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Temperature regimes, growth, and food consumption for female and male adult walleye in Lake Huron and Lake Erie: a bioenergetics analysis

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Abstract: Bioenergetics modeling was used to assess the relative importance of food availability and water temperature in determining walleye (*Sander vitreus*) growth. Temperature regimes experienced by both female and male adult walleye in three basins of Lake Huron and in Lake Erie were determined by use of surgically implanted temperature loggers and acoustic telemetry. Temperatures experienced by walleye were higher in Lake Erie than in Lake Huron. Walleye from Lake Erie grew at nearly double the rate of walleye from Lake Huron, and mass at age for adult females averaged about 50% greater than that for adult males in both lakes. Food consumption rate for an average adult walleye in Lake Erie was nearly twice as high as that in Lake Huron. Interbasin and interlake variability in temperature regimes accounted for a moderate degree of variability in walleye growth. We concluded that the driver for faster growth in Lake Erie compared with Lake Huron was higher food availability in Lake Erie compared with Lake Huron. The sex difference in temperature regimes explained 15% of the sex difference in Lake Erie walleye growth.

Résumé : La modélisation de la bioénergétique a été utilisée pour évaluer l'importance relative de la disponibilité de nourriture et de la température de l'eau comme facteurs déterminants de la croissance des dorés jaunes (*Sander vitreus*). Les régimes thermiques auxquels sont exposés les dorés adultes femelles et mâles dans trois bassins du lac Huron et dans le lac Érié ont été déterminés en utilisant des enregistreurs de température implantés chirurgicalement et la télémétrie acoustique. Les températures étaient plus élevées pour les dorés dans le lac Érié que pour ceux dans le lac Huron. Le taux de croissance des dorés du lac Érié était presque le double de celui des dorés du lac Huron, et le poids en fonction de l'âge pour les femelles adultes était en moyenne 50 % supérieur à celui des mâles adultes dans les deux lacs. Le taux de consommation de nourriture pour un doré adulte moyen dans le lac Érié était presque deux fois plus grand que dans le lac Huron. La variabilité des régimes thermiques entre bassins et entre lacs explique un degré modéré de variabilité de la croissance des dorés. Nous concluons que le facteur expliquant la croissance plus rapide dans le lac Érié que dans lac Huron est une plus grande disponibilité de nourriture dans le lac Érié. La différence entre les sexes sur le plan des régimes thermiques explique 15 % de la différence entre les sexes sur le plan de la croissance des dorés du lac Érié. [Traduit par la Rédaction]

Introduction

For a given species of fish, individual-level growth of fish is a function of food availability and the temperature regime experienced by the fish (Hewett and Johnson 1992; Jobling 1994; Quinn and Deriso 1999; Enberg et al. 2008). Food availability is a complex function of several factors, including prey abundance, prey size, and handling times (Werner 1974; Persson and Greenberg 1990; Rennie and Venturelli 2015). Typically, metabolic costs for the fish increase with increasing water temperature, and metabolic costs represent a substantial energy loss for fish (Hewett and Johnson 1992; Jobling 1994; Quinn and Deriso 1999; Enberg et al. 2008). Thus, if the rate of food consumption is identical in two aquatic ecosystems, and other factors affecting growth other than water temperature are also identical across the two ecosystems, then fish growth would be expected to be faster in the aquatic ecosystem with the lower temperatures experienced by fish compared with fish growth in the other aquatic ecosystem, owing to higher metabolic costs in the warmer ecosystem (Hewett and Johnson 1992; Kao et al. 2015*a*, 2015*b*).

Bioenergetics modeling has proven invaluable in assessing the effects of various factors, including temperature regime, on fish

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growth (Chipps and Wahl 2008; Madenjian 2011; Deslauriers et al. 2017). A fish bioenergetics model represents an energy budget for a fish. Energy input via food consumption is equal to metabolic losses, waste losses, and growth:

$$C = (R + A + \mathrm{SDA}) + (F + U) + G$$

where C = consumption, R = standard metabolism, A = energy expenditure due to activity, SDA = specific dynamic action (energy required to digest food), F = egestion, U = excretion, and G = growth. Standard metabolism is typically modeled as an exponential function of water temperature. Bioenergetics model applications to evaluate the effects of various factors on fish growth are well illustrated in the study by Hayward and Margraf (1987), who used bioenergetics modeling to show that faster growth of yellow perch (*Perca flavescens*) in the central basin of Lake Erie compared with the western basin of Lake Erie was due to an interbasin difference in food availability rather than an interbasin difference in temperature regime.

Coupling archival temperature tag technology with acoustic telemetry has recently enabled researchers to record thermal histories of fish within different basins of the same lake, as well as within lakes connected by waterways (Cooke et al. 2013; Hayden et al. 2014; Peat et al. 2015). By constructing an appropriate acoustic receiver network, interbasin and (or) interlake movement of fish can be detected. Implanting both an acoustic transmitter and an archival temperature tag in each fish, and subsequent monitoring of any interbasin and interlake movements of the fish using acoustic telemetry, can be used by researchers to determine temperature regimes experienced by fish while confined to a specific basin or lake.

To date, the effects of both interbasin and interlake variability in temperatures experienced by fish on fish growth in a two-lake system, with a connecting waterway between the two lakes, have not been investigated. Moreover, the effect of a difference in temperature regimes between the sexes of a fish population on the difference in growth between the sexes has yet to be assessed for any fish population. Use of archival temperature tagging and acoustic telemetry, in conjunction with fish bioenergetics modeling, affords the opportunity to pursue these new lines of research. In turn, these new lines of research may have fishery management implications, because knowledge of movement and spatial ecology of fishes provides critical information to managers about how fishes are distributed in both space and time (Lucas and Baras 2000; Landsman et al. 2011). For example, bioenergetics analysis of growth of a piscivorous fish within a two-lake system may be useful in accurately characterizing the fish's role as a piscivore in both lakes.

Walleye (*Sander vitreus*) populations support valuable recreational and (or) commercial fisheries in many North American lakes, reservoirs, and rivers (Feiner and Höök 2015). Moreover, this species fulfills the ecological role as a top predator in the aquatic ecosystems that it inhabits (Feiner and Höök 2015; He et al. 2015). Female walleye grow substantially faster than male walleye, but reasons for this sexually dimorphic growth are not clear (Bozek et al. 2011; Rennie and Venturelli 2015). In the Laurentian Great Lakes, the most valuable walleye fisheries are situated in Lake Huron and Lake Erie (Roseman et al. 2008; Melstrom and Lupi 2013; Fielder et al. 2014). Despite the importance of the Lake Huron and Lake Erie walleye fisheries, a direct and rigorous comparison of walleye growth in Lake Huron with walleye growth in Lake Erie has yet to be undertaken.

Walleye in Lake Huron exhibit three migration behaviors, as elucidated from an acoustic telemetry study (Hayden et al. 2014). Walleye may reside in Saginaw Bay throughout the year or out-migrate to the main basin of Lake Huron for residence during the summer and fall. Those walleye out-migrating to the main basin

reside in either the northern main basin or the southern main basin (Hayden et al. 2014). Walleye remaining in Saginaw Bay are expected to experience warmer temperatures than those walleye out-migrating to the main basin, while food availability for walleye is presumably higher in Saginaw Bay than in the main basin (Fielder et al. 2014; Hayden et al. 2014; Peat et al. 2015).

The primary goals of our study were to compare walleye growth in Lake Huron with walleye growth in Lake Erie and to assess the relative importance of food availability and temperature regime as determinants of walleye growth in the Lake Huron – Lake Erie system. A secondary goal of our study was to evaluate the effect of sex differences in temperature regimes on sex differences in walleye growth. Specific objectives included (*i*) using temperature loggers and acoustic telemetry to determine temperatures experienced by female and male walleye in Saginaw Bay, the northern main basin of Lake Huron, the southern main basin of Lake Huron, and Lake Erie, (*ii*) developing growth trajectories for female and male walleye in both Lake Huron and Lake Erie and then compare growth between the two lakes, (*iii*) using bioenergetics modeling to estimate food consumption by female and male walleye in Saginaw Bay, northern main basin of Lake Huron, southern main basin of Lake Huron, and Lake Erie, (*iv*) using a bioenergetics modeling framework to exchange temperature regimes experienced by walleye between basins and lakes to assess the effects of interbasin and interlake variability in temperature regimes experienced by walleye on walleye growth, and (*v*) again using a bioenergetics modeling framework to exchange temperature regimes experienced by walleye between the sexes to evaluate the effect of sex differences in temperature regimes on sex differences in walleye growth.

