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RESEARCH ARTICLE

Habitat-dependent metabolic costs for a wild cold-water fish

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Abstract

Bioenergetics models for fishes are useful for understanding ecological processes (e.g., survivorship, growth, and reproduction) and can also inform fisheries management. Yet, current bioenergetics models are unable to ascertain direct energetic costs associated with standard and active metabolism for wild, free-swimming fishes. The use of telemetry with accelerometer sensors, calibrated in the laboratory using swim tunnel respirometers, have made it possible to estimate field metabolic activity in wild fish. Our objectives were to determine seasonal thermal habitat use and habitat-dependent metabolic costs associated with standard, active, and maximum metabolism in a ~1400 ha multibasin lake in Québec, Canada. We implanted 47 wild, free-swimming Lake Trout (*Salvelinus namaycush*) with either acoustic transmitters equipped with temperature and depth sensors or an acceleration sensor. Three sets of water temperature loggers (one set for each basin) were deployed at 2, 4, 6, 10, and 18 or 20 m to measure seasonally available thermal habitat. Thermal profiles of lake water temperature varied among basins with the thermocline being ~5 m in the smallest basin (north basin) and ~7.5 m in the largest basin (east basin). Thermal habitat used by Lake Trout varied seasonally, coupled with seasonal and basin differences in standard and maximum metabolism. Daily active metabolism loosely followed seasonal changes in thermal habitat use but was largely unaffected by differences in thermal habitat use among capture basins. The theoretical scope-for-activity followed seasonal trends and was estimated to range between 47% and 74% of theoretical aerobic scope. Our observations suggest that available thermal habitats influence Lake Trout thermal habitat use, and thus metabolic costs associated with swimming. These changes in thermal habitats could have metabolic consequences for individuals in a population, resulting in altered fitness metrics (i.e., survival, growth, and/or reproduction). Reductions in the volume and availability of optimal thermal habitats for Lake Trout are likely to occur under climate change scenarios. Our study indicates that the species can adjust metabolic costs throughout the year even when thermal habitats appear to be limiting, which may inform future evidence-based management decisions.

Keywords Lake trout · Thermal habitat · Metabolism · Acoustic telemetry

Introduction

Understanding why animals move provides insight into ecological processes that are focal points of conservation and resource management (e.g., predator–prey dynamics, energetics, resource partitioning, and habitat selection; Hugie and Dill 1994; Morris 2003; Nathan et al. 2008). The energy an individual consumes, retains, and excretes alters its capacity for movement that in turn impacts its survival, growth, and reproductive success (i.e., fitness), thereby affecting population-level processes for the species (Tytler and Calow 1985). Understanding how energy is transferred between an ecosystem and an organism is the study of bioenergetics and is of fundamental interest to ecology, conservation, and

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resource management (Kitchell 1983; Hansen et al. 1993; Chipps and Wahl 2008). Bioenergetics models are energy-balance equations based on the first law of thermodynamics where energy is consumed and transformed for various uses such as metabolism, growth, and waste, with active metabolism considered energetically costly (Kitchell et al. 1977; Kitchell 1983; Hansen et al. 1993).

Temperature, for ectothermic organisms such as fishes, has a substantial influence on energy use, and is one of the most important drivers of biological processes due to its effects on the physiological mechanisms that dictate movement, survival, growth, and reproduction (Fry 1947). Many fishes are stenothermal, relying on thermal habitats defined by a narrow range of temperatures for survival. Thermal habitats of many aquatic environments are currently being altered by human-induced climate change and other anthropogenic stressors (Reid et al. 2019; Jane et al. 2021; Kraemer et al. 2021). In the face of thermal habitat loss, fishes have three potential options: (1) endure warming thermal habitats, (2) seek the next best thermal habitat by seasonally shifting habitat use which might increase energy demands and the potential for a mismatch between predator and prey (Thackeray et al. 2010), or (3) if available, use deeper, cooler water, that might be unsuitable in other ways (e.g., having limited dissolved oxygen or light conditions; Hansen 2021). Each of these options will have different consequences for fish movement and energetics, therefore understanding how movement within and among thermal habitats influences metabolism and theoretical aerobic scope (AS; i.e., the difference between standard and maximum metabolic rates) in the wild is important for ongoing conservation and management of climate-affected species.

Lake Trout (*Salvelinus namaycush*) are a stenothermal, cold-water fish native to oligotrophic aquatic ecosystems within northern North America (Shuter et al. 1998; Muir et al. 2016; Muir et al. 2021; Gunn and Louste-Fillion 2022). Access to cold water is vital for the species, with reports of the species using temperatures ranging from 4–18 °C (Martin and Olver 1980; Morbey et al. 2006), with metabolic optimum documented between 8–12 °C (Stewart et al. 1983; Rottier 1993; Evans et al. 2007), and multiple studies indicating that the species often uses thermal habitats ≤ 15 °C (Evans 2007; Plumb et al. 2009; Guzzo et al. 2017). Climatic changes to thermal habitats (e.g., warmer water extending deeper, and/or longer stratified periods) could impact Lake Trout populations in a variety of ways including by forcing the species to shift seasonal habitat use, resulting in increased metabolic costs and reduced growth rates (Schindler et al. 1996; Sharma et al. 2007; Plumb et al. 2014; Guzzo et al. 2017). Understanding how Lake Trout metabolism (i.e., standard, SMR; active, RMR; and maximum metabolic rates, MMR) will change in response to changing thermal habitats will provide scientists, fisheries managers, and conservation organizations more information to sustainably conserve and manage the species (Zimmerman and Krueger 2009).

