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Foraging activity and habitat use throughout an annual migration of adult walleye (*Sander vitreus*) from the Trent River in eastern Lake Ontario

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Abstract

Background Mature walleye (*Sander vitreus*) that spawn in the Trent River conduct long-distance annual migrations into eastern Lake Ontario that begin and end in the Bay of Quinte. This scale of movement likely reflects seasonal spawning activity in the spring and a combination of temperature and foraging preferences at other times of the year. This study used a combination of acoustic transmitters and pop-off data storage tags to collect high-resolution data on temperature, depth, rate of vertical movement (ROVM), and rate of horizontal movement (ROHM) during these migrations. We tested the theory that post-spawn fish migrating to Lake Ontario experience colder water temperatures than those remaining in the upper Bay of Quinte, and offset this cost with greater foraging, as indicated by ROVM. We also documented the trends in these variables seasonally at the daily and hourly level.

Results Temperature experienced by walleye in the lake (11.56 °C; SE±0.1) was on average 5.33 °C colder than in the upper bay (16.89 °C; SE±0.3), and there was a 15.5% increase in ROVM for fish in the lake. All the measured variables had significant seasonal trends, while only temperature, depth, and ROVM had significant hour of day trends. Sex based differences were limited to males having greater annual ROVM than females.

Conclusions There were differences in thermal habitat selection and vertical activity measures between the upper bay and Lake Ontario, which supported the current conceptual model of post-spawn walleye migration from the Bay of Quinte. Vertical activity peaked during crepuscular periods during the summer and fall when water temperatures promoted growth. This study demonstrates the value of combining tagging techniques to collect high-resolution data across multiple aspects of annual fish migrations.

Keywords Walleye, Acoustic telemetry, Pop-off data storage tags, Lake Ontario, Bay of Quinte

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Background

Many walleye (Sander vitreus) in eastern Lake Ontario migrate seasonally, utilizing spawning tributaries that flow into the Bay of Quinte and foraging in eastern Lake Ontario [1, 2]. They are the most abundant nearshore piscivorous fish in these regions of the lake and thus have an important influence on the fish community assemblage [3-8]. To better understand their role in the eastern Lake Ontario ecosystem, it is necessary to characterize their broad-scale movements, as well as their localized behaviour. Walleye display strong thermal-optical preferences, which dictate their location within the water column [9]. Chu et al. [10] modelled the habitat availability based on these preferences by walleye within the Bay of Quinte using fixed monitoring stations during the summer months. They found that walleye habitat use was consistent with this modelled habitat availability during the spring. After spawning was complete, however, fish movements became larger in scale, which was thought to be related to greater prey resources outside of the bay. Bowlby and Hoyle [1] also surmised that the post-spawn movements of mature walleye from the Bay of Quinte into the colder waters of Lake Ontario may be offset by the increased availability of alewife (Alosa pseudoharengus). These studies relied upon fixed monitoring sites and index netting programs to collect data, but lacked the ability to gather continuous observations directly from free-swimming walleye.

Over the last decade, acoustic telemetry has become a more widely used tool to document seasonal habitat use and annual migrations of walleye populations across the Laurentian Great Lakes [2, 11–13]. Walleye movements have been examined in relation to temperature [14], lake depth [15], and thermal-optical habitat [13]. Earlier non-telemetry studies have linked post-spawning migrations to the search for preferred foraging habitat with abundant soft-rayed prey species [5, 16]. A common theme emerging from these studies is that walleye migration is not typically driven by any single factor, but is often attributed to a combination of abiotic and biotic drivers [1, 14, 16]. To assess these factors simultaneously, researchers look to new types of tagging methods beyond traditional acoustic transmitters.

Advances in transmitter technology now allow for the incorporation of various sensors to provide in situ data on tagged fishes, such as temperature, depth, and acceleration [17]. One drawback to tags that transmit data is that, until recently, they did not have any logging capabilities, therefore telemetry data were limited to the time of detection by a passive receiver (or when active tracking). In the Laurentian Great Lakes, a collection of various receiver networks, each deployed to address project-specific objectives, provide the framework to address

whole-lake movement questions [18]. Despite this cooperative network, the scale of these waterbodies is such that data are often non-continuous and potentially biased depending on spatio-temporal coverage of receivers in the system. While gridded receiver arrays improve detection efficiency in these large systems [19], they often lack randomized coverage across all available bathy-thermal habitats [20].

Past studies have attempted to overcome the challenge of limited receiver spatial coverage in large lakes by internally tagging walleye with a combination of acoustic transmitters and independent temperature loggers; however, in these studies the loggers acquired data at long time intervals (4 h) and required the fish to be harvested in order to retrieve the data [14, 21]. Sample sizes in these studies ranged from 61-70 tags returned, representing 8-18% of tagged individuals. Pop-off data storage tags (pDSTs) with a logging rate of 70 s have been used in Lake Ontario to capture high-resolution temperature and depth observations from salmonids, however, they lacked positional data [22, 23]. With increasing memory capabilities, pDSTs are now able to record at a logging rate of every 2 s and last longer than a year, providing very high-resolution data to produce more accurate measures of activity such as vertical rate of movement [20]. While increased activity may not directly indicate successful foraging [24], vertical activity has been associated with foraging in other species [25, 26]. For walleye, general activity has been observed to peak at crepuscular periods [27, 28] when walleye are known to actively forage [29, 30]. Combining acoustic telemetry and pDST tagging methods provides an opportunity to collect positional data and high-resolution observations of thermal and vertical habitat selection, from which it is possible to derive the associated activity levels throughout a fishes' migration. Since walleye from the Bay of Quinte grow large enough to handle the burden of an acoustic transmitter and pDST, we can now use the expanding acoustic receiver coverage in Lake Ontario to address outstanding questions on habitat use and the drivers of activity during annual migrations posed over a decade ago by Bowlby and Hoyle [1].