Materials and methods

Field methods

Walleye in this study were captured and tagged as part of a large project to understand movement of two adfluvial walleye populations in the Great Lakes. A detailed description of walleye capture and tagging is found elsewhere (Hayden et al. 2014; Peat et al. 2015). Walleye in spawning condition were captured using boat-mounted electroshocking gear in the Tittabawassee River (Lake Huron watershed) immediately downstream of Dow Dam (Midland, Michigan) and near Orleans Park in the Maumee River (tributary to Lake Erie) during March–April in 2011 and 2012. The primary spawning area in the Tittabawassee River is located approximately 2–3 km downstream of the Dow Dam and approximately 100 km upstream of the mouth of the Saginaw River in Saginaw Bay. Primary walleye spawning grounds in the Maumee River are located approximately 25–30 km upstream of the Maumee River mouth in Lake Erie. After capture, biological measurements (total length (TL) in millimetres, sex) and dorsal fin spine clips were collected from each walleye chosen for transmitter implanting, and paired t-bar tags (Floy Tag, Inc., Seattle, Washington) were inserted below the base of the second dorsal fin. T-bar tags allowed identification of walleye during the implanting process and informed anglers of the presence of an internal acoustic transmitter in the event the fish was caught after release. Dorsal fin spine clips were used for nonlethal age (in years) estimation. Fish were then transferred to streamside holding tanks for surgical implantation of an acoustic transmitter and a temperature logger. Walleye selected for implanting transmitters in the Maumee and Tittabawassee rivers were greater than 381 mm, which represented the minimum length limit for recreational angling limit for Michigan waters of Lake Huron and Ohio waters of Lake Erie during 2011–2012. In total, 199 walleye were implanted with transmitters in the Tittabawassee River, and 200 walleye were implanted with transmitters in the Maumee River in 2011. In 2012, 60 walleye were implanted with transmitters in the Tittabawassee River, and 33 walleye were implanted with transmitters in the Maumee River. Our research project was reviewed and

approved by the Carleton University Animal Care Committee in accordance with the Canadian Council of Animal Care Guidelines for the Use of Fish in Research (project No. 8890; approval No. B10-29).

Each walleye was implanted with an acoustic transmitter programmed to emit a unique code (frequency of 69 kHz) at random intervals between 60 and 180 s (mean: 120 s) (Vemco, Halifax, Nova Scotia; model V16-4x; 16 mm diameter × 86 mm, 24 g; battery life = 1338 days). Each acoustic transmitter was outfitted with an iButton temperature logger (DS1921z; resolution = ±0.1 °C, precision = 0.2 ± 0.3 °C, accuracy = 0.4 ± 0.3 °C; Maxim Integrated Products, Inc., Sunnyvale, California) programmed to record temperatures at 4 h intervals for a period of approximately 1 year (Donaldson et al. 2009). All iButtons were attached to acoustic transmitters using hot glue and dipped in an inert waterproof coating (Plasti Dip, Performix Brand, Blaine, Minnesota) prior to implantation.

Walleye were anesthetized prior to surgery using a Smith-Root (Vancouver, Washington) portable electroanesthesia system operating at 35 V pulsed direct current. Treatments of 3 s induced stage-4 anesthesia for several minutes (Vandergoot et al. 2011). All surgeries were conducted on fish supported in a v-shaped surgical table lined with soft nonslip material. Walleye received a constant supply of fresh river water pumped across gills during surgery, and all surgical tools and transmitters were cleaned with povidone iodine prior to surgery. Acoustic transmitters with attached iButtons were inserted into the coelomic cavity through a small incision located along the ventral side of each fish, posterior to the pelvic girdle. Incisions were closed using two to three interrupted sutures (absorbable monofilament, PDS-II, 3-0, Ethicon, Somerville, New Hampshire). After surgery, fish were placed in holding tanks until fish were able to maintain balance in the water (approximately 30 min), and then fish were released near the capture site.

The acoustic receiver array was deployed as part of the Great Lakes Acoustic Telemetry Observation System network (http://data. glos.us/glatos) and consisted of approximately 140 omnidirectional receivers operating at 69 kHz (VR2W, Vemco, Halifax, Nova Scotia). Hayden et al. (2014) and Peat et al. (2015) provide complete details of anchoring acoustic receivers and receiver line detection probabilities. All receivers were suspended in the water column and retrieved annually for maintenance and data download. Deployment locations of acoustic receivers during 2011–2012 in Lake Huron consisted of multiple receivers near the Tittabawassee and Saginaw river mouths, double receiver lines located across Saginaw Bay, and multiple-receiver lines extending perpendicular to the shoreline to depths <40 m (extending 3–10 km offshore; Fig. 1). Receiver lines were deployed to monitor walleye movements in and out of the Saginaw Bay, movements in and out of the Tittabawassee and Saginaw rivers, and nearshore movements in Lake Huron. Acoustic receivers were deployed in the St. Clair River flowing out of Lake Huron and Detroit River to monitor walleye movement between Lake Huron and Lake Erie through the Huron–Erie corridor (Fig. 1). Acoustic receivers were deployed near the mouth of the Maumee River in Lake Erie to monitor walleye movements in and out of the river. Thermal data were obtained via returned transmitter–iButtons from fish caught in recreational and commercial fisheries. A US$100 reward was offered to anyone that returned the acoustic transmitter with the attached iButton to the investigators. All acoustic detection data were screened for false positives caused by environmental noise and signal collisions using the short-interval criteria described by Pincock (2009). False detections were detections that were not accompanied by at least one other detection from the same transmitter on the same receiver within 1 h and were removed from the analysis. Of all of the detections, 99% of them passed the false detection filter.

We used acoustic telemetry detections to classify the walleye recaptured by anglers and commercial fishers into four geographic areas: (1) northern main basin of Lake Huron, (2) southern main basin of Lake Huron, (3) Saginaw Bay, and (4) Lake Erie (Fig. 1).

Please refer to Hayden et al. (2014) and Peat et al. (2015) for more details on the classification assignments.

Temperature regimes

We followed the procedure described by Bergstedt et al. (2003), Madenjian et al. (2003, 2006), and He et al. (2015) to develop temperature regimes for both female and male walleye from each of the above-mentioned four geographic areas. The calendar year was divided into half-month intervals. For each combination of geographic area and sex, temperatures recorded on the iButton temperature loggers were averaged within each half-month interval, and the standard error of the mean was also calculated. The mean temperature for each half-month interval was assigned to the midpoint day, in time, for the half-month interval. Temperatures for days between consecutive midpoints were estimated via linear interpolation. Thus, each day of the calendar year was assigned a temperature.

In 15 cases, the calculated mean temperature for the half-month interval was less than 0.10 °C. To successfully perform the bioenergetics model simulations, all calculated mean temperatures less than 0.10 °C were assigned the value of 0.10 °C. Waste loss components of the bioenergetics model yielded inaccurate estimates of waste losses for temperatures less than 0.10 °C (Kao et al. 2015a, 2015b), and therefore these assignments were necessary to successfully complete the bioenergetics modeling.

We were well justified in developing temperature regimes by sex and geographic area, for four reasons. First, two of the objectives of our study were to assess the effects of interbasin and interlake variability in temperature regimes on walleye growth and to assess the effect of the sex difference in temperature regimes on the sex difference in walleye growth. Development of temperature regimes by sex and geographic area was necessary to accomplish these two objectives. Second, previous research has shown that, on average, (i) surface water temperatures in Saginaw Bay are higher than those in the main basin of Lake Huron, (ii) surface water temperatures in the southern section of Lake Huron's main basin are higher than those in the northern main basin of Lake Huron, and (iii) surface water temperatures in Lake Erie are higher than those in any of the basins of Lake Huron (Moukomla and Blanken 2016). Third, habitat use may vary with sex both in the Saginaw Bay walleye population and in the Lake Erie population (Madenjian et al. 1998; Wang et al. 2007). Fourth, female walleye grow considerably faster than male walleye (Bozek et al. 2011; Rennie and Venturelli 2015).

Growth trajectories

We estimated growth trajectories for both female and male walleye from Lake Huron based on data from annual gillnet surveys conducted by the Michigan Department of Natural Resources (DNR) each September in Saginaw Bay (Fielder and Thomas 2014). TL (to the nearest millimeter), mass (to the nearest gram), and age (in years) of each walleye caught in the gill nets were determined. We pooled survey data from years 2010–2012, which closely corresponded with the years of our acoustic telemetry study, and then fitted von Bertalanffy growth curves to the TL at age data for both sexes. In addition, a mass–length regression curve was fitted to TL and mass data for each sex. Total lengths at age for ages 3–13 years were calculated from the fitted von Bertalanffy growth curves for both sexes. Then, these TLs at age were substituted into the fitted mass–length regression equations to estimate masses at age. We focused on ages 3–13 years because this range of ages is used in the population models developed for the Lake Huron walleye population (Fielder and Bence 2014; Fielder and Thomas 2014; He et al. 2015). Walleye growth trajectories were assumed not to vary across the basins (i.e., northern main basin, southern main basin, and Saginaw Bay) of Lake Huron. A similar assumption was made by He et al. (2015) in quantifying piscivory patterns in Lake Huron. Standard errors were calculated for masses at age by first calculating

