wisconsin. Murphy et al. (1990) used 114 walleye populations from across North America to develop a standard-weight relationship for walleye. The mean relative weight for only 18% of the Muskegon system walleye population fell in the recommended target range of 95 to 105, compared to 35% from other populations (Wege and Anderson 1978; Anderson 1980; Murphy et al. 1990). However, Hansen and Nate (2005) suggested a relative weight target range of 86 to 92 for Wisconsin and other states of the upper Midwest, where colder conditions most likely constrain growth of walleye. The results of the Muskegon study more closely reflect those of Wisconsin. In Wisconsin, quartile values were 79 (25th quartile), 86 (50th quartile), and 92 (75th quartile; Hansen and Nate 2005), while in the Muskegon system quartile values were 81 (25th quartile), 88 (50th quartile), and 96 (75th quartile). This study suggests the relative weight of walleye in the Muskegon system should be assessed in the objective range of 88 to 96.

For walleye 551 to 650 mm in length, there was a significant difference in relative weight between seasons, where walleye captured in summer had higher relative weight values compared to spring. These increases in relative weight probably indicate high forage abundance and growth for larger walleye. Walleye at these lengths were able to ingest all prey sizes, subsequently improving their overall body condition. Smaller walleye might have been gape-limited to consume only smaller individuals of the larger forage items, especially larger prey with high-energy content, such as rainbow trout in the Muskegon River and alewife in Muskegon Lake.

Walleye inhabiting the Muskegon River and Muskegon Lake ingested high-energy prey items when available. In the Muskegon River, high-energy prey such as Chinook salmon and rainbow trout were abundant during spring and early summer. While both salmonids have high caloric content, rainbow trout were larger on average (174 ± 6.0 mm) compared to Chinook salmon (48 ± 1.7 mm). In Muskegon Lake, high-energy prey items such as alewife were abundant during summer. Alewife moved into Muskegon Lake from Lake Michigan when temperature was optimal for spawning (13 to 16^{o}C), and subsequently became the main diet item of walleye inhabiting the lake during summer.

Temperature in the Muskegon system rose faster and reached a higher maximum value in 2005 compared to 2004. In 2004, temperature in the Muskegon River and Muskegon Lake was in the optimal range in terms of walleye growth for nearly one month. Therefore, if larger prey were available during this time, the potential for walleye growth was substantial. In 2004, walleye inhabiting the Muskegon River during optimal temperatures consumed mainly Chinook salmon and rainbow trout, while walleye in Muskegon Lake exclusively consumed alewife. The significant difference in walleye relative weight between seasons, as well as the increased length of walleye inhabiting the Muskegon system in 2005, implies that favorable temperature and forage conditions in 2004 resulted in increased walleye growth over the course of the year.

Various limitations, biases, and assumptions arose during this study. One such limitation was the lack of sex determination of walleye in the Muskegon system. Since walleye captured during this study were released alive, sex could only be determined during spawning when walleye were expressing gonadal material. However, determining the sex of walleye inhabiting the Muskegon River and Muskegon Lake throughout the year could provide insight into walleye behavior and movement. In a study performed in Lake Huron's Saginaw Bay, Madenjian et al. (1998) reported that adult male walleye spent most of the year in the Saginaw River system, while adult females spent the majority of their time in Saginaw Bay. In the Muskegon River in 2005, after peak spawning occurred the first week of April, males tended to stay in the river longer than females. During peak spawning, 51% of walleye captured were male, while 86% of walleye captured the rest of April were male. While the explanation is beyond the extent of these studies, in Saginaw Bay, Michigan (Madenjian et al. 1998), Lake Winnebago, Wisconsin (Priegel 1970), Falcon Lake, Manitoba (Ellis and Giles 1965), and the Muskegon system post-spawning adult male walleye show partiality toward riverine habitats.

The most influential factor affecting sampling in the Muskegon River was water level. In 2004, the Muskegon area received 10 inches of rain during May, significantly increasing water levels in the Muskegon system. Due to increased water levels and relatively mild summer weather (average water temperature = 18^{o}C), sampling on the Muskegon River was possible through the third week of August. In 2005, the Muskegon area was very dry, with more sunny days and higher temperatures than 2004. The water level of the Muskegon River was very low, making sampling on the river impossible using a boom-electroshocker after the middle of July.