Bioenergetics models for Lake Trout were developed in the 1980s to assist in population rehabilitation and inform management (Stewart et al. 1983; Hansen et al. 1993). Subsequent studies used bioenergetics to explore contaminant assimilation (Madenjian et al. 2000), sexual differences and/or the influence thermal habitat has on prey consumption and growth (McDonald et al. 1996; Madenjian and O'Connor 1999; Madenjian et al. 2000, 2010; Kao et al. 2015), food web structure and trophic dynamics (Pazzia et al. 2002; Sherwood et al. 2002; Harvey et al. 2003), morphotype differences (Kepler et al. 2014), and growth and metabolism (Evans 2007; Guzzo et al. 2019). These studies have provided novel information but have relied on laboratory-derived measurements of metabolism, or do not directly assess metabolic costs for wild, free-swimming populations (Madenjian et al. 2013). These limitations inevitably constrain the ability to accurately understand how anthropogenic stressors will impact the metabolic costs of Lake Trout and the availability of suitable thermal habitats for the species (Plumb et al. 2014). Recent work though has provided insight on metabolic costs for wild, free-swimming fish, by using a combination of respirometry and acoustic telemetry (Cruz-Font et al. 2016). Our study furthers this work by providing context on how a complex freshwater ecosystem influences metabolic costs, including theoretical SMR, MMR, AS, and estimated RMR and scope-for-activity (i.e., the difference between theoretical MMR and estimated RMR) for Lake Trout throughout an entire year.

The objective of this study was to determine whether thermal habitats influence theoretical SMR, MMR, AS, and estimated RMR and scope-for-activity for wild Lake Trout as inferred by variation in locomotor activity and thermal habitat use. We hypothesized that within a multibasin lake, seasonal thermal habitats would be influenced by basin size resulting in changes in Lake Trout thermal habitat use, theoretical SMR and MMR, and estimated RMR and scope-for-activity, and thus influence metabolic costs for the species. We predicted that fish that primarily use smaller basins with limited thermal habitat (volume of water ≤ 12 °C) would exhibit reduced activity and metabolic costs because movement and access to preferred resources (e.g., habitat and/or prey) is limited compared with fish that use larger basins.

Methods

Study site

Lake Papineau (45.815120° N, 74.770875° W) lies within the boundaries of a privately owned 26,305 ha fish and game reserve named Kenauk Nature X Limited Partnership Landholdings (hereafter referred to as Kenauk Nature), near Montebello, Québec, Canada. Lake Papineau is a 1,357-ha, oligotrophic lake with three basins: the east basin is 714 ha, maximum depth ~90 m; the west basin is 409 ha, maximum depth ~27 m; and the north basin is 234 ha, max depth ~50 m (Fig. 1). The basins are connected by narrow, shallow channels (100–250 m wide, ≤ 10 m deep) that may act as physical (e.g., ice) and thermal barriers preventing fish movement between basins (Fig. 1). Each basin has a large hypolimnetic volume during summer stratification (east basin, 169.9 billion liters or 72.3% of east basin; west basin, 18.9 billion liters or 33.5% of west basin; and north basin, 22.3 billion liters or 54.3% of north basin), providing thermal refugia for Lake Trout.

Acoustic telemetry

An acoustic telemetry array was deployed in Lake Papineau from fall 2017 to summer 2021 (Fig. 1). Seventeen acoustic receivers (VR2W—69 kHZ, Innovasea Systems Inc., Halifax, NS, CA) were deployed in September 2017 among the three basins: east ($n = 8$), west ($n = 5$), and north basin ($n = 4$; Fig. 1). An additional four receivers were deployed in July 2018, two in the east basin ($n_{total} = 10$) and two in the west basin ($n_{total} = 7$). In June 2019, one additional receiver was deployed in the southern portion of the west basin ($n_{total} = 8$). That receiver was relocated in November 2019, to a Lake Trout spawning reef in the east basin ($n_{total} = 11$) as part of a separate study on spawning movements. Receivers were moored 3–5 m off the lakebed using two 30 kg sandbags with a single floating line running to a sub-surface buoy (2–3 m below the surface). Detection range and efficiency were determined by using one representative receiver in each basin (Supplementary Fig. 1). Sentinel transmitters (V13; 840–960 s delays, Innovasea Systems Inc., Halifax, NS, CA) were deployed at a distance where approximately 50% of detections within 24 h would be heard (Brownscombe et al. 2020). The distance at which 50% of detections were heard varied in each basin between 270 m and 340 m. Thermal habitats were measured in Lake Papineau by deploying five temperature loggers (Vemco Mini-logger II, Innovasea Systems Inc., Halifax, NS, CA) in July 2018 to the mooring line of one receiver in the east and west basins (Supplementary Fig. 1) at ~2, 4, 6, 10, and 20 m and one receiver in the north basin at ~2, 4, 6, 10, and 18 m. Loggers recorded temperature every 10 min to determine the timing of spring and fall turnover, and the thermocline depth during summer stratification. Data were downloaded from receivers and temperature loggers in June or July of each year.

