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Seasonal thermal ecology of adult walleye (*Sander vitreus*) in Lake Huron and Lake Erie



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ABSTRACT

The purpose of this study was to characterize thermal patterns and generate occupancy models for adult walleye from lakes Erie and Huron with internally implanted biologgers coupled with a telemetry study to assess the effects of sex, fish size, diel periods, and lake. Sex, size, and diel periods had no effect on thermal occupancy of adult walleye in either lake. Thermal occupancy differed between lakes and seasons. Walleye from Lake Erie generally experienced higher temperatures throughout the spring and summer months than did walleye in Lake Huron, due to limnological differences between the lakes. Tagged walleye that remained in Saginaw Bay, Lake Huron (i.e., adjacent to the release location), as opposed to those migrating to the main basin of Lake Huron, experienced higher temperatures, and thus accumulated more thermal units (the amount of temperature units amassed over time) throughout the year. Walleye that migrated toward the southern end of Lake Huron occupied higher temperatures than those that moved toward the north. Consequently, walleye that emigrated from Saginaw Bay experienced thermal environments that were more favorable for growth as they spent more time within their thermal optimas than those that remained in Saginaw Bay. Results presented in this paper provide information on the thermal experience of wild fish in a large lake, and could be used to refine sex- and lake-specific bioenergetics models of walleye in the Great Lakes to enable the testing of ecological hypotheses.

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1. Introduction

Walleye *Sander vitreus* provides an economically valuable resource in the Laurentian Great Lakes of North America to recreational and commercial fisheries that generate tens of millions of dollars annually (Fielder et al., 2014; Melstrom and Lupi, 2013; Roseman et al., 2008). Commercial fisheries in Lake Huron date back to the 1880s and once supported the second largest walleye fishery in North America, producing an average of 458 tonnes of fish annually (Brown et al., 1999; Baldwin and Salfeld, 1962). However, walleye populations declined during the 1950s due to

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http://dx.doi.org/10.1016/j.jtherbio.2015.08.009 0306-4565/© 2015 Elsevier Ltd. All rights reserved. overfishing and a series of poor year classes, presumably due to diminished water quality and degraded spawning habitat (Schneider and Leach, 1977), and fry predation by the invasive alewife *Alosa pseudoharengus* (Madenjian et al., 2008). Reestablishment of walleye populations occurred during the 1980s as a direct result of improvements in water quality and fingerling stocking (Schneider and Leach, 1977; Fielder and Baker, 2004) and due to a collapse of alewife populations in the 2000s (Madenjian et al., 2008) leading to a full recovery in 2009 of the Saginaw Bay stock of walleyes (the single largest source within Lake Huron; Fielder and Thomas, 2014).

Lake Erie has the largest walleye fishery of all five Laurentian Great Lakes (Roseman et al., 2008; Fielder, 2002). Historically, commercial records indicate that the harvest of walleye stocks in Lake Erie date back to 1867 (Baldwin et al., 2002) with yields increasing until the mid-1950s reaching a peak of approximately 7000 tonnes (Nepszy, 1977; Schneider and Leach, 1977). Walleye populations of Lake Erie collapsed to low levels by 1960 as a direct result of the overexploitation of walleye stocks, combined with the effects of pollution, eutrophication, and severe spawning habitat modifications (Koonce et al., 1996). The enactment of fishing quotas coupled with habitat remediation efforts (Hatch et al., 1987; Ryan et al., 2003) have since allowed walleye populations to recover in Lake Erie.

As ectotherms, temperature has been labeled the "master" abiotic factor (Brett, 1971), and variations in ambient water temperatures can affect physiological (e.g., growth, swimming speed, and digestion), biochemical (e.g., enzymatic activities), and lifehistory activities (e.g., maturation, reproduction, and migrations) (Fry, 1971). For many fish species (see Pierce et al. (2013) and Tirsgaard et al. (2015)), laboratory studies have shown that thermal optima occur throughout ontogeny. With walleye, thermal optimas for early life stages (22 °C; Koenst and Smith 1976; Huh et al., 1976; Kelso, 1972) have been determined to be slightly higher than optimas for mature fish (18–22 °C; Christie and Regier, 1988). Although a general understanding exists for many species of fish of the potential effects of temperature, little is known on the available thermal habitat of Lake Erie and Lake Huron, and thus further knowledge regarding the thermal regimes experienced by Great Lakes walleye is required to aid in better understanding growth rates, maturation schedules, foraging behavior, and year-class strength of wild walleye in relation to changes in environmental temperatures.

We focused on the thermal biology of two adult walleye populations in two physically and limnologically distinct lakes. Specifically, we investigated walleye in Lake Huron that used the Tittabawassee River for spawning, and walleye from Lake Erie that spawned in the Maumee River. Our objectives were to (1) describe and compare seasonal patterns of temperature occupancy by adult walleye and assess the effects of sex, size, diel periods, and location on those patterns, (2) model the annual thermal experience of Lake Erie and Lake Huron walleye, and (3) determine whether differences exist in the thermal experience of Lake Huron walleye by comparing accumulated thermal units among walleye from the subpopulation resident in Saginaw Bay (adjacent to the release site) vs. walleve using northern Lake Huron during summer and fall, vs. walleye using southern Lake Huron during summer and fall. Results presented in this paper provide information on the thermal experience of wild fish in a large lake, and could be used to refine sex- and lake-specific bioenergetics models of walleye in the Great Lakes to improve management (Hansen et al., 1993) and enable the testing of ecological hypotheses.