In 2005, sampling walleye from Muskegon Lake was difficult as well. Walleye tend to concentrate in deeper water during summer due to higher temperatures found in shallow water (Holt et al. 1977), and only move into shallow water to feed at night. In 2005, lower water levels and higher water temperatures (average temperature = 21^{o}C) led to severe algal blooms and stagnant water along the shore of Muskegon Lake. A concurrent study performed in 2005 by J. Hanson (University of Michigan, personal communication) used telemetry to monitor walleye movement in Muskegon Lake over several 24-hour periods throughout summer. This study demonstrated that walleye remained in the deeper waters they inhabited during the day and did not come up to shallow water at night to feed (Hanson, personal communication). During summer 2005, walleye were found in shallow water ($\leq$ 3 m) less than 1% of the time (Hanson, personal communication), making boom-electroshocking for walleye along the shore of Muskegon Lake relatively unsuccessful.

It was hypothesized that movement of walleye was correlated with selecting conditions of prey availability and temperature that would optimize growth. This study assumed that movement of walleye into the Muskegon River was due to spawning in spring, and return movements to Muskegon Lake and Lake Michigan were due to searching for optimal growth conditions during the remainder of the year. However, genetic influences and prior experiences were not taken into account. A walleye that came from Lake Michigan and inhabited the Muskegon River only during spawning was more likely to leave the river to return to feeding grounds in Lake Michigan regardless of riverine conditions. Alternatively, a walleye that inhabited the Muskegon River its entire life was less likely to leave the river, even if conditions were less than optimal for growth.

Several studies demonstrate heritable preferences of walleye for feeding and spawning habitats (Olson et al. 1978; Jennings et al. 1996; Rasmussen et al. 2002). A study conducted by Jennings et al. (1996) found heritable preferences for spawning and feeding habitats between river and lake populations of walleye. When introduced into a system containing lacustrine and riverine habitats, offspring from the lake-spawning walleye population were found more frequently in lake habitats, while river-spawning offspring were found more often in riverine habitats (Jennings et al. 1996). Therefore, the movement of walleye from the Muskegon River to Muskegon Lake or Lake Michigan after spawning could at least partially be due to familiarity with each habitat and genetic or experiential differences in spawning and feeding habitats rather than conditions for growth.

An essential assumption made throughout this study was that walleye captured in Muskegon Lake had inhabited the lake for some period of time. However, some walleye captured in Muskegon Lake could have recently moved from the Muskegon River and may have resided in the river for a longer period of time. This factor was particularly important when examining walleye growth. The similarities in relative weight and growth between walleye captured in the Muskegon River and Muskegon Lake could be due to the movement of walleye between these two systems and not due to differences in temperature and prey availability.

An important aspect of this study was the relative similarity of conditions in the Muskegon River and Muskegon Lake. Both the Muskegon River and Muskegon Lake had periods of time when high-energy prey items were available, although the prey types and availability differed both within and between these systems. Temperature in the Muskegon River may have warmed more slowly and stayed a few degrees cooler than Muskegon Lake, but walleye inhabiting Muskegon Lake could seek refuge in cooler, deep waters. The similarities in prey availability and temperature in both the Muskegon River and Muskegon Lake led to comparable lengths-at-age, relative weight values, and overall body condition and growth of walleye.

While the Muskegon River and Muskegon Lake have relatively similar conditions, there is a difference in the nature of the forage base between each system. Walleye inhabiting the Muskegon River after spawning mainly consume rainbow trout stocked by the MDNR. These rainbow trout are important, energy-rich food items, and if they were not stocked in large numbers during spring, walleye inhabiting the Muskegon River would be forced to consume smaller Chinook salmon or cyprinids. Thus, reduced or delayed stocking would likely decrease the growth and overall body condition of those walleye remaining in the river, or influence walleye to move out of the river. Alewife that move into Muskegon Lake from Lake Michigan are a naturally reproducing population of an exotic fish species. They are not supported by stocking, but do show annual fluctuations based mainly on the intensity of forage demand from the stocked populations of Pacific salmon in Lake Michigan (Madenjian et al. 2005). Therefore, variations in the number of alewife available for walleye consumption are based on more natural yearly fluctuations but are also indirectly influenced by human decisions. Timing and magnitude of stocking for rainbow trout in the river and Pacific salmon in Lake Michigan could have major implications for feeding, movements, and growth of walleye in Great Lakes tributaries.

