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Does behavioural thermoregulation underlie seasonal movements in Lake Erie walleye?

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Abstract: Thermoregulation is presumed to be a widespread determinant of behaviour in fishes, but has not often been investigated as a mechanism shaping long-distance migrations. We used acoustic telemetry and animal-borne thermal loggers to test the hypothesis that seasonal migration in adult walleye (*Sander vitreus*) in Lake Erie is size- and (or) sex-specific and related to behavioural thermoregulation. Female walleye migrated out of the warm, shallow western basin earlier than did males and were 1.8 times more likely to be detected on acoustic receivers in the deeper and cooler eastern basin. The few fish that remained in the western basin were restricted to a smaller range of higher temperatures (≥20 °C) than those that migrated to the central and eastern basins (~16–21 °C). However, temperature records from walleye in the central basin were nearly indistinguishable from those in the eastern basin, suggesting thermal preferences alone could not explain migration to the eastern basin. As such, our effort to understand the mechanisms that cause migratory behaviours has generated mixed evidence on the role of temperature and that factors like foraging opportunities may have synergistic roles in the migration.

Résumé : S'il est présumé que la thermorégulation est un déterminant répandu du comportement chez les poissons, la possibilité qu'elle puisse moduler les migrations sur de longues distances n'a pas souvent été examinée. Nous avons utilisé la télémétrie acoustique et des enregistreurs de température installés sur des animaux pour vérifier l'hypothèse selon laquelle la migration saisonnière chez les dorés jaunes (*Sander vitreus*) adultes du lac Érié dépend de la taille ou du sexe et est associée à la thermorégulation comportementale. La migration des dorés femelles pour sortir du bassin ouest plus chaud et moins profond a eu lieu plus tôt que celle des mâles, et les femelles étaient 1,8 fois plus susceptibles d'être détectées par des récepteurs acoustiques dans le bassin est plus profond et frais. Les quelques poissons qui étaient restés dans le bassin ouest étaient limités à une petite fourchette de températures plus élevées (≥20 °C) que celles caractérisant les poissons ayant migré vers les bassins central ou est (~16–21 °C). Cependant, les registres de températures des dorés dans le bassin central étaient presque identiques à ceux du bassin est, ce qui indiquerait que les préférences thermiques ne peuvent à elles seules expliquer la migration vers le bassin est. Ainsi, nos efforts visant à comprendre les mécanismes qui modulent les comportements migratoires ont fait ressortir des indications mitigées sur le rôle de la température et le fait que des facteurs comme les occasions d'approvisionnement pourraient jouer des rôles synergiques dans la migration. [Traduit par la Rédaction]

Introduction

Understanding why animals migrate is fundamental to ecology, evolution, and the conservation of migratory species and their habitat (Wilcove and Wikelski 2008). Migration can be driven by a variety of variables such as foraging opportunities or participation in spawning aggregations (Bowlin et al. 2010). Among the most important variables in the life of ectotherms is environmental temperature. Temperature is an important dimension of habitat (Hutchison and Maness 1979) and, for fishes, has been referred to as an ecological resource because the efficiency with which fishes dynamically adjust their thermal habitat via locomotory movement (i.e., behavioural thermoregulation) can affect their

fitness through bioenergetic costs and benefits (Magnuson et al. 1979). Behavioural thermoregulation is often thought of as happening on smaller scales than what would be classified as long-distance migration, particularly among freshwater fishes, often involving vertical movements (in thermally stratified waters) or horizontal movements of a few metres or kilometres (e.g., Baird and Krueger 2003; Sims et al. 2006).

Walleye (*Sander vitreus*) of Lake Erie are one of the most economically valuable populations of freshwater fish in North America (Schmalz et al. 2011; Kayle et al. 2015). The majority of Lake Erie's walleye spawn on rocky offshore reefs or in the tributaries of the lake's shallow western basin in early spring (March–April; Vandergoot et al. 2010). Based on long-term mark–recapture studies, many

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Aaron T. Fisk currently serves as an Associate Editor; peer review and editorial decisions regarding this manuscript were handled by Suzanne Gray.

adult walleye migrate out of the western basin after spawning (Wang et al. 2007; Vandergoot and Brenden 2014), a behaviour that is believed to be driven, at least in part, by behavioural thermoregulation (Kershner et al. 1999; Wang et al. 2007; Vandergoot and Brenden 2014). The western basin is warm and typically isothermal, averaging ~24 °C during the summer (June–September; Mortimer 1987), which is above what is considered thermally optimal for adult walleye (20–23 °C; Hokanson 1977; Barton and Barry 2011). Summer surface temperatures are 2–3 °C cooler in the central and eastern basins than in the western basin; these basins also become thermally stratified in the summer (Mortimer 1987; Kershner et al. 1999). As a result, a bioenergetics model predicted that western basin fish that migrate to the central basin should achieve higher growth rates given the same food intake; these migrating fish theoretically spend more of the summer at or near their thermal optima for growth as compared with fish that remain in the warmer western basin (Kershner et al. 1999). In addition, the central basin is shallower than the eastern basin, and in most years, this situation leads to seasonal hypoxia in the hypolimnion (Burns et al. 2005; Conroy et al. 2011), reducing the volume of thermally optimal habitat that walleye may occupy. Currently, a lack of information exists on whether walleye remain in marginal habitats of the central basin or move to more suitable habitats in the eastern basin. Fishery-dependent recaptures of walleye in the eastern basin were more common in large females, suggesting a size- and (or) sex-specific migration pattern (Wang et al. 2007), which may have been driven by a preference for lower temperatures as compared with males and small females.