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Fig. 1. Map of study area. Circles denote locations for acoustic receivers, and triangles denote tagging locations. Base map data taken from the Great Lakes Information Network (2017).
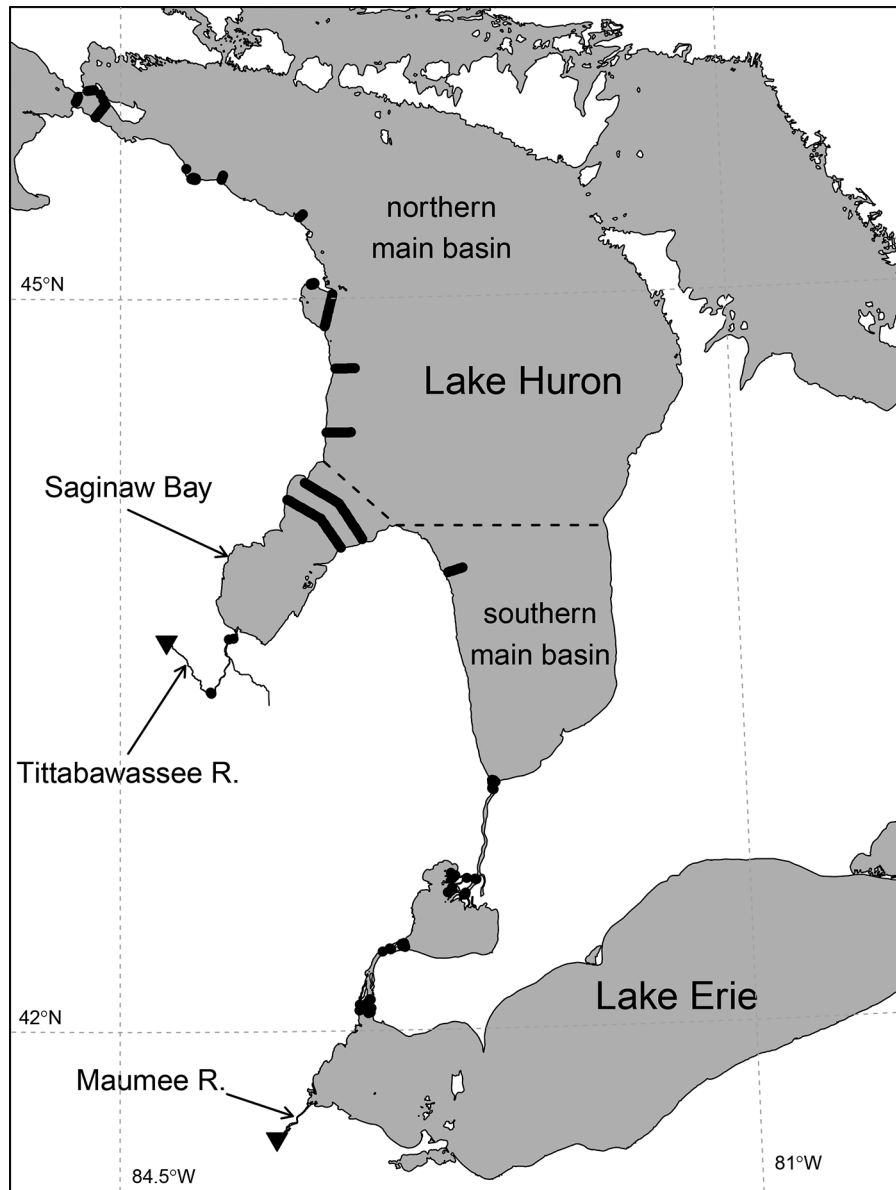
standard errors for TLs at age, using routines described by Ogle (2016), and then substituting the error bounds for TLs at age into the fitted mass–length equations.

Growth trajectories for Lake Erie were based on data from annual gillnet surveys conducted by the Michigan DNR, Ohio DNR, and Ontario Ministry of Natural Resources and Forestry (OMNRF) each October in the western and central basins of Lake Erie (Ohio Division of Wildlife 2011, 2012, 2013). Again, TL (to the nearest millimetre), mass (to the nearest gram), and age (in years) of each walleye caught in the gill nets were determined, and survey data from years 2010–2012 were pooled. von Bertalanffy growth curves were fitted to TLs at age for both sexes, and mass–length regression curves were fitted to TL and mass data for both sexes. Masses at age were estimated by substituting TLs at age into the fitted mass–length regression equations. Standard errors were calculated for masses at age using the same procedures described above.

To determine whether walleye growth significantly differed between the two lakes and between the sexes, we applied *t* tests for paired comparisons to the above-mentioned estimated masses at

ages 3–13. Specifically, *t* tests for paired comparisons were used to (*i*) compare mass at age of Lake Huron female walleye with mass at age of Lake Erie female walleye, (*ii*) compare mass at age of Lake Huron male walleye with mass at age of Lake Erie male walleye, (*iii*) compare mass at age of Lake Huron female walleye with mass at age of Lake Huron male walleye, and (*iv*) compare mass at age of Lake Erie female walleye with mass at age of Lake Erie male walleye.

Bioenergetics modeling: fit to observed growth

The Wisconsin walleye bioenergetics model, originally developed by Kitchell et al. (1977) and refined by Hewett and Johnson (1992), was used to estimate food consumption by both female and male walleye in each of the four geographic areas. Bioenergetics model simulations were performed using the Fish Bioenergetics 4.0 software developed by Deslauriers et al. (2017). The model was fit to observed growth, as represented by the growth trajectory, to estimate food consumption. For each combination of geographic area and sex, the appropriate temperature regime, as derived from our iButton temperature logger data, was used in the bioen-

Table 1. Diet schedule for adult walleye from Lake Erie.

Month(s)	Shiners	Clupeids	*Morone* spp.	Rainbow smelt	Yellow perch	Round goby	Other fish	Invertebrates
April–May	0.39	0.19	0.02	0.37	0.00	0.02	0.01	0.00
June	0.65	0.04	0.04	0.21	0.01	0.03	0.00	0.02
July	0.47	0.00	0.00	0.34	0.08	0.08	0.00	0.03
August	0.25	0.23	0.10	0.14	0.09	0.19	0.00	0.00
September	0.21	0.60	0.12	0.01	0.04	0.01	0.01	0.00
October–November	0.19	0.74	0.01	0.06	0.00	0.00	0.00	0.00
December–March	0.29	0.47	0.01	0.22	0.00	0.01	0.00	0.00

Note: Numeric table entries represent estimated proportions in diet, on a wet mass basis.

ergetics model simulations. Each bioenergetics model simulation was 1 year in duration, and thus 10 simulations were run to estimate food consumption by an average walleye from age 3 through age 13 for each combination of geographic area and sex. The bioenergetics model operated on a daily time step (Hewett and Johnson 1992).

With regard to bioenergetics modeling for Lake Huron walleye, inputs for diet composition, prey energy density, and walleye energy density were taken from Pothoven et al. (2017). Because 8 September represented the typical midpoint date for the duration of the Michigan DNR gillnet survey in Saginaw Bay, we assigned 8 September as the starting day for the bioenergetics model simulations. Spawning day was assigned 4 April for Lake Huron walleye (Madenjian et al. 1998). Spawning was simulated by females and males losing 22.1% and 2.9%, respectively, of their body mass on the spawning day (Madenjian et al. 1998). Females and males were assumed to mature by ages 5 and 4 years, respectively (Wang et al. 2009; Fielder 2014; Fielder and Thomas 2014).

With regard to bioenergetics modeling for Lake Erie walleye, diet composition was based on stomach contents data for age-2 and older walleye caught by the Ohio DNR during monthly bottom trawl surveys from May through October and fall gillnet surveys (late September through early November) during 2000–2015 (Ohio Division of Wildlife 2016). Bottom trawls were conducted from sunrise to sunset, and gill nets were set overnight on the bottom or suspended approximately 1.5–3 m from the surface. All fish were held on ice in coolers <12 h until being processed. In the laboratory, TL of each walleye was measured to the nearest millimetre, and wet mass was recorded to the nearest gram. For stomach contents analysis, prey items were examined macroscopically, identified to the lowest taxonomic level possible, and measured to the nearest millimetre. Whole prey items were measured for TL, while partially digested items were measured for standard, fork, or backbone lengths. All prey lengths were converted to TL when necessary and subsequently converted to wet mass using available data (Ohio Division of Wildlife 2016). Prey items were grouped into the following eight diet categories: shiners (primarily emerald shiner (*Notropis atherinoides*)), clupeids (primarily gizzard shad (*Dorosoma cepedianum*)), *Morone* spp. (primarily white perch (*Morone americana*)), rainbow smelt (*Osmerus mordax*), yellow perch, round goby (*Neogobius melanostomus*), miscellaneous fish (primarily rainbow trout (*Oncorhynchus mykiss*)), and invertebrates (burrowing mayflies, other ephemeropterans, amphipods, *Bythotrephes longimanus*, chironomids, other dipterans, isopods, and trichopterans). Wet masses of individual prey were used to calculate percent diet composition of each prey category for each walleye, and mean percent diet composition was calculated across individuals for each month (May through October; Table 1). Percent composition of unidentified fish was distributed proportionally across the identified finfish species each month. Diet composition for April and November was assumed to be equal to that for May and October, respectively. Diet composition for December through March was assumed to be equal to the average diet composition for months May and October. A total of 7860 walleye stomachs were examined. Of these, 3449 contained prey items and 4411 were empty.

Table 2. Energy densities for prey of adult walleye from Lake Erie.

Prey category	Energy density (J·g⁻¹)	Source
Shiners	6372	This study
Clupeids	5014	Kershner 1996
Morone spp.	3760	Kershner 1996
Rainbow smelt	5241	This study
Yellow perch	3823	Kershner 1996
Round goby	3621	Bunnell et al. 2005
Other fish	4512	Pothoven et al. 2017
Invertebrates	3134	Cummins and Wuycheck 1971

Note: Numeric table entries represent energy densities, on a wet mass basis.