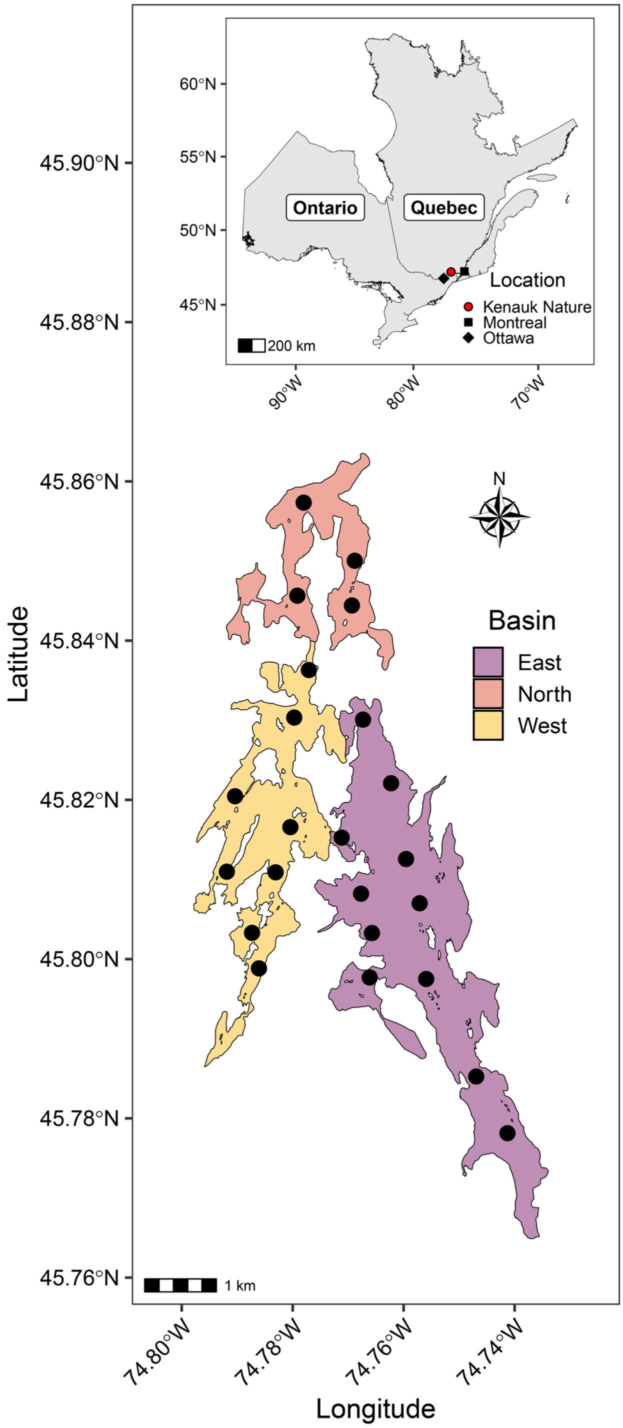


Fig. 1 Papineau Lake lies within the boundaries of Kenauk Nature, QC, Canada (inset map). Filled black circles denote locations of the 23 acoustic telemetry receivers deployed and maintained across the east, west, and north basins from September 2017—July 2021

Table 1 Number of Lake Trout (*n*) captured per basin per year in Lake Papineau, Québec, Canada and implanted with an acoustic transmitter. Transmitter type is specified as either accelerometer (Acc), or temperature and depth transmitter (T/P). Mean total length, fork length, and weight are reported as mean ± standard error of the mean (SEM)

Year	Capture basin	Transmitter type	*n*	Total length (mm)	Fork length (mm)	Weight (g)
2017	East	Acc	1	575	530	1902
2017	East	T/P	4	500 ± 24	455 ± 23	860 ± 349
2017	North	T/P	4	496 ± 24	454 ± 23	801 ± 349
2017	West	Acc	1	455	410	669
2017	West	T/P	7	494 ± 18	455 ± 17	871 ± 264
2018	East	T/P	3	490 ± 28	454 ± 27	768 ± 404
2018	West	T/P	7	498 ± 18	459 ± 17	809 ± 264
2019	East	Acc	7	469 ± 18	429 ± 17	764 ± 264
2019	East	T/P	1	705	660	4850
2019	North	Acc	4	477 ± 24	436 ± 23	881 ± 349
2019	West	Acc	9	522 ± 16	474 ± 15	1200 ± 223

Animal care protocols, in accordance with the Animal Care Council of Canada guidelines as administered by Carleton University, were followed throughout this study. All animal collection was done under provincial scientific collection permits administered by the Québec Ministère des Forêts, de la Faune et des Parcs. Forty-eight Lake Trout (Table 1) were captured across all three basins by rod and reel or multipaneled monofilament gill nets (64 m × 1.8 m; 8 m panels; stretch mesh sizes of 57, 64, 70, 76, 89, 102, 114, and 127 mm). Gill nets were used in either spring or fall with a soak duration of 1–2 h. Fish were immobilized for surgery using electronarcosis (Vandergoot et al. 2011). All instruments were sterilized prior to surgery using betadine (povidone iodine, 10%). A small mid-ventral incision (~25 mm) was made to implant an acoustic transmitter into the body cavity. An acoustic transmitter with accelerometer sensor was internally tethered with Vicryl sutures (Ethicon VCP423, 3–0 FS-2 cutting) near the incision site following implant protocols described in Cruz-Font et al. (2016) and Brownscombe et al. (2014). The incision was closed by two or three Vicryl sutures (Ethicon VCP423, 3–0 FS-2 cutting) tied with a double surgeon's knot. The transmitter-to-body weight ratio was < 2% for all fish (Winter 1996). All fish were measured (total length; TL, mm) and weighed (g). For fish where weight was unattainable because of issues with scale stability, weight was derived from length–weight relationship calculated from regressing $\log_{10}$ transformed length and weight of Lake Papineau Lake Trout (Piccolo et al. 1993). An external T-bar anchor tag (Floy Tag and Mfg., Inc.) was inserted into the fish musculature behind the dorsal fin as an external identifier for researchers and recreational anglers. After surgery, all fish were placed in a recovery tank and monitored until they regained equilibrium. Each procedure lasted 2–4 min and all fish were released within 10 min of the surgery near the site of capture within each basin ($n = 16$ east basin; $n = 24$ west basin; and $n = 8$ north basin; Table 1).

Seventeen of the 47 Lake Trout captured in September 2017 were implanted with Innovasea transmitters: V13TP (80–160 s delays, $n = 15$), and V13A (90–180 s delays, $n = 2$, swim activity rate of 5 HZ, i.e., five samples of acceleration per second, with 25-s sampling duration). An additional ten Lake Trout were tagged in spring 2018 with V13TP (80–160 s delays) and 20 Lake Trout in spring 2019 with V13A (320–640 s delays, tailbeat sampled at a rate of 10 HZ, i.e., ten samples of acceleration per second, with a 45-s sampling duration). One Lake Trout tagged in spring 2018 with an V13TP was lethally captured in spring 2019 and its transmitter was implanted into another fish in spring 2019 (Table 1). All transmitters (emitting) and receivers (recording) were set to a frequency of 69 kHZ.

