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ARTICLE

Comparative thermal biology and depth distribution of largemouth bass (*Micropterus salmoides*) and northern pike (*Esox lucius*) in an urban harbour of the Laurentian Great Lakes

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Abstract: Understanding how individuals are distributed in space and time, as well as how they interact with dynamic environmental conditions, represent fundamental knowledge gaps for many fish species. Using acoustic telemetry tags, we monitored the temperatures and depths used by northern pike (*Esox lucius* L., 1758) and largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) in Toronto Harbour (Lake Ontario). Northern pike and largemouth bass had similar thermal experiences throughout the year, except during summer, when northern pike were observed in cooler waters than largemouth bass. Both species used different depths throughout the year, with northern pike occupying deeper depths. Statistical modelling indicated that depth usage was influenced by all variables (season, species, and body size) and interactions between them, whereas thermal preferences were influenced by the main effects and interactions between species:season and species : body size. Both species were observed at temperatures warmer than those in the vicinity of nearby telemetry stations, but as station temperatures exceeded 20 °C, northern pike moved into cooler water, indicating active thermoregulation. These data will be useful for refining our understanding of the spatial ecology of fish and for informing fisheries and habitat management in this and other urban harbours of the Laurentian Great Lakes.

Key words: Great Lakes, temperature, thermoregulation, northern pike, *Esox lucius*, largemouth bass, *Micropterus salmoides*.

Résumé : Il existe des lacunes fondamentales en matière de connaissances sur de nombreuses espèces de poissons pour ce qui est de comprendre la répartition des individus dans l'espace et le temps et leurs interactions avec des conditions ambiantes dynamiques. À l'aide d'étiquettes de télémétrie acoustique, nous avons surveillé les températures et les profondeurs fréquentées par les grands brochets (*Esox lucius* L., 1758) et les achigans à grande bouche (*Micropterus salmoides* (Lacepède, 1802)) dans la baie portuaire de Toronto (lac Ontario). Les grands brochets et les achigans à grande bouche présentent des expériences thermiques semblables durant toute l'année, sauf l'été, quand les brochets sont observés dans des eaux plus froides que les achigans à grande bouche. Les deux espèces fréquentent des profondeurs différentes tout au long de l'année, les grands brochets occupant de plus grandes profondeurs. La modélisation statistique indique que les profondeurs fréquentées sont influencées par toutes les variables (saisons, espèce et taille du corps) et leurs interactions, alors que les préférences thermiques sont influencées par les principaux effets et les interactions espèce:saison et espèce : taille du corps. Les deux espèces sont observées à des températures plus élevées que les températures au voisinage de stations de télémétrie situées à proximité, mais quand les températures des stations dépassent 20 °C, les grands brochets se déplacent vers des eaux plus froides, un indice de thermorégulation active. Ces données seront utiles pour parfaire la compréhension de l'écologie spatiale des poissons et éclairer la gestion des pêches et des habitats dans cette baie et d'autres baies portuaires urbaines des Grands Lacs laurentiens. [Traduit par la Rédaction]

Mots-clés : Grands Lacs, température, thermorégulation, grand brochet, *Esox lucius*, achigan à grande bouche, *Micropterus salmoides*.

Introduction

Understanding how individual organisms are distributed in space and time is fundamental to ecology (Elton 2001). Many environments are spatially (within and across different habitat types) and temporally (over diel or seasonal period) heterogeneous (Wiens et al. 1993) and it is generally assumed that animals distribute themselves in a manner that maximizes fitness (Huey 1991), particularly as it relates to acquiring resources (e.g., food, mates) and avoiding predators. Fish live in aquatic systems that provide a multidimensional environment where animals can access resources that are distributed laterally or vertically. Yet, researchers who study fish are faced with inherent challenges given the diffi-

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culty of studying free-living fish in the wild (reviewed in Lucas and Baras 2000). The advent of various biotelemetry tools has provided ecologists with new opportunities for understanding how fish are distributed in space and time (Cooke et al. 2013; Hussey et al. 2015). Various sensors incorporated into electronic tags (see Cooke et al. 2004) can provide detailed information on depth use and environmental conditions experienced by the fish (e.g., water temperature). Nonetheless, these developments are relatively recent and many knowledge gaps remain with respect to understanding how fish interact with their environment across different spatial and temporal scales. Such information would not only enhance our understanding of animal–environment relationships and ecological processes, but also inform activities such as fisheries management or habitat restoration (Hussey et al. 2015; Cooke et al. 2016).

Northern pike (*Esox lucius* L., 1758) and largemouth bass (*Micropterus salmoides* (Lacepède, 1802)) are two popular fish species that are intensively managed (Bence and Smith 1999) and for which there is great interest in understanding animal–environment interactions given that they are top predators in many freshwater ecosystems. Northern pike are a broadly distributed fish species, occurring in a majority of northern lakes and rivers across North America, much of the United Kingdom (excluding Scotland; Lefevre 1999), and in Europe (Crossman 1996; Harvey 2009). Ideal northern pike habitat has been identified as vegetated areas that are <4 m in depth (Harvey 2009). Largemouth bass is a ubiquitous freshwater fish species, inhabiting a majority of aquatic habitats in North America (Brown et al. 2009). Typically, largemouth bass prefer lacustrine environments with shallow (<6 m) littoral zones (Essington and Kitchell 1999) that are capable of supporting widespread vegetation, as well as high structural habitat complexity (Prince and Maughan 1979; Schlagenhaft and Murphy 1985; Mesing and Wicker 1986). There is therefore considerable overlap in the preferred habitat of both species. Although much is known about both northern pike and largemouth bass ecology, there is still relatively little known about how they are distributed vertically and the water temperatures that they occupy over the course of a day or across seasons.

As ectotherms, temperature plays a vital role influencing many physiological processes affecting growth for both northern pike and largemouth bass. Temperature is traditionally regarded as the "master" abiotic factor (Brett 1971), and variations in ambient water temperatures can have an assortment of effects on all biochemical (such as enzymatic activities), physiological (such as growth, swimming speed, and digestion), and life-history (such as maturation, reproduction, and migration) processes (Fry 1971). Northern pike are classified as a cool-water fish species and thus have considerably lower thermal optimums compared with largemouth bass, a warm-water species. Optimal growth of juvenile and adult northern pike has been known to occur at temperatures ranging from 19 to 21 °C (Casselman and Lewis 1996), whereas largemouth bass prefer temperatures ranging from 24 to 30 °C (Stuber et al. 1982). Although detailed information exists on the thermal optima of northern pike and largemouth bass (see Strawn 1961; Casselman 1978; Casselman and Lewis 1996; Brown et al. 2009), information on thermal habitat usage derived from wild fish is relatively absent from the literature and we are unaware of any studies in which they have been explicitly compared within the same waterbody.