The notion that larger fish may prefer, or perform better in, colder water than do small fish has support in the literature (Lafrance et al. 2005; Daufresne et al. 2009; Morita et al. 2010), although the physiological mechanisms that lead to thermal performance curves being body size-dependent remain a subject of vigorous debate (Ohlberger 2013; Lefevre et al. 2017). In contrast, few examples of sex-specific thermal preferences exist in the literature, and these seem to suggest females prefer warmer waters than do males (Johansen and Cross 1980; Swain 1997), the opposite of what has been suggested for adult walleye in Lake Erie (Wang et al. 2007). For many ectotherms, some degree of sexual size dimorphism exists, with females growing to larger sizes than do males — conventionally explained by correlations in females among body size, fecundity, and lifetime reproductive fitness (i.e., Darwin's fecundity advantage model; Shine 1988). Any trends relating to migration patterns and temperature preference in large female walleye may therefore simply be related to body size, rather than sex. As body size increases in ectotherms, both across and within species, lower thermal optima for growth and a behavioural preference for lower temperatures typically occur (Lafrance et al. 2005; Daufresne et al. 2009; Morita et al. 2010). As a result, we hypothesized that large adult walleye in Lake Erie behaviourally down-regulate their body temperature by eastward migration from the western basin to deeper (eastern basin mean depth 24.4 m; 18.5 m in central basin) and cooler habitats (Wang et al. 2007).

The goal of this study was to determine whether behavioural thermoregulation plays a role in long-distance eastward migrations some walleye make after spawning in Lake Erie. Using acoustic telemetry and animal-borne temperature loggers, we tested three predictions: (i) large females migrate farther east than do males or small females; (ii) large females select cooler temperatures during summer than do small females and males; and (iii) the timing of postspawning departure from the western basin occurs at a threshold water temperature, which varies by date according to the annual warming pattern of the lake. The latter prediction (iii) was included because the relationship between the timing of migration and water tem-

perature (Trepanier et al. 1996; Sims et al. 2004) is relevant to the hypothesis that thermoregulation is a driving force behind the migration. For Lake Erie walleye, recent efforts to improve population assessments and spatial resource management would benefit from an improved understanding of size, sex, or population-specific movements across fishery quota areas (Kayle et al. 2015). More generally, this study provides insights about migratory phenotypes expressed by a freshwater teleost with potential application in predicting responses to climatic change.

Methods

Fish capture and telemetry tagging

All fish capture, handling, and surgery methods followed best practices for animal care and fish surgery (e.g., Wagner et al. 2011) and have been described in depth elsewhere (Hayden et al. 2014). Walleye (N = 758 fish) were captured at four spawning areas in early spring (March–April) from 2011 through 2015 (Fig. 1): the Detroit River (2014, 2015), Maumee River (2011, 2012, 2014), Niagara Reef (2014), Toussaint Reef (2013, 2014), and Sandusky River (2014, 2015). For management purposes, these spawning aggregations are considered part of the western basin walleye population (Ryan et al. 2003). Fish were captured by electrofishing gear in tributaries or using 1–2 h gill net sets on open-water reefs and then held in large flow-through tanks at the capture site (either on adjacent land or onboard a large vessel) for processing and tagging. Walleye implanted with acoustic transmitters also received an external tag (i.e., t-bar anchor tags, internal anchor tags, or loop tags; Floy Manufacturing, Seattle, Washington, USA) to facilitate reporting of recaptures by commercial or recreational fisheries. Fish were measured (total length, mm) and the three leading dorsal spines were removed from each fish to estimate age via annual growth increments (Isermann et al. 2003). For each year and location, sampling targeted equal numbers of males and females throughout the spawning period. Efforts were also made to tag a representative distribution of fish sizes (see online Supplementary material, Fig. S1[1]). Overall, 360 females and 398 males were immobilized via electro-narcosis (Vandergoot et al. 2011) and implanted with acoustic transmitters (model V16-4H; 16 mm diameter, 86 mm long, 24 g, estimated battery life = 3.67 years, power output = 158 dB; Vemco, Halifax, Nova Scotia, Canada) outfitted with an iButton thermal logger (DS1921Z; resolution = 0.125 °C, accuracy ±1 °C; Maxim Integrated Products, Sunnyvale, California, USA, set to record every 4 h for 341 days = 2048 records) attached to the nontransmitting end of the transmitter with a waterproof coating (Plasti Dip, Performix Brand, Blaine, Minnesota; Donaldson et al. 2009). Each transmitter was programmed to emit a unique 69 kHz code at random time intervals ranging between 60 and 180 s (mean = 120 s) to reduce the likelihood of collisions with transmissions made by other nearby acoustic tags.

Acoustic telemetry tracking

Movements of tagged fish were determined using a network of 69 kHz acoustic receivers (Vemco, Bedford, Nova Scotia, Canada) installed at spawning areas and at other key points throughout Lake Erie and the corridor between Lakes Erie and Huron (Fig. 1). Although tagging began in 2011, many sections of the receiver network were not installed until mid-2013. As a result, analyses for this paper focused on the movements of walleye in 2014 and 2015 when relatively full spatiotemporal receiver coverage of Lake Erie occurred. Some receivers were seasonally moved to different locations to meet the objectives of several studies, but in general, receivers were deployed to capture walleye migrations throughout the lake (video showing receiver deployment places and times can be found online at https://youtu.be/_vQrDQYQTRI).

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0145.