2. Methods

2.1. Study site and fish collection

Adult walleye were captured at two sites using boat-mounted electrofishing gear, during the spring spawning (between March and April 2011) run: (1) below Dow Dam on the Tittabawassee River (43 °36'24.2''N 84 °14'23.1''W) of Lake Huron, and (2) Orleans Park along the Maumee River (41 °33'37.2''N 83 °38'38.1'W) of Lake Erie (Fig. 1). Fish selected for tagging were limited to those at or above the legal recreational angling length limit in Michigan and Ohio (> 381 mm) and were transferred to 380 L holding tanks after total length, weight, and sex were recorded for each individual. Dorsal spines were taken to non-lethally (see Brusher and Schull (2009)) estimate the age of individual walleye, a procedure that is routinely used by management agencies in the Great Lakes Basin (Erickson, 1983). In total, 199 individuals from Lake Huron (101 females and 98 males), and 200 (97 females and 103 males) individuals from Lake Erie, were implanted with acoustic transmitters (V16-4x; 16 mm dia. \times 86 mm, 24 g; battery life=1338 d, Vemco, Halifax, Nova Scotia). The acoustic transmitters were set to emit a tag-specific code (69 kHz) at intervals between 60 and 180 s (mean: 120 s) and were coupled with an thermal (DS1921z; iButton logger resolution = +0.1 °C: accuracy= 0.4 ± 0.3 °C, precision= 0.2 ± 0.3 °C, Maxim Integrated Products, Inc., Sunnyvale, California) (Donaldson et al., 2009) using a hot glue gun and the affixed logger was dipped in a waterproof coating (Plasti Dip, Performix Brand, Blaine, MN). iButtons were programmed to record temperatures at four-hour intervals for a period of approximately one year.

2.2. Acoustic tag and thermistor implanting

Prior to surgery, a walleye was transferred from a holding tank and anesthetized using a portable electroanesthesia system (PES; Smith-Root, Vancouver, Washington) operating at 35 V pulsed direct current. Electroanesthesia using pulsed direct current results in immediate induction, quick recovery, and high survival of walleye (Vandergoot et al., 2011). Treatments of three seconds induced stage-4 anesthesia for several minutes, allowing sufficient time for surgical implantation of the acoustic transmitters-iButtons. All surgical procedures followed guidelines outlined by Cooke et al. (2011). While sedated, fish were placed on a v-shaped



Fig. 1. Collection sites for adult walleye (*Sander vitreus*) for Lake Erie (Orleans Park, Maumee River) and Lake Huron (Dow Dam, Tittabawassee River). Red dots represent the locations of individual VR2W acoustic telemetry receivers positioned in Lake Erie, Lake Huron, and along the Huron–Erie corridor, which includes the St. Clair River, Lake St. Clair, and the Detroit River. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

surgical table, lined with soft, non-slip material. A constant flow of fresh water was pumped using a recirculation pump across each individual's gills to provide oxygen. All surgical tools were cleaned with povidone iodine and rinsed with deionized water before surgery; transmitters were similarly disinfected prior to being implanted. A small incision was made along the ventral side of each fish, posterior to the pelvic girdle. Each acoustic tag with iButton was placed into the coelom and the incision was closed with two to three absorbable monofilament sutures (PDS-II, 3-0, Ethicon, Somerville, NJ). A single experienced surgeon implanted all transmitters to reduce variation in fish survival and recovery: average surgery time was 142 s. Each fish was also tagged with two external anchor tags (Flov Manufacturing, Seattle, Washington) inserted between the dorsal pterygiophores to allow for identification of fish implanted with transmitters and promoted return of tags from walleye caught in the fishery. After surgery, fish were returned into holding tanks to recover. After the recovery period (30 min), individuals were released near the location where captured.

2.3. Experimental design

During summer 2010, 140 stationary receivers (VR2W, 69 kHz, Vemco; Fig. 1) were installed in Lake Huron where they remained throughout the study period, except for periods of maintenance and data downloads (See Hayden et al., 2014). Receivers were placed in several perpendicular lines out from the shoreline, across bay mouths, and in rivers to monitor walleye movement (Fig. 1). Double receiver lines were deployed across Saginaw Bay to gather information regarding walleye movement in and out of Saginaw Bay. Receiver lines positioned perpendicular to the shoreline were restricted to depths < 40 m, extending 3–10 km offshore. In shallower depths (less than 2 m), deployed receivers were attached to existing structure or steel anchor posts buried in the substrate. Receivers deployed in deep waters (>2 m) were attached to a concrete anchor connected to a buoy. Receivers were placed on stainless steel cable, suspended at depths of 1-3 m above the lake bottom. Refer to Hayden et al. (2014) for complete information on static range testing, and receiver line detection probabilities. Thermal data were obtained via returned transmitter/iButton units from tagged fish caught in the fisheries. A monetary reward of \$100 USD was offered to anyone that harvested tagged walleye and returned the acoustic tag and iButton to the investigators.

2.4. Data analysis

To test for seasonal differences in thermal experiences of walleve in lakes Erie and Huron, two-sample *t*-tests were performed on minimum, maximum, and average temperatures for each season in order to estimate the differences in the thermal extremes walleye may experience in either lake. F-tests were done on average temperatures for each season to determine any variability between lakes. Maximum and minimum values for each lake were determined by averaging the highest and lowest of temperatures experienced by individual walleye during each season. Spring corresponded to dates between March 20th, 2011 and June 20th, 2011; summer corresponded to dates between June 21st, 2011 and September 21st, 2011; fall corresponded to dates between September 22nd, 2011 and December 20th, 2011; and winter corresponded to dates between December 21st, 2011, and March 19th, 2012. As a result of variations in the timing of fish being caught (i.e., the majority of walleye being caught earlier in the year), estimates of thermal experiences were restricted to data from fewer individuals during later parts of the year (see Fig. 2 for exact numbers).



Fig. 2. Thermal data for walleye (*Sander vitreus*) mean maximum seasonal temperatures (panel a), mean seasonal temperatures (panel b), and mean minimum seasonal temperatures (panel c) for both Lake Erie (labeled LE) and Lake Huron (labeled LH) individuals. Values below lake labels represent the total number of individuals for each season. Asterisks represent significant differences between lakes within seasons (P < 0.05). The horizontal lines represent the means of each group. Whiskers represent the largest and smallest observations within each group that fall within 1.5 × of the interquartile range. Observations that exceed this interquartile range are plotted as open circles. Mean maximum and minimum values for each lake were determined by averaging the highest and lowest of temperatures experienced by individual walleye during each season.

Based on seasonal temperature variations experienced by walleye over time for lakes Erie and Huron, non-linear relationships existed between temperature experienced and time. Because time was a covariate of interest, time was analyzed for its effect on the response variable (temperature) using a generalized additive mixed model (GAMM) that included individual fish ID as a random effect (random intercept model). In addition, a correlation structure and variance structure were included to account for autocorrelation in the residuals and heterogeneity across months, respectively (Zuur et al., 2009). To determine the final model, the significance of variables (i.e., sex, size, diel periods, locations, and any interactions that may be occurring) was assessed using backwards model selection from a global model (i.e., model containing all variables of interest). Using this approach, we initially fitted our model using all of our variables of interest and continued on by sequentially dropping the least significant variable, as long as it was not significant at our chosen value of $\alpha = 0.025$. For this analysis, we used a more conservative P-value to assess the importance of each variable (Wood, 2006). Model residuals were plotted and examined to validate that model assumptions were not violated (Zuur et al., 2009).