Situated on the northwestern shore of Lake Ontario, Toronto Harbour experiences an enhanced thermocline upwelling effect (amplitudes over 11 m) due to the large escarpment at the end of the Outer Harbour (Huang et al. 2010; Hlevca et al. 2015); therefore, temperature fluctuations of 10–16 °C during a 24 h interval are common and can occur numerous times throughout the stratified season (Hlevca et al. 2015). Additionally, the superposition of Poincaré waves (mean amplitudes of 4 m) may have an important modulation effect on major thermocline oscillations and increase thermal variability especially in the more exposed half of the Outer Harbour (Hlevca et al. 2015). Temperature fluctuations caused by lake–embayment exchanges have been identified as a major factor contributing to habitat suitability (Murphy et al. 2011), fish distribution, and adequate growing seasons (Murphy et al. 2012*a*, 2012*b*, 2012*c*) for warm-water fish species. Populations of yellow perch (*Perca flavescens* (Mitchill, 1814)), largemouth bass, and pumpkinseed (*Lepomis gibbosus* (L., 1758)) have been shown to move among embayments, effectively creating a metapopulation and allowing individuals to compensate for variations in the thermal habitat of different embayments in Toronto Harbour that would otherwise act as ecological traps (Murphy et al. 2012*a*, 2012*b*, 2012*c*). Thus, we hypothesize that the intrinsic thermal variability in the harbour will influence the thermal habitat usage of northern pike and largemouth bass.

In this study, we monitored the temperatures and depths used by northern pike and largemouth bass in Toronto Harbour (Lake Ontario), and explored the possibility of either species thermoregulating when temperatures permitted. We hypothesized that, on average, northern pike would be found at greater depths and cooler temperatures than largemouth bass, and when necessary, both species would seek thermal refuge to exploit more favourable temperatures. The objectives of this paper were to compare the thermal biology and vertical distribution (i.e., depth use) of northern pike and largemouth bass. Specifically, we (*i*) characterize the temperature and depth use for both species of fish on a seasonal basis, (*ii*) evaluate how temperature and depth use are influenced by biotic and abiotic factors (e.g., individual size, species, time of year), and (*iii*) evaluate evidence of thermoregulation for either species. Collectively, this information will contribute to our understanding of the animal–environment interactions for wild fish while simultaneously informing habitat management efforts and the development and validation of habitat-based models for these species.

Materials and methods

Study site and fish collection

This study took place in Toronto Harbour, a large nearshore feature situated on the northwestern shore of Lake Ontario and adjacent to the largest population centre in Canada. Toronto Harbour is often described as being two separate harbours: the Inner Harbour, which is defined by the area of water enclosed by the Toronto Islands, and the Outer Harbour, which is defined by the area of water enclosed by Tommy Thompson Park (see Figs. 1A–1C).

Adult northern pike and largemouth bass were caught using boat-mounted electrofishing gear (Smith-Root electrofishing model SR 18.EH; 250 V and 7 A for intervals of ~1000 s) at a number of target locations including the Toronto Islands, embayment C, cell 2, and cell 3 (see Fig. 1C). Captured fish were retained in a flow-through livewell for 1 to 3 h prior to tagging. In total, 74 northern pike and 83 largemouth bass were implanted with acoustic transmitters (V9TP: 9 mm diameter × 39 mm length, 4.6 g, accuracy = ±0.5 °C and ±2.5 m, resolution = ±0.15 °C and ±0.22 m; V13TP: 13 mm diameter × 45 mm, 12 g, accuracy = ±0.5 °C and ±2.5 m, resolution = ±0.15 °C and ±0.22 m; Vemco, Halifax, Nova Scotia, Canada; for summary information see Table 1) capable of measuring depth (derived from pressure) and fish temperature. Acoustic transmitters were set to emit a tag-specific code (at 69 kHz) randomly at time intervals between 90 and 150 s to reduce possible code collisions, which can occur when transmissions from two 69 kHz tag IDs interfere and produce a single incomplete or incorrect tag ID.

Fish tagging

Fish were tagged during the spring and fall of 2010 to 2013. Prior to surgery, individual northern pike and largemouth bass were transferred from a holding tank and anesthetized using either a portable electroanesthesia system (PES; Smith-Root, Vancouver, Washington, USA) operating at 35 V pulsed direct current or a

Fig. 1. Map of study area and positions of acoustic receiver arrays in Toronto Harbour, Toronto, Ontario, Canada. Deployment years ranged between 2010 and 2013, and are specified by the different sizes of solid and open circles for each station.