This study established that growth of walleye was strongly related to forage abundance and temperature. Significant changes in temperature or prey availability could have severe effects on walleye growth. For instance, a year-class failure of alewife due to a severely cold winter or limited food availability could have devastating effects on the health of walleye inhabiting Muskegon Lake. Similarly, even if prey are abundant, high water temperatures will negatively affect walleye growth due to reduced activity and consumption (Momot et al. 1977; Kocovsky and Carline 2001; Quist et al. 2002). Throughout this study, walleye consumption declined from spring through summer, since the percent of empty walleye stomachs increased throughout the summer as temperatures increased (Tables 3 and 4).

Understanding the influence of temperature and prey availability on walleye growth and movement can help direct fisheries management decisions, such as stocking walleye in the Muskegon system. Stocking decisions for walleye should be based on the status of the natural walleye population, and an important aspect to consider when conducting population estimates is the time of year. Studies conducted in spring give insight into the spawning walleye population from both the Muskegon system and Lake Michigan. Studies performed during summer focus on the Muskegon system walleye population, and could provide low population estimates if the summer conditions included high water temperature and reduced activity of walleye. Since prey availability and temperature affect the growth and overall health of walleye populations, these factors should be monitored on a yearly basis to more accurately determine the health and growth of the walleye population inhabiting the Muskegon system each year. Monitoring each of these factors will aid management decisions concerning the number of walleye to be stocked each year.

I hypothesized that walleye would remain in the Muskegon River after spawning until prey availability and/or temperature became less than optimal in terms of growth. Immediately after spawning, the dense stocking of rainbow trout provided an excellent forage base for walleye in the Muskegon River. Shortly afterwards, the movement of alewife into Muskegon Lake also provided an excellent forage base for walleye inhabiting Muskegon Lake. The similarity of forage and temperature conditions in the Muskegon River and Muskegon Lake facilitated movement between the two systems and led to comparable length-at-age and relative weight values for walleye in either system. Therefore, significant yearly variations in prey abundance and temperature in the Muskegon system should more strongly affect walleye feeding and growth compared to the smaller differences in these conditions between the Muskegon River and Muskegon Lake within a year.

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Table 1. Mean length-at-age (± 1 SE) and sample size (N) of walleye captured during spring (April and May) and summer (June, July, and August) from the Muskegon River and Muskegon Lake during 2004 and 2005.

	2004		**2005**	
Age	**N**	**Mean Length ± SE**	**N**	**Mean Length ± SE**
2**	6	301 ± 4.4	9	252 ± 12.6
3*	17	365 ± 10.4	48	427 ± 4.5
4*	33	451 ± 10.3	50	486 ± 4.8
5*	34	521 ± 6.6	60	535 ± 4.0
6*	24	581 ± 4.9	97	591 ± 3.6
7	10	629 ± 11.1	38	629 ± 6.7
8	5	655 ± 17.9	34	676 ± 5.4

* Significant difference between years (ANOVA; $p < 0.05$), with length-at-age of walleye smaller in 2004 than in 2005.

**Significant difference between years (ANOVA; $p < 0.05$), with length-at-age of walleye larger in 2004 than in 2005.

Table 2. Mean relative weight (± 1 SE) for each 50-mm size interval of walleye collected in spring (April and May) and summer (June, July, and August) from the Muskegon River and Muskegon Lake. Relative weight was calculated for all 50-mm length intervals with N ≥ 10.

		Spring		**Summer**	
Length (mm)	**p-value**	**N**	**Relative Weight ± SE**	**N**	**Relative Weight ± SE**
351-400	−	2	−	16	85.7 ± 3.1
401-450	0.390	23	79.6 ± 2.7	24	83.7 ± 3.7
451-500	0.530	28	88.0 ± 2.5	28	90.3 ± 2.5
501-550	0.384	39	90.2 ± 2.7	33	93.1 ± 1.8
551-600	0.003	46	87.9 ± 1.6	42	95.8 ± 1.9
601-650	0.043	33	88.7 ± 2.1	20	96.0 ± 3.0
651-700	−	26	85.2 ± 1.8	7	−
701-750	−	36	88.1 ± 1.6	1	−
751-800	−	13	82.6 ± 2.6	0	−

Table 3. Numeric proportion of prey items from walleye captured during spring and summer from the Muskegon River. The number of walleye examined and the percent of walleye stomachs containing prey items are also given.