Fig. 1. Bathymetric map of Lake Erie with receiver locations in 2015 (circles) and all the locations (triangles) at which fish were captured, tagged, and released throughout the study. The terms in bold italics denote the five migration zones to which fish were assigned for analyses, based on telemetry detections (corresponding to the data in Fig. 3): north (i.e., Lake Huron), WB (western basin), CBW (west-central basin), CBE (east-central basin), EB (eastern basin).
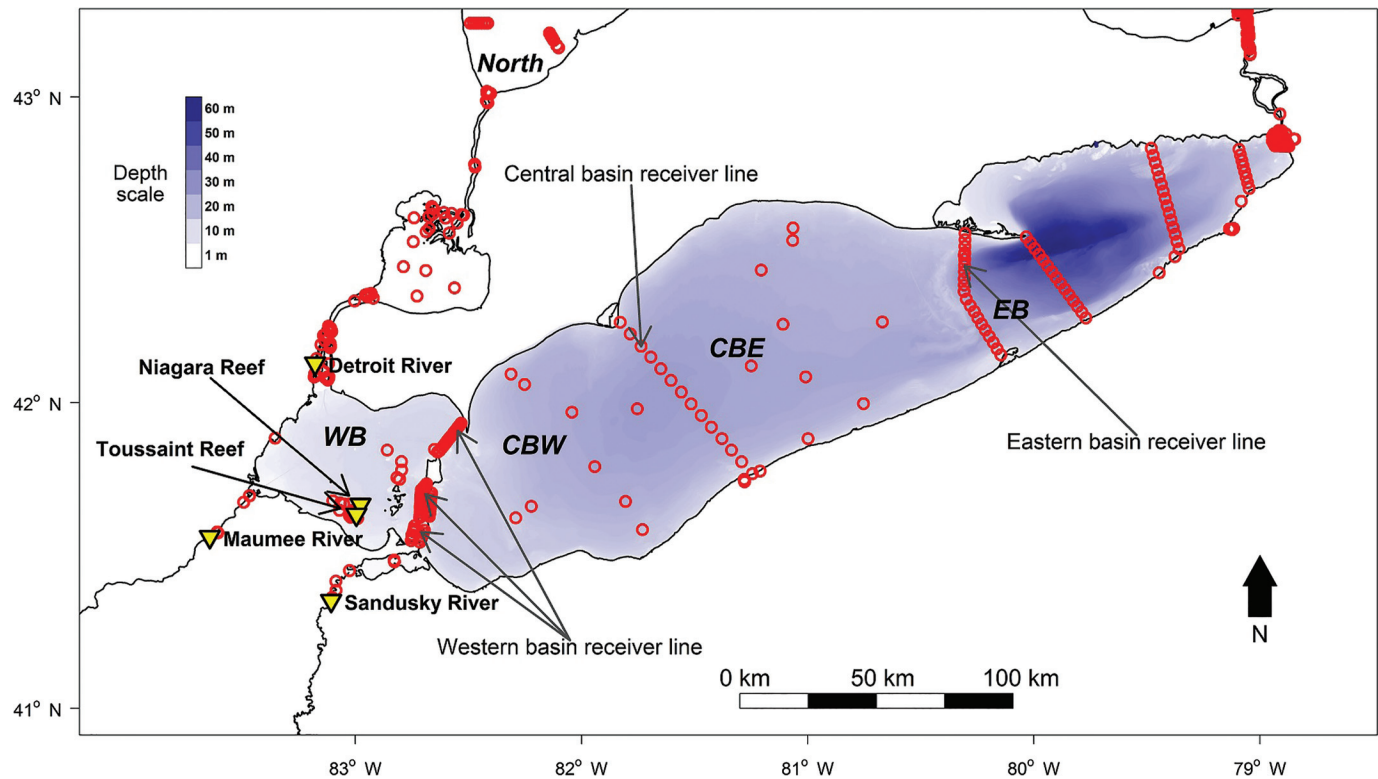
Identification of surviving fish

To avoid the influence of natural, tagging-induced, or fishing mortality on analyses of seasonal movements in 2014 and 2015, we only included fish if they survived until the end of the calendar year (or beyond). This included some fish that were tagged in 2013 or earlier (and survived through 2014, 2015, or both) or fish tagged in either study year (i.e., 2014 and 2015), which were required to be at liberty and alive from the time they were tagged through to 1 January of the following year (1 January 2015 or 1 January 2016) or later. Fish were assumed to have survived the calendar year if they were detected on 1 January or later in a way that made it evident that the fish was likely to be alive. On the other hand, some fish died at or near receiver stations, which was evident based on a year or more of continuous or intermittent detections at the same receiver. Fish were also included if they were recaptured in fisheries after 15 September of either of the 2 study years, a time late enough in the year deemed sufficient to assess a fish's propensity for temperature-driven migration (see online Supplementary material for further detail[1]).

Timing of outmigration from the western basin

Timing of outmigration of fish from the western basin was compared with water temperatures at 2 m depth at 13 locations throughout the western basin of Lake Erie (Fig. S2[1]). To quantify postspawning outmigration timing from the western basin, we fitted Kaplan–Meier (K-M) time-to-event functions with 95% confidence intervals (using the package "survival" in R; Therneau 2015). A departure event was defined as a fish moving east from the western basin line (Fig. 1), after having been inside the western basin during the spawning period (see online Supplementary material for further details on how this was assessed[1]). To assess whether two or more survival curves were statistically different, we used the "survdiff" function (R package: "survival"). These analy-

ses focused on fish that spawned and were released west of the western basin receiver line (Fig. 1), which included Toussaint Reef and Niagara Reef (grouped for analyses), the Maumee River, and the Detroit River. Sandusky River fish were excluded from this portion of the analyses because this river empties into the central basin. The total number of fish used from these stocks was $N = 137$ fish in 2014 and $N = 73$ fish in 2015. Sixty fish were present in both the 2014 and 2015 data sets; therefore, these data were not independent. For the time-to-event analyses, the data sets were analyzed separately by year in most cases; both years were pooled for data visualizations (e.g., for comparing sexes).