Data analysis

Acoustic telemetry detection data were cleaned by first removing detections from unknown transmitter identifiers (IDs). A minimum lag filter (i.e., time between detections) was then applied to each transmitter ID, because the delays for each transmitter varied (Pincock 2012; see Supplementary Material 1.1). Data were further inspected visually using abacus plots to identify any additional suspicious detections that were subsequently removed. A minimum of three detections were needed every hour for a fish to be considered present and the data valid (Papastamatiou et al. 2010). A total of 10 out of 48 tagged fish were never detected, with the remaining 38 individuals detected throughout the study time period.

We measured thermal habitat use of Lake Trout by calculating daily mean fish temperature (°C) obtained from 26 acoustically implanted Lake Trout. Daily metabolic costs (SMR, MMR, and RMR; mg O_2 h^{-1} kg^{-1}) were calculated for each individual Lake Trout. Standard, maximum, and active metabolism were estimated using formulae described in the Supplementary Material

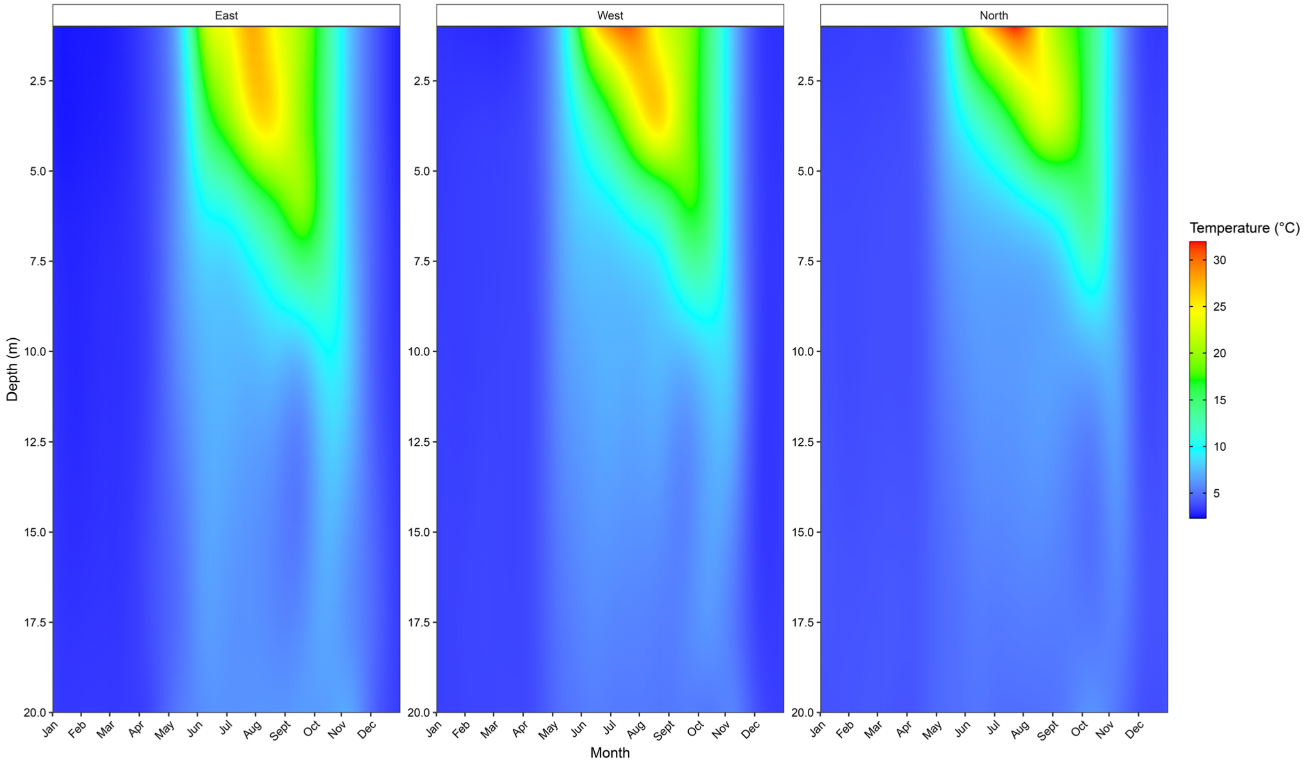


Fig. 2 Papineau Lake temperature profiles interpolated for each basin generated from generalized additive mixed effects models (GAMMs) for July 2018 to July 2021. The thermocline was identified using 15 °C isothermal throughout periods of stratification (June to October) of each year. We choose to use 15 °C isothermal because multiple studies have documented the importance of thermal habitats ≤ 15 °C for Lake Trout (Evans et al. 2007; Plumb et al. 2009; and Guzzo et al. 2017)