		Spring		**Summer**	
Year	**Species**	**April**	**May**	**June**	**July**
2004	Chinook salmon* *Oncorhynchus tshawytscha*	–	88.0	9.4	0
	Cyprinidae*	–	0	43.8	100
	Rainbow trout* *Oncorhynchus mykiss*	–	9.6	25.0	0
	Unknown fish	–	2.4	21.9	0
	No. of walleye examined	–	23	21	5
	Percent stomachs with items	–	78.3	76.2	40.0
2005	Brook trout *Salvelinus fontinalis*	0	0	2.3	0
	Brown trout *Salmo trutta*	7.9	0	0	0
	Chinook salmon* *Oncorhynchus tshawytscha*	18.4	38.8	77.3	0
	Cyprinidae*	5.3	2.4	2.7	0
	Mottled sculpin *Cottus bairdi*	0	0	0	33.3
	Rainbow darter *Etheostoma caeruleum*	2.6	0	0	0
	Rainbow trout* *Oncorhynchus mykiss*	36.8	44.7	5.1	33.3
	Invertebrates	2.6	7.1	9.8	0
	Other fish	5.3	2.4	1.2	33.3
	Unknown fish	21.1	4.7	1.6	0
	No. of walleye examined	57	24	42	3
	Percent stomachs with items	36.8	79.2	85.7	0

*Significantly different proportion of prey between months (Chi-square; $p < 0.05$).

Table 4. Numeric proportion of prey items from walleye captured during spring and summer from Muskegon Lake. The number of walleye examined and the percent of walleye stomachs containing prey items are also given.

		Spring		**Summer**		
Year	**Species**	**April**	**May**	**June**	**July**	**August**
2004	Alewife* *Alosa pseudoharengus*	–	6.2	75.0	33.3	0
	Chinook salmon *Oncorhynchus tshawytscha*	–	0	6.2	0	0
	Cyprinidae*	–	31.3	0	0	4.3
	Gizzard shad *Dorosoma cepedianum*	–	0	0	0	34.8
	Unknown fish	–	62.5	18.8	66.7	60.9
	No. of walleye examined	–	19	15	23	37
	Percent stomachs with items	–	57.9	60.0	34.8	29.7
2005	Alewife* *Alosa pseudoharengus*	0	48.0	100	0	100
	Brook stickleback *Culaea inconstans*	0	0	0	100	0
	Cyprinidae*	17.6	16.0	0	0	0
	Round goby *Neogobius melanostomus*	0	4.0	0	0	0
	Western banded killifish *Fundulus diaphanous*	0	4.0	0	0	0
	Invertebrate*	76.5	20.0	0	0	0
	Other fish	5.9	8.0	0	0	0
	No. of walleye examined	6	22	3	5	3
	Percent stomachs with items	50.0	50.0	66.7	20.0	33.3

*Significantly different proportion of prey between months (Chi-square; < 0.05).

Table 5. Mean total lengths-at-age (mm) ± 1 SE of walleye captured in spring 2005 in the Muskegon River, compared to walleye captured in 1998 spring surveys in Lake Erie (Thomas and Haas 2000), and the 2000 Michigan state average of walleye captured from January through May (Schneider 2000). Sample size of walleye collected is given in parentheses.

	Survey Location				
	Muskegon		**Lake Erie**		**Michigan Average**
Age	**Males**	**Females**	**Males**	**Females**	**Combined**
3	434 ± 3.7 (16)	–	408 ± 3.5 (49)	–	353
4	494 ± 2.6 (15)	–	446 ± 1.4 (323)	488 ± 4.8 (29)	401
5	531 ± 2.2 (22)	571 (1)	478 ± 2.1 (198)	532 ± 12.3 (7)	447
6	564 ± 2.2 (34)	626 ± 5.2 (8)	512 ± 5.3 (37)	588 ± 16.2 (4)	488
7	597 ± 2.7 (13)	653 ± 4.1 (5)	521 ± 2.3 (147)	605 ± 10.1 (11)	523
8	–	682 ± 1.5 (14)	549 ± 4.3 (58)	636 ± 11.7 (9)	549
9	–	704 ± 1.4 (29)	575 ± 5.6 (46)	648 ± 7.8 (8)	569
10	–	736 ± 1.8 (22)	585 ± 5.4 (45)	677 ± 8.2 (18)	586
11	–	759 ± 1.8 (12)	593 ± 9.0 (13)	688 ± 17.3 (6)	–