To detect differences in the thermal experiences of walleye that migrate out of Saginaw Bay into Lake Huron versus walleye that remain in Saginaw Bay, a Tukey's range test was used in conjunction with a one-way analysis of variance (ANOVA) using temperature data from Lake Huron walleye. For this analysis, accumulated thermal units were used in order to provide an estimate of the effect emigrating out of Saginaw Bay has on the thermal experience of Lake Huron walleye. The dependent variable in the ANOVA was accumulated thermal units (ATUs) and the main effect was subpopulation (three levels: Saginaw Bay subpopulation, northward-migrating subpopulation, southward-migrating subpopulation). We calculated ATUs by first averaging recorded temperatures for each day, and then summing average daily temperature from 5 April 2011 through 11 October 2011. The final day for ATU calculations was 11 October 2011 to optimize sample size for each of the three groups. Statistical significance was set at P < 0.05. This part of the analysis was limited to specifically Lake Huron walleye, as previous studies have already examined the potential benefits of migrating walleye in Lake Erie (see Wang et al. (2007) and Kershner et al. (1999)). All analyses used the R statistical programming environment (R Development Core Team, 2012). Analyses completed by Hayden et al. (2014) on walleye movement in Lake Huron were used to classify each of the tagged Lake Huron walleye into one of the three subpopulations.

3. Results

3.1. Thermal experiences of Lake Erie and Lake Huron walleye

Thermal data was downloaded from 70 tagged individuals (18% of total tagged) caught in the fishery (see Table 1 for summary information). Walleye experienced different temperatures in Lake Erie vs. Lake Huron during specific periods of the year as judged by mean maximum water temperature recorded. Lake Erie walleye used warmer maximum temperature water during the summer (25.0 °C) and fall (18.3 °C) than Lake Huron fish (23.6 °C, 16.5 °C respectively, P < 0.05, Fig. 2.a). During the summer, Lake Erie walleye resided in warmer temperature water, on average, than Lake Huron fish (mean 21.14 °C vs. 19.30 °C, P=0.004, Fig. 2b). Mean temperatures experienced of Lake Erie walleye were less

Table 1

Summary of physical attributes (e.g., sex, number of individuals, length, and age) and days at liberty after tagging of adult walleye (*Sander vitreus*) caught by the Lake Erie and Lake Huron fisheries as of October of 2013. Age was determined using dorsal spine samples. Length refers to an individual's total-length. Days at liberty refer to the time individual walleye spent in each lake before being caught.

	Lake Huron		Lake Erie	
Sex	М	F	М	F
Total numbers	17	28	14	11
Mean age (years)	8	8	7	10
Maximum	13	14	12	13
Minimum	4	4	4	8
Standard deviation	2.24	2.42	2.48	2.14
Mean length (mm)	528	588	525	652
Maximum	712	781	602	781
Minimum	450	456	450	590
Standard deviation	56.8	71.2	43.3	56.0
Mean days at liberty	167	187	85	207
Maximum	338	338	341	341
Minimum	33	22	3	63
Standard deviation	115.4	129.3	112.6	122.9

variable throughout the fall (F=0.049, P<0.01) and winter (F=0.006, P<0.001) seasons, when compared to individuals from Lake Huron. Similarly, the mean minimum water temperature recorded for Lake Erie walleye in spring and summer was higher than for Lake Huron walleye (Fig. 2c). A few individuals from Lake Huron were recorded occupying temperatures warmer than 15 °C during parts of the winter season.

3.2. Effects of sex, size, and diel periods

Overall, walleye thermal regimes closely reflected normal temporal temperature patterns with water temperatures warming throughout the spring season, reaching a maximum in late summer and declining through the fall and into the winter (Fig. 3). No differences in thermal experiences between the sexes of mature walleye were found within either lake (P > 0.025). Likewise, the thermal experience of walleye was not related to their total length or diel period (P > 0.025). In contrast, season and location (i.e. Lake Huron and Lake Erie) explained temperatures experienced by walleye (P < 0.025), and these two variables explained 92% of the variation in the data (Table 2; $R^2 = 0.92$). Based on the model, the expected thermal experiences of walleye were plotted throughout the year; yielding an estimate of the range of temperatures walleye can be found at any given time for both lakes in 2012 (see Fig. 4, dashed lines represent the 95% confidence intervals).

3.3. Thermal variability between different groups of migrating walleye in Lake Huron

Of the 45 individuals evaluated from Lake Huron, 64% (n=29) remained within Saginaw Bay after spawning, whereas 18% (n=8) migrated to the northern portion of Lake Huron and 18% (n=8)migrated to the southern portion of Lake Huron. Of the individuals that remained in Saginaw Bay, 59% were female, with an average age of 7.2 years (SD=2.27) and an average length of 550 mm (SD=70.2). Of the individuals that migrated to northern parts of Lake Huron, 63% were female, with an average age of 9.4 years (SD=2.32) and an average length of 590 mm (SD=71.4). Similarly, of the individuals that migrated to southern parts of Lake Huron, 75% were female with an average age of 6.8 years (SD=0.834) and an average length of 560 mm (SD=51.5). Results of the one-way ANOVA revealed differences in thermal experiences among the three walleye subpopulations (F(2,17) = 32.319, P < 0.001, Fig. 5). Individuals remaining in Saginaw Bay accumulated 648 more ATUs than individuals migrating to the north (P < 0.0001, Table 3), and 461 more ATUs than to the south (P < 0.0001, Table 3).