The purpose of this study was to evaluate the current conceptual model of walleye migration from the Bay of Quinte. We used a combination of pDSTs and acoustic telemetry to provide information on habitat (temperature, and depth) and activity (rate of vertical movement, ROVM and rate of horizontal movement, ROHM) throughout an annual migration of Trent River walleye as they moved from the Bay of Quinte to eastern Lake Ontario and back again. Specifically, our objectives were to: (1) evaluate the current conceptual model proposed by Bowlby and Hoyle [1] that early-migrating walleye

which make post-spawn movements out of the Bay of Quinte encounter colder water temperatures which are offset by greater foraging; and (2) model seasonal patterns of temperature, depth, ROVM, and ROHM at the daily and hourly level to further our understanding of these annual migrations. We hypothesize that during the immediate post-spawn period (~1 month after spawning), early-migrating walleye to Lake Ontario will occupy colder water temperatures and record greater ROVM (indicative of feeding behaviour) than their conspecifics that delay migration or remain resident in the upper Bay of Quinte.

Methods

Study area

The Trent River flows into the Bay of Quinte at its northwesternmost end, approximately 75 km from the bay mouth, which connects to the eastern basin of Lake Ontario (Fig. 1). The Bay of Quinte is a narrow embayment located on the northern shore of Lake Ontario. The bay is divided into three regions, the upper bay, middle bay, and lower bay, which transition from shallow eutrophic habitat to deeper mesotrophic habitat, respectively.

Acoustic detections from migrating adult walleye were recorded using VR2W-69 kHz and VR2TX-69 kHz (Innovasea, Halifax, NS) omnidirectional receivers. The primary receiver array for this project consisted of 62 receivers, which were deployed consistently throughout the entire duration of the study period (April 1, 2019-April 23, 2020) (Fig. 1). Receivers were attached to anchored float lines ~1 m above the lake bottom with a secondary grapple line used for recovery purposes. Receivers in the Trent and Moira Rivers were attached to marina dock anchor lines to accommodate for water flow and boat traffic in these areas. The Bay of Quinte had receivers deployed in a series of gates (receiver spacing within gates ~ 500 m) at narrow points or locations of interest, while in eastern Lake Ontario receivers were arranged primarily in a grid (receiver spacing~7 km), supplemented with additional gates in areas of interest. Detections for this project were primarily acquired using these receivers which form the Eastern Lake Ontario Multi-Species Array (ELOMA). Additional detections from the New York region of the eastern basin of Lake Ontario were provided from the Eastern Lake Ontario Cisco and Lake Trout (ELOCS) array through the Great Lakes Acoustic Telemetry Observation System (GLA-TOS) network (Fig. 1). The downloaded detections were



Fig. 1 Map of the eastern basin of Lake Ontario showing the acoustic receivers (grey circles) used from the GLATOS network for this study. Receivers were grouped into 4 discrete regions based on locations from Bowlby and Hoyle [1]. The Bay of Quinte is divided into upper bay, middle bay, and lower bay, while the remainder of the receivers in the eastern basin form the lake region

uploaded to the GLATOS network to allow cooperative data collection across Lake Ontario.

Fish tagging

Boat-mounted electrofishing gear was used to collect walleye from suspected spawning habitat within the Trent River from April 2-16, 2019 in collaboration with the Lake Ontario Management Unit of the Ontario Ministry of Natural Resources and Forestry. Post-capture, fish were placed in a large recirculating holding tank to allow recovery from the electrofishing event. Ten males and ten females were selected to receive an acoustic transmitter and pDST based on a visual assessment of health and size. A minimum weight threshold of 2.1 kg was used to account for the total weight of both tags (42 g) and a tag burden not exceeding 2% body weight. Prior to surgery, all fish were measured for total length (mm), weighed (kg), and visually sexed by applying a small amount of pressure on the abdominal cavity and assessing the type of gamete released. Males averaged 650 mm in length (range 631-680 mm) and 3.04 kg in weight (range 2.65-3.53 kg), while females averaged 708 mm in length (range 648-746 mm) and 3.55 kg in weight (range 2.72-4.25 kg). Fish were immobilized for the procedure using electric fish handling gloves on the lowest setting (current output 4 mA; Smith-Root, Vancouver, WA). To implant the acoustic transmitters, fish were laid dorsally into a cradle lined with a soft non-slip mesh, and a constant supply of freshwater was gently sprayed across their gills. A small~3 cm incision was made slightly anterior of the anus, next to the central line of the ventral surface. Tags were inserted into the coelomic cavity and the incisions were closed with 2-3 interrupted absorbable Monocryl sutures (FS-1, 3-0, Ethicon, Somerville, NJ). Acoustic transmitters used for this study (V16-4H-69 kHz, 16×68 mm dia, 24 g in air, Innovasea, Halifax, NS) emitted a coded signal every 80-160 s (nominal delay 120 s) and had an estimated battery life of 1825 days. After the sutures were completed, scales were taken from behind the pectoral fin for ageing purposes.