Analyses of the extent of eastward migration

Based upon postspawning detection histories (up to 31 December), each fish was classified by its most distant detection into four categories: (*i*) detected in the eastern basin, (*ii*) detected in the east-central basin (including on the central basin line), (*iii*) detected in the west-central basin, or (*iv*) no detections outside of the western basin (termed western basin residents; Fig. 1). The detection efficiency for the western basin receiver line (1 km between adjacent receivers) was 99.7%, for the central basin line (5.6 km spacing) was 83.9%, and for the eastern basin line (2.5 km spacing) was 100% (see online Supplementary material for further detail[1]). We further specified that western basin residents were those that remained inside the western basin until 1 October or later. By comparison, fish migrating out of the western basin were those detected east of the western basin receiver line before 1 October **and** after the spawning period. For simplicity and because so few fish remained inside the western basin ($N = 8$ in each of the 2 years), these residents were pooled with west-central basin migrants for statistical analyses. Two fish migrated north into Lake Huron (one in each year) and were excluded from the analyses.

Fig. 2. Kaplan–Meier survival curves (left y axis) based on the outmigration timing of western basin walleye (with 95% confidence intervals, shaded in light grey). The right panel includes the water temperature profiles for the western basin (right y axis), which represent the mean ± one standard deviation based on the temperature data taken from 2 m depth at 13 locations (shown in Fig. S2[1]) in the western basin using a thermal forecast model. The right panel is a comparison of all fish from both years (stocks and sexes pooled; N = 137 in 2014, N = 73 in 2015, with 60 of these 73 also present in the 2014 sample), while the left panel is a male–female comparison (both years, all stocks pooled).
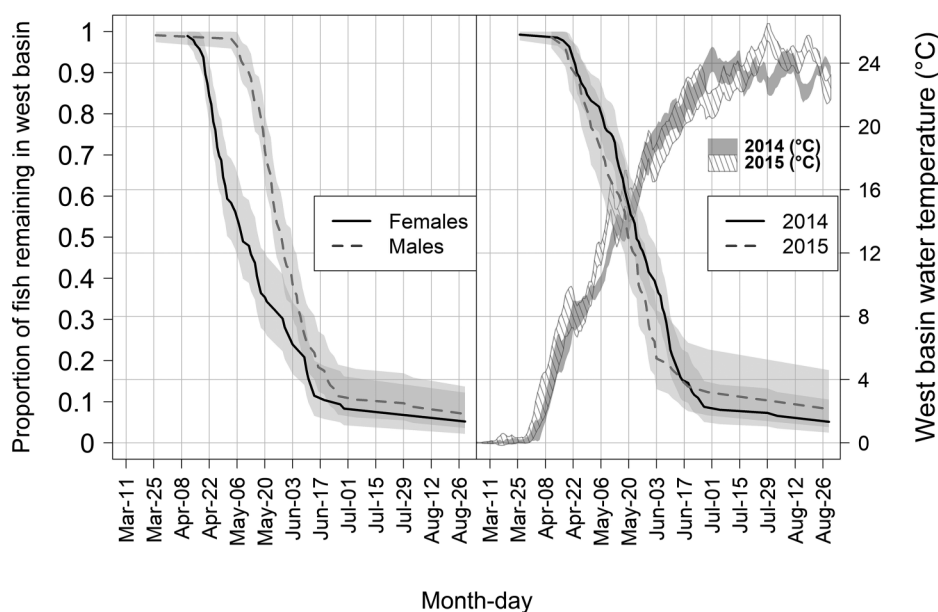
Extent of eastward migration was inferred from estimates of the probability of detection in each area of the lake. These probabilities were modeled with three separate binomial logistic regressions, one for each detection outcome: western half of the lake, east-central basin, and eastern basin (as defined above). In the regressions, we assessed effects of sex, size (continuous predictor), and age (treated as a continuous predictor; range 3–14). Age was not quantified for a small number of individuals; models were rerun with the full sample of fish in cases where age was not significant or included in final models. Model selection was achieved using AIC with the stepAIC function in R (package MASS; Venables and Ripley 2002; see online Supplementary materials for additional details[1]).

Modeling animal-borne temperature measurements during summer

To evaluate the prediction that females and large fish would occupy colder waters than would males and smaller fish, we focused on summer (21 June – 21 September), when the lake was thermally stratified and the greatest range of environmental temperatures was likely to be present (both vertically and horizontally across the lake). Thus, summer is when sex- or size-specific behavioural thermoregulation would be expected to be evident, particularly if fish were motivated to seek lower temperatures. Data were downloaded from N = 89 temperature loggers available, but only N = 61 had records that extended into summer. These loggers recorded temperature every 4 h for each fish. Unlike the analyses of fish movements, these analyses ultimately included data during 2013–2015. We modelled summer temperature time series with generalized additive mixed models (GAMMs, using package "mgcv" in R; Wood 2017). Time of day, day of year, sex, and size were included as explanatory variables, individual fish ID was included as a random effect, and a temporal autocorrelation structure was used. Modeling and diagnostics followed procedures described by Zuur et al. (2009; see online Supplementary material for further detail[1]).