4. Discussion

4.1. Inter-lake thermal variability of Great Lakes walleye

Differences in the thermal experiences of walleye is partly attributable to differences in the physical features between the two lakes. Lake Erie, being further south and the smaller and shallower of the two lakes (Fuller et al., 1995), warms more quickly in the spring and summer months, and on average possesses mean surface water temperatures more than 5 °C higher than Lake Huron during mid-summer (Dobiesz and Lester, 2009). Temperature plays a key role in the growth and maturation of walleye, with optimal temperatures ranging between 18 and 22 °C. Individuals occupying habitats within this range undergo the highest levels of growth, as well as generate strong subsequent year classes, as individuals can allocate more energy to gamete production (Kitchell et al., 1977). However, increases in temperatures above these limits can lead to adverse effects on the physiology of fish.



Fig. 3. Example thermal profiles typifying two female adult walleye (*Sander vitreus*) from Lake Erie and Lake Huron (panels A and C respectively), and two male adult walleye (*Sander vitreus*) from Lake Erie and Lake Huron (panels B and D respectively). The solid black line represents the moving average of temperatures experienced by walleye in each lake and shaded areas represent 95% confidence intervals.

Table 2

The importance of fixed terms, variance covariate (β), and correlation structure (TimelFish ID) for our model predicting the thermal experience of walleye (*Sander vitreus*) in Lake Erie and Lake Huron. The approximate significance of the smoother (Month) for Lake Erie was ($F_{8,231}$ =95.72, P < 0.0001) and for Lake Huron ($F_{8,240}$ =209.0, P < 0.0001). Length, sex, size, diel period, were all insignificant in our model (P > 0.025).

Model term	L ratio	df	P-value
Location Month (TimeIFish ID)	18.99 461.4 1590	1 12 2	< 0.001 < 0.001 < 0.001 $R^{2} = 0.92$

Temperatures exceeding optimal levels are correlated with decreased growth rates (Kershner et al., 1999), higher metabolic costs (Clarke and Johnston, 1999), and increased natural mortality rates (Houde, 1989). As such, fish residing in the warm waters of Lake Erie may experience a higher rate of early season growth, followed by a period of decreased growth rates during periods in the summer, when compared to individuals from Lake Huron, as temperatures in excess of 25 °C have been recorded. However, Lake Erie walleye may compensate for this by migrating toward the central and eastern basins where cool water habitat exists (Ryan et al., 2003; Wang et al., 2007).

Abnormally high temperatures experienced by some Lake Huron walleye in the winter were likely the result of fish occupying thermal effluents associated with manufacturing establishments along the shore of Lake Huron. Telemetry data has revealed these individuals overwintered in Saginaw Bay, and Lake St. Clair (Hayden et al., 2014). Historically, increases in water temperatures up to 10 °C have been observed in the Tittabawassee River as a



Fig. 4. Predicted temperatures experienced by adult walleye (*Sander vitreus*) in Lake Huron (A) and Lake Erie (B) throughout the course of a year, with dashed lines representing 95% confidence intervals. Values for predicted temperatures of each lake were obtained using a generalized additive mixed model.



Fig. 5. Box and whisker plot of the accumulated thermal units (ATUs) of walleye (*Sander vitreus*) who migrate north, remain in Saginaw Bay, or migrate south. The horizontal lines represent the means of each group. Whiskers represent the largest and smallest observations within each group that fall within $1.5 \times$ of the interquartile range. Observations that exceed this interquartile range are plotted as open circles. Different letters are representative of significant differences between groups.

Table 3

Results of one-way ANOVA and Tukey's range test applied to accumulated thermal units (ATUs) for walleye (*Sander vitreus*) from the following three Lake Huron subpopulations: (1) those fish migrating to northern Lake Huron, (2) those fish remaining in Saginaw Bay, and (3) those fish migrating to southern Lake Huron. Both *F*- and *P*-values were obtained through Tukey's range test.

Location	Accumulated thermal units	F value	Significance
North Saginaw Bay South	2601 3249 2789	40.75 7.65 2.08	P < 0.0001 P = 0.053

result of water being used for cooling purposes (Gannon, 1963). Hence, a few individuals may have selected specific locations of Lake Huron that are exposed to thermal effluents, explaining the increased temperatures we observed. Previous telemetry studies on yellow perch, a similar cool-water fish, have shown high numbers of individuals actively selecting areas in a thermal discharge bay for much of the winter (Ross and Sniff, 1982). Consequently, walleye inhabiting thermal plumes throughout winter months may show an analogous preference for areas of increased water temperatures and, in turn, benefit from a lengthened growing season that extends into the winter months.

4.2. Intra-lake thermal variability of Great Lakes walleye

Individuals that remained in Saginaw Bay were able to accumulate more thermal units as they occupied higher water temperatures when compared to fish that migrated out of Saginaw Bay and into the main basin of Lake Huron. As such, walleye that remain in Saginaw Bay have the potential to be at a disadvantage during the summer, as temperatures exceeded thermal optima, and could result in depressed growth. Although individuals that remained in Saginaw Bay did not migrate into other parts of Lake Huron, due to the incomplete coverage of our receiver lines in the lake, we could not determine whether northern or southern moving fish reversed and took paths outside of our detection ranges along the shores of Lake Huron. As such, walleye could possibly be detected on northern receivers but then turn south without being detected.

In Lake Erie, walleye move during the summer to the central and eastern basins that have cooler water than the western basin (Wang et al., 2007). Western basin walleye that showed eastward migrations were larger and older than those individuals that did not migrate from the western basin. A bioenergetic analysis by Kershner et al. (1999) revealed two growth peaks associated with eastward migratory walleve, and only a single growth peak for individuals that remained in the western basin. As the western basin warmed at a greater rate than the other basins, optimal growth periods occurred earlier in the season and these periods would eventually shift eastward to the central basin in the early summer. Consequently, migratory fish exploited growth peaks in both basins and experienced optimal temperatures for a longer period of time. Thus, migratory individuals achieved a thermal advantage and experienced higher growth rates than their nonmigratory counterparts (Kershner et al., 1999). Walleye that emigrated from Saginaw Bay were likely demonstrating analogous behavior to walleye from Lake Erie and thus behaviorally thermoregulating to access optimal growth periods and temperatures associated with Saginaw Bay and northern and southern basins of Lake Huron. Migratory walleye in both lakes may also have benefited through behavioral thermoregulation by avoiding the damaging effects on fish that become evident as temperatures approach upper critical thresholds. High summer temperatures are known to cause significant losses in optimal thermal habitat for cool and cold-water species (Eaton and Scheller, 1996), and result in weight loss and stunted growth (Kitchell et al., 1977), an increase in the occurrences of bacterial and viral diseases (Snieszko, 1974), and ultimately increase in mortality rates when temperatures exceed maximum tolerable levels.