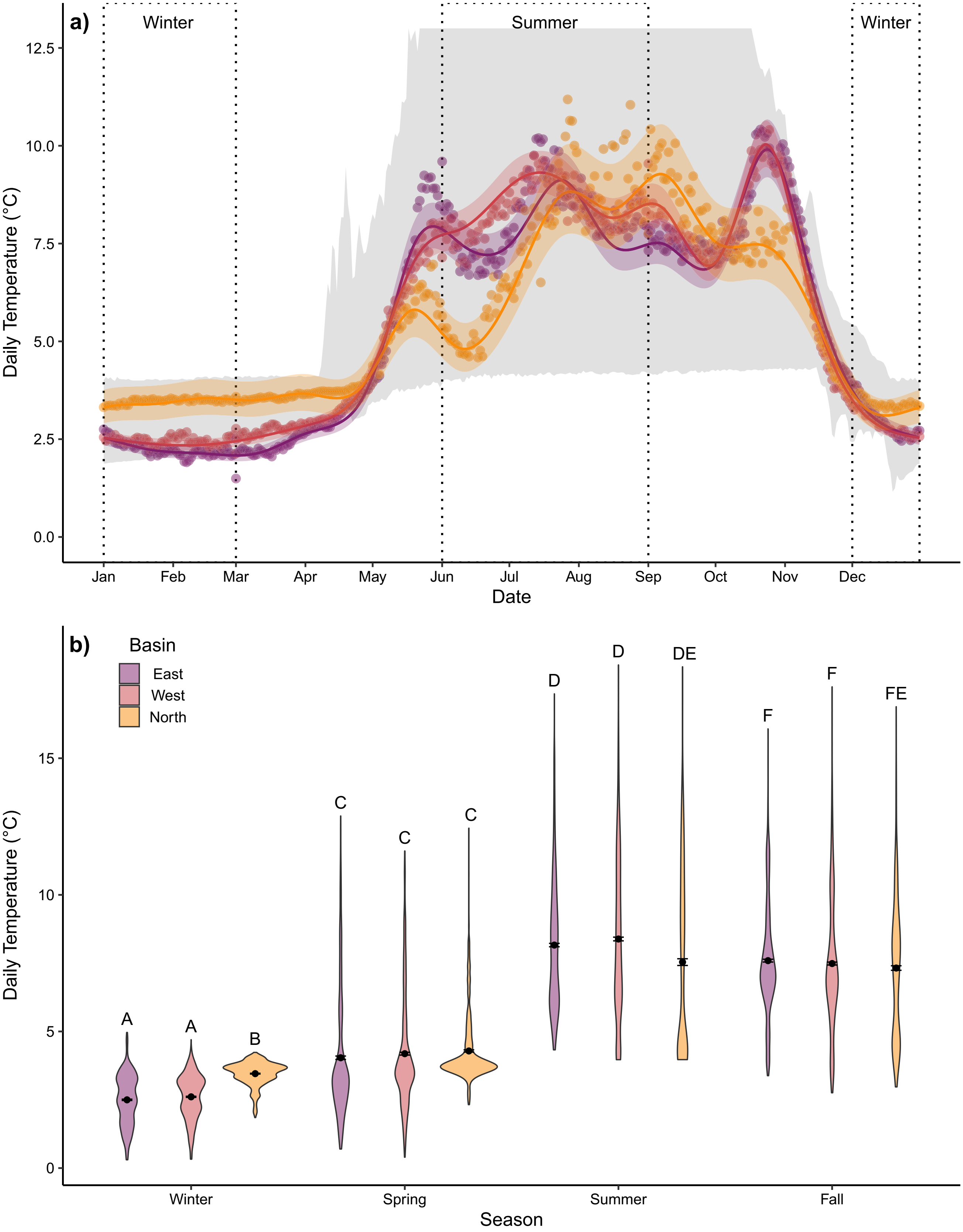
sections. 1.2.1, 1.2.2, and 1.2.3 using individual temperature or acceleration detections, weight of each Lake Trout, and the mean laboratory weight of Lake Trout used by Cruz-Font et al. (2016). Raw acceleration detections from accelerometer acoustic transmitters (0–255 arbitrary units; a.u.) were used in calculations of active metabolism, following a protocol in Cruz-Font et al. (2016). These raw values capture varying tail beat frequency of the fish and are linearly related to the acceleration $[\, accleation\left(m \bullet s^{-2}\right) = 0 + 0.01922(a.u.)\,]$ experienced by the transmitter in the two directions perpendicular to the anterior–posterior axis of the fish. Detections that produced an a.u. value ≤ 8 a.u. were removed because they were considered "inactive" based on laboratory measurements and visual observations from Cruz-Font et al. (2016) that indicated fish were at rest. Daily theoretical AS for 26 wild free-swimming Lake Trout was estimated by taking the difference between daily mean MMR and daily mean SMR (AS; mg O_2 h^{-1} kg^{-1}; for formula see Supplementary Material 1.2.4). The remaining daily scope-for-activity was calculated by taking the difference between daily mean MMR and daily mean RMR (mg O_2 h^{-1} kg^{-1}; for formula see Supplementary Materials 1.2.5).

Statistical analysis

Data cleaning, visualization, mapping, and statistical analyses were conducted in R v4.2.3. Distributions and heteroscedasticity were assessed using {moments}, {fitdistrplus}, and {cars} packages.

To determine the relationship that day-of-year (DOY) and lake basin have on lake water temperature profiles, daily mean water temperature (°C) at each depth interval (2, 4, 6, 8, and 18 or 20 m) for each basin from July 2018 to July 2021 were analyzed using generalized additive mixed effects models (GAMMs) from the {mgcv} package. Models used a gamma error distribution with the link function set to log. Interpolated temperature values for each basin were determined using the model for every ~0.2 m from 0 to 20 m. The thermocline was identified by estimating depth that 15 °C isothermal occured throughout periods of stratification (June–October) of each year. We choose to use 15 °C isothermal because multiple studies have documented the importance of thermal habitats ≤ 15 °C for Lake Trout (Evans et al. 2007; Plumb et al. 2009; and Guzzo et al. 2017).

To understand the relationship that day-of-year and capture basin have on daily fish temperature use and RMR,


a)
Winter
Summer
Winter
Daily Temperature (°C)
12.5
10.0
7.5
5.0
2.5
0.0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date
b)
Basin
East
West
North
Daily Temperature (°C)
15
10
5
0
A
A
B
C
C
C
D
D
DE
F
F
FE
Winter
Spring
Summer
Fall
Season

◂**Fig. 3** Generalized additive mixed effects models and their 95% confidence intervals (**a**) were used to determine differences in mean daily thermal habitat use (colored points) for each basin in Lake Papineau by Lake Trout. Violin plots (**b**) represent the seasonal distribution of daily thermal habitat use for each basin by Lake Trout. Black circles denote the seasonal mean for each basin with error bars representing ± SEM. Statistical differences were determined by generalized linear mixed effects models and are denoted by upper case letters. Color denotes basin while shading in **a** denotes the available thermal habitat throughout the lake regardless of basin. The *y*-axis has been limited to 13 °C for scaling and interpretation purposes. Dotted boxes in **a** denote summer and winter. Data were collected from September 2017 to October 2020

we used GAMMs with a Gamma error distribution with either a log or identity link function. The relationship that day-of-year has on daily mean RMR, regardless of basin, was also analyzed using a GAMM with a Gaussian error distribution with a log link function. To obtain multiple comparisons, linear predictors (seasons, e.g., spring defined as March, April, and May and capture basin), and random effects from GAMMs for daily fish temperature, SMR, and RMR, were further tested using generalized linear mixed effects models (GLMMs) from the {glmmTMB} package. Models used Gaussian or gamma error distributions with a log link function.