Fish were then inverted in the cradle, so they laid ventrally to attach the pDST and accompanying harness through the dorsal musculature. The pDST tags used in this study (G5 pDST, 64 MB memory, 15×61 mm dia, 18 g in air, Cefas Technologies Limited, Suffolk, UK) were contained within orange floating collars and outfitted with timed release mechanisms utilizing corroding metal loops. Each tag included an information window which provided an ID number, contact name, phone number, website address, and indicated "Reward". The pop-off date was set for approximately one year from tagging (March 25, 2020) when fish were expected to be within or near the Trent River for spawning the following year. This date was chosen to gather a full year of data and to increase the recovery probability by reducing the search radius for tags when they detached from the fish and floated to the lake surface. The pDSTs were programmed to record depth (10 bar sensor) and temperature every 2 s until April 25, 2020 to allow approximately one month of data beyond the pop-off date. The complete procedure for attaching the pDSTs is described in detail within the methods of Elliott et al. [20]. Briefly, harnesses made from 300 lb monofilament fishing line, stainless steel crimps, and plastic brackets to maintain spacing, were attached through two entry points in the dorsal musculature of the fish. The fishing line was adjusted and crimped so that the pDST was positioned in the gap between the spiny and soft dorsal fins where it would not interfere with swimming ability or rub against the fins. The aims of this harness style were to distribute the force of the pDST evenly between the two entry points and keep the tag close to the body to reduce its impact on the fish. Tools and tags were bathed in 95% ethanol before and between surgeries. Fish were kept in a large recirculating holding tank post-procedure to allow recovery before being released back into the river.

pDST returns

Thirteen of the 20 pDSTs were recovered (65% return rate) roughly 1-18 mo after walleye were released (May 9, 2019-Dec 1, 2020). Tags were recovered and returned by members of the public, and only three tags correctly popped-off during the pre-determined period. Other recoveries were provided through angler recaptures, fish mortalities or premature failure of the release mechanism [20]. A \$100 CAD monetary reward was provided in exchange for the physical tag, and information regarding when, where and how the tag was recovered. Tags were downloaded and raw data were visually examined to determine when the tag physically released from the fish as indicated by a constant surface pressure reading. The dataset for an individual walleye was trimmed to start one day post-surgery until one day before the pDST released from the fish or the fish was captured (Table 1).

Data analysis

All analyses were conducted using R version 4.0.3 [31] and functions other than base are cited when noted. A significance level of $\alpha = 0.05$ was used for all analyses included in this study. ROVM was calculated for each fish individually using the sum of the differences between each two second depth record over the course of an hour. This produced a high-resolution measure of ROVM in m/h for each fish at each hour for the length of their respective datasets. The full temperature and depth pDST datasets were condensed into hourly averages

ID	Sex	TL (mm)	Weight (kg)	Last day of useable data	Number of days with useable data	Locations detected for objective 1	Migrated out of the Bay of Quinte
03	F	708	3.65	04/23/20	373	LO	Y
04	F	693	3.11	04/23/20	379	LO	Υ
05	F	739	3.83	06/22/19	68	UB	Ν
09	F	682	2.72	09/03/19	146	UB, MB, LB	Υ
10	F	706	3.73	10/07/19	175	LO	Υ
11	Μ	640	2.65	11/12/19	223	LO	Υ
12	F	648	2.74	06/30/19	81	UB, MB, LB	Ν
15	Μ	654	2.74	04/23/20	386	LB, LO	Υ
17	Μ	658	2.98	04/04/19	0	NA	NA
18	Μ	652	2.95	09/08/19	159	LO	Υ
21	Μ	638	3.01	08/30/19	149	LO	Υ
24	Μ	650	3.30	09/04/19	154	UB, LB, LO	Y
25	М	680	3.53	06/23/19	81	MB, LB, LO	Υ

 Table 1
 Summary of 13 walleye with recovered pDSTs tagged in April 2019

The amount of data collected was based on the number of days at-large in the system and was variable for each fish. Possible locations detected for objective 1 were upper bay (UB), middle bay (MB), lower bay (LB), and Lake Ontario (LO)

for each fish to match the sampling rate of ROVM and ROHM.