Energy densities for gizzard shad, *Morone* spp., yellow perch, and round goby from Lake Erie were taken from Kershner (1996) and Bunnell et al. (2005) (Table 2). Energy densities for miscellaneous fish and invertebrates from Lake Erie were based on previous studies (Cummins and Wuycheck 1971; Pothoven et al. 2017). To determine energy densities of Lake Erie emerald shiner and rainbow smelt, we used bottom trawling to sample emerald shiner and rainbow smelt from Lake Erie during May–October 2005–2007. In total, three composite samples of emerald shiners and five composite samples of rainbow smelt were homogenized in a blender. Number of emerald shiners and rainbow smelt per composite ranged from 12 to 25 fish and from 10 to 23 fish, respectively. Energy density (in J·g⁻¹ wet mass) was determined for each composite using a Parr 1261 isoperibol bomb calorimeter (Parr Instrument Company, Moline, Illinois), following the procedure outlined by Pothoven et al. (2012). For both emerald shiners and rainbow smelt, energy densities were averaged across the composite samples to determine mean energy density (Table 2). Energy densities for Lake Erie walleye were determined by capturing 41 walleye in Lake Erie using gill nets during May 2005 (Pothoven et al. 2008). Upon capture, each walleye was individually wrapped in foil, bagged, and frozen until processing. In the laboratory, frozen fish were homogenized using a commercial blender. To determine dry-to-wet mass, we dried a 20–30 g subsample of ground fish tissue at 70 °C to a constant mass (about 3 days). For energy density (J·g⁻¹ wet mass), the dried material was ground with a mortar and pestle, and then a 1 g subsample was combusted in a Parr 1261 isoperibol bomb calorimeter that was standardized with benzoic acid. To estimate within-fish variability for bomb calorimetry, we initially quantified energy density in triplicate. The mean coefficient of variation for individual fish was 1.02% ($n = 10$); thus, we subsequently quantified energy density using only one subsample per fish following the procedure outlined by Pothoven et al. (2017). Walleye energy density increased with increasing walleye mass, and therefore we fitted a straight line, using simple linear regression analysis, to walleye energy density as a function of walleye mass. Walleye masses ranged from 487 to 6426 g. We used the fitted regression line $ED = 7776 + 0.231M$, where ED is walleye energy density (J·g⁻¹ wet mass) and M is walleye wet mass (g), for the bioenergetics modeling of Lake Erie walleye. Because energy

density did not significantly differ between the sexes of Lake Erie walleye, this fitted regression line was used for both sexes. Similarly, energy density did not significantly differ between the sexes of Lake Huron walleye, and therefore the walleye energy density function used by Pothoven et al. (2017) was applied to both sexes in our Lake Huron simulations.

Because 15 October represented the typical midpoint date for the duration of the Ohio DNR fall gillnet survey in Lake Erie, we assigned 15 October as the starting day for the Lake Erie bioenergetics model simulations. Spawning day was assigned 10 April for Lake Erie walleye (Ohio Division of Wildlife 2011, 2012, 2013). Again, spawning was simulated by females and males losing 22.1% and 2.9%, respectively, of their body mass on the spawning day. Females and males were assumed to mature by ages 4 and 3 years, respectively (Ohio Division of Wildlife 2011, 2012, 2013).

Bioenergetics modeling: exchanging temperature regimes between areas and sexes

Walleye growth is affected by both food availability and the temperature regime experienced by the walleye. One of the steps in identifying which of these two factors is the more influential determinant of walleye growth in the Lake Huron – Lake Erie system is to assess the scope for changes in walleye growth brought about by geographic variation in temperature regimes. Results from this scoping exercise can then be compared with observed geographic differences in walleye growth within the Lake Huron – Lake Erie system solely attributable to food availability, and then relative importance of the two factors can be determined. To assess the scope for changes in walleye growth brought about by geographic variation in temperature regimes, we performed the following set of bioenergetics model simulations. For a specific combination of geographic area and sex, walleye growth was predicted using the food consumption schedule for that specific combination of geographic area and sex (as determined by the fit-to-growth simulations) but replacing the temperature regime for that specific combination of geographic area and sex with the temperature regimes for the other three geographic areas and the same sex. The food consumption schedule was the total amount of food consumed by an average walleye over the course of the year for each of the 10 simulation years from age 3 through age 13, as determined by the 10 fit-to-growth simulations. Observed mass at age 3 was the starting walleye mass, and walleye growth was predicted over ages 4–13. For each age between 4 and 13, predicted walleye mass was compared with observed walleye mass. For example, consider the case of northern Lake Huron female walleye. We predicted female walleye growth from age 3 through age 13, using the feeding schedule for northern Lake Huron females and maintaining bioenergetics model inputs specific for northern Lake Huron females other than temperature regime, under the following three temperature regimes: (*i*) southern Lake Huron female walleye, (*ii*) Saginaw Bay female walleye, and (*iii*) Lake Erie female walleye. The starting mass for each of these three scenarios was the observed mass at age 3 for Lake Huron female walleye. For each of the three scenarios, predicted mass at age was compared with observed mass at age for Lake Huron female walleye. Percent changes from observed mass at age were recorded.

In our bioenergetics model simulations, we kept food consumption constant while subjecting the fish to temperature regimes from other geographic areas to assess the effect of geographic variation in temperature regimes on fish growth. Our approach was similar to that of Kao et al. (2015*a*, 2015*b*), who inputted the present-day food consumption schedule into fish bioenergetics models while subjecting the fish to a temperature regime predicted for the future using climate change models. The goal of the Kao et al. (2015*a*, 2015*b*) studies was to forecast the effects of climate change on fish growth in the Laurentian Great Lakes.

To assess the effect of variability in temperature regimes between the sexes on walleye growth, we performed the following set of bioenergetics model simulations. For a specific combination of geographic area and sex, walleye growth was predicted using the food consumption schedule for that specific combination of geographic area and sex (as determined by the fit-to-growth simulations) but replacing the temperature regime for that specific combination of geographic area and sex with the temperature regime for that specific geographic area but for the opposite sex. Again, observed mass at age 3 was the starting walleye mass, and walleye growth was predicted over ages 4–13. Predicted walleye mass was compared with observed walleye mass for ages 4–13. Consider the case of northern Lake Huron female walleye as an example. We predicted female walleye growth from age 3 through age 13, using the feeding schedule for northern Lake Huron females and maintaining bioenergetics model inputs specific for northern Lake Huron females other than temperature regime, but we replaced the temperature regime for northern Lake Huron female walleye with the temperature regime for northern Lake Huron male walleye. Initial mass was the observed mass at age 3 for Lake Huron female walleye. Predicted mass at age was compared with observed mass at age for Lake Huron female walleye over ages 4–13, and percent changes from observed mass at age were recorded. We did not assess the effect of variation in food availability between the sexes on the sex difference in walleye growth, because factors other than a sex difference in food availability likely were responsible for faster growth by females compared with males (Bozek et al. 2011; Rennie and Venturelli 2015). In contrast, assessment of the effect of a sex difference in temperature regimes on the sex difference in growth was a secondary goal of our study.

Results

Temperature regimes

Temperature data downloaded from temperature loggers implanted in 81 individuals (16% of total number of implanted individuals) were used to derive temperature regimes experienced by walleye. Temperature data from five females and three males were used to characterize the temperature regimes for walleye inhabiting northern Lake Huron, whereas the temperature regimes for walleye inhabiting southern Lake Huron were based on data from seven females and two males. In addition, temperature data from 18 females and 17 males and from 13 females and 16 males were used to characterize the temperature regimes for walleye residing in Saginaw Bay and Lake Erie, respectively. Ages of the walleye from Lake Huron ranged from 4 to 14 years, and only one of these walleye was an age-14 fish. Similarly, ages of walleye from Lake Erie ranged from 4 to 13 years.

On average, temperatures experienced by the walleye were lowest for northern Lake Huron walleye and highest for Lake Erie walleye (Fig. 2). Over the course of the calendar year, mean temperatures experienced by female and male walleye from northern Lake Huron were 8.7 and 8.6 °C, respectively. Temperature regimes were slightly higher for southern Lake Huron walleye compared with northern Lake Huron walleye, with female and male walleye from southern Lake Huron experiencing average temperatures of 9.3 and 8.9 °C, respectively, over the course of the calendar year. Saginaw Bay walleye experienced higher temperatures than walleye from the main basin of Lake Huron, as female and male walleye from Saginaw Bay experienced mean temperatures of 10.8 and 10.5 °C, respectively, during the year (Fig. 2). Temperatures experienced by female and male walleye from Lake Erie averaged 11.1 and 11.5 °C, respectively. Thus, on average, temperature regimes for female walleye were higher than those for male walleye in the main basin of Lake Huron and Saginaw Bay, whereas the temperature regime for male walleye from Lake Erie averaged a higher value than the temperature regime for female walleye from Lake Erie. Peak temperatures experienced by female walleye were 20.6, 21.3, 23.8, and 23.4 °C in northern Lake Huron, southern Lake Huron,