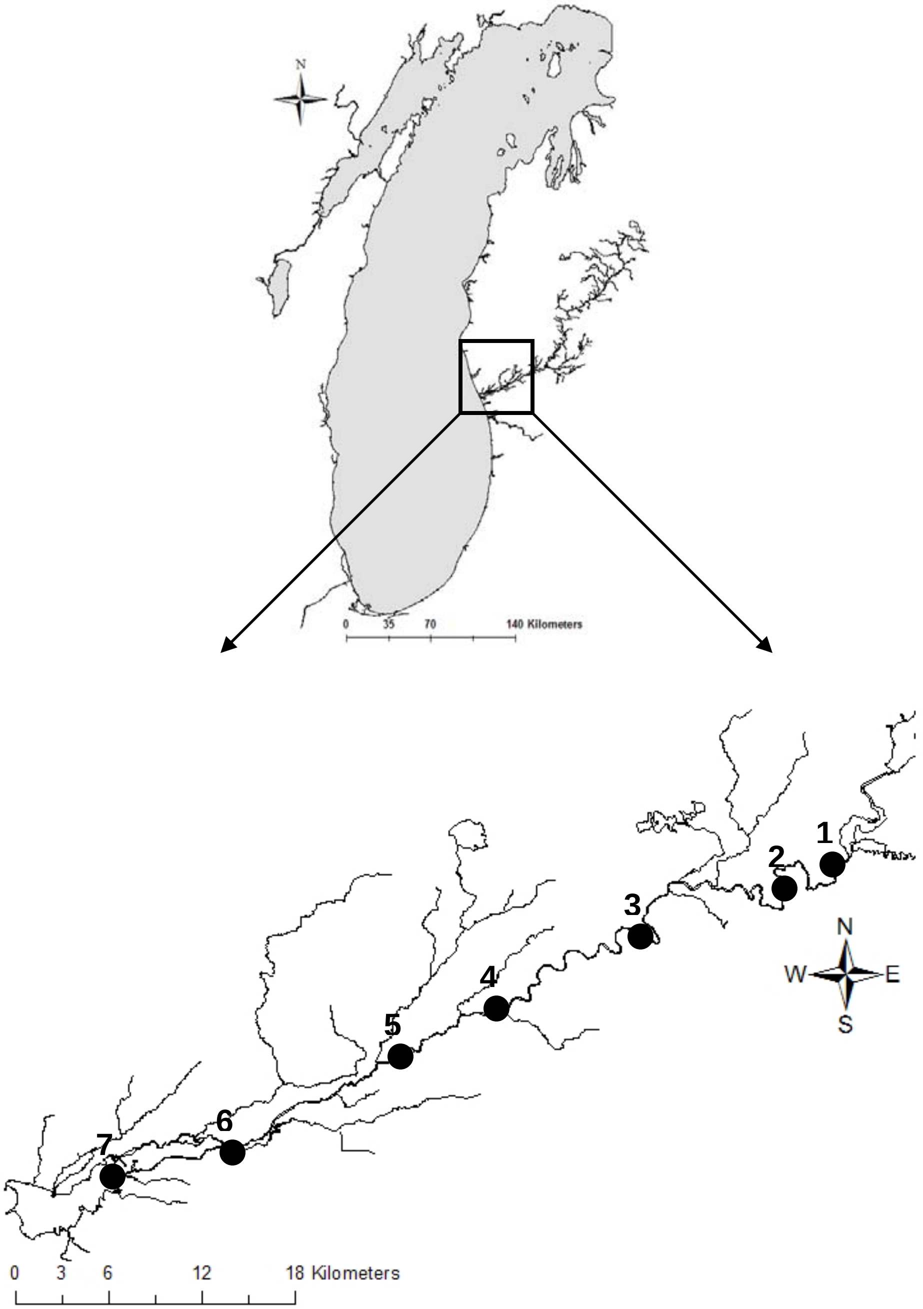

Figure 1. Map of the Muskegon River watershed, Michigan, including Muskegon Lake and the 80-km study area of the Muskegon River downstream of Croton Dam. Sites 1 through 6 were located on the Muskegon River, while site 7 was on Muskegon Lake.