Detection data from acoustic transmitters were exported from the GLATOS database and organized in R using the GLATOS package [32]. Potential false positives in the dataset that can arise due to tag collisions or environmental noise were screened using short interval criteria [33]. Detections were identified as false if they were a single detection on a receiver within a 1 h period. Only 0.4% of the total detections were removed from the dataset as potential false positives. Acoustic data were trimmed to match the length of time that pDST data were collected for an individual fish. Raw acoustic detections were converted to an estimated position every hour using the interpolate_path function from the GLATOS package. Interpolated positions were determined using the shortest straight-line path between two consecutive receiver detections and accounting for the difference in timestamps between the two detections before splitting into estimated hourly positions [34, 35]. Interpolated positions for individuals were used on average 3.3 times as often as detections (SD = 1.9) during the study period. If the most direct path attempted to cross land, a non-linear shortest path was used to produce only movements that utilized water. The Bay of Quinte and eastern Lake Ontario have many irregular shorelines, therefore the interpolated non-linear pathways provide more realistic estimates of the minimum swimming distance. While this method provides a more realistic estimate of minimum swimming distance, it is likely that fish do not swim in linear paths between detections and therefore the true distances travelled could be much greater. For each fish,

the distance between interpolated positions was calculated in metres to produce hourly estimates of ROHM (m/h).

Hourly measures of temperature, depth, ROVM, ROHM were merged with animal ID, sex, Julian day (JD), month, and hour of day to produce the full dataset. Model assumptions for linear models were assessed using the gvlma function in R which provides a global statistic to evaluate the assumptions of linear models and provides a P-value used to determine significant deviations from acceptable assumptions [36].

Receivers from the ELOMA and ELOCS arrays were grouped into four regions: upper bay, middle bay, lower bay and lake to align with regions from Bowlby and Hoyle [1] (Fig. 1). Migration sequences were created for individual fish with daily timesteps using the most frequented region for each day to represent a single location for each timestep. For days where there were no detections, the last-observation-carried-forward method was used [37, 38], based on the assumption that fish remain in a region until they are detected in a subsequent region. To examine differences between early- and late-migrating walleye to Lake Ontario (objective 1), daily averages of temperature and ROVM were calculated for each fish at each location from May 14 to June 22, 2019. These dates corresponded to the peak of migratory walleye entering Lake Ontario [2] and the last day with data from all 12 individuals. It encompassed the period when > 50% of fish in the population had completed their post-spawn foraging migrations. Since fish were migrating through the system during this period a single fish could

provide detections in multiple locations. Differences in temperature and ROVM between locations were tested using linear mixed effects models in the lme4 package [39] with animal ID included as a random intercept to account for repeated daily observations from individuals. ROVM required a logarithmic transformation to normalize residuals. Visual inspections of diagnostic plots did not reveal any obvious deviations from linearity or homoscedasticity and residuals were normally distributed. Likelihood ratio tests were used with hierarchical models which compared the full model against the models without location to obtain P-values for the significance of location. Post hoc Tukey tests were used to determine differences between specific locations using the glht function from the multcomp package [40].

To examine habitat use and activity throughout the annual migration (objective 2), temperature (°C), depth (m), ROVM (m/h), and ROHM (m/h) were separately modelled by Julian day (smoothed), hour of day (separate smoothing functions by month), and sex (linear), using generalized additive mixed models (GAMMs) with the mgcv R package [41]. Animal ID was included as a random intercept for the models to account for repeated observations on the same individuals. Individual variance structures were included for the month term in the model (Jan-Mar, Apr-Jul, Aug-Oct, Nov-Dec) to remedy heteroscedasticity violations using the 'varIdent' function from the nlme R package [42]. Since time series datasets such as these are typically highly autocorrelated, we followed a similar procedure to Raby et al. [23] and randomly subsampled the full dataset to only include four hourly observations per day from each fish. A temporal autocorrelation structure was also included in each model using the corARMA function from the mgcv R package as described by Zurr et al. [43]. Likelihood ratio tests were used with hierarchical models, which compared the full model against a series of models without the individual effects in order to obtain P-values for the significance of individual predictor variables within each model separately. Model assumptions were visually checked using the residuals plotted against fitted values and the predictor variables, as well as the autocorrelation function of the residuals. Hour of day with separate smoothing functions by month were used to assess diel or crepuscular patterns in temperature, depth, and ROVM. ROHM was not assessed at the hourly level since it was not a significant term in the full model. Significant effective degrees of freedom (EDF) at each monthly level were used to determine the level of hourly change in the response variables, where a greater EDF indicated increased non-linearity across hourly values.

Results

The temperatures occupied by walleye and their activity levels varied across the four regions during the period directly following the post-spawn migration (Fig. 2). The upper bay had 48 detection days from four individuals, the middle bay had 15 detection days from three individuals, the lower bay had 29 detection days from five individuals, and the lake had 307 detection days from nine individuals. There were statistically significant differences among the regions for both temperature (Likelihood ratio test; Chi-squared = 53.2; df = 3; P-value < 0.001) and ROVM (likelihood ratio test; Chi-squared = 23.0; df = 3; *P*-value < 0.001). Specifically, temperature experienced by walleye in the lake (11.56 °C; $SE \pm 0.1$) was on average 5.33 °C colder than in the upper bay (16.89 °C; SE \pm 0.3), and there was a 15.5% increase in ROVM for fish in the lake (68.1 m/h; SE \pm 1.9) compared to those in the upper bay (54.4 m/h; $SE \pm 2.9$). The full statistical output from every regional contrast can be found in Table 2. A 24-h period of observed depth data from an individual in the upper bay and an individual in the lake are presented to provide an example of how ROVM differs between the regions (Fig. 3).