Fig. 2. Temperature regimes experienced by walleye in the northern main basin of Lake Huron, southern main basin of Lake Huron, Saginaw Bay, and Lake Erie, by sex. Each bar represents one standard error. Error bar width may be less than the diameter of the symbol marker used to denote mean temperature and therefore not visible. See Temperature regimes subsection of Materials and methods for more details.
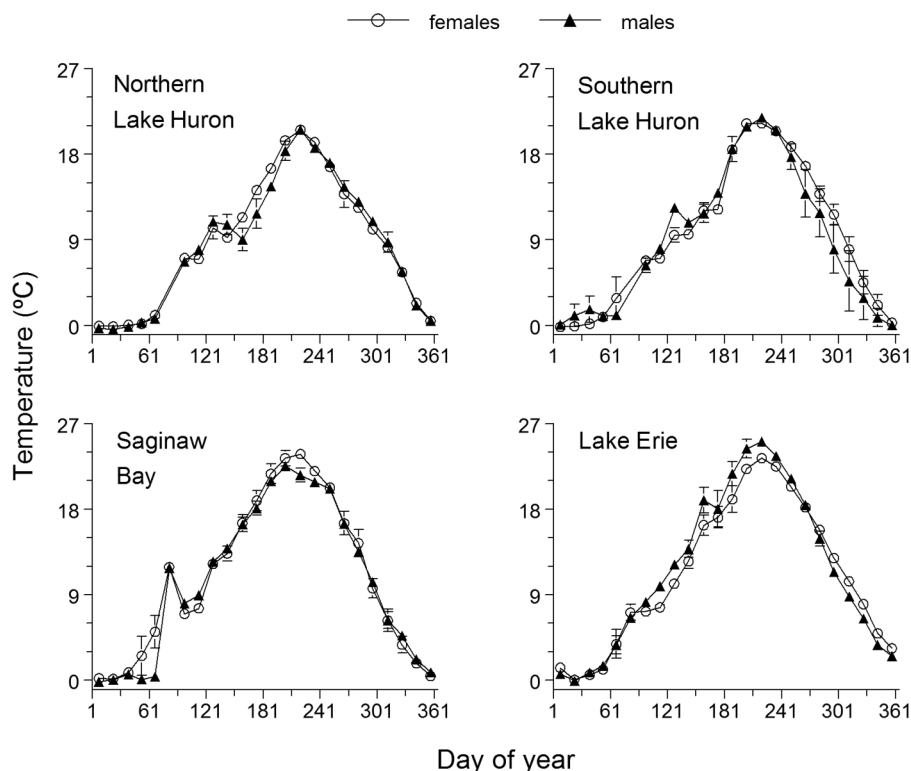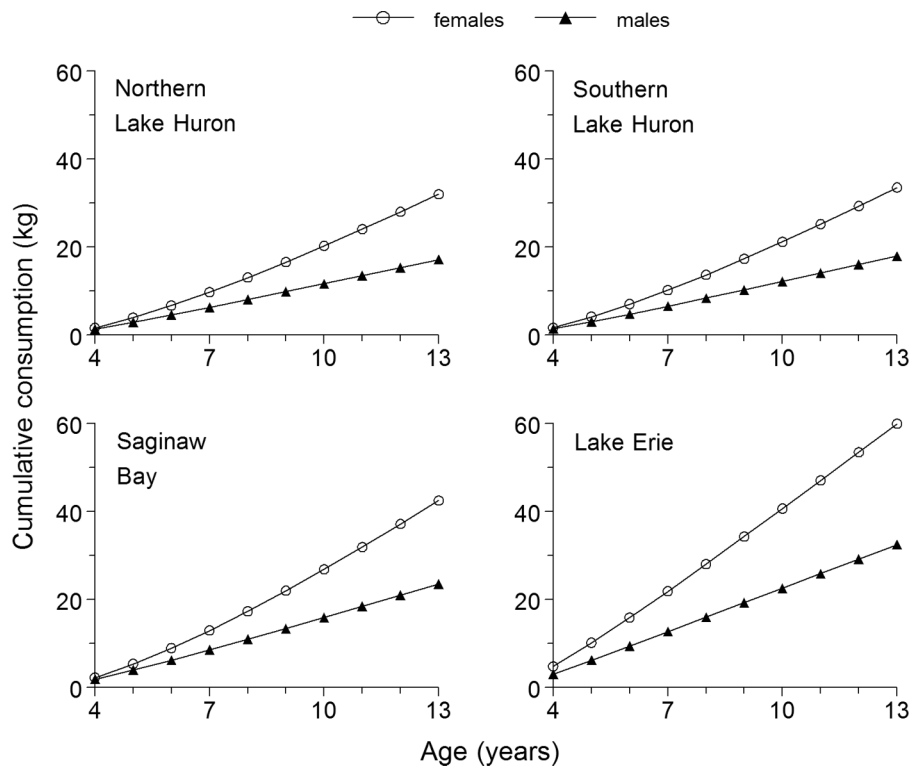

Saginaw Bay, and Lake Erie, respectively (Fig. 2). Peak temperatures experienced by male walleye were 20.6, 21.8, 22.5, and 25.1 °C in northern Lake Huron, southern Lake Huron, Saginaw Bay, and Lake Erie, respectively.

Growth trajectories

Walleye attained much larger sizes in Lake Erie than in Lake Huron (Fig. 3; Table 3). Age-3 female walleye in Lake Erie were 2.5 times greater in mass than age-3 female walleye in Lake Huron, and age-3 male walleye in Lake Erie were 2.2 times greater in mass than age-3 male walleye in Lake Huron. At age 8, female and male walleye in Lake Erie were 84% and 72%, respectively, greater in mass than female and male walleye in Lake Huron (Fig. 3). At age 13, mean mass of female walleye, as estimated from our analysis, was 3.2 kg in Lake Erie compared with 2.1 kg in Lake Huron. For males, we estimated mean mass in Lake Erie to be 1.9 kg compared with 1.2 kg in Lake Huron. Averaging across ages 3–13, female walleye from Lake Erie exceeded female walleye from Lake Huron in mass by 92%. Similarly, averaging across ages 3–13, male walleye from Lake Erie were 78% greater in mass than male walleye from Lake Huron. Averaging across ages and sexes, walleye growth in Lake Erie was 85% greater than walleye growth in Lake Huron.

Females grew substantially faster than males in both Lake Huron and Lake Erie (Fig. 3). Averaging across ages 3–13, female walleye from Lake Huron were 47% greater in mass than Lake Huron male walleye. Similarly, averaging across ages 3–13, female walleye from Lake Erie were 56% greater in mass than Lake Erie male walleye.

Based on results from t tests for paired comparisons, Lake Erie female walleye at a given age were significantly greater in mass than Lake Huron female walleye ($t = 28.74$; df = 10; $P < 0.0001$). Likewise, Lake Erie male walleye at a given age were significantly greater in mass than Lake Huron male walleye ($t = 56.74$; df = 10; $P < 0.0001$). At a given age, female walleye were significantly greater

Table 3. Parameter estimates from fitting von Bertalanffy growth curves to total length and age data for walleye caught in Saginaw Bay of Lake Huron during September and walleye caught in western and central Lake Erie during October, years 2010–2012.

Lake and sex	L_∞ (mm)	K (year^{-1})	t_0 (years)
Lake Huron females	629 (14)	0.226 (0.015)	−0.596 (0.125)
Lake Huron males	509 (5)	0.361 (0.017)	−0.079 (0.090)
Lake Erie females	661 (1)	0.374 (0.004)	−0.113 (0.020)
Lake Erie males	558 (1)	0.468 (0.006)	−0.193 (0.025)

Note: L_∞ = asymptotic mean total length, K = Brody growth coefficient, and t_0 = age at which mean total length is equal to zero. Standard error is enclosed within parentheses.

in mass than male walleye in both Lake Huron ($t = 5.56$; df = 10; $P = 0.0002$) and Lake Erie ($t = 9.45$; df = 10; $P < 0.0001$).

Bioenergetics modeling: fit to observed growth

On average, the rate of food consumption by Lake Erie walleye was nearly double the rate of food consumption by Lake Huron walleye (Fig. 4). At age 13, cumulative consumption by female and male walleye from Lake Erie was 59.9 and 32.4 kg, respectively. In contrast, cumulative consumption at age 13 by female and male walleye from Lake Huron ranged from 32.0 and 17.2 kg, respectively, in northern Lake Huron to 42.5 and 23.5 kg, respectively, in Saginaw Bay (Fig. 4). Thus, cumulative consumption at age 13 in Saginaw Bay was roughly 30% greater than cumulative consumption in the main basin of Lake Huron. Averaging cumulative consumption across ages 4–13, mean cumulative consumption for Lake Erie walleye was greater than that for Lake Huron (averaging across the three geographic areas) by factors of 2.0 and 1.8 for females and males, respectively.

On average, the rate of food consumption by female walleye exceeded the rate of food consumption by male walleye by a factor

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Fig. 3. Growth trajectories for walleye in Lake Huron and Lake Erie, by sex. Estimated mass at age based on gillnet surveys in Saginaw Bay (Lake Huron) during September 2010–2012 and gillnet surveys in Lake Erie during October 2010–2012. Each bar represents one standard error. Error bar width may be less than the diameter of the symbol marker used to denote mean mass at age and therefore not visible. See Growth trajectories subsection of Materials and methods for more details.
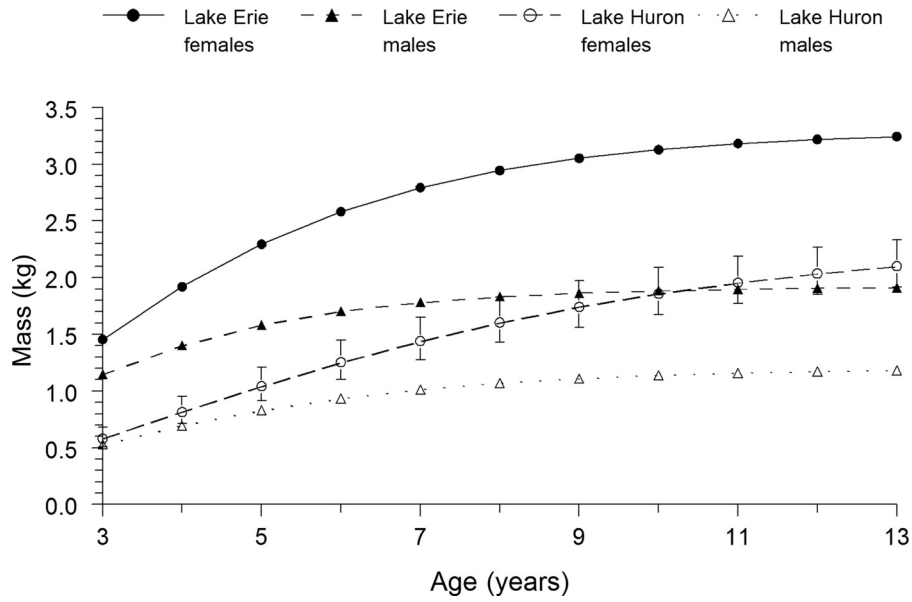
Fig. 4. Cumulative food consumption by walleye, beginning at age 3, in the northern main basin of Lake Huron, southern main basin of Lake Huron, Saginaw Bay, and Lake Erie, by sex. Food consumption was estimated by application of a walleye bioenergetics model (Kitchell et al. 1977; Hewett and Johnson 1992) to observed growth trajectories. See Bioenergetics modeling: fit to observed growth subsection of Materials and methods for more details.

of 1.6 (Fig. 4). Averaging cumulative consumption across ages 4–13, mean cumulative consumption by females was greater than that by males by factors of 1.6, 1.6, 1.6, and 1.7 for northern Lake Huron, southern Lake Huron, Saginaw Bay, and Lake Erie, respectively.