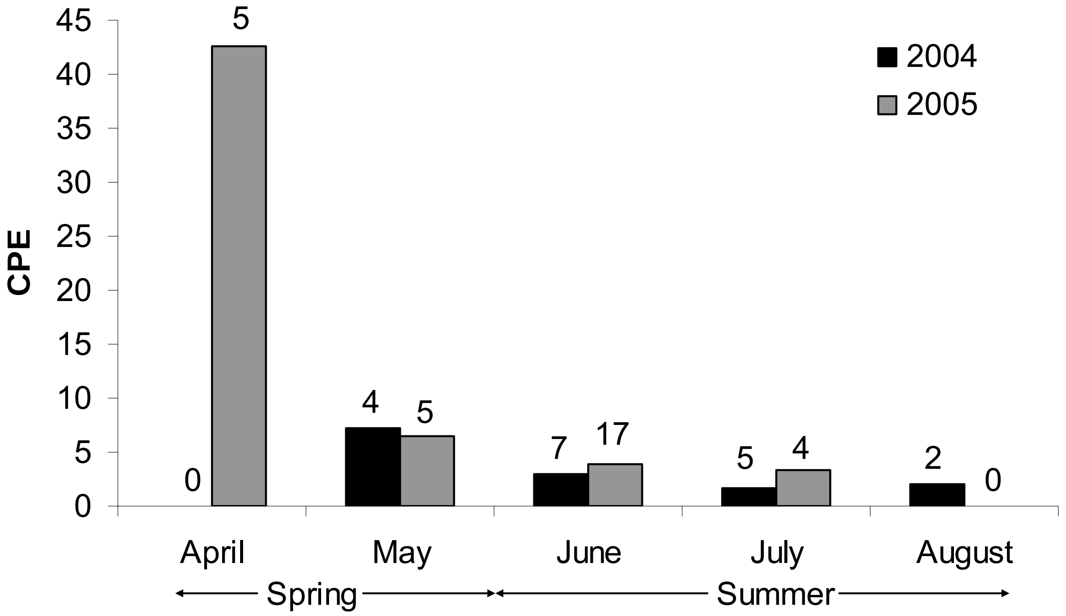

Figure 2. Number of walleye captured per hour (CPE) in the Muskegon River from April through August 2004 and 2005. The numbers above each bar indicate the number of collections.