A series of four separate GAMMs were used to model temperature, depth, ROVM, and ROHM for walleye over the course of an entire year (Fig. 4). Each model included terms for Julian day, hour of day, and sex, however total length was not included in the model as females in this study were significantly larger than males (linear regression; $R^2 = 0.50$; df = 10; *P*-value = 0.010). The linear model testing the relationship of sex and total length met all the assumptions of a linear model (gvlma global stat = 1.9; P-value = 0.759). Weight was similarly excluded for the same reason. Due to the uncertainty in the predicted values at the right-hand tails for each GAMM, these values were not described as part of the overall trends. Temperature occupied by tagged walleye reached a global minimum in February (JD: 45; 0.67 °C; SE \pm 0.5), increased through spring and summer, and peaked in August (JD: 218; 23.1 °C; SE \pm 0.4), at which point it declined into the fall and winter months. Depth was shallowest during spawning activity in April (JD: 97; 3.5 m; $SE \pm 1.9$) and a maximum depth was realized in October (JD: 291; 15.1 m; SE \pm 1.0) before the walleye moved shallower during winter. ROVM had a bimodal distribution with the first peak occurring in late June (JD: 181; 74.9 m/h; SE \pm 5.6), the second peak in October (JD: 280; 75.4 m/h; SE \pm 7.3) and was at its minimum in February (JD: 38; 26.2 m/h; SE \pm 8.1). ROHM had a localized peak in movement during the post-spawn migration in May (JD: 141; 114.8 m/h; SE ± 10.9), a localized minimum in July (JD: 196; 65.2 m/h; SE ± 12.1), a global maximum in late October (JD: 299; 133.6 m/h; $SE \pm 14.8$), and a global



Fig. 2 Boxplots of average individual daily **A** temperature and **B** ROVM, of tagged walleye at the four different regions (Fig. 1) after completing their post-spawn migration (May 14–June 22, 2019). The upper bay (n=48 detection days, fish=4), the lower bay (n=29 detection days, fish=5), and the lake (n=307 detection days, fish=9) all had resident individuals, while the middle bay (n=15 detection days, fish=3) was only used by transient walleye. Bold lines represent the medians, the boxes represent the interquartile ranges, whiskers show the extent of the data, and outliers are shown as points. Regions that share a letter were not found to be significantly different (Table 2)

Table 2 Output from post hoc Tukey tests contrastingtemperature and depth across the four regions (upper bay,middle bay, lower bay, and lake) in the period following the post-spawn migration (May 14–June 22, 2019)

Region contrasts	Estimate	Std. error	Z-value	P-value	
Temperature (°C)					
Upper bay–Middle bay	- 2.74	0.788	- 3.47	0.003	
Upper bay–Lower bay	- 4.85	0.711	- 6.82	< 0.001	
Upper bay–Lake	- 3.57	0.546	- 6.54	< 0.001	
Middle bay–Lower bay	- 2.11	0.585	- 3.61	0.002	
Middle bay–Lake	- 0.828	0.705	- 1.18	0.634	
Lower bay–Lake	1.28	0.626	2.05	0.163	
ROVM (m/h)					
Upper bay–Middle bay	- 0.190	0.164	- 1.15	0.647	
Upper bay–Lower bay	- 0.269	0.145	- 1.85	0.242	
Upper bay–Lake	0.321	0.109	2.96	0.016	
Middle bay–Lower bay	- 0.079	0.132	- 0.599	0.929	
Middle bay–Lake	0.511	0.144	3.55	0.002	
Lower bay–Lake	0.589	0.123	4.80	< 0.001	

minimum in early January (JD: 1; 29.8 m/h; SE \pm 18.1). Significance of the individual model terms were tested against their respective full models (Table 3). Julian day was significant in all four models (*P*-value < 0.001), hour of day was significant for temperature (*P*-value < 0.001),

depth (*P*-value < 0.001), and ROVM (*P*-value < 0.001). Sex was only significant for ROVM (*P*-value = 0.023) such that males moved on average 12.1 m/h (106 km per year) more than females based on the model intercepts.

The effect of hour of day was modelled for temperature, depth and ROVM using month-specific smoothing functions. Temperature and depth had months with smoothing terms that were significantly non-linear, however there were no months with trends that were biologically significant. Over a 24-h period temperature typically varied by less than 1 °C (except July: 1.4 °C) and depth typically varied by less than 1 m (except July and November: <2 m). ROVM had the strongest crepuscular patterns with activity peaking at dusk and dawn from May through October (Table 4, Fig. 5). A summary of the month-specific hour of day model terms and significance levels for temperature, depth, and ROVM can be found in Table 4.