To explain the relationship that day-of-year has on the daily mean theoretical SMR, MMR, and AS, we used GAMMs with a gamma error distribution with either an identity, inverse, or log link function. To illustrate the relationship that day-of-year has on the remaining daily mean scope-for-activity, we used GAMMs with an inverse link function.

Multiple comparison for GLMMs were conducted using {emmeans} with a Tukey multiplicity adjustment to evaluate capture basin differences within a season and seasonal differences for each capture basin (Supplementary Materials Table 1). To compensate for autocorrelation, autocorrelation structures were added to the models using the package {itsadug}or {glmmTMB}. For all response variables, several models were fitted and the model that retained the predictors of interest, fitted the data appropriately, and produced the lowest AIC value (evaluated using the function *simulateResiduals()* from {DHARMa} or mgcv::*gam.check()*; Supplementary Materials Table 2) were selected and are reported below.

Results

Lake Papineau temperature profiles

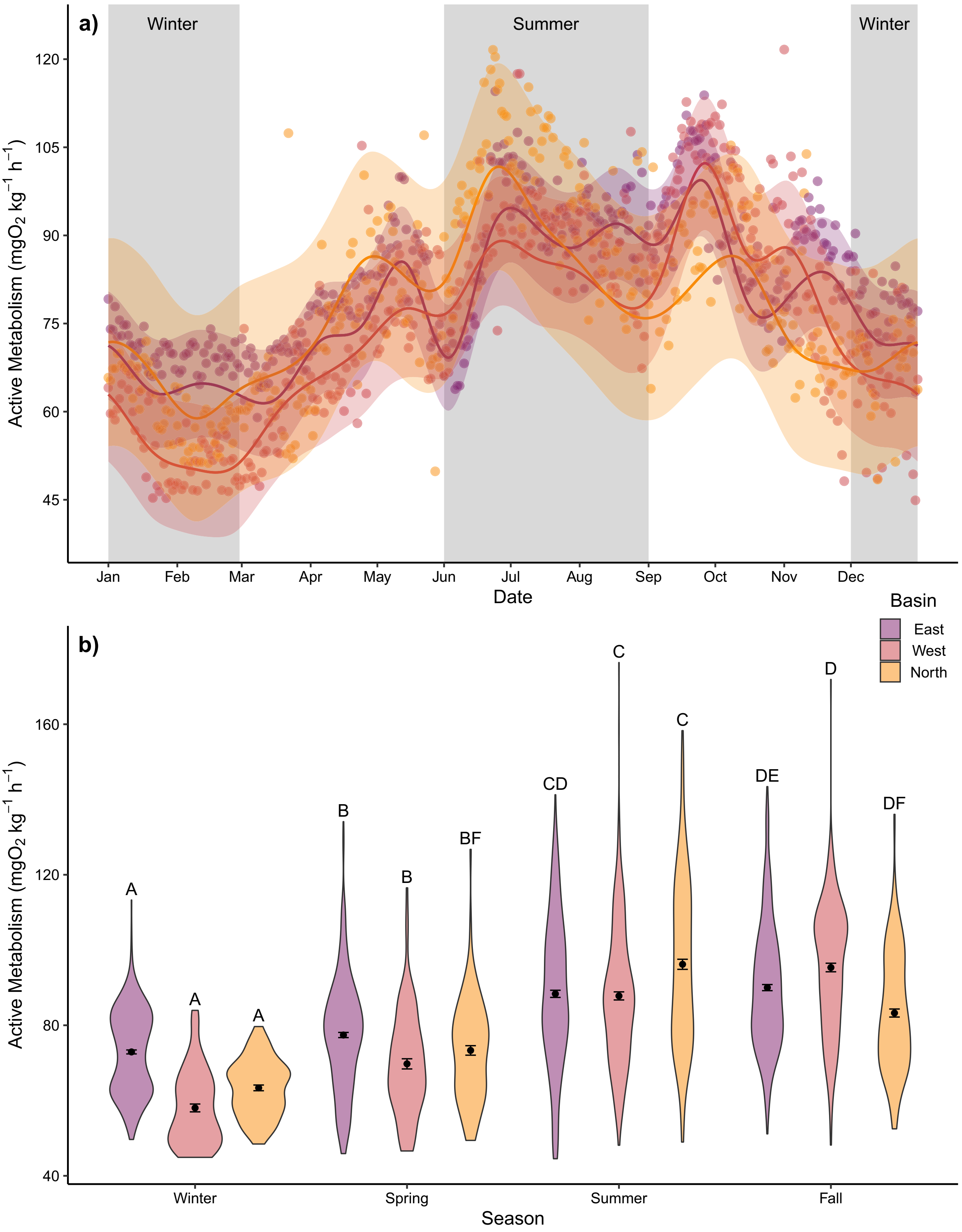
Thermal stratification occurred each year (2018–2021), starting in late-May to mid-June and ending in mid- to late-October. Thermocline depth (i.e., 15 °C) in all basins started shallow (2 m) in early summer (late-May to mid-June), and increased in depth through late summer to between approximately 5 m to 7.5 m in August and September (smoothers of DOY interacting with depth by basin—$F = 331.2–336.3$, effective degrees of freedom (edf) = 47.6–49.0, reference degrees of freedom (ref. df) = 65, $p \leq 0.001$). The maximum thermocline depth was estimated from the models to occur late-September and be 5.41 m in the north basin, 6.95 m in the west basin, and 7.53 m in the east basin (Fig. 2; GAMM depth—$F = 357$, df = 1, $p \leq 0.001$; basin—$F = 10.43$, df = 2, $p = 0.005$). Model selection resulted in the following model: mean daily water temperature at a given depth was regressed against lake basin and depth as linear predictors and four smoothers, with year as a random effect [Akaike information criterion (AIC) = 17,942.8, Supplementary Material Table 2]. The lake started to destratify in mid- to late-October, becoming isothermal (8 °C) by early- to mid-November.