Bioenergetics modeling: exchanging temperature regimes between areas and sexes

Averaging across ages 4–13, changes in mass at age resulting from exchanging temperature regimes between geographical areas did not exceed 16% for female walleye and did not exceed 29%

Fig. 5. Predicted changes in walleye mass at age by replacing the temperature regime experienced by walleye in the northern main basin of Lake Huron with the temperature regime for southern main basin of Lake Huron walleye (upper panel), Saginaw Bay walleye (middle panel), and Lake Erie walleye (lower panel), by sex. See Bioenergetics modeling: exchanging temperature regimes between areas and sexes subsection of the Materials and methods for more details.

Fig. 6. Predicted changes in walleye mass at age by replacing the temperature regime experienced by walleye in the southern main basin of Lake Huron with the temperature regime for northern main basin of Lake Huron walleye (upper panel), Saginaw Bay walleye (middle panel), and Lake Erie walleye (lower panel), by sex. See Bioenergetics modeling: exchanging temperature regimes between areas and sexes subsection of the Materials and methods for more details.
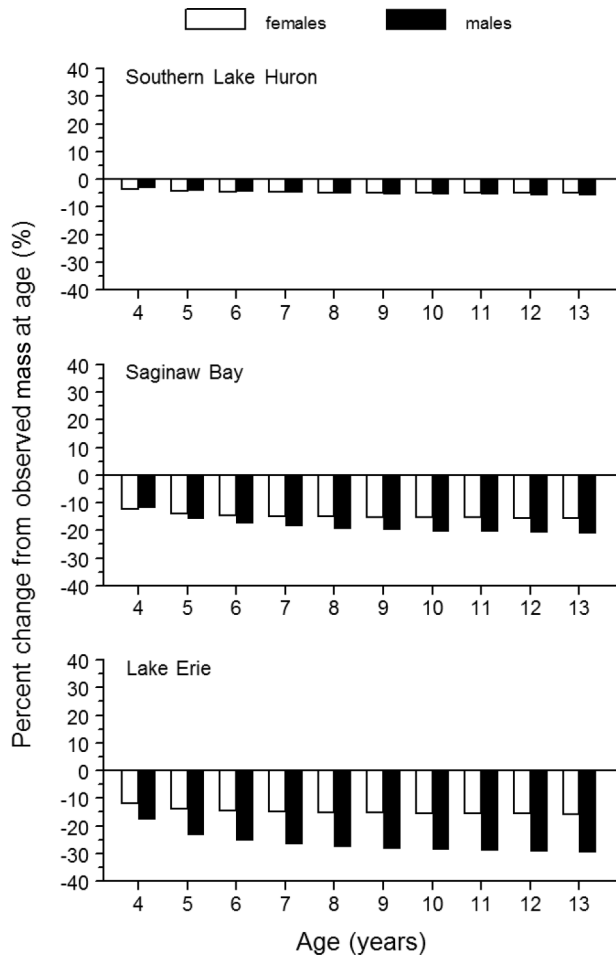

for male walleye (Figs. 5–8). For northern Lake Huron, mass at age for female and male walleye decreased, on average, by 15% and 26%, respectively, when the Lake Erie temperature regimes were imposed (Fig. 5). In contrast, mass at age decreased, on average, by only 5% for both female and male walleye when the southern Lake Huron temperature regimes were imposed in northern Lake Huron. For southern Lake Huron, mass at age for female and male walleye decreased, on average, by 11% and 23%, respectively, when the Lake Erie temperature regimes were imposed (Fig. 6). However, mass at age increased by 5%, on average, for both female and male walleye when the northern Lake Huron temperatures were imposed in southern Lake Huron. For Saginaw Bay, mass at age of female and male walleye increased, on average, by 16% and 21% when northern Lake Huron temperatures were imposed (Fig. 7). When Lake Erie temperatures were imposed in Saginaw Bay, mass at age of female and male walleye decreased, on average, by <1% and 10%, respectively. For Lake Erie, mass at age of female and male walleye increased, on average, by 14% and 29%, respectively, when northern Lake Huron temperatures were used in the bioenergetics model simulations (Fig. 8). In contrast, mass at age of female and male walleye increased, on average, by only 1% and 9%, respectively, when the Saginaw Bay temperature regimes were imposed.
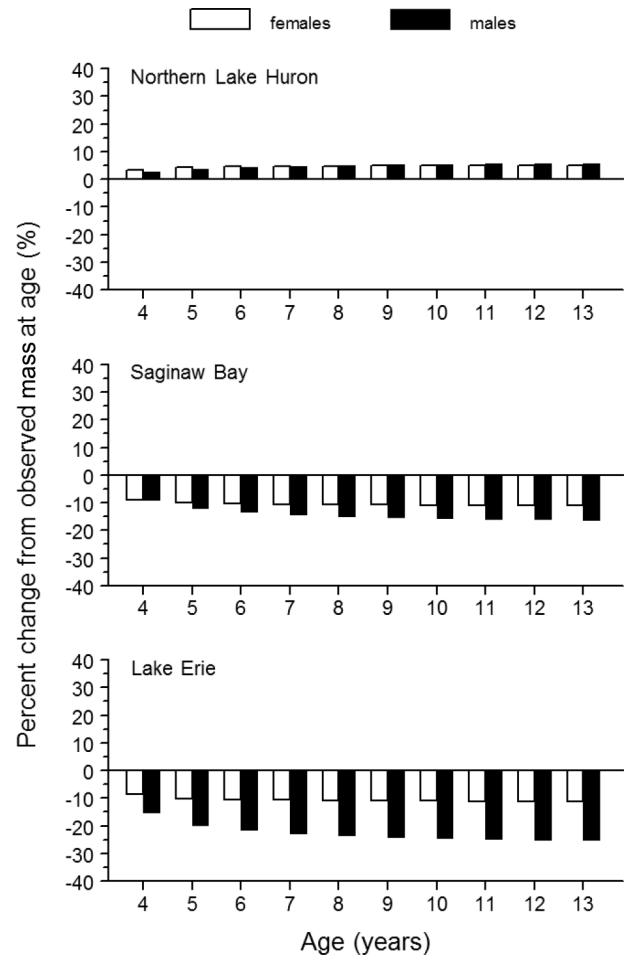
Changes in walleye mass at age were less than 7% when temperature regimes were exchanged between sexes in the bioenergetics model simulations (Fig. 9). For northern Lake Huron, mass at age of females increased by 1%, on average, while mass at age of males decreased by 2%, on, average, when temperature regimes were exchanged between the sexes. For southern Lake Huron, mass at age of females increased by 3%, on average, while mass at age of males decreased by 3%, on average, when temperatures were swapped between the sexes. For Saginaw Bay, mass at age of females increased by 3%, on average, whereas mass at age of males decreased by 3%, on average, when temperatures were exchanged between the sexes (Fig. 9). Finally, for Lake Erie, mass at age of females decreased by 3%, on average, while mass at age of males increased by 5%, on average, when temperature regimes were exchanged between the sexes.

Discussion

The observed difference in temperature regimes experienced by walleye between the two lakes made no contribution whatsoever toward the faster walleye growth in Lake Erie compared with Lake Huron. Data from our iButton temperature loggers implanted in fish indicated that Lake Erie walleye experienced higher temper-