Results

Timing of postspawning migration

Walleye departed Lake Erie's western basin following a similar schedule in 2014 and 2015 ($\chi^2_{1,209}$ = 0.5, P = 0.47). The thermal profile of the western basin when this outmigration occurred was also similar between years (Fig. 2, right panel). Fish began departing the western basin in mid-April, and departures continued at a relatively steady pace through mid-June (Fig. 2, right panel). In both years, by the time the western basin warmed to 20 °C, most of the tagged walleye had departed (~70% in 2014, ~80% in 2015), and once the western basin reached the upper end of the optimal thermal range (thought to be 23 °C, ca. 20 June – 1 July; Barton and Barry 2011), no additional outmigration was observed (a total of eight fish remained in the western basin in each year; see section on Extent of eastward migration, below). An absolute temperature associated with outmigration could not be identified because fish departed at a relatively similar rate across a wide range of absolute temperatures (~8–20 °C; Fig. 2). When all western basin stocks were pooled, females departed the western basin earlier than did males (2014: $\chi^2_{1,136}$ = 22.1, P < 0.001; 2015: $\chi^2_{1,72}$ = 8.8, P = 0.003; both years pooled in Fig. 2, left panel). The main difference occurred during the early part of the migration period; more females left the western basin than did males in April and early May (Fig. 2, left panel). This difference between sexes was mostly driven by fish tagged on the western basin reef complex, where the median departure dates for females were 17 and 24 days earlier than for males in 2014 and 2015, respectively (not shown graphically; 2014: $\chi^2_{1,100}$ = 25.4, P < 0.001; 2015: $\chi^2_{1,50}$ = 16.1, P < 0.001). Outmigration from the western basin tended to begin ~2 weeks later for fish from the Maumee and Detroit rivers than in reef-spawning fish (2014: $\chi^2_{1,136}$ = 14.2, P < 0.001; 2015: $\chi^2_{1,72}$ = 8.2, P = 0.004). Because outmigration timing was stock- and sex-specific, our ability to further differentiate size effects was limited to western basin reef fish in 2014 (55 males, 45 females). Two size groups for each sex (small and large) were defined based on the median length (for females, 676.3 cm TL; for males, 572 cm). No size dif-

Fig. 3. Sex-specific and overall broad-scale movement patterns for western Lake Erie walleye in 2014 (N = 168 fish) and 2015 (N = 119 fish) shown as the percentage of fish that migrated to each part of the lake. For the year-specific estimates, the estimated percentage of females that migrated to each area is shown in grey triangles, while males are shown in black circles (with error bars). The error bars represent 95% confidence intervals for the estimates and were calculated using the Clopper–Pearson exact method. Each panel provides the percentage of fish (within that sex–year group, or overall) that were determined to have migrated to each of the five migration zones shown in Fig. 1 (based on telemetry detections; see Methods).
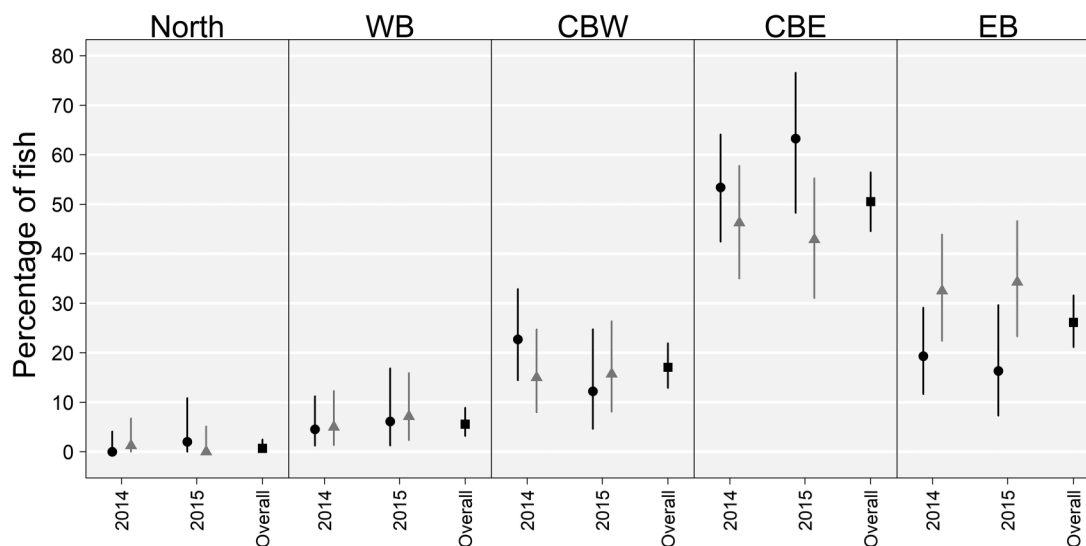
ference in outmigration timing was detected for males (P = 0.55), but small females tended to leave the western basin later than large females (χ^2 = 5.4, P = 0.02; Fig. S3[1]).

Extent of the eastward migration

The extent and characteristics of postspawning eastward migration among western Lake Erie walleye stocks was similar during 2014 and 2015. For example, the percentage of fish that migrated to each of the four zones (western basin, west-central basin, east-central basin, eastern basin) was nearly identical between the 2 years (Fig. 3). The majority of fish migrated into the eastern half of the lake, with 26% overall (Fig. 3) being detected on the eastern basin receiver line (Fig. 1) or further east. Only two fish were detected moving north into Lake Huron — one Maumee River fish in 2014 and a Detroit River-tagged fish in 2015. Among the 119 fish included in the 2015 sample, 76 (64%) were also part of the 2014 sample (N = 168 total fish in 2014). Sixty-two of these 76 fish (82%) migrated to the same zone in both years, indicating some coarse-level longitudinal fidelity to summer residence areas. Fourteen of 76 fish were assigned a different eastward migration zone in 2015 than in 2014. Among these 14 fish, each between-year change was to an adjacent zone (e.g., switched from east-central basin to eastern basin), except for one fish from the Sandusky River that reached the eastern basin in 2015 despite remaining in the west-central basin in 2014. Neither year nor tagging location had any effect on which part of the lake a fish was assigned to (binary logistic regressions; P > 0.2 for stock and year for all three locations and a lower AIC value using a null model in each case), so these variables were left out of subsequent analyses of the factors driving the eastward migration.

The likelihood of fish reaching the east-central basin ("CBE" in Fig. 1) was unaffected by all variables in 2014 (all P > 0.4), with lower AIC scores for a null model than models with any combination of predictor variables. In 2015, the best model included a term for sex (P = 0.03), which offered a marginal improvement over a null model (i.e., McFadden R^2 = 0.04), while sex was not significant in a model combining data from both years (P = 0.14). Likewise, sex, size, age, and associated interactions were not significant predictors of the likelihood of fish remaining in the western half of the lake ("CBW" plus "WB" in Fig. 1) — either by analyzing each

year separately or by combining years (all P > 0.3). We therefore focused on presenting models examining the likelihood of fish being detected on eastern basin receivers.