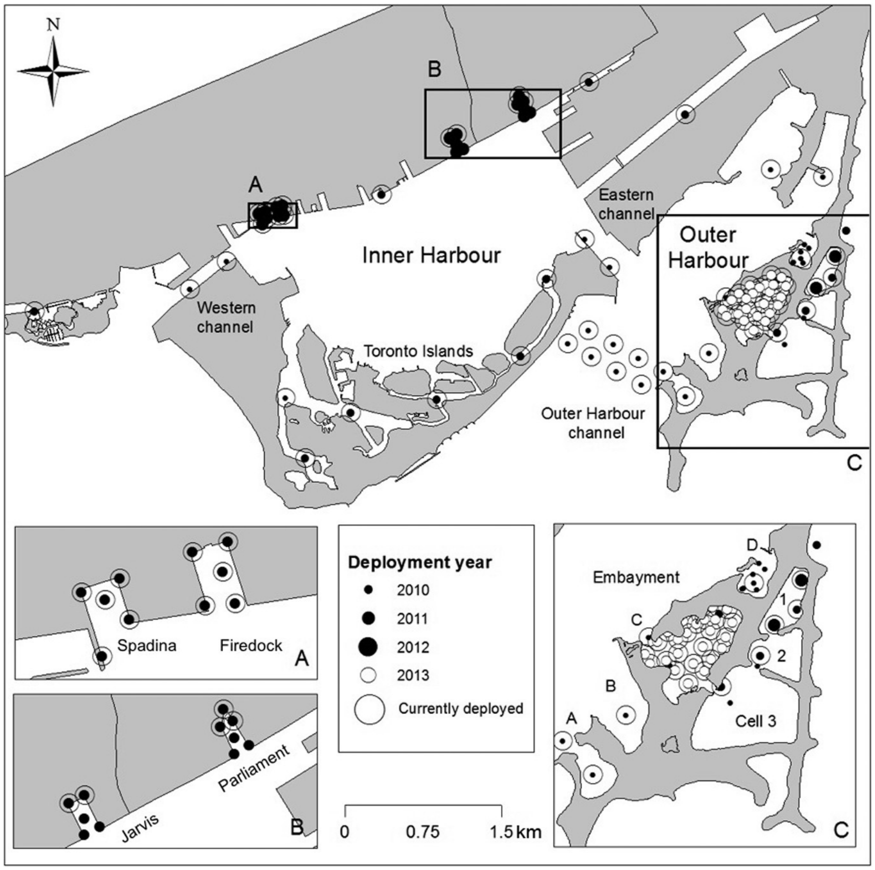


Table 1. Summary of physical attributes (e.g., sex, length, mass) of tagged northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) in Toronto Harbour, Toronto, Ontario, Canada, as of November 2013.

	Northern pike			Largemouth bass		
	Male	Female	Unknown	Male	Female	Unknown
Total numbers	12	22	40	12	21	50
Length (mm)						
Mean	655	798	729	401	467	382
SD	99	104	164	65	40	111
SE	8	5	4	5	2	2
Mass (g)						
Mean	1856	3373	1938	1140	1907	1191
SD	791	1384	1252	555	527	774
SE	66	66	63	46	25	16

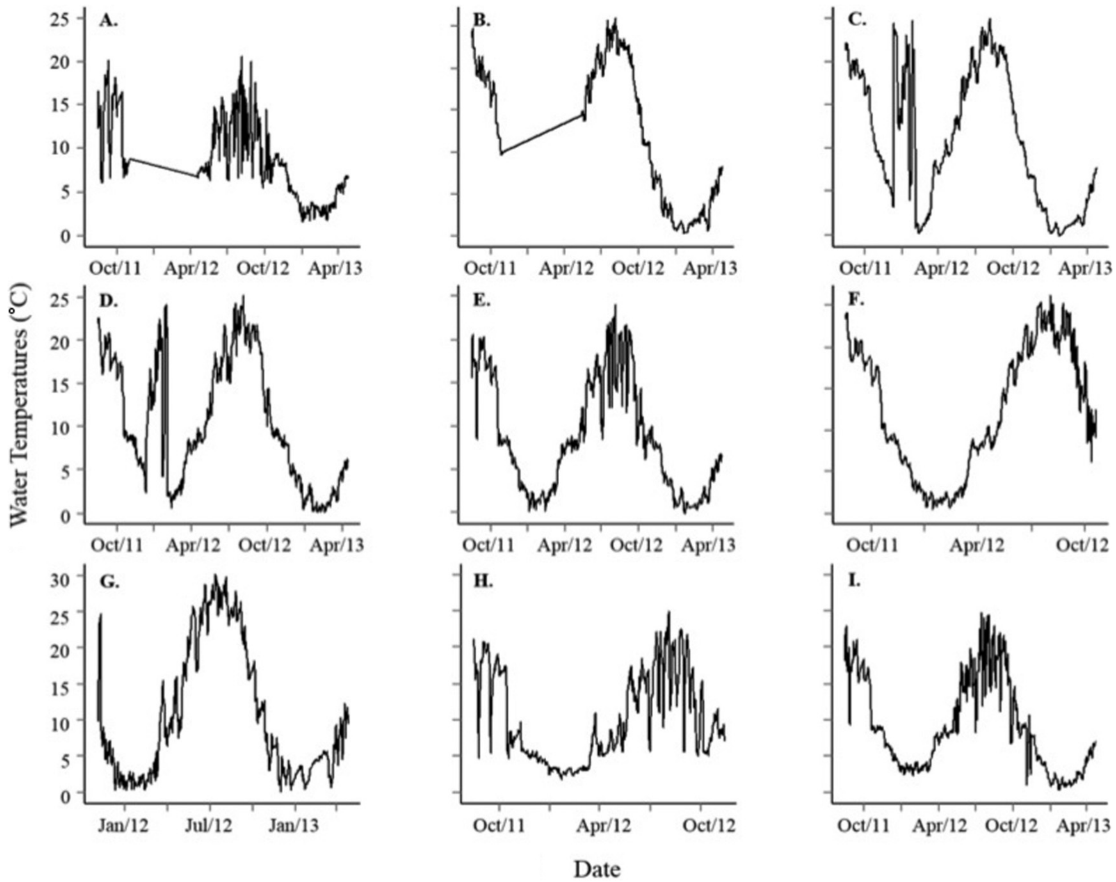
Note: In total 74 northern pike and 83 largemouth bass of various sizes were caught and tagged with either Vemco V9TP or V13TP acoustic tags. SD represents the standard deviation, whereas SE represents the standard error.

60 ppm clove oil bath (emulsified in ETOH) until stage-4 anesthesia was achieved. Electroanesthesia using pulsed direct current is known to result in immediate induction, quick recovery, and high survival for many species (Vandergoot et al. 2011; Rous et al. 2015), including largemouth bass. Treatments of 3 s induced stage-4 anesthesia for several minutes, allowing sufficient time for surgical implantation of the acoustic transmitters. Despite evidence of high survivorship of northern pike with respect to electroanesthesia (Walker et al. 1994), preliminary observations revealed 6 of 18 northern pike tagged in 2011 using the PES unit died within the first month after being released. As such, all further tagging activities for that species used clove oil. All surgical procedures followed guidelines outlined by Cooke et al. (2011). While sedated, fish were placed on a v-shaped surgical table, lined with soft, nonslip rubberized material. A constant flow of water was pumped across the gills with a recirculating pump to provide oxygen. All surgical tools were cleaned with povidone iodine and rinsed with deionized water before surgery; transmitters were similarly disinfected prior to being implanted. A small incision (1–3 cm) was made along the ventral midline of each fish, posterior to the pelvic girdle for largemouth bass and anterior to the pelvic girdle for northern pike. Each tag was then placed into the coelom and incisions were closed with absorbable monofilament sutures (PDS-II, 3-0; Ethicon, Somerville, New Jersey, USA). An experienced surgeon implanted all transmitters to reduce variation in fish survival and recovery, with the mean surgery time being 180 s; some surgeries, however, lasted upwards of 660 s because of attempts to determine the sex of individuals with a borescope. After surgery, fish were returned to holding tanks to recover for a period of approximately 30–120 min. Following this recovery period, individuals were released at their respective capture locations.