Discussion

This study documented thermal and vertical habitat use, as well as activity levels, during an entire annual migration cycle for adult walleye that spawn in the Bay of Quinte and spend the summer in Lake Ontario. The combination of high-resolution tagging methods used in this study provided insight into spatially distinct behaviours of walleye along their migration route. The conceptual



Fig. 3 Observed 24-h depth data for an individual from the upper bay (black line, maximum = 6.59 m) and an individual from the lake (grey line, maximum = 19.03 m) during the peak of the post-migration period decribed in objective 1. This exemplifies the different ranges of vertical movements made in these two locations. The maximum depth available in the upper bay is ~ 8 m, while available depths in the eastern basin of Lake Ontario can exceed 75 m

model for post-spawn walleye movements in this region proposed by Bowlby and Hoyle [1] was supported with our data collected from tracking free-swimming individuals. We showed that post-spawn water temperatures and ROVM differed for walleye depending upon the spatial regions occupied. The pDSTs revealed that walleye demonstrate strong patterns of daily vertical activity that varies seasonally. ROVM peaked during crepuscular periods when walleye are known to increase prey consumption [29, 30], providing support that ROVM is likely indicative of feeding behaviour. Estimates of ROVM collected with high-resolution data logging were almost equivalent to estimates of migration movements (ROHM) within the acoustic telemetry array, highlighting the importance of the vertical dimension to overall fish activity. The information obtained here has implications for bioenergetics modelling where activity levels are often assumed and can induce large errors into the predicted values for growth and consumption [44].

Walleye that made post-spawn migrations to the lake occupied colder water temperatures and had significantly higher ROVM than those that remained in the upper bay. The average post-spawn migration to the lake required walleye to occupy water ~ 10 °C colder than their preferred water temperature range of 20–23.2 °C [45]. Although high ROVM is likely indicative of feeding behaviours, it is important to note that foraging and consumption were not directly measured in this study. Future research validating the association of ROVM and foraging for walleye will be required. Nevertheless, these

observations provide support to the conceptual model first proposed by Bowlby and Hoyle [1] that increased foraging on alewife by post-spawn walleye in Lake Ontario could offset the associated colder water temperatures in the lake at that time of year. Despite Lake Ontario providing greater summer thermal refuge for large adult walleye compared to the Bay of Quinte [7], there is an early thermal disadvantage associated with lake migrations during the post-spawn period. This is consistent with walleye tracked in Lake Erie, where behavioural thermoregulation was not found to be the primary reason for large adult females to migrate into the colder regions [14]. It was concluded that other factors, such as foraging behaviours, likely play an important role in postspawn migrations. Hoyle et al. [5] also argued that access to increased foraging opportunities in Lake Ontario may be a larger driver than temperature for walleye from the Bay of Quinte. The lake-wide forage base in Lake Ontario is primarily composed of alewife, representing more than 90% of pelagic prey caught in annual assessments [46]. While a small proportion of the adult walleye population remain resident in the bay throughout the year ($\sim 9\%$, [2]), the vast majority migrate to the lake during the postspawn period, likely to take advantage of these foraging opportunities. Although there is variation in the timing of these migrations, individuals are highly consistent with their behaviours [47] and may rely on previously successful feeding strategies to reinforce future migratory behaviours. Taken together, the results from free-swimming individuals demonstrating increased ROVM in colder



Fig. 4 Fitted seasonal smoothing functions for A temperature, B Depth, C ROVM, and D ROHM based on individual GAMMs (Table 3). The number of individual walleye included in the models ranged from 3 to 12 based on when data were available (Table 1). Black lines are the daily fitted averages and shaded regions represent 95% confidence intervals around the averages

water during the post-spawn period and the conclusions drawn from other studies [1, 5, 14] provide growing evidence that foraging opportunities are likely the major driver of post-spawn migrations for walleye in the Great Lakes.

The results from tracking the annual migrations of free-swimming individuals in this study provided continuous information on the temperature, depth, and rates of movement throughout the year. Temperature experienced by the walleye peaked in early August at 23.1 °C, just below the upper preferred temperature threshold (20–23.2 °C; [45]). However, this observed peak in temperature is not reflective of the ambient peak in water temperatures of the eastern basin, which generally occurs in September–October (~24 °C) across water depths ranging from 4 to 15 m [48]. Rather, the results of this study indicate that once walleye reached their upper threshold of 23 °C, they moved deeper, perhaps as a strategy to avoid thermal stress near the surface. These results indicate that vertical movements in the late summer may be a strategy for behavioural thermoregulation utilized by walleye in Lake Ontario at that time of year. Upon returning to the Bay of Quinte in November, walleye experienced a decline in water temperatures at an increased rate compared to when they were in the eastern basin (Fig. 4A). The rapid warming and cooling of the Bay of Quinte relative to Lake Ontario resulted in notable thermal disruptions to walleye during their annual migrations as they exited and returned to the bay. Both disruptions occurred at times of the year when abundant foraging opportunities for alewife and gizzard shad (*Dorosoma cepedianum*) were available in the lake and lower bay, respectively [1]. It may be that increased foraging opportunities are able to offset localized thermal disadvantages encountered by walleye during their migrations.