A numerically greater proportion of females were detected on eastern basin receivers than were males in both years (Fig. 3), but no evidence existed for an effect of size or an interaction between size and sex on migration to the eastern basin. Sex had a significant effect on the likelihood of fish reaching the eastern basin both years (P = 0.047 for the 2014 model; P = 0.038 for the 2015 model; Table S2[1]). Total length and its interaction with sex were insignificant predictors of arrival at eastern basin receivers for both years. With both years combined, the effect of sex was the sole variable in the best model, but the sex term was not significant (P = 0.07; Table S1[1]). Nevertheless, although sex had a significant effect for each year (separately), the models predicting likelihood of migration to the eastern basin using sex as a variable offered a negligible improvement over null models (2014: McFadden R^2 = 0.02; 2015: McFadden R^2 = 0.03). Thus, while a higher percentage of females were detected in the eastern basin than were males (33% versus 18%), sex was a statistically weak predictor of an individual fish's likelihood of reaching the eastern basin (Table S2[1]).

Animal-borne temperature measurements during summer

The best model fit for walleye summer temperature data (Table 1) used three separate smoothing functions for day of the year (one for each year; Fig. S4[1]) and included separate time-of-day smoothers based on the size class of the fish (Fig. S5[1]). Size-specific time-of-day smoothers were initially fit using three size classes (small, medium, large), but the medium and large groups showed an identical diel pattern so were combined as one group, which further improved model fit (i.e., one smoother for "small" fish (<525 mm) and one for average and large-sized fish (>525 mm)). The time-of-day smoothers revealed no diel pattern in temperature for small fish, whereas the remaining fish tended to experience a subtle day–night differences in temperature (~1 °C warmer during the day; Fig. S5[1]). Controlling for day of the year and time-of-day patterns that arose (Fig. S5[1]), we detected no effects of size, sex, or their interaction (all P > 0.1). The model explained only a modest portion of the overall variation in the iButton tempera-

Table 1. The importance of each of the two smoothing function terms (day of the year by year and time of day by size grouping), the size-specific variance covariate, and the correlation structure (Time|Animal ID) to the fit of our model predicting the thermal experience of walleye in Lake Erie during summer (21 June – 21 September).

Model term	L ratio	df	P value
Day of the year (by year) smoothing function	321.4	7	<0.001
Time of day (by size class) smoothing function	552.7	11	<0.001
Size class (variance structure)	287.7	12	<0.001
Time	Animal ID (temporal correlation function)	2340.5	12	<0.001
			Model R^2 = 0.164

Note: The terms in the table are based on a comparison of models with and without each of the components listed using the "anova" function in R. Terms for fish length, sex, and their interaction were all insignificant ($P > 0.05$) when added to the model, as was fish age. The approximate significance of the day of the year (by year) smoothing functions within the model were as follows: for 2013: $F_{[7.2]} = 36.7$, $P < 0.001$; for 2014: $F_{[7.2]} = 17.7$, $P < 0.001$; for 2015: $F_{[5.9]} = 21.6$, $P < 0.001$. For the time-of-day smoothing functions, the approximate significance was $F_{[7.5]} = 76.7$, $P < 0.001$ (medium and large fish) and $F_{[4.3]} = 3.9$, $P < 0.001$ (small fish).

ture data ($R^2 = 0.164$), which is perhaps unsurprising given the large range of temperatures available to walleye during this period, when most of the lake was thermally stratified (Fig. S6[1]).

The effect of location (basin) could not be sufficiently assessed in these models because of poor temporal coverage and low sample sizes for the western and eastern basins (i.e., low numbers of fish with iButton data that could be matched to these locations across all levels of our smoothing functions). For example, only one iButton-retrieved fish was confirmed as having been continuously inside the western basin throughout summer, while the seven others that registered summer detections there were only confirmed to be in the western basin sporadically (based on detection on the western basin receiver line). Likewise, only three fish in the sample were confirmed as having spent time in the eastern basin during summer. As a result, inclusion of basin as a factor in models (using a smaller subset of the data for which basin is known) did not improve model fit and the basin term was not significant ($P > 0.1$; Fig. 4). However, overall comparisons among basins (Fig. 4) revealed that in the summer, fish in the western basin were generally restricted to the upper range of temperatures experienced by fish in the central and eastern basins. Only one iButton-retrieved fish was able to be confirmed as spending some time in the eastern basin in 2014, but its residency there was only for ~2 weeks in September so its data were pooled with the central basin data (Fig. 4, right panel). Two fish whose iButtons were retrieved were confirmed as spending their entire summer in the eastern basin in 2015. The median and maximum temperatures experienced by these two fish in the eastern basin were slightly lower than those for fish in the central basin, but otherwise substantial overlap occurred (Fig. 4, left panel).

Discussion

### The role of temperature in migratory behaviours

The hypothesis that walleye migrate from Lake Erie's western basin to its eastern basin due to a preference for colder water was not supported here. Although we had limited data on the temperature histories of fish that were confirmed via telemetry detections to be in the eastern basin during the summer, the thermal data logged by fish in the central basin show that fish there have access to and use a broad range of temperatures, likely similar to the range of water temperatures available. Moreover, fish in the central basin spent a considerable portion of their time at temperatures reported to be suboptimal for walleye based on labo-

ratory experiments (i.e., below 20 °C; Barton and Barry 2011). The limited data from the eastern basin (Fig. 4) showed that median and maximum temperatures for fish that resided there during summer were slightly (0.5–1 °C) cooler than in the other basins, but this subtle difference seems unlikely to be reason alone to motivate fish to swim an extra 200+ km (round-trip) to the eastern basin. However, the possibility that thermal preference was a contributing factor cannot be ruled out. Our findings partially supported the prediction that large females migrate to the eastern basin more frequently than do smaller fish and males (Wang et al. 2007); females were about 1.8 times as likely than males to be detected in the eastern basin, but no effect of size was observed. However, large walleye were mostly females. For example, among the walleye tracked for this project (2011–2015), the median size was 567 mm (total length: min. = 420 mm, max. = 781 mm); 75% of females were above this median size, whereas only 27% of males were longer than 567 mm.