Receiver configuration

An acoustic array was used to evaluate the thermal ecology and thermal habitat use of northern pike and largemouth bass in Toronto Harbour. In general, receiver locations were selected using previous known techniques to maximize fish detection throughout the harbour but with some limitations. Such methods included the use of curtain arrays (a line of receivers that stretch across a shoreline) at transition points to detect any fish leaving or returning to the array system, and overlapping receiver placements to maximize the detection of fish within our system. Costs and complications associated with high boat or shipping traffic in

Fig. 2. Water temperatures of Toronto Harbour, Toronto, Ontario, Canada, from October 2011 through April 2013. Temperatures were recorded every 600 s daily by HOBO temperature loggers fixed at receiver stations: (A) temperatures observed in Cherry Beach; (B) temperatures taken from cell 2; (C) temperatures taken from cell 3; (D) temperatures taken from the Toronto Islands; (E) temperatures taken from embayment A; (F) temperatures taken from embayment C; (G) temperatures taken from embayment D; (H) temperatures taken from Lake Ontario; (I) temperatures taken from the Outer Harbour Marina.



this area required receivers be placed only in key transition points and areas of interest, rather than in an array covering the entire harbour. As such, receivers (69 kHz VR2W; Vemco) were placed at the following locations: cell 1, cell 2, cell 3, embayment A, embayment B, embayment C, embayment D, the Toronto Islands, Western Gap, Eastern Gap, Jarvis Slip, Parliament Slip, Spadina Slip, Fire Dock, and the Outer Harbour Channel, which connects the Outer Harbour to Lake Ontario (Figs. 1A–1C). Receivers were also placed in areas recognized early in the study to be overwintering aggregation sites for northern pike and largemouth bass to facilitate collection of temperature and depth data throughout the winter months. In total, 93 receivers were deployed in Toronto Harbour during the study period (see Figs. 1A–1C).

A variety of deployment methods were used to overcome the challenges associated with having acoustic receivers in Toronto Harbour (boat traffic, ice floes, etc.). Stations located in shallower waters were typically anchored to the bottom using a large cement block (60 cm × 60 cm × 10 cm) embedded with PVC pipes large enough to contain the receivers. The use of these cement blocks proved to be ideal because they were light enough to be maneuvered by hand, yet heavy enough to resist movements caused by currents and dissuade vandals. Stations were either tethered to shore using aircraft cable (coated high-tensile steel cable) connected to a t-bar hidden in brush, or by tethering the station to a nearby retaining wall, out of reach of pedestrians. Receivers placed offshore in relatively shallow waters (5–10 m) were either attached to mooring buoys right below the surface of the water or anchored to the substrate and coupled with a float that was deep enough under the surface of the water to avoid boat traffic, but shallow enough to be seen and recovered. Lastly, receivers that were placed in deep offshore waters (typically depths >10 m) were anchored using two sewer grates connected by a rope or cable. Retrieval of these stations required the use of a grapple and mechanical winch because each grate weighed upwards of 60 kg. GPS coordinates of each receiver were taken at the time of deployment to facilitate station retrieval. Despite the relatively long battery life of VR2W receivers, downloads of receiver data occurred at frequent intervals and batteries were changed every 12 months to avoid complications with potential data gaps caused by dead batteries or lost receivers.

Water temperature measurements

An array of over 200 individual thermistor loggers (benthic and subsurface; attached to receiver stations) was deployed during the periods of April–November in 2012 and 2013. Thermistor loggers remained in the water throughout the duration of a whole year and data were downloaded concurrently with receiver downloads. Thermistors on chains were placed at 1 m intervals on ropes, which were kept vertical by submerged buoys. All thermistors used were time-synchronized Onset HOBO U22 Water Temp Pro V2, and recorded the temperature every 600 s, with an accuracy of ±0.1 °C, and an annual drift under 0.1 °C. This thermal accuracy is comparable with measurements made within the fish using acoustic tags. All the thermistor loggers were tested and calibrated in laboratory conditions before deployment. In a companion study, Hlevca et al. (2015) provide detailed information about temperature and velocity measurements in the various zones of the Inner Harbour and Outer Harbour.

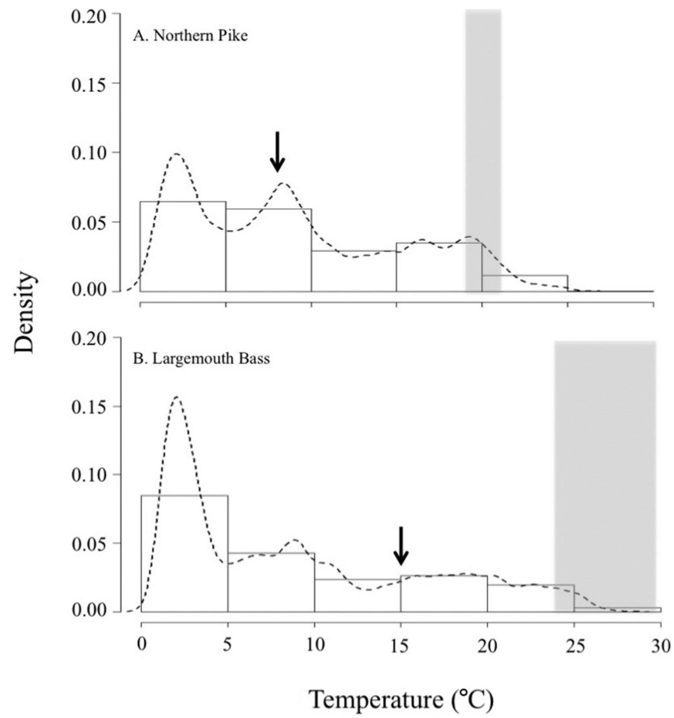
Data management and analysis

All temperature and fish tracking data were downloaded at two (three in earlier years of the project) separate events each year, usually once in the spring and once in the fall. Data were imported into a Microsoft Access database and filtering system, which allowed for the extraction of specific data and the ability to remove erroneous detections by identifying detections that appeared to be logically impossible (e.g., a fish being detected at two stations at the same time, or detections where fish appear to move an improbable distance given the time frame of detections). Data for northern pike and largemouth bass were then extracted from the database, which contained all true detections from September 2010 to November 2013. We separated seasons by classifying spring to correspond with dates between 1 March and 31 May; summer to correspond with dates between 1 June and 31 August; fall to correspond with dates between 1 September and 30 November; and winter to correspond with dates between 1 December and 28 February. Variation in the timing of tagging, fish mortality, and battery life of the acoustic tags may have led to an imbalance in the number of observations for each fish.