Migration from Saginaw Bay could also be the result of the quest for greater availability of forage fish. In Lake Ontario, specifically the Bay of Quinte, Bowlby and Hoyle (2011) show that many mature walleye migrated out of the bay into the deeper and cooler waters of Lake Ontario throughout the summer and early fall months to forage on alewife. The authors noted that the concentrated amounts of alewife might offset any disadvantages associated with lower temperatures than available in the Bay of Quinte. Similarly, movement of Lake Erie walleye has also been linked to spatial patterns of prey abundance, specifically soft-rayed fish (i.e., rainbow smelt *Osmerus mordax*, emerald *Notropis atherinoides* and spottail shiners *Notropis hudsonius*) that reside in the central and eastern basins in the summer (Wang et al., 2007).

A more extensive study by Hayden et al. (2014), reported 57% of individuals remained in Saginaw Bay throughout the year and 43% emigrated to either northern or southern parts of Lake Huron. Discrepancy in our results is likely caused by us only using the biologger data from individuals caught earlier than when the majority of walleye left the bay, whereas the outmigration rates presented by Hayden et al. (2014) included individuals at liberty as well as those harvested. It is also important to note that this study is limited to one year of temperature data due to the characteristics of the biologgers. Interpretation of our statistical results should thus be taken carefully as the benefits and/or disadvantages of remaining in Saginaw Bay is likely to change with the annual variation in water temperatures of Lake Huron. For example, during a cooler than normal year individuals that remain in Saginaw Bay may be at an advantage, as temperatures would be unlikely to exceed thermal limits, compared to individuals that migrate out of the bay.

4.3. Variables influencing thermal habitat experience

Despite the growing body of evidence regarding the effects of interspecific variables on the thermal biology of ectothermic organisms (Sagonas et al., 2013; Tang et al., 2013; Huey and Pianka, 2007), few studies have focused on fish. In addition to field experiments, Pearson et al. (2003) stated that research on the thermal biology of an organism should also include a laboratory component so that thermal preferences observed in the wild can be compared to those observed under controlled conditions. We did not incorporate a laboratory component in our study given the extensive body of work already published on walleve. Previous studies with adult walleve have suggested thermal optima for growth ranging between 18 and 22 °C (Christie and Regier, 1988). However, individuals that we observed spent a relatively small proportion of their time within this optimal temperature range due to the seasonal variation in water temperatures during an entire year and so we examined various other biological variables that may have contributed to the annual thermal regimes of walleye in lakes Huron and Erie.

Adult walleye are negatively phototactic organisms (Bulkowski and Meade, 1983) and progressively move into deep/cool waters during their ontogeny. If walleye in either lake were forced into deep waters of the hypoliminion during daytime, we would anticipate diel movement to occur with regards to their thermal habitat. However, our results showed no differences between day and night temperatures (P > 0.025). A possible explanation for the lack of any day/night fluctuations can be explained by periodic thermal mixing within both lakes. When testing the effects of each variable, we did so over the course of an entire year. Stratification properties of northern temperate lakes reveal isothermal profiles for the majority of the year (Baj et al., 2013). In central and eastern Lake Erie, stratification is first established in early July and continues until late September or early October; stratification typically does not occur in western Lake Erie (Schertzer et al., 1987). Full stratification of Lake Huron does not occur until mid-July and lasts until waters become fully isothermal again by mid-October (Sheng and Rao, 2006). As these dates translate into roughly a third of the year, any effects that diel period may have on walleye thermal ecology may be masked by the isothermal conditions that occur during most of the year. Nonetheless, walleye temperatures were highly variable during parts of the summer months and random daily fluctuations, up to 8.9 °C, were observed. Walleye in West Blue Lake, Manitoba, revealed similar patterns with regards to day and night thermal variation (Kelso, 1976). Adult walleye, between the ages of 2 and 5, used the epilimnion between 5 and 10 m, and chose a fairly constant range of temperatures between 10.6 and 11.7 °C, despite having temperatures from 5.1 to 14.7 °C available.

Our results revealed no differences in thermal experiences between the sexes of mature walleye in either lake. Likewise, thermal habitat experience of walleye was not related to their total length. Female walleyes tend to be larger at a specific age than their male counterparts (Rennie et al., 2008). Similar work on differences in freshwater fish species revealed no differences in thermal selectivity and responses between sexes (Cherry et al., 1975). Only mature walleye were used in this study. If immature fish had been tagged, differences in thermal experience may have emerged between immature and mature individuals. Many species of fish show size-dependent thermal preferences (McCauley and Huggins, 1979) such that optimal temperatures required for growth decrease with increasing body sizes (Morita et al., 2010). For example, clear differences in ontogenetic thermal preferences of yellow perch were documented with juveniles selecting temperatures within a range of 20-20.3 °C while adults selected a range between 17.6 and 20.1 °C (McCauley and Read, 1973). Similarly, juvenile walleye experienced optimal growth at water temperatures of 26 °C (Hokanson and Koenst, 1986), whereas mature walleye prefer temperatures between 18 and 22 °C (Christie and Regier, 1988). Consideration of ontogenetic differences of the thermal preferences of walleye is needed to fully understand growth performances and thermal experiences of walleye.

The annual thermal experience of adult walleye in lakes Erie and Huron reported here will provide an important management tool to refine bioenergetics models for walleye in both lakes (Hartman and Kitchell, 2008; Hanson et al., 1997). For example, fish bioenergetics modeling has been used in managing the Chinook salmon (Oncorhynchus tshawytscha) fishery in Lake Michigan (Tsehaye et al., 2014; Madenjian, 2011; Hansen et al., 1993) and the entire predator community of Lake Huron (He et al., 2014). Population models for salmonines have been coupled with fish bioenergetics models to generate estimates of annual consumption of prey fish. In turn, salmonine stocking rates have been adjusted based on model predictions. Petersen and Kitchell (2001) used bioenergetic modeling to predict changes in predation on juvenile salmon with climate change, and thus provided managers with a tool to predict future mortality on juvenile salmon and ultimately aid in recovery of the salmon stock.