Based on an examination of the temperatures encountered by fish in different basins (Fig. 4), this study did not provide support for temperature as the reason for migration to the eastern basin, although it seems reasonable that outmigration from the western basin into the central basin could be related to water temperature (Wang et al. 2007). However, it is difficult to disentangle temperature from alternate hypotheses that may be temperature-related. For example, some walleye may have pursued aggregations of soft-rayed forage fishes, like rainbow smelt (*Osmerus mordax*) and emerald shiner (*Notropis atherinoides*), into the central and eastern basins after spawning. These forage species are abundant in the eastern basin during summer while at the same time their abundances tend to be low in the western basin (Biesinger et al. 2017). Moreover, these same soft-finned species, along with round goby (*Neogobius melanostomus*), comprise the majority of walleye forage in the central and eastern basins during summer (Biesinger et al. 2017). Although they are generalist piscivores, previous evidence suggests walleye prefer soft-finned forage fishes over spiny rayed fish like yellow perch (*Perca flavescens*) and white perch (*Morone americana*), two of the prey species that predominate in the western basin during the summer (Knight et al. 1984; Hartman and Margraf 1992). Trawl surveys conducted by fisheries management agencies in Lake Erie do not occur with sufficient spatiotemporal coverage to enable a clear evaluation of whether certain forage fishes move from west to east during the summer. Sex-specific foraging preferences, which to our knowledge have not been studied in Lake Erie walleye, may also relate to why our study and a previous study (Wang et al. 2007) found that more females migrated to the eastern basin than did males. Females grow to significantly larger size than do males and in the spring may have a body mass that is up to 25% gonads (versus 1%–3% for males; Colby et al. 1979; Moles et al. 2008). As a result, females may, after reaching maturity, have a stronger incentive to maximize somatic growth and energy intake (Henderson and Nepszy 1994).

Along with pursuit of foraging opportunities or cooler waters to the east, multiple reasons exist for adult walleye to avoid the western end of the lake during summer. For example, departure from the western basin may be selected for as a means of fish avoiding high conspecific density and competition (Hartman and Margraf 1992) and (or) because it could reduce intraspecific cannibalism of young life stages (i.e., ages 0–1 walleye). Moreover, the western basin and adjacent areas in the central basin are where most of the fishing pressure occurs in Lake Erie (Wills et al. 2016), which could act as a selective pressure against fish remaining resident there year-round. Negative aspects of habitat quality other than high fishing pressure and water temperatures also tend to predominate in the western basin or in the western half of the lake (e.g., harmful algal blooms, sediment pollution; Regier and Hartman 1973; Carter and Hites 1992; Michalak et al. 2013).

Fig. 4. Box-and-whisker comparisons among Lake Erie's three basins of the visceral temperature of walleye during summer
(21 June – 21 September). Numbers along the bottom of each boxplot indicate sample sizes (total number of measurements and the
number of unique individuals). The thick horizontal line in the middle of each box denotes the median (middle 50% value), the lower
and upper edges of each box correspond to the first and third quartiles, respectively (i.e., the box shows the middle 50% of the data
distribution), and upper and lower whiskers are 1.5× the interquartile range (or the most extreme high or low value, respectively, in the
data set, whichever is closer to the median). Note that eastern basin was not distinguished from the central basin in 2014 because only
one fish in our iButton data set was confirmed as having been in the eastern basin in 2014, and its presence was restricted to September,
precluding a whole-summer comparison — the two basins were therefore pooled.
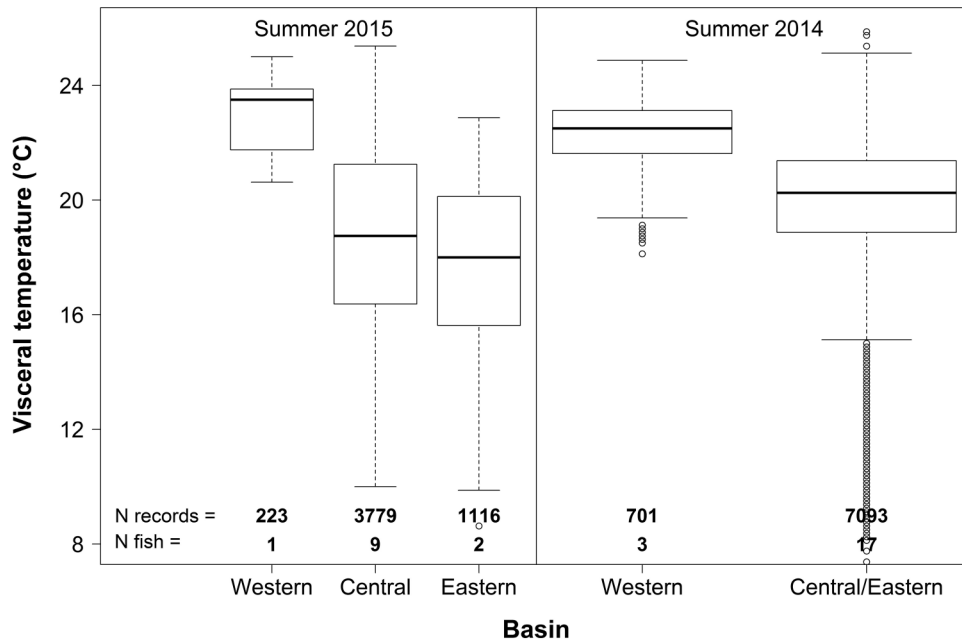
In contrast with our prediction, outmigration from the western basin appeared to be asynchronous and took place over a period of 6–8 weeks. This pattern contrasted with some animal migrations in which nearly all individuals initiate migration within a short time frame (e.g., 2–4 weeks) in response to an environmental cue (e.g., Hagan et al. 1991; Orell et al. 2007). In both 2014 and 2015, outmigration was completed around the time when western basin temperatures exceeded the reported optimal range (>23 °C; Barton and Barry 2011), which suggests that for some walleye, temperature may have been a factor in the timing of outmigration. However, the rate at which fish departed appeared to remain consistent from ~10 °C through 20–22 °C. If a fish chooses to spend its limited post-spawning energy reserves on a 100+ km migration to the east and does so when the temperature is 15 °C (as an example) **and** is doing so for thermal reasons, this implies the fish's thermal preference at that time is for temperatures below 15 °C. Alternatively, the consistent warming throughout spring in the western basin could indicate to fish that supra-optimal temperatures are imminent. It is also possible that migratory behaviours or timing are learned or initiated through social interactions (e.g., young fish may follow older fish; Olson et al. 1978; Brown and Laland 2011) or that these behaviours have been genetically encoded by long-term selection pressures that favour migration.