There was an observed minimum in occupied depth during the month of April, when fish were within the Trent River while presumably spawning. For most of the year (Jan–Sept), fitted depth ranged from 5–10 m, which is consistent with netting results from Lake Ontario [1], **Table 3** Significance of model terms in a series of separate GAMMs modelling water temperature and depth occupancy, as well as rate of vertical movement (ROVM) and rate of horizontal movement (ROHM) for migratory walleye (n = 12) in eastern Lake Ontario

Temperature (°C)	$R^2 = 0.95$		
Model term	L ratio	P-value	
Julian day (smoothed)	762.0	< 0.001	
Hour of day (month-specific smoothing functions)	125.6	< 0.001	
Sex (linear)	0.9	0.335	
Depth (m)	$R^2 = 0.46$		
Model term	L ratio	<i>P</i> -value	
Julian day (smoothed)	153.7	< 0.001	
Hour of day (month-specific smoothing functions)	74.4	< 0.001	
Sex (linear)	1.7	0.195	
ROVM (m/h)	$R^2 = 0.30$		
Model term	L ratio	<i>P</i> -value	
Julian day (smoothed)	547.9	< 0.001	
Hour of day (month-specific smoothing functions)	363.4	< 0.001	
Sex (linear)	5.2	0.023	
ROHM (m/h)	$R^2 = 0.03$		
Model term	L ratio	P-value	
Julian day (smoothed)	68.2	< 0.001	
Hour of day (month-specific smoothing functions)	7.2	0.067	
Sex (linear)	1.6	0.212	

Each model also included a month-based individual variance structure and a temporal autocorrelation structure. Model R² is provided and the significance of each term was tested using a series of likelihood ratio tests

Table 4 Monthly-level smoothing functions and their output for hour of day effects from three separate GAMMs predicting water temperature, depth, and rate of vertical movement (ROVM) by tagged walleye in eastern Lake Ontario

	Temper	ature		Depth			ROVM		
Month	EDF	F	P-value	EDF	F	P-value	EDF	F	P-value
January	1.0	0.953	0.329	3.8	12.218	< 0.001	1.0	4.570	0.033
February	1.0	0.416	0.519	2.1	4.150	0.014	2.6	3.925	0.008
March	6.3	37.408	< 0.001	1.0	0.909	0.340	1.0	0.004	0.949
April	4.5	17.118	< 0.001	1.0	1.291	0.256	1.0	0.000	0.984
May	1.0	12.853	< 0.001	3.4	13.382	< 0.001	3.3	10.731	< 0.001
June	4.6	22.976	< 0.001	4.0	14.900	< 0.001	8.2	49.461	< 0.001
July	6.8	36.923	< 0.001	6.3	12.154	< 0.001	8.0	50.088	< 0.001
August	3.6	10.374	< 0.001	1.0	0.003	0.957	7.2	8.916	< 0.001
September	5.5	3.569	0.016	1.0	1.321	0.250	6.4	20.207	< 0.001
October	4.0	7.716	< 0.001	1.0	5.787	0.016	7.0	20.529	< 0.001
November	1.0	17.812	< 0.001	7.5	6.406	< 0.001	1.0	2.666	0.102
December	1.0	1.378	0.240	1.0	0.049	0.825	1.0	0.676	0.411

An EDF of one indicates a linear relationship, and higher EDF values indicate increasingly non-linear relationships

however shallower than acoustic telemetry results from Lake Erie (10.8–13.9 m) [49]. This depth range is deeper than where optimal light conditions have previously occurred for walleye in this system (2–6 m; [9, 10]). This may indicate that thermal limitations at shallower water depths are driving walleye away from their optimal light levels, if these conditions have persisted over the last two decades. Alternatively, increasing water clarity may be forcing walleye deeper than previously modelled for this region [50]. The available habitat becomes a tradeoff



Fig. 5 Hour of day smoothing functions by month for ROVM based on fitted results from a GAMM (Table 4). The number of individual walleye included in the models ranged from 3 to 12 based on when data were available (Table 1). Black lines are the daily fitted averages and shaded regions represent 95% confidence intervals around the averages

between depths deep enough to not exceed thermal preferences, yet shallow enough for optimal light levels. As lake-wide temperatures increased into the late summer, walleye occupied deeper depths. Walleye remain deep until after the thermocline dissipates, which happens in October in eastern Lake Ontario [48], at which time they begin to move shallower. These results are consistent with observations from walleye tagged in Lake Erie, which occupied deeper depths during stratification, than during pre- and post-stratification periods [49]. With no vertical thermal constraints post-stratification, the depth of walleye may be more influenced by light attenuation, location in the system, bathymetry, and vertical foraging opportunities.

Both ROVM and ROHM decreased in August when temperatures were at their maximum (Fig. 4). It is possible that walleye minimize activity at that time of year because metabolic demands could out-weigh the benefits of foraging as supported by bioenergetics modelling showing growth ceases beyond 23.5 °C [7]. As the walleye moved deeper and the temperatures decreased, there was a subsequent peak in both ROVM and ROHM. Walleye are perhaps able to simultaneously expend energy on feeding and migratory behaviours in October because their energy reserves are increased from the period of feeding activity in the early summer [51]. Movement was minimized as walleye over-wintered in the Bay of Quinte. Lower levels of activity during winter would be expected for walleye based on previous work [52]. Although activity levels were minimized during the winter months, it is noteworthy that they were not negligible. Some degree of over-winter foraging was likely occurring, behaviour which has been reported for other cool-water species [53].