We used a similar method to Baird and Krueger (2003) to evaluate whether there was evidence of thermoregulation in the area. Fish temperatures recorded from the implanted acoustic tags were compared with station temperatures corresponding with the dates of detection. Fish temperatures were then plotted against water temperatures and the differences between the two were calculated for each species. Due to thermal loggers being deployed later on in the study period, data for the thermoregulation analysis was limited to the dates of April 2012 to November 2013. To estimate the relative amounts of time individuals of each species were spending within certain ranges of temperatures, we used kernal density estimations using all temperature data. Data exploration and analyses were all carried out in the R statistical environment (R Core Team 2014).

To test for seasonal differences in thermal and depth experiences of northern pike and largemouth bass in Toronto Harbour, we used generalized linear mixed models (GLMM) where individual ID was treated as a random effect. Prior to the analysis, depth (4.8 million observations) and temperature (3.05 million observations) data were examined for outliers, collinearity, and relationships between response and explanatory variables using Cleveland dot plots, scatter plots, and conditional box and whisker plots. Depth and temperature were then $\log_e$-transformed and modelled using GLMM where the residuals were assumed to follow a Gaussian distribution. Explanatory variables included species, season (categorical), and body size (categorical; based on quartiles of length for individuals by species). All model terms, including the random effect, were evaluated using Akaike's information criterion (AIC) model selection (Akaike 1998). The R package "nlme" was used to model the data (Pinheiro et al. 2014). To identify the factors that best explained fish depth and fish temperature, two sets of candidate models (N = 5) were a priori hypothesized and compared using second-order AIC (Mazerolle 2015). GLMM fit was further evaluated using marginal (fixed effects) and conditional (fixed and random effects) R^2 (Nakagawa and Schielzeth 2013). Due to heterogeneity of variance among seasons, both sets of models were further fitted with a variance structure to allow residual variance to depend on season (Zuur et al. 2009). All candidate models were validated by plotting the normalized residuals against the fitted values and each covariate.

Fig. 3. Relative amount of time spent within specific ranges of temperatures for tagged northern pike (*Esox lucius*) (A) and largemouth bass (*Micropterus salmoides*) (B). Presented is a histogram paired with a kernal density estimation (broken line), which estimates the likelihood of a random variable (e.g., temperature) to take on a given value. Shaded regions represent literature values for optimal growth ranges of each species and the arrows represent the minimum temperature needed for growth for each species.



Results

Harbour water temperature

Temperatures in Toronto Harbour are highly variable throughout the year (Figs. 2A–2I). The highest recorded station temperatures were in the surface waters and shallow, protected regions, and occurred from July through to early October. Mean station temperatures throughout the winter months (i.e., December–February) were 2.7 °C (with temperatures ranging from 0 to 24.7 °C), 6.9 °C in the spring (March–May; with temperatures ranging from 0.7 to 25.8 °C), 17.9 °C in the summer (June–August; with temperatures ranging from 4.8 to 30.1 °C), and 11.6 °C in the fall (September–November; with temperatures ranging from 1.0 to 27.6 °C). Overall, the mean annual water temperature of Toronto Harbour was 8.9 °C. Using kernal density estimations, our results revealed that northern pike were often in water temperatures that would permit maximum growth rate for the species, i.e., within its optimal thermal range. The full range of optimal water temperatures were not always available to largemouth bass, which may partly explain the species' distribution in Toronto Harbour (Figs. 3A, 3B).

Effects of size, species, and season on temperature and depth distributions

Filtering depth and temperature data into daily mean values for each individual per season yielded 462 and 410 mean depth and temperature values, respectively. Largemouth bass were found at temperatures ranging from 1.4 to 24.6 °C, whereas northern pike were found at temperatures ranging from 1.6 to 21.8 °C (see Table 2). With respect to depths, largemouth bass were found at depths ranging from 0.34 to 12.35 m, whereas northern pike were found at depths ranging from 0.17 to 12.09 m (see Table 2).

Table 2. Summary statistics calculated from data on the depths and temperatures of northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) observed in Toronto Harbour, Toronto, Ontario, Canada.

	Temperature statistics (°C)		Depth statistics (m)	
	Northern pike	Largemouth bass	Northern pike	Largemouth bass
Mean minimum	1.6	1.4	0.17	0.34
First quartile	6.8	6.1	2.17	1.07
Median	11.2	10.9	3.76	2.36
Third quartile	16.7	18.6	6.08	3.80
Mean maximum	21.8	24.6	12.09	12.35

Table 3. Model selection statistics from generalized linear mixed models (GLMMs) on the log temperature and log depth of tagged largemouth bass (*Micropterus salmoides*) and northern pike (*Esox lucius*) in Toronto Harbour, Toronto, Ontario, Canada.

Model	Fixed terms	k	AIC_c	ΔAIC_c	AIC_c weight	Cumulative Akaike weight	Log-likelihood of the model
Temperature							
M4	Species + season + species × TL + species × season	17	–12.60	0.00	0.97	0.97	24.08
M1	Species + season	10	–5.03	7.57	0.02	1.00	12.79
M3	Species + season + species × TL	14	–0.58	12.01	0.00	1.00	14.82
M2	Species × season × TL	29	1.20	13.80	0.00	1.00	30.69
M5	Species + season + species × TL + season × TL	20	9.96	22.56	0.00	1.00	16.10
Depth							
M2	Species × season × TL	29	746.12	0.00	0.93	0.93	–324.04
M4	Species + season + species × TL + species × season	17	751.35	5.23	0.07	1.00	–357.98
M5	Species + season + species × TL + season × TL	20	757.56	11.44	0.00	1.00	–357.83
M3	Species + season + species × TL	14	759.73	13.61	0.00	1.00	–365.39
M1	Species + season	10	763.09	16.98	0.00	1.00	–371.30

Note: k is the number of parameters; AIC_c is the bias-corrected Akaike's information criterion; ΔAIC_c is the difference in the bias-corrected AIC between a given model and the top-ranked model; AIC_c weight is the relative weight of the bias-corrected AIC; TL is total length. All models contain individual fish ID as a random intercept. Models are fitted with an additional variance structure to allow for different variances for each stratum of season.