We suspect that many walleye leave the western basin on a schedule that is relatively fixed to the time at which they complete spawning activity, which itself is thought to be linked to ice-out timing and water temperatures (Colby et al. 1979; Schneider et al. 2010). Our data showed that western basin reef-spawning males linger in the western basin longer than do females. Across their distribution, male walleye typically arrive at spawning areas before females do and remain for a period of time after females have left (Colby et al. 1979). This behaviour may be adaptive because males can spawn several times within a season and with multiple mates; staying in the western basin provides this opportunity. In contrast, females

typically release all of their eggs within hours (Colby et al. 1979). We favour these aspects of spawning behaviour as a more likely explanation for the difference in departure timing between the sexes for reef-spawning fish than sex-specific behavioural thermoregulation.

Sex- or size-specific thermal preferences

Similar to previous findings with Maumee River walleye (Peat et al. 2015), we found no overall effect of sex or size on the thermal experiences of adult walleye in Lake Erie. As a result, we suspect that sex-specific behavioural thermoregulation was unlikely to be a primary reason why female walleye migrated to the eastern basin in greater numbers than did males. The animal-borne temperature data in our study were highly variable within most fish during summer (Fig. S6[1]), most likely indicating that fish regularly moved through a thermocline, which in summer in Lake Erie can sometimes represent a change of more than 10 °C for a vertical movement of only 3–4 m (Brandt et al. 2011). Our data do not rule out the possibility that large females tend to **prefer** colder water during summer months than do small males. Temperatures experienced by fish may often be by-products of other behaviours unrelated to thermoregulation. The best ways to assess thermal optima in the laboratory are to measure temperature-specific growth rates (e.g., Khan et al. 2014) or to use a shuttle-box system (e.g., Konecki et al. 1995) that allows fish to behaviourally demonstrate their preferred temperature. To our knowledge, a shuttle-box experiment has not been performed using adult walleye, and growth rate experiments with adult walleye have only extended to waters as warm as 20 °C (Kelso 1972). Nevertheless, no evidence for sex- or size-specific behavioural thermoregulation occurred here or in a previous study (Peat et al. 2015), which lends confidence that our result was not a false negative.

Conclusion, future work, and importance

Collectively, our results supported the hypothesis that postspawning emigration of Lake Erie walleye from the western basin was, at least partially, driven by temperature, but that future research into other factors (e.g., foraging) will be required to explain the extended migration that some fish made to the lake's eastern basin. Avoidance of high conspecific density and competition combined with foraging opportunities may be particularly important covariates of outmigration from the western basin given that overall walleye abundance is highest in the west end of the lake based on netting surveys (Kayle et al. 2015).

Investigating mechanisms involved in the appearance or disappearance of migratory phenotypes is fundamentally challenging because these questions do not easily lend themselves to experimental manipulation. Lake Erie, like most large ecosystems, is heterogeneous in several ways, many of which might contribute to the development of migratory phenotypes. A more detailed investigation into differences among fish that seasonally migrate to different areas (e.g., growth rates, diet composition, thermal preferences) across years with contrasting thermal regimes could provide further insight into the selective advantages and disadvantages of different migratory behaviours as they relate to temperature. Future research could incorporate a comparative analysis of the role of other habitat variables known to be important to walleye habitat, like turbidity and light levels (Colby et al. 1979). Counterintuitively, while seasonal hypoxia in the hypolimnion of the central basin of Lake Erie may eliminate thermal refuge habitats, bioenergetics modeling indicated that concentration of prey in marginal habitats could increase suitability of the central basin for walleye (Brandt et al. 2011). This intriguing idea may, in part, explain why some walleye migrate to and remain in the central basin throughout summer. Lake Erie walleye may be a good system for such questions, given the apparent repeatability of migratory behaviours and the relatively high long-term fisheries-recapture rates for our telemetry-tagged walleye (~30%), which can enable recovery of animal-borne data loggers (e.g., temperature, acceleration, depth) and analysis of growth patterns (otoliths). Such knowledge would aid in the larger effort to understand the causes, ontogeny, and functional effects of different migratory behaviours (Wilcove and Wikelski 2008; Bowlin et al. 2010; Lennox et al. 2016), each of which has important conservation implications (Caro 1999).

Acknowledgements

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