Lake Trout thermal habitat use

Daily thermal habitat use was more variable for each capture basin in summer and fall compared with spring and winter (Fig. 3a; GAMM DOY by capture basin smoothers—$F = 1133.8–6089.8$, edf = 12.8–12.9, ref. df = 13, $p \leq 0.001$). The best candidate model included daily thermal habitat use as a response, with capture basin as a linear predictor, two smoothers, and fish ID and year as random effects (AIC = 55,781; Supplementary Material Table 2). In spring, the thermal habitat used was warmer than in winter but cooler than in summer and fall. Summer and fall thermal habitat use differed for the east and west basins, while in fish from the north basin, thermal habitat use did not differ between summer and fall. Winter thermal habitat use was the least variable when compared to other seasons. North basin fish used warmer temperatures in winter compared with fish in the east and west basins (Fig. 3b; GLMM season—$\chi^2 = 24{,}253$, df = 3, $p \leq 0.001$; season *capture basin—$\chi^2 = 546$, df = 6, $p \leq 0.001$; Supplementary Material Table 1).

Lake trout active metabolism

Daily RMR increased during warmer months and decreased during cooler months, with no observable differences between capture basins (Fig. 4a; GAMM DOY by capture basin smoothers—$F = 315.7–3940.2$, edf = 13.6–17.2, df = 18, $p \leq 0.001$; Fig. 5a; GAMM DOY smoother—$F = 1271.51$, edf = 12.0, df = 13, $p \leq 0.001$). Model selection indicated the best model contained RMR as a response, with capture basin as a linear predictor, two smoothers, and fish ID as random effect (AIC = 24,530; Supplementary Material Table 2). Lake Trout were more active in spring than in winter, but activity in spring was lower than in summer and


a)
Winter
Summer
Winter
Active Metabolism ($mgO_2\ kg^{-1}\ h^{-1}$)
120
105
90
75
60
45
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date
Basin
East
West
North
b)
Active Metabolism ($mgO_2\ kg^{-1}\ h^{-1}$)
160
120
80
40
A
A
A
B
B
BF
CD
C
C
DE
D
DF
Winter
Spring
Summer
Fall
Season

◂**Fig. 4** Generalized additive mixed effects models and their 95% confidence intervals (**a**) were used to determine differences in mean daily active metabolism (colored points) for Lake Trout. Violin plots (**b**) represent the seasonal distribution of daily active metabolism for each basin by Lake Trout. Black circles denote the seasonal mean for each basin with error bars representing ± SEM. Statistical differences were determined by generalized linear mixed effects models and are denoted by upper case letters. Color denotes basin while the lack of shading in **a** denotes spring and fall. Data were collected from May 2019 to April 2020

fall. Fish in the north basin did not differ in RMR between spring and fall, while levels of RMR in summer regardless of basin were the highest compared with every other season. Levels of activity of fish in the east basin, however, did not differ between summer and fall (Fig. 4b; GLMM season—$\chi^2 = 878.2$, $df = 2$, $p \leq 0.001$; season *capture basin—$\chi^2 = 121.7$, $df = 6$, $p \leq 0.001$; Supplementary Material Table 1).

Lake trout standard and maximum metabolism

Theoretical daily SMR and MMR for Lake Trout were influenced across months and seasons, with warmer months exhibiting greater estimates of SMR and MMR than cooler months (Fig. 5a; SMR—GAMM DOY smoothers—$F = 12{,}054.23$, $edf = 15.8$, $df = 16$, $p \leq 0.001$; MMR—GAMM DOY smoothers—$F = 9939$, $edf = 14.8$, $df = 15$, $p \leq 0.001$). The best model described daily SMR or MMR as the response, one smoother, and fish ID and year as random effects (SMR—AIC = 96,491; MMR—AIC = 142,434; Supplementary Material Table 2). Lake Trout had greater SMR and MMR in spring than in winter, but SMR and MMR in spring was lower than in summer and fall. Daily SMR and MMR were greater in summer compared to any other season but at times were comparable to fall levels. Winter SMR and MMR estimates were the lowest compared with every other season (Fig. 5a).