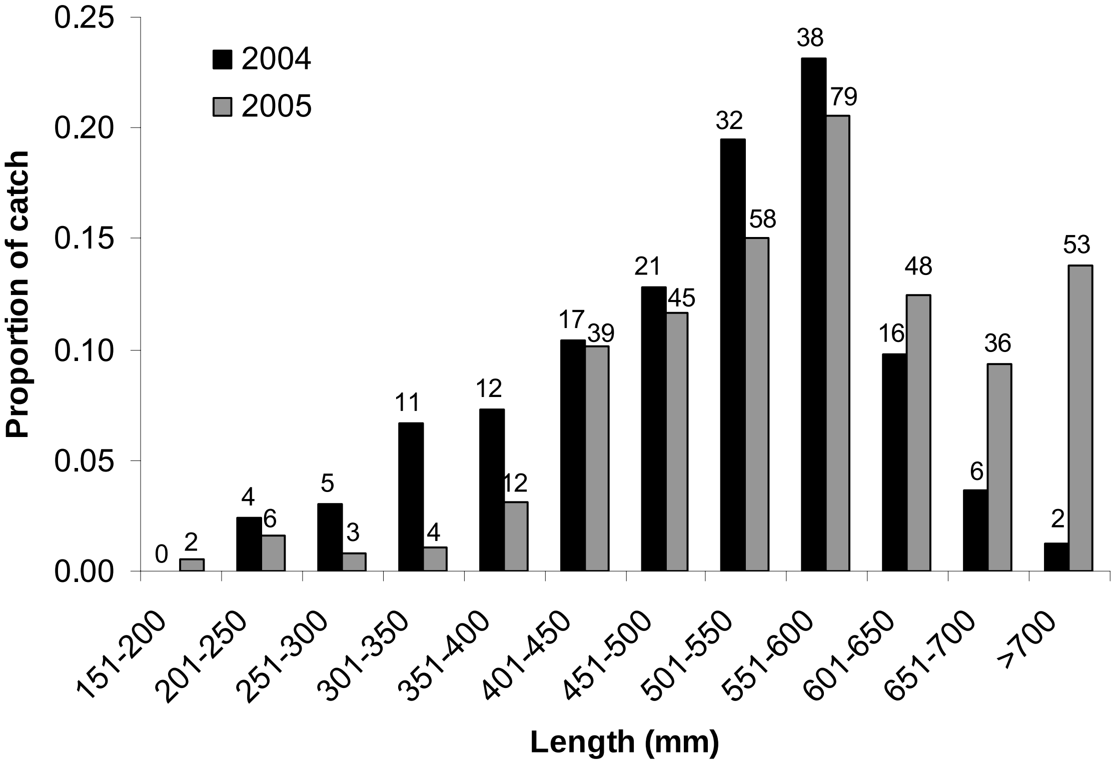

Figure 3. Length frequencies (in 50-mm intervals) of walleye captured in the Muskegon River and Muskegon Lake from May through August 2004 and April through August 2005. The numbers above each bar indicate sample size.

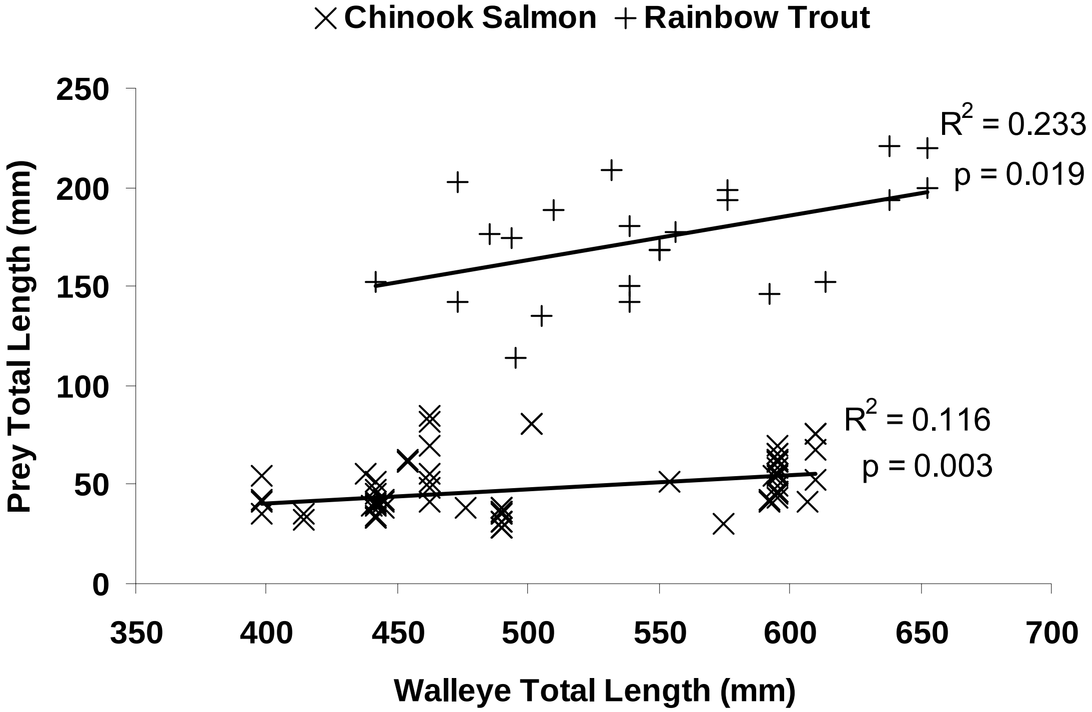

Figure 4. Linear regression of Chinook salmon and rainbow trout total length compared to walleye total length. Walleye were captured in the Muskegon River and Muskegon Lake from April through August 2005. Prey total length was measured from Chinook salmon and rainbow trout ingested by these walleye.