In the near future, temperature is predicted to increase with climate change (Hayhoe et al., 2010; Magnuson et al., 1997), resulting in higher water temperatures. Magnuson et al. (1997) predict climate change to cause a number of physical and biological changes including increases in thermocline depths, decreases of dissolved oxygen below thermocline, increases in phyto- and zooplankton, increases of warm-, cool-, and cold-water habitats in deep stratified lakes (opposite for shallow stratified lakes), and changes in the growth and production of fish species. Although some work has been done on predicting potential effects of climate change on different species on fish in lakes Michigan and Erie (Magnuson et al., 1990), future studies should consider how climate change might affect available thermal habitat for native populations of fish (i.e. walleye) in all the Great Lakes.

Differences in thermal regimes experienced by walleye between lakes Erie and Huron were largely driven by differences in bathymetry between the two lakes, with Lake Erie being substantially shallower and warmer than Lake Huron. However, concluding that observed differences in the thermal experiences of walleye were caused solely by limnological differences would be an oversimplification. Walleye are likely faced with a decision to either stay in areas of the lake where temperatures exceed optimum levels and benefit from not having to expend energy, or alternatively to search for more thermally optimal areas and if found, benefit from reduced metabolic costs associated with colder temperatures. Thus, future research is needed to identify potential explanations as to why such differential behavior exists within a population.

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References

- Bai, X., Wang, J., Schwab, D.J., Yang, Y., Luo, L., Leshkevich, G.A., Liu, S., 2013. Modeling 1993–2008 climatology of seasonal general circulation and thermal structure in the Great Lakes using FVCOM. Ocean Model. 65, 40–63. http://dx. doi.org/10.1016/j.ocemod.2013.02.003.
- Baldwin, N.S., Saalfeld, R.W., 1962. Commercial Fish Production in the Great Lakes, 1867–1960. No. 3, Great Lakes Fishery Commission, Ann Arbor, Michigan. Baldwin, N.S., Saalfeld, R.W., Dochoda, M.R., Buettner, H.J., Eshenroder, R.L., 2002.
- Commercial Fish Production in the Great Lakes 1867–2000.
- Bowlby, J.N., Hoyle, J.A., 2011. Distribution and movement of Bay of Quinte walleye in relation to temperature, prey availability and Dreissenid colonization. J. Aquat. Ecosyst. Health 14, 56–65. http://dx.doi.org/10.1080/ 14634988.2011.548298.
- Brett, J.R., 1971. Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). Am. Zool. 11, 99–113. http://dx.doi.org/10.1093/icb/ 11.1.99.
- Brown, R.W., Ebener, M., Gorenflo, T., 1999. Great Lakes commercial fisheries: historical overview and prognosis for the future. Great Lakes Fisheries Policy and Management: A Binational Perspective. Michigan State University Press, East Lansing, Michigan.
- Brusher, J.H., Schull, J., 2009. Non-lethal age determination for juvenile goliath grouper Epinephelus itajara from southwest Florida. Endangered Species Research 7, 205–212.
- Bulkowski, L., Meade, J.W., 1983. Changes in phototaxis during early development of walleye. Trans. Am. Fish. Soc. 112, 445–447. http://dx.doi.org/10.1577/ 1548-8659 (1983)112 < 445:CIPDED > 2.0.CO;2.
- Cherry, D.S., Dickson, K.L., Cairns Jr., J., 1975. Temperatures selected and avoided by fish at various acclimation temperatures. J. Fish. Res. Board Can. 32, 485–491. http://dx.doi.org/10.1139/f75-059.
- Christie, G.C., Regier, H.A., 1988. Measures of optimal thermal habitat and their relationship to yields for four commercial fish species. Can. J. Fish. Aquat. Sci. 45, 301–314. http://dx.doi.org/10.1139/f88-036.
- Clarke, A., Johnston, N.M., 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. J. Anim. Ecol. 68, 893–905. http://dx.doi.org/ 10.1046/j.1365-2656.1999.00337.x.
- Cooke, S.J., Wagner, G.N., Brown, R.S., Deters, K.A., 2011. Training considerations for the intracoelomic implantation of electronic tags in fish with a summary of common surgical errors. Rev. Fish. Biol. Fish. 21, 11–24. http://dx.doi.org/ 10.1007/s11160-010-9184-4.
- Donaldson, M.R., Cooke, S.J., Patterson, D.A., Hinch, S.G., Robichaud, D., Hanson, K.C., Olsson, I., Crossin, G.T., English, K.K., Farrell, A.P., 2009. Limited behavioural thermoregulation by adult upriver-migrating sockeye salmon (*Oncorhynchus nerka*) in the Lower Fraser River, British Columbia. Can. J. Zool. 87, 480–490. http://dx.doi.org/10.1139/Z09-032.
- Dobiesz, N.E., Lester, N.P., 2009. Changes in mid-summer water temperature and clarity across the Great Lakes between 1968 and 2002. J. Gt. Lakes Res. 35, 371–384. http://dx.doi.org/10.1016/j.jglr.2009.05.002.
- Eaton, J.G., Scheller, R.M., 1996. Effects of climate warming on fish thermal habitat in streams of the United States. Limnol. Oceanogr. 41, 1109–1115.
- Erickson, C.M., 1983. Age determination of Manitoban walleyes using otoliths, dorsal spines, and scales. N. Am. J. Fish. Manag. 3, 176–181. http://dx.doi.org/ 10.1577/1548-8659 (1983)3 < 176:ADOMWU > 2.0.CO;2.
- Fielder, D.G., 2002. Sources of walleye recruitment in Saginaw Bay, Lake Huron. N. Am. J. Fish. Manag. 22, 1032–1040. http://dx.doi.org/10.1577/1548-8675 (2002) 022 < 1032:SOWRIS > 2.0.CO;2.
- Fielder, D.G., Baker, J.P., 2004. Strategy and Options for Completing the Recovery of Walleye in Saginaw Bay, Lake Huron.
- Fielder, D.G., Kolb, T.L., Goniea, T.M., Wesander, D.L., Schrouder, K.S., 2014. Fisheries of Saginaw Bay, Lake Huron 1986–2010. Michigan Department of Natural Resources, Lansing, Michigan.
- Fielder, D.G., Thomas, M.V., 2014. Status and Trends of the Fish Community of Saginaw Bay, Lake Huron 2005–2011. Michigan Department of Natural Resources, Lansing, Michigan.
- Fry, F.E.J., 1971. The effect of environmental factors on the physiology of fish. Fish Physiol. 6, 1–98. http://dx.doi.org/10.1016/S1546-5098(08)60146-6.
- Fuller, K., Shear, H., Wittig, J., 1995. The Great Lakes: an Environmental Atlas and Resource Book. Great Lakes National Program Office, U.S. Environmental Protection Agency, Chicago, IL.
- Gannon, J.J., 1963. River BOD Abnormalities, a Case Study Approach: the Clinton River below Pontiac, Michigan, the Tittabawassee River below Midland, Michigan. College of Engineering – Technical Report.
- Hansen, M.J., Boisclair, D., Brandt, S.B., Hewett, S.W., Kitchell, J.F., Lucas, M.C., Ney, J. J., 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here. Trans. Am. Fish. Soc. 122, 1019–1030. http://dx.doi.org/10.1577/1548-8659 (1993)122 < 1019:AOBMTF > 2.3.CO;2.