AIC indicated a random effect should be included in both temperature and depth models ($AIC_{\text{random effect – depth}} = 900$; $AIC_{\text{intercept only – depth}} = 1137$; $AIC_{\text{random effect – temperature}} = 887$; $AIC_{\text{intercept only – temperature}} = 889$). The top model (where ΔAIC_c was <2) for depth was the global model, which included all main effects and all possible interactions between season, species, and body size (M2; Table 3). The marginal R^2 and the conditional R^2 in the global model of depth use was 25.4% and 86.2%, respectively. The top model for fish temperature included all main effects, an interaction between species and body size, and an interaction between species and season (M4; Table 3). Fixed effects alone explained 91.5% of the variance, whereas fixed and random effects together explained 92.8% of the variance in the top model for temperature. Northern pike and largemouth bass depth use was highly dependent on the season and body size of the individual (Fig. 4). Across all seasons, large northern pike (857–1003 mm total length (TL)) were detected in relatively deep locations compared with medium-sized (396–434 mm TL) and large (478–535 mm TL) largemouth bass (Fig. 4). These differences were most evident in the fall and winter. Similarly, regardless of season, small (325–635 mm TL) northern pike depth use tended to overlap that of all sizes of largemouth bass, including the smallest individuals (271–396 mm TL), but was considerably shallower than medium-sized and large northern pike. Depth use was deepest during the winter for both species and all body sizes and generally shallowest during the summer.

Although depth use differed among body sizes and between species during winter (with the exception of largemouth bass in the fall and winter), temperatures used in this season averaged 2.7 °C for northern pike (95% CI = 2.4 and 3.0 °C) and 3.1 °C for largemouth bass (95% CI = 2.8 and 3.4 °C) with little variation among body sizes (Fig. 5). Similarly, no differences in temperatures between species or among body sizes were observed in the spring and fall seasons. Only during the summer were temperature differences apparent between species and among body sizes. In summer, small to large northern pike were predicted by the model to occur along a declining gradient of temperatures with large individuals having a mean temperature of 17.2 °C (95% CI = 16.0 and 18.6 °C), whereas small to large largemouth bass were predicted to occur along a rising gradient of temperatures up to a mean of 20.3 °C (95% CI = 18.8 and 21.9 °C; Fig. 5).

Evidence of thermoregulation in Toronto Harbour

Study fish were found to use specific thermal habitats of Toronto Harbour during much of the year. When station temperatures were observed to be >10 °C, the mean difference between station and fish temperatures throughout the year was found to be 0.7 °C higher for northern pike and 0.9 °C higher for largemouth bass (Table 4). The maximum difference observed for northern pike was 12.6 °C higher, and 13 °C higher for largemouth bass. Given that the two species differed with respect to their thermal optima, we examined differences between fish and water temperatures when water temperatures were >20 °C. At these higher temperatures, the mean difference between station and northern pike temperatures was found to be 0.4 °C colder, whereas for largemouth bass the mean difference was 0.7 °C warmer (Figs. 6A, 6B).

Discussion

Seasonal patterns of species-specific variability in temperature and depth use

When comparing the thermal and depth experiences of both northern pike and largemouth bass in Toronto Harbour, our results revealed similarities in thermal experiences for much of the year, despite northern pike occupying deeper depths. Differences

Fig. 4. Mean (±95% CI) fitted values for northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) depth use (m) in Toronto Harbour, Toronto, Ontario, Canada. Body sizes are illustrated as circles (small; minimum to 25% quartile), triangles (moderate; 25% to 75% quartiles), and squares (large; 75% quartile to maximum).

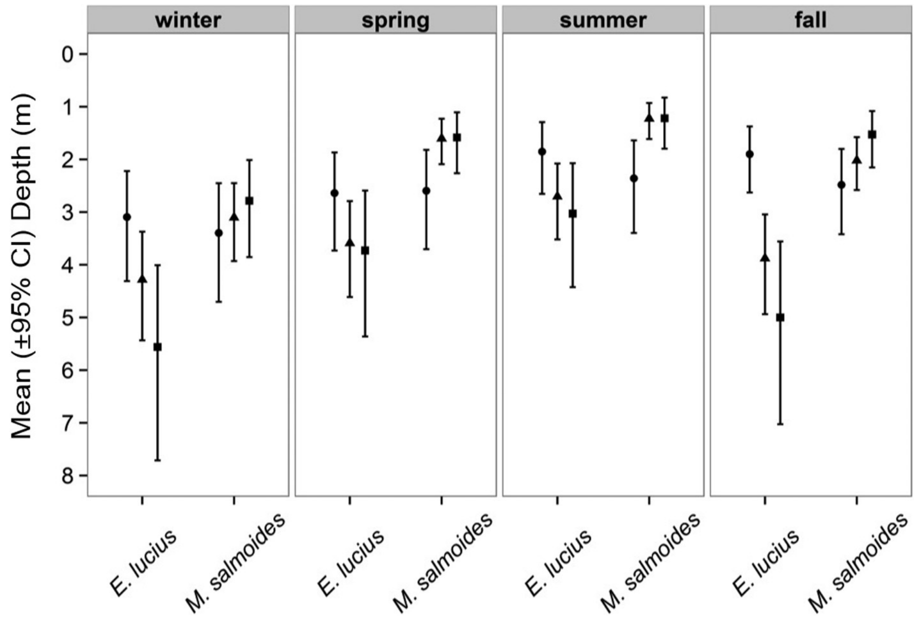
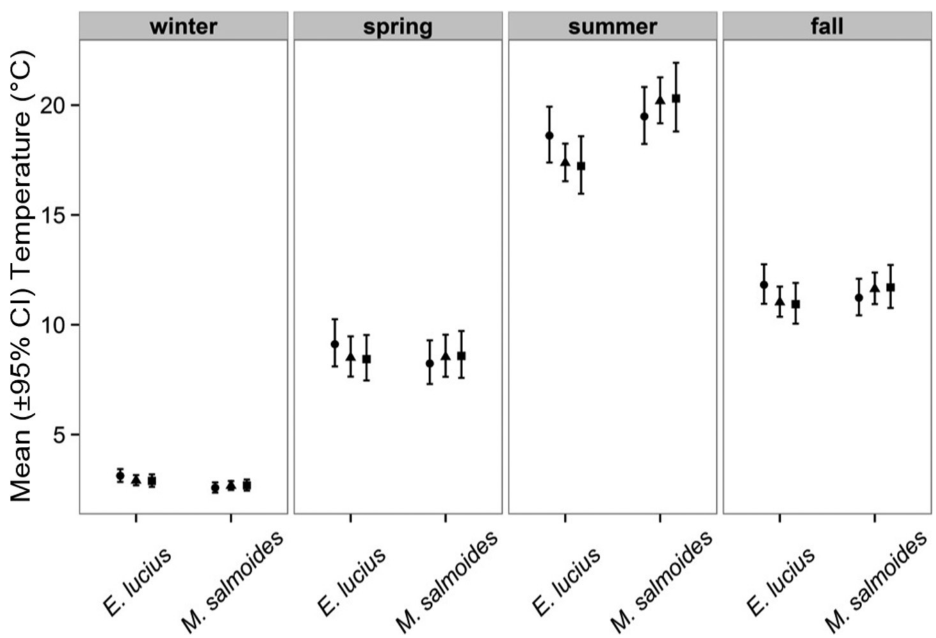