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Fig. 7. Predicted changes in walleye mass at age by replacing the temperature regime experienced by walleye in Saginaw Bay with the temperature regime from the northern main basin of Lake Huron walleye (upper panel), the southern main basin of Lake Huron walleye (middle panel), and Lake Erie walleye (lower panel), by sex. See Bioenergetics modeling: exchanging temperature regimes between areas and sexes subsection of the Materials and methods for more details.
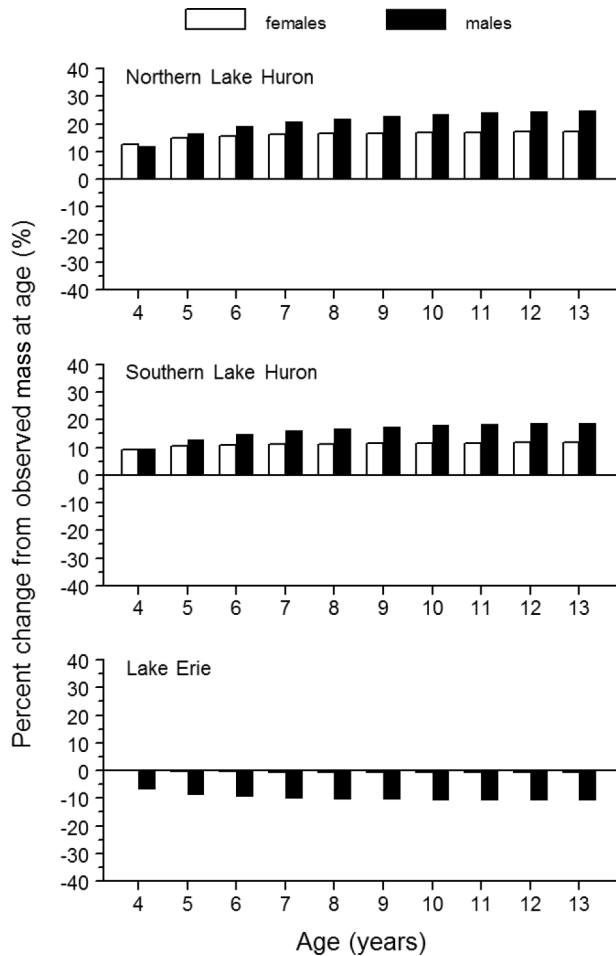
Fig. 8. Predicted changes in walleye mass at age by replacing the temperature regime experienced by walleye in Lake Erie with the temperature regime from the northern main basin of Lake Huron walleye (upper panel), the southern main basin of Lake Huron walleye (middle panel), and Saginaw Bay walleye (lower panel), by sex. See Bioenergetics modeling: exchanging temperature regimes between areas and sexes subsection of the Materials and methods for more details.
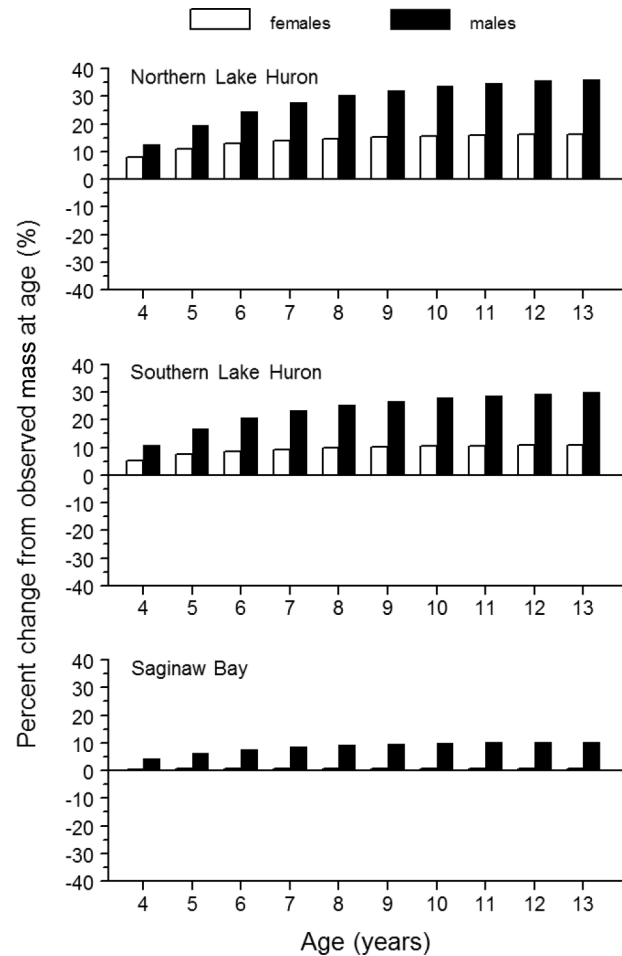
atures than Lake Huron walleye. Thus, if food availability, as indexed by food consumption, did not differ between the two lakes and all other factors (other than temperature regime) affecting growth were identical between the two lakes, then walleye growth would have been expected to be faster in Lake Huron than in Lake Erie. Moreover, results from our bioenergetics model simulations showed that walleye growth in Lake Huron would decrease if Lake Erie temperature regimes were imposed in Lake Huron and that walleye growth in Lake Erie would increase if Lake Huron temperature regimes were imposed in Lake Erie.

We conclude that faster walleye growth in Lake Erie compared with walleye growth in Lake Huron was most likely due to much greater food availability in Lake Erie compared with that in Lake Huron. This conclusion was supported by the available data from prey fish hydroacoustics surveys from both lakes. Lake-wide mean pelagic prey fish biomass density in Lake Huron was about 8 kg·ha⁻¹ during 2011–2012, based on results from the lake-wide hydroacoustics survey (Warner et al. 2013). The dominant pelagic prey fish species in Lake Huron included rainbow smelt and bloater (*Coregonus hoyi*), and each species contributed approximately 50% to the overall biomass density. In contrast with Lake Huron, acoustic estimates of mean biomass density of yearling and older

rainbow smelt in central and eastern Lake Erie during 2011–2012 ranged from 69 to 85 kg·ha⁻¹ (Forage Task Group 2012, 2013; Patrick Kocovsky, US Geological Survey, Great Lakes Science Center, personal communication). Our conclusion was also supported by the available data on lake primary production. Estimates of annual primary production in Lake Erie and Lake Huron during 2008, the only recent year for which these estimates were available, were 5.4 and 0.8 kt C·ha⁻¹, respectively, where 1 kt C = 1000 metric tons of carbon fixed by photosynthesis during the year (Great Lakes Primary Production Model 2017). Thus, from a primary production standpoint, Lake Erie had potential to support a substantially higher prey fish biomass density than Lake Huron.

The higher food availability in Lake Erie compared with Lake Huron was not due to the biomass density of walleye in Lake Huron being substantially greater than that in Lake Erie. As density of a fish population increases, intraspecific competition for food within the fish population is expected to increase, and consequently growth of individual fish within the population would be expected to decrease (Lorenzen and Enberg 2002). Thus, as biomass density of the fish population increases, availability of food for an individual fish in the population tends to decrease, and growth of individual fish tends to decrease as well. Adult walleye population

Fig. 9. Predicted changes in walleye mass at age by exchanging temperature regimes experienced by the walleye between the sexes for each of the four geographic areas: northern main basin of Lake Huron, southern main basin of Lake Huron, Saginaw Bay, and Lake Erie. See Bioenergetics modeling: exchanging temperature regimes between areas and sexes subsection of the Materials and methods for more details.
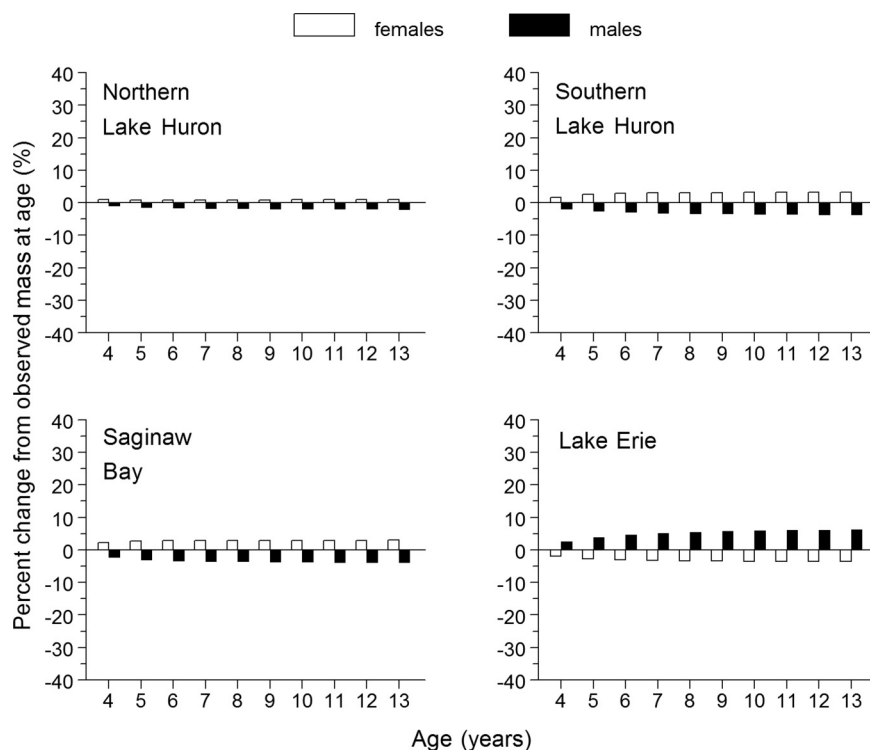
biomass in Saginaw Bay and the main basin of Lake Huron averaged 1.6 kt during 2011–2012 (Fielder and Bence 2014). Assuming that the bulk of the walleye population in the main basin of Lake Huron inhabits waters corresponding to bottom depths less than 23 m deep, and including all of Saginaw Bay as habitable by walleye, the surface area available to walleye in the main basin of Lake Huron and Saginaw Bay would be 7057 km² (Wang et al. 2015). This assumption appeared to be a reasonable one (Fielder and Bence 2014). Thus, adult walleye biomass density in the habitable region of Lake Huron's main basin and Saginaw Bay was estimated to be 2 kg·ha⁻¹. Adult walleye population biomass in Lake Erie averaged 65.4 kt during 2011–2012 (Walleye Task Group 2016), and all of Lake Erie's surface area of 25 690 km² was considered habitable by walleye (Ryan et al. 2003; Pandit et al. 2013). Thus, adult walleye biomass density in Lake Erie was estimated to be 25 kg·ha⁻¹, a value more than an order of magnitude higher than that for Lake Huron. Clearly, the higher food availability in Lake Erie was not attributable to greater adult walleye biomass density in Lake Huron compared with that for Lake Huron.