- Hanson, P.C., Johnson, T.B., Schindler, D.E., Kitchell, J.F., 1997. Fish Bioenergetics 3.0. University of Wisconsin Sea Grant Institute Rep. WIS-CU-T-97-001, Madison, Wisconsin.
- Hartman, K.J., Kitchell, J.F., 2008. Bioenergetics modelling: progress since the 1992 symposium. Trans. Am. Fish. Soc. 137, 216–223. http://dx.doi.org/10.1577/ T07-040.1.
- Hatch, R.W., Nepszy, S.J., Muth, K.M., Baker, C.T., 1987. Dynamics of the recovery of the western Lake Erie walleye (*Stizostedium vitreum vitreum*) stock. Can. J. Fish. Aquat. Sci. 44, 15–22.
- Hayden, T.A., Holbrook, C.M., Fielder, D.G., Vandergoot, C.S., Bergstedt, R.A., Dettmers, J.M., Krueger, C.C., Cooke, S.J., 2014. Acoustic telemetry reveals large-scale migration patterns of walleye in Lake Huron. PLOS One 9, e114833. http://dx. doi.org/10.1371/journal.pone.0114833.
- Hayhoe, K., VanDorn, J., Croley, T., Schlegal, N., Wuebbles, D., 2010. Regional climate change projections for Chicago and the US Great Lakes. J. Gt. Lakes Res. 36, 7–21.
- He, J.X., Bence, J.R., Madenjian, C.P., Pothoven, S.A., Dobiesz, N.D., Fielder, D.G., Johnson, J.E., Cottrill, A.R., Mohr, L.C., Kroproski, S.R., 2014. Coupling agestructured stock assessment and fish bioenergetics models: a system of timevarying models for quantifying piscivory patterns during the rapid trophic shift in the main basin of Lake Huron. Can. J. Fish. Aquat. Sci. 72, 7–23.
- Hokanson, K.E., Koenst, W.M., 1986. Revised estimates of growth requirements and lethal temperature limits of juvenile walleyes. Prog. Fish. Cult. 48, 90–94. http: //dx.doi.org/10.1577/1548-8640 (1986)48 < 90:REOGRA > 2.0.CO;2.
- Houde, E.D., 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. B – NOAA 87, 471–495.
- Huey, R.B., Pianka, E.R., 2007. Lizard thermal biology: do genders differ? Am. Nat. 170, 473–478.
- Huh, H.T., Calbert, H.E., Stuiber, D.A., 1976. Effects of temperature and light on growth of yellow perch and walleye using formulated feed. Trans. Am. Fish. Soc. 105, 254–258.
- Kelso, J.R.M., 1972. Conversion, maintenance, and assimilation for walleye (*Stizos-tedion vitreum vitreum*), as affected by size, diet, and temperature. J. Fish. Res. Board Can. 29, 1181–1192.
- Kelso, J.R.M., 1976. Diel movement of walleye, *Stizostedion vitreum vitreum*, in West Blue Lake, Manitoba, as determined by ultrasonic tracking. J. Fish. Res. Board Can. 33, 2070–2072. http://dx.doi.org/10.1139/f76-255.
- Kershner, M.W., Schael, D.M., Knight, R.L., Stein, R.A., Marschall, E.A., 1999. Modeling sources of variation for growth and predatory demand of Lake Erie walleye (*Stizostedion vitreum*), 1986–1995. Can. J. Fish. Aquat. Sci. 56, 527–538. http://dx.doi.org/10.1139/f98-193.
- Kitchell, J.F., Stewart, D.J., Weininger, D., 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34, 1910–1921. http://dx.doi.org/10.1139/f77-258.
- Koenst, W.M., Smith Jr., L.L., 1976. Thermal requirements of the early life history of walleye (*Stizostedion vitreum vitreum*) and sauger (*Stizostedion canadense*). J. Fish. Res. Board Can. 33 (5), 1130–1136.
- Koonce, J.F., Busch, W.-D.N., Czapla, T., 1996. Restoration of Lake Erie: contribution of water quality and natural resource management. Can. J. Fish. Aquat. Sci. 53, 105–112.
- Magnuson, J.J., Meisner, J.D., Hill, D.K., 1990. Potential changes in the thermal habitat of Great Lakes fish after global climate warming. Trans. Am. Fish. Soc. 119, 254–264.
- Magnuson, J.J., Webster, K.E., Assel, R.A., Bowser, C.J., Dillon, P.J., Eaton, J.G., Quinn, F. H., 1997. Potential effects of climate changes on aquatic systems: Laurentian Great Lakes and Precambrian Shield Region. Hydrol. Process. 11, 825–871.
- Madenjian, C.P., 2011. Bioenergetics in ecosystems. In: Farrell, A.P. (Ed.), Encyclopedia of Fish Physiology: From Genome to Environment. Elsevier, Oxford, pp. 1675–1680.
- Madenjian, C.P., O'Gorman, R., Bunnell, D.B., Argyle, R.L., Roseman, E.F., Warner, D. M., Stockwell, J.D., Stapanian, M.A., 2008. Adverse effects of alewives on Laurentian Great Lakes fish communities. N. Am. J. Fish. Manag. 28, 263–282. http: //dx.doi.org/10.1577/M07-012.1.
- McCauley, R.W., Read, L.A.A., 1973. Temperature selection by juvenile and adult yellow perch (*Perca flavescens*) acclimated to 24 °C. J. Fishes. Res. Board Can. 30, 1253–1255. http://dx.doi.org/10.1139/f73-202.
- McCauley, R.W., Huggins, N.W., 1979. Ontogenetic and non-thermal seasonal effects on thermal preferenda of fish. Am. Zool. 19, 267–271. http://dx.doi.org/10.1093/ icb/19.1.267.
- Melstrom, R.T., Lupi, F., 2013. Valuing recreational fishing in the Great Lakes. N. Am. J. Fish. Manag. 33, 1184–1193. http://dx.doi.org/10.1080/02755947.2013.835293.
- Morita, K., Fukuwaka, M.A., Tanimata, N., Yamamura, O., 2010. Size-dependent thermal preferences in a pelagic fish. OIKOS 119, 1265–1272. http://dx.doi.org/ 10.1111/j.1600-0706.2009.18125.x.
- Nepszy, SJ., 1977. Changes in percid populations and species interactions in Lake Erie, J. Fish. Res. Board Can. 34, 1861–1868.
- Pearson, D., Shine, R., Williams, A., 2003. Thermal biology of large snakes in cool climates: a radio-telemetric study of carpet pythons (*Morelia spilota imbricata*) in south-western Australia. J. Therm. Biol. 28, 117–131. http://dx.doi.org/ 10.1016/S0306-4565(02)00048-7.
- Petersen, J.H., Kitchell, J.F., 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile salmon. Can. J. Fish. Aquat. Sci. 58, 1831–1841. http://dx.doi.org/10.1139/f01-111.
- Pierce, R.B., Carlson, A.J., Carlson, B.M., Hudson, D., Staples, D.F., 2013. Depths and thermal habitat used by large versus small Northern Pike in three Minnesota lakes. Trans. Am. Fish. Soc. 142, 1629–1639.