Fig. 5. Mean (±95% CI) fitted values for northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) temperature use (°C) in Toronto Harbour, Toronto, Ontario, Canada. Body sizes are illustrated as circles (small; minimum to 25% quartile), triangles (moderate; 25% to 75% quartiles), and squares (large; 75% quartile to maximum).



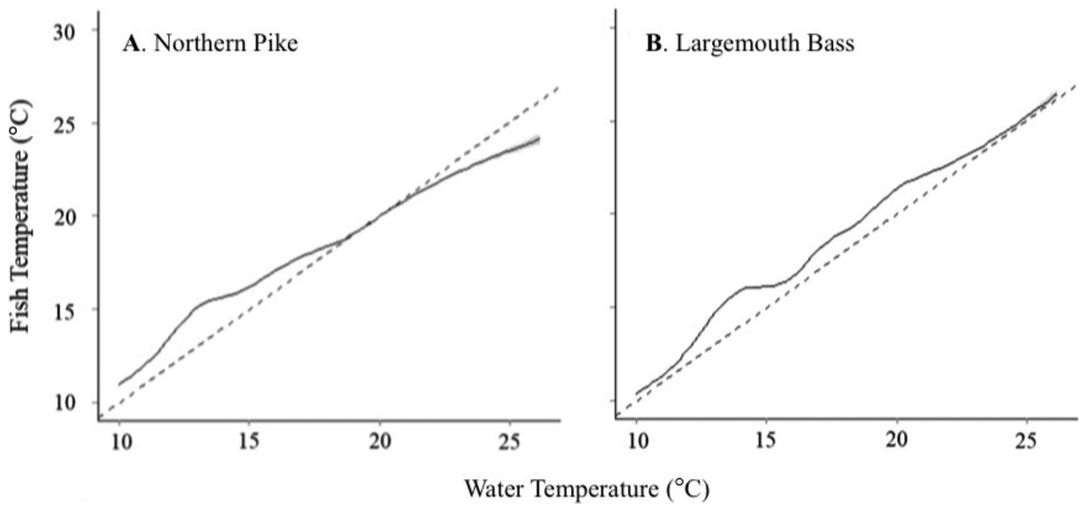
in the observed depth preferences of each species can be attributed to their respective habitat requirements. Largemouth bass are known to prefer shallow littoral zones, consisting of areas with widespread aquatic vegetation and enough space to allow for overwintering (Winter 1977; Stuber et al. 1982; Brown et al. 2009). In Ontario, optimal habitat for largemouth bass typically consists of lakes with shallow (<6 m) (Essington and Kitchell 1999) areas capable of supporting widespread vegetation, as well as high structural habitat complexity (Prince and Maughan 1979; Schlagenhaft and Murphy 1985; Mesing and Wicker 1986). Northern pike are characteristically found in fairly shallow and vegetated waters, usually <4 m (Casselman and Lewis 1996), but can sometimes be found in waters as deep as 12 m during the summer. Differences in the depth preferences of northern pike are known to be dependent on life stage, but have also been linked to the potential advantages of being versatile (e.g., locating greater abundances of prey and exploiting optimal temperatures) (Pierce et al. 2013). Studies show large and small northern pike differ significantly with respect to their depth preferences (Chapman and Mackay 1984; Pierce et al. 2013); with larger individuals using both open water and vegetated habitats, whereas smaller individuals were usually limited to shallow vegetated areas only (Chapman and

Table 4. Mean fish and water temperatures (°C) of northern pike (*Esox lucius*) and largemouth bass (*Micropterus salmoides*) in Toronto Harbour, Toronto, Ontario, Canada.

	Temperature >10 °C					Temperature >20 °C				
	Mean	SE	Minimum	Maximum	*N*	Mean	SE	Minimum	Maximum	*N*
Northern pike										
Fish	17.2	0.02	7.1	27.2	39124	21.4	0.02	12.4	27.2	7857
Water	16.5	0.02	10.0	26.2	39124	21.8	0.01	20.0	26.2	7857
Difference	0.7	0.01	0.0003	12.6	39124	−0.4	0.02	0.0009	4.6	7857
Largemouth bass										
Fish	17.1	0.02	6.1	28.3	48555	23.1	0.03	6.1	28.3	10740
Water	16.3	0.02	10.0	26.2	48555	22.4	0.02	20.0	26.2	10740
Difference	0.9	0.01	0.0012	13.0	48555	0.7	0.03	0.0001	5.4	10740

Note: Differences are between the fish temperature and the corresponding water temperature of the station at which each observation was detected. Negative values represent periods where the fish temperature of fish was less than that of the water temperatures. Observations for when water temperatures were >10 °C are shown, along with those for when water temperatures were >20 °C. *N* represents the total number of observations for each species.

Fig. 6. Northern pike (*Esox lucius*) (A) and largemouth bass (*Micropterus salmoides*) (B) fish temperatures versus water temperatures in Toronto Harbour, Toronto, Ontario, Canada. Plotted is a LOESS smoother and 95% CI (shaded areas). The broken line represents the point at which water temperature is equal to fish temperature.



Mackay 1984; Casselman and Lewis 1996). Therefore, it is not surprising that northern pike in Toronto Harbour were observed using both mid-depth water and shallow-water areas, with largemouth bass being limited to shallower areas throughout the year.