We also conclude that food availability was considerably more important in determining walleye growth in the Lake Huron – Lake Erie system than temperature regime. The faster walleye growth in Lake Erie than in Lake Huron was solely attributable to greater food availability in Lake Erie than in Lake Huron. On average, Lake Erie walleye grew 85% faster than Lake Huron walleye. Our bioenergetics modeling results indicated that variability in temperature regimes among geographic areas of the Lake Huron – Lake Erie system could account for up to a 16% change in the growth of female walleye and a 29% change in the growth of male walleye. More specifically, we showed that variation in temperature regimes between the three basins of Lake Huron could account for as high as a 16% change in growth of female walleye and as high as a 21% change in growth of male walleye. In addition, variation in temperature regimes between the two lakes could account for as high as a 15% change in growth of female walleye and as high as a

29% change in growth of male walleye. Clearly, of these two factors affecting walleye growth, food availability was the dominant factor in the Lake Huron – Lake Erie system.

The faster walleye growth in Lake Erie compared with that in Lake Huron was not explained by differences in prey and (or) walleye energy densities between the two lakes. If the ratio of walleye energy density to prey energy density was greater for Lake Huron than for Lake Erie, then walleye would have to consume more food in Lake Huron than in Lake Erie to achieve the same amount of growth, all other factors being equal. Thus, this scenario would contribute toward faster walleye growth in Lake Erie than in Lake Huron. However, the ratio of walleye energy density to prey energy density for Lake Erie was greater than that for Lake Huron. Averaging across ages 3–13, walleye energy densities were 6311 and 8288 J·g⁻¹ in Lake Huron and Lake Erie, respectively. Weighted (weighting by the proportion of each prey type eaten) averages of prey energy densities were 4888, 4251, and 5350 J·g⁻¹ in the main basin of Lake Huron, Saginaw Bay, and Lake Erie, respectively. Consequently, values of the ratio of walleye energy density to prey energy density were 1.29, 1.48, and 1.55 for the main basin of Lake Huron, Saginaw Bay, and Lake Erie, respectively. Thus, Lake Erie walleye had to consume more food than Lake Huron walleye to achieve the same amount of growth, all other factors being equal. And Lake Erie walleye grew nearly twice as fast as Lake Huron walleye. In sum, differences in walleye and prey energy densities between the two lakes did not contribute toward the faster walleye growth in Lake Erie.

Our research has provided new insights into the effect of variation in temperature regimes between the sexes on the difference in walleye growth between the sexes. For all three basins of Lake Huron, females experienced slightly higher temperatures, on average, than males. Exchanging temperature regimes between the sexes of Lake Huron walleye resulted in slight (<5%) increases in growth of females and slight decreases in growth of males. Thus, sex differences in temperature regimes could not account for any

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portion of the observed difference in growth between the sexes of
Lake Huron walleye, as observed mass at age of females averaged
47% higher than that of males over ages 3–13. For Lake Erie, males
experienced slightly higher temperatures than females. Exchang-
ing temperature regimes between the sexes of Lake Erie walleye
led to a 3% decrease, on average, in growth of females and a 5%
increase, on average, in growth of males. Thus, the sex difference
in temperature regimes could account for females being about 8%
greater in mass at age than males from Lake Erie. Females were
observed to be 56% greater, on average, in mass at age than males
from Lake Erie. We conclude that the sex difference in tempera-
ture regimes explained 15% of the observed difference in growth
between the sexes of Lake Erie walleye, but none of the observed
sex difference in growth of Lake Huron walleye. More research is
needed to identify the predominant causes underlying sexually
dimorphic growth in fish. We also note that the slightly higher
temperature regime experienced by male walleye compared with
female walleye in Lake Erie was expected based on results reported
by Wang et al. (2007). Using data from a long-term mark and
recapture study, these researchers showed that male walleye were
more likely to reside in the western basin of Lake Erie throughout
the year than female walleye. On average, surface water tempera-
tures in the western basin are higher than those in the central or
eastern basins of Lake Erie (Moukomla and Blanken 2016), and
therefore higher temperatures experienced by males would be
presumed. Reasons for the slightly higher temperatures experi-
enced by females compared with males in Lake Huron were un-
clear.

One caveat for our findings was that the growth trajectories
that we developed for walleye from Lake Huron were specifically
for the Saginaw Bay walleye stock, which inhabits Saginaw Bay and
the main basin of Lake Huron (Fielder and Bence 2014; Hayden et al.
2014). Walleye stocks also inhabit both Georgian Bay and the
North Channel of Lake Huron, but these walleye stocks do not mix
with the Saginaw Bay stock (Fielder et al. 2010; Stepien et al. 2010).
Walleye grew faster in Georgian Bay and the North Channel than
in the main basin of Lake Huron during 1982–2003 (Chu and
Koops 2007), and this difference in growth appears to hold true
today as well (Arunas Liskauskas and Adam Cottrill, Ontario Min-
istry of Natural Resources and Forestry, personal communica-
tion).

Another caveat for our findings was that the temperature re-
gimes that we developed for walleye residing in the main basin of
Lake Huron were based on relatively low numbers of recaptured
walleye. Temperature regimes for the northern main basin of Lake
Huron were based on data from five females and three males, and
temperature regimes for the southern main basin of Lake Huron
were based on data from seven females and two males. However,
despite the low sample sizes with regard to number of walleye
recaptured, the temperature regimes did indeed show that wall-
eye experienced slightly higher temperatures in the southern
main basin than in the northern main basin and that walleye
experienced higher temperatures in Saginaw Bay than in the
main basin of Lake Huron, as would be expected based on the
long-term observations of surface water temperatures by Moukomla
and Blanken (2016). To perform a bioenergetics analysis for walleye
growth in Georgian Bay and the North Channel of Lake Huron
analogous to that from our study, temperature regimes for Geor-
gian Bay walleye and North Channel walleye would need to be
developed. This would involve implanting Georgian Bay walleye
and North Channel walleye with temperature loggers.

Our results should be useful in refining and updating models
for quantifying the role of walleye as a piscivore in the Lake Huron
and Lake Erie ecosystems. He et al. (2015) coupled age-structured
population models with fish bioenergetics models to assess the
effect of piscivory by Chinook salmon (*Oncorhynchus tshawytscha*),
lake trout (*Salvelinus namaycush*), walleye, and lake whitefish (*Coregonus
clupeaformis*) on Lake Huron prey fish populations. For modeling

purposes, these researchers assumed that the temperature re-
gime experienced by walleye was equivalent to the long-term
mean temperature profile from daily water temperature records
kept at the Bay Metro Water Treatment Plant, which drew water
directly from Saginaw Bay. Their modeling effort could be refined
and updated by applying the temperature regimes developed in
our study based on data from iButton temperature loggers im-
planted in Lake Huron walleye. With regard to assessing the role
of piscivory by the Lake Erie walleye population on prey fish pop-
ulations, previous efforts have relied on temperature regimes de-
rived from measurements of water temperatures in Lake Erie
(Hartman and Margraf 1992; Kershner et al. 1999), rather than
derived from in situ measurements from temperature loggers im-
planted in Lake Erie walleye. Application of our temperature re-
gimes based on data from the iButton temperature loggers would
lead to more accurate estimates of prey fish consumption by the
Lake Erie walleye population. Moreover, the two above-mentioned bio-
energetics model applications to the Lake Erie walleye population
were not based on energy density determinations specifically for
Lake Erie walleye. Rather, energy density of Lake Erie walleye was
assumed to equal that of a typical value for fishes (Winberg 1956;
Hewett and Johnson 1992). Use of our energy density determina-
tions specifically for Lake Erie walleye would improve the accu-
racy of the bioenergetics model applications to the Lake Erie
walleye population. Finally, detailed studies on walleye diet in
Lake Erie, like the studies conducted during the late 1970s and
1980s (Knight et al. 1984; Hartman and Margraf 1992), have rarely
been published since 1995. Our study provided a detailed diet
schedule for Lake Erie walleye, from spring through fall based on
more than 3000 non-empty stomachs, by summarizing stomach
contents data over years 2000–2015. This diet schedule will be
invaluable in updating and refining models used to quantify the
effects of piscivory by the Lake Erie walleye population on Lake
Erie prey fish populations. Once the models for quantifying pis-
civory by the walleye population have been refined, these new
models would contribute toward ecosystem-based management,
as advocated by Link (2002), Pikitch et al. (2004), Tsehaye et al.
(2014), and Grüss et al. (2017), of the important fisheries operating
in both lakes.

Our study was innovative, from two perspectives. First, our study
represented the first assessment of the effect of a sex difference in
temperature regimes on the sex difference in growth within a fish
population. We found that the sex difference in temperature re-
gimes for Lake Huron walleye made no contribution at all to the
observed faster growth of females compared with males. In the
case of Lake Erie walleye, the sex difference in temperature re-
gimes accounted for 15% of the observed difference in growth
between the sexes. Thus, although the sex difference in tempera-
ture regimes contributed to the observed sex difference in growth
of Lake Erie walleye, it was not the primary driver of the sexually
dimorphic walleye growth. Second, we were the first to evaluate
the effects of both interbasin and interlake variability in temper-
ature regimes on fish growth in a two-lake system with a water-
way connection between the two lakes. Results showed that
interbasin and interlake variability in temperature regimes had
just a moderate effect on walleye growth in the Lake Huron – Lake
Erie system. Further, food availability was the dominant factor
affecting walleye growth in this two-lake system. Coupling of
archival temperature tagging and acoustic telemetry with fish
bioenergetics modeling should continue to provide new insights
into the relative importance of temperature regime as a factor
influencing fish growth in fish populations from multi-lake sys-
tems around the world.

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