R Development Core Team, 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: (http://www.r-project.org/).

Rennie, M.D., Purchase, C.F., Lester, N., Collins, N.C., Shuter, B.J., Abrams, P.A., 2008. Lazy males? Bioenergetic differences in energy acquisition and metabolism help to explain sexual size dimorphism in percids. J. Anim. Ecol. 77, 916–926. http://dx.doi.org/10.1111/j.1365-2656.2008.01412.x.

Roseman, E.F., Knight, R.L., Wright, E., Einhouse, D., Kayle, K., Newman, K., Hoopes, R., 2008. Ecology and International Governance of Lake Erie's Percid Fisheries. In International Governance of Fisheries Ecosystems: Learning from the Past, Finding Solutions for the Future. American Fisheries Society, Bethesda, Maryland, pp. 145–169.

Ross, M.J., Siniff, D.B., 1982. Temperatures selected in a power plant thermal effluent by adult yellow perch (*Perca flavescens*) in winter. Can. J. Fish. Aquat. Sci. 2, 346–349.

Ryan, P.A., Knight, R., MacGregor, R., Towns, G., Hoopes, R., Culligan, W., 2003. Fish-Community Goals and Objectives for Lake Erie.

Sagonas, K., Meiri, S., Valakos, E.D., Pafilis, P., 2013. The effect of body size on the thermoregulation of lizards on hot, dry Mediterranean islands. J. Therm. Biol. 38, 92–97. http://dx.doi.org/10.1016/j.jtherbio.2012.11.006.

Schertzer, W.M., Saylor, J.H., Boyce, F.M., Robertson, D.G., Rosa, F., 1987. Seasonal thermal cycle of Lake Erie. J. Gt. Lakes Res. 13, 468–486. http://dx.doi.org/ 10.1016/S0380-1330(87)71667-0.

Schneider, J.C., Leach, J.H., 1977. Walleye (*Stizostedion vitreum vitreum*) fluctuations in the Great Lakes and possible causes, 1800–1975. J. Fish. Res. Board Can. 34, 1878–1889. http://dx.doi.org/10.1139/f77-254.

Sheng, J., Rao, Y.R., 2006. Circulation and thermal structure in Lake Huron and

Georgian Bay: application of a nested-grid hydrodynamic model. Cont. Shelf Res. 26, 1496–1518. http://dx.doi.org/10.1016/j.csr.2006.01.019.

Snieszko, S.F., 1974. The effects of environmental stress on outbreaks of infectious diseases of fishes. J. Fish. Biol. 6, 197–208.

Tang, X.L., Yue, F., He, J.Z., Wang, N.B., Ma, M., Mo, J.R., Chen, Q., 2013. Ontogenetic and sexual differences of thermal biology and locomotor performance in a lacertid lizard, *Eremias multiocellata*. Zoology 116, 331–335. http://dx.doi.org/ 10.1016/j.zool.2013.08.006.

Tirsgaard, B., Behrens, J.W., Steffensen, J.F., 2015. The effect of temperature and body size on metabolic scope of activity in juvenile Atlantic cod Gadus morhua L. Comp. Biochem. Physiol. Part A: Mol. Integr. Physiol. 179, 89–94.

Tsehaye, I., Jones, M.L., Bence, J.R., Brenden, T.O., Madenjian, C.P., Warner, D.M., 2014. A multispecies statistical age-structured model to assess predator-prey balance: application to an intensively managed Lake Michigan pelagic fish community. Can. J. Fish. Aquat. Sci. 71, 627–644. http://dx.doi.org/10.1139/ cifas-2013-0313.

Vandergoot, C.S., Murchie, K.J., Cooke, S.J., Dettmers, J.M., Bergstedt, R.A., Fielder, D. G., 2011. Evaluation of two forms of electroanesthesia and carbon dioxide for short-term anesthesia in walleye. N. Am. J. Fish. Manag. 31, 914–922. http://dx. doi.org/10.1080/02755947.2011.629717.

Wang, H., Cook, H.A., Einhouse, D.W., Haas, R.C., Johnson, T.B., Kenyon, R., Locke, B., Turner, M.W., 2007. Movement of walleye in lakes Erie and St. Clair inferred from tag return and fisheries data. Trans. Am. Fish. Soc. 136, 539–551.

Wood, S., 2006. Generalized Additive Models: an Introduction with R. CRC Press, Boca Raton, Florida.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York City, New York.