Results from our analysis indicated that differences in thermal experiences were dependent on species, season, and body size. Species-specific differences are presumably driven by differences in the optimal thermal requirements of northern pike and largemouth bass. Northern pike used cooler temperatures throughout the summer months than largemouth bass. Northern pike are a cool-water fish species and thus prefer water temperatures that are considerably cooler than largemouth bass (optimal temperature range of 19–21 vs. 24–30 °C for northern pike and largemouth bass, respectively; Stuber et al. 1982; Casselman and Lewis 1996). Small northern pike (325–635 mm TL) and largemouth bass (271–396 mm TL) were observed to use higher temperatures than larger northern pike (857–1003 mm TL). Previous studies have suggested that thermal preferences for northern pike and largemouth bass have been linked to the ontogeny of each species (Casselman and Lewis 1996). Stuber et al. (1982) have reported optimal thermal habitat of mature largemouth bass occurring at temperatures ranging from 24 to 30 °C, whereas juvenile largemouth bass prefer slightly warmer temperatures ranging from 27 to 30 °C (Strawn 1961; Brown et al. 2009). For northern pike, Casselman and Lewis (1996) reported optimum temperature ranges of 22–23 °C for young-of-the-year fish and 19–21 °C for mature fish. Our results are consistent with results from Pierce et al. (2013), who examined thermal habitat usage of northern pike in different Minnesota lakes. Their study revealed that small northern pike (<710 mm) generally preferred warmer water and were mostly found in shallow areas consisting of heavy vegetation. Large individuals (>710 mm) were consistently found at temperatures around 19 °C, with individuals following the thermocline into deeper waters as the summer progressed.

Fish temperatures were stable throughout the winter due to the consistency of water temperatures during this season. In contrast, extensive variation in fish temperature was observed throughout the spring, summer, and fall seasons. High variations in temperatures are likely a result of the thermal profiles and stratification properties of Lake Ontario and, more specifically, the thermodynamics of Toronto Harbour (see Hlevca et al. 2015). In Lake Ontario, stratification is first established between mid-May and early July (Rodgers 1987) and continues until late September or early October. Thus, individuals experience large changes in water temperatures as the water warms throughout the spring and cools during the fall. Variations throughout the summer can be explained through the frequent coastal upwelling events and internal waves (seiches, Kelvin waves, and Poincaré waves) that occur in the area (see Hlevca et al. 2015). These result in cooler, hypolimnetic water upwelling along shorelines (Lam and Schertzer 1999). As such, variation in fish temperatures throughout the spring, summer, and fall months can be at least partially linked to the hydrodynamics of Toronto Harbour.

Species-specific and seasonal aspects of thermoregulation in Toronto Harbour

The breadth of temperatures available in the Toronto Harbour provided northern pike and largemouth bass with environmental temperatures close to or within the known optimal ranges for these species at multiple stages of development. Additionally, individuals could access water temperatures for active thermoregulation, which is likely a common behaviour to avoid temperatures above or below thermal limits. Temperatures exceeding optimal levels have been correlated with decreased growth rates (Kershner et al. 1999), higher metabolic costs (Clarke and Johnston, 1999), and increased natural mortality rates (Houde 1989). Suboptimal temperatures have also been known to limit species distributions in aquatic ecosystems (Magnuson et al. 1997). Studies on smallmouth bass (*Micropterus dolomieu* Lacepède, 1802) revealed that July temperatures of <15 °C restricted young-of-the-year individuals from achieving a required body size needed to overwinter, preventing the sustainability of the species (Shuter et al. 1980). Specifically, within Toronto Harbour, previous work using bioenergetic simulations suggested that for bluegill (*Lepomis macrochirus* Rafinesque, 1819) many embayments were too cool for sufficient summer growth and that these habitats may act as ecological sinks during cooler years (Murphy et al. 2012*a*, 2012*b*, 2012*c*). Thus, behavioural thermoregulation of northern pike and largemouth bass in Toronto Harbour is likely an adaptive response to avoid temperatures that limit growth potential.

When station temperatures exceeded 20 °C (i.e., in the summer), the thermoregulation of northern pike reversed and individuals were observed at temperatures cooler than recorded at the stations where they were detected. This indicates that northern pike actively select temperatures that fall within or close to their thermal optima to facilitate metabolic rates needed for foraging and growth. When Pierce et al. (2013) evaluated the thermal habitat usage of northern pike in three different lakes, they observed northern pike following the thermocline into deeper waters and occupying temperatures lower than expected based on previous knowledge of thermal optima. Large pike in Toronto Harbour may be exhibiting a similar behaviour, and thus occupying deeper depths and cooler temperatures. In contrast, largemouth bass were consistently found at temperatures higher than station temperatures throughout the entire year. Optimal thermal ranges for largemouth bass are between 24 and 30 °C for mature individuals, but throughout the harbour, it was uncommon for water temperatures to exceed 25 °C during the summer months (see Figs. 2A–2I) except in very shallow and protected areas such as embayment D. Largemouth bass were consequently more likely to actively seek out areas with higher water temperatures because the majority of thermal habitats in Toronto Harbour was only capable of supporting the growth of largemouth bass for a relatively short period of time (see Figs. 3A, 3B) and very rarely reached their optimal temperature range.

Conclusions and management implications

The results from the study indicate the thermal experiences and depth preferences of northern pike and largemouth bass are dependent on a specific set of factors (i.e., species, total length, and time of year), and that the available habitat was thermally hetereogenous, allowing both northern pike and largemouth bass to effectively thermoregulate especially as water temperature differences increased. As mean temperatures increased above 10 °C, both northern pike and largemouth bass actively thermoregulated such that fish temperatures of individuals were higher than ambient temperatures; however, when ambient temperatures exceeded 20 °C, northern pike sought cooler temperatures.

Currently, Aquatic Habitat Toronto (a conglomerate of Toronto Region Conservation Authority, Ontario Ministry of Natural Resources and Forestry, Environment and Climate Change Canada, Fisheries and Oceans Canada, and the City of Toronto) is implementing the Toronto Waterfront Aquatic Habitat Restoration Strategy (TWAHRS) to restore and recreate aquatic habitat in both the central waterfront of Toronto Harbour and the Toronto Region in general. Aquatic habitat has been improved in the slips, as well as created through offset plans in Tommy Thompson Park and Lake Ontario Park. Future plans include the restoration of some key features in the Lower Don Lands. Construction is ongoing throughout much of the year in these areas and can have a negative short-term impact on local fish communities. Information presented here may help managers not only with future enhancement projects focusing on the provision of different thermal habitats but also by informing local construction schedules based on the likely seasonal spatial distribution of fish in Toronto Harbour. Indeed, our work revealed that largemouth bass began to move into shallower waters several weeks earlier than had been anticipated by managers, suggesting that the construction window for in-water works should potentially be narrowed. In general, these data will support more effective habitat management (protection and restoration) and development or validation of more robust habitat models. Moreover, the findings from this study are relevant to other urban harbours in the Laurentian Great Lakes.

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