Temperature, depth, and ROVM all displayed significant seasonal hour of day effects, while ROHM did not. Walleye are primarily visual feeders, relying on their scotopic vision that allows for more efficient crepuscular and nocturnal feeding [54]. Therefore, it is not surprising that the most prominent differences were related to increases in ROVM (inferred feeding activity) during crepuscular and nocturnal periods, consistent with other studies of walleye [27, 28]. Seasonally, the greatest diel variations in ROVM were during the summer and fall months (June-October) which may reflect differences in vertical prey pursuit related to thermal stratification during this period of the year. June and July showed the most prominent diel change in depth, and likely resulted in the observed ~1 °C increase in water temperature as fish move into shallower, warmer water. Modelled diel temperature increases and depth variations (~1 m) in our study were similar to those found in tagging studies of Lake Erie walleye [14, 49]. However, it is important to note that these modelled trends do not reflect the full scale of daily variation that can occur at the individual level [20].

Increased ROVM at crepuscular and nocturnal periods aligns with periods of predatory advantage for the walleye due to scotopic vision and increased prey availability at their occupied depths. In Lake Ontario, alewife display a diel vertical migration moving from deeper water during the day, towards the surface at night [55]. Considering alewife are the preferred prey for walleye in the eastern basin [5], it may be that the nightly change in walleye ROVM is synchronous with the vertical migration of alewife. While daytime activity is lower during summer months, a significant portion of this activity is directed downwards when fish are in the lake (Fig. 3). These dives can be quite extensive and numerous during the summer [20] and may be used as foraging excursions for alewife that are occupying deeper and colder depths during the daytime. There was a notable difference in daily ROVM patterns at the seasonal level, such that during November through May the typical crepuscular patterns break down. This seasonal period includes consistent depth selection throughout the day and water temperatures dropping below 11 °C. According to Lester et al. [9], at these colder temperatures walleye growth is reduced below 50% of its peak (which occurs at 21 °C). The lack of crepuscular ROVM patterns from November through May aligns with this period of reduced growth in colder water. This likely indicates that walleye are making efforts to conserve energy in the winter rather than actively foraging to the degree that was observed in June through October.

There were no statistically significant differences in annual temperature experiences between the sexes observed in this study. This is consistent with results for walleve in Lake Erie and Lake Huron [14, 21], despite females being larger and incurring higher metabolic costs at warm temperatures [16]. In contrast to walleye from Lake Erie [15], our results did not indicate a significant difference in annual depth selection between the sexes. The researchers in Lake Erie analysed depth habitat selection using receiver deployment depth as a proxy for fish depth at each detection. Our study used depth observations from animal-borne tags, which may account for the differences between the studies. It is possible that in both lakes the two sexes occupy similar depths, however utilize alternative regions with different available depths. Our analyses indicated that males vertically travelled 12.1 m further per hour (106 km per year) than females. Henderson et al. [56] proposed that the inferior growth efficiency of males is a function of their greater activity levels, which is consistent with the observed activity levels of males found in our study. They also found that mature females have higher growth rates from not only higher growth efficiency, but also greater consumption. Further study will be required to better understand the prey selection and activity differences between the sexes, specifically during the summer and fall months when consumption is at its highest.

Conclusions

This study was able to use a novel combination of acoustic transmitters and pDSTs to collect data from piscivores in a large freshwater system. Specifically, our approach allowed us to examine habitat use and activity by adult walleye as they undertook an annual post-spawning migration through a large and complex system-the Trent River, Bay of Quinte and into Lake Ontario. Walleye that migrated to Lake Ontario immediately postspawn encountered colder water temperatures and showed higher ROVM, indicative of increased foraging behaviour, consistent with the current conceptual model proposed by Bowlby and Hoyle [1]. The observed seasonal trends based on an annual migration cycle of free-swimming individuals provide further support that walleye migrations are likely driven by a combination of thermal preferences and foraging opportunities in Lake Ontario. These interpretations are also consistent with walleye migrations from other populations across the Great Lakes [14, 16]. Our results derived from freeswimming individuals also provided rates of vertical movement at a higher resolution than previously available for this species. The collection of this data would not have been possible using only acoustic transmitters and required the addition of pDSTs to achieve the necessary sampling frequency [20]. Notably, the data revealed that vertical movement is extensive and nearly equivalent to horizontal movement at certain times of the year. Bioenergetic models for walleye would benefit from including measures of vertical activity since it has now been shown that walleye must be allocating a significant amount of energy to this aspect of movement. The cost of pDSTs and the challenges in obtaining their data can often limit the sample sizes for studies using these tags. Future studies with a greater number of individual fish double tagged with these types of loggers will be beneficial to confirm if the observed trends are representative of the entire population and continue to expand our understanding of seasonal crepuscular movements. Until then, these findings shed new light on the habitats occupied and activity patterns of adult walleye through an annual migration cycle.

Abbreviations

pDST	Pop-off data storage tag
ROVM	Rate of vertical movement
ROHM	Rate of horizontal movement
ELOMA	Eastern Lake Ontario multi-species array
ELOCS	Eastern Lake Ontario cisco and lake trout
GLATOS	Great Lakes acoustic telemetry observation system
JD	Julian day
GAMM	Generalized additive mixed model
EDF	Effective degrees of freedom

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Author contributions

CE was responsible for fieldwork, data analysis, and drafted the manuscript. CE, MR, PB, and BT were all responsible for project conception, data interpretation, and manuscript preparation. All authors read and approved the final manuscript.

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Availability of data and materials

The data from this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

All research was conducted in accordance with Protocol Number 2019–1916 approved by the University Animal Care Committee at Queen's University.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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