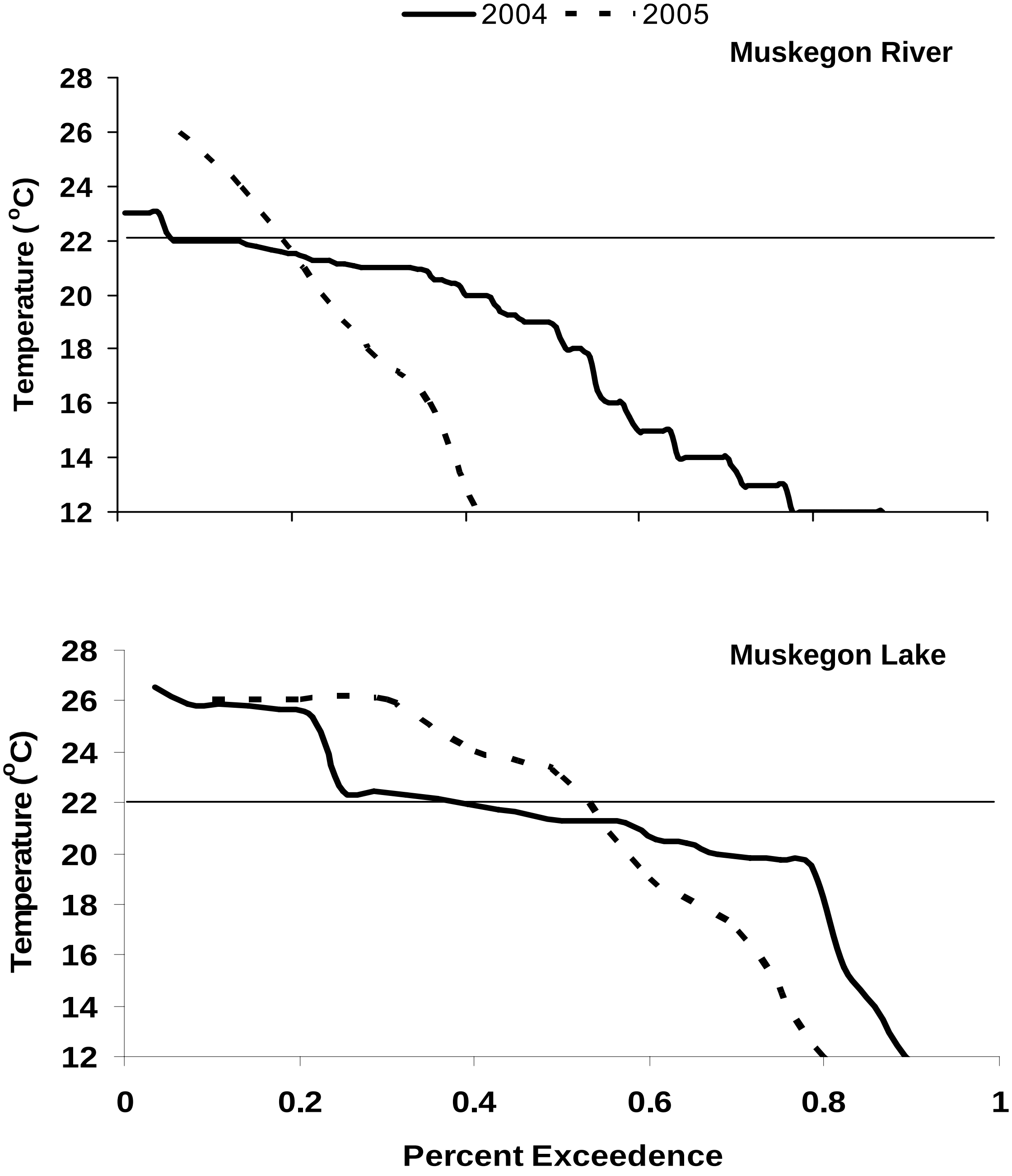

Figure 5. Surface water temperatures from the Muskegon River and Muskegon Lake from May through August 2004 and April through August 2005. The line at 22°C indicates optimal temperature for walleye consumption and growth.