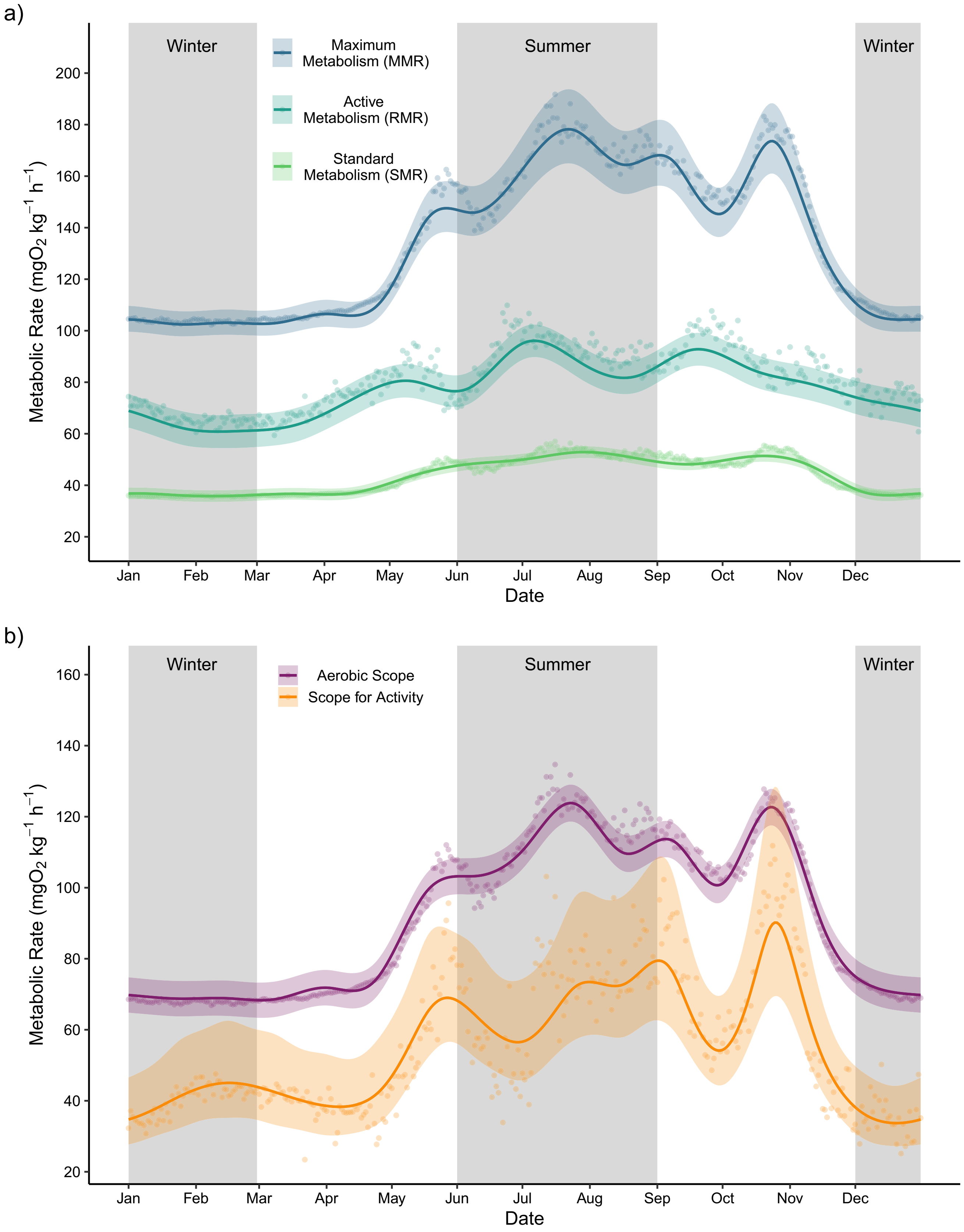
Lake trout aerobic scope and scope-for-activity

Estimates of daily AS and scope-for-activity for Lake Trout varied among months and seasons with warmer months resulting in increases in aerobic scope than cooler months (Fig. 5b; AS—GAMM DOY—$F = 3086.37$, $edf = 14.9$, $df = 15$, $p \leq 0.001$; scope-for-activity—GAMM DOY—$F = 566.21$, $edf = 14.3$, $df = 15$, $p \leq 0.001$). The best model described daily AS or scope-for-activity as the response, one smoother, and year as random effect (AS—AIC = 134,887; scope-for-activity—AIC = 9549; Supplementary Material Table 2). Aerobic scope was greater during summer than during any other period, however, estimates of aerobic scope during fall were momentarily at levels comparable with estimates during summer (Fig. 5b). Scope-for-activity followed similar trajectories annually (i.e., greater during summer and lower during winter) but was greatest late fall when water temperature starts to cool, and Lake Trout become more active. The theoretical scope-for-activity was estimated to range between 47% and 74% of theoretical aerobic scope.

Discussion

Our observations indicated that thermal habitat availability (Fig. 2) dictated Lake Trout habitat use (Fig. 3), and in turn influenced their RMR, aerobic scope, and scope-for-activity (Fig. 4 and 5). We did not observe fish captured from the smaller basins to exhibit reduced activity and metabolic costs caused by a lack of suitable thermal habitats, and thus we reject our proposed hypothesis (Fig. 3). We did observe unexpected increases in scope-for-activity when least expected (i.e., fall and winter; Fig. 5b) that were likely related to changes in thermal habitat availability and thermal habitat use (Figs. 2 and 3). Scope-for-activity followed seasonal trends but at times was much closer to aerobic scope, thus potentially affecting the ability of Lake Trout to allocate energy towards other processes such as somatic and/or gonadal growth (Fig. 5b).

The influence of temperature on aerobic scope and scope-for-activity is well-established (Fry 1971), but in wild populations other factors can influence aerobic scope and scope-for-activity such as phenotypic variation, food availability, and hypoxia (Evans 2007; Enders and Boisclair 2016; Metcalfe et al. 2016). Our observations of theoretical SMR and MMR, and estimated RMR, indicated that other environmental factors might be influencing metabolic processes for Lake Trout in Lake Papineau (Fig. 5a). Food availability can cause salmonid species to exhibit phenotypic plasticity in metabolic processes, with individuals that have greater flexibility in SMR, MMR, and AS, having greater growth rates than less-flexible conspecifics (Norin and Malte 2012; Auer et al. 2015a, b). Prey diversity in Lake Papineau is quite limited for Lake Trout with only one pelagic prey fish, rainbow smelt *Osmerus mordax*, documented (Pers. Comm. Québec Ministère des Forêts, de la Faune et des Parcs). This limitation in prey could be contributing to changes in RMR and scope-for-activity for Lake Trout, particularly in winter when food availability might become even more limited. Changes in food availability has been shown to affect SMR and activity in salmonids, with individuals that experience reductions in food having lower SMR but exhibiting higher rates of activity and greater lipid reserves (Byström et al. 2006; Auer et al. 2016). Flexibility in aerobic scope in response to changing food resources can allow energy to be allocated to other processes, such as scope-for-activity, and thus Lake Trout


a)
Winter
Summer
Winter
Maximum Metabolism (MMR)
Active Metabolism (RMR)
Standard Metabolism (SMR)
Metabolic Rate ($mgO_2\ kg^{-1}\ h^{-1}$)
200
180
160
140
120
100
80
60
40
20
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date
b)
Winter
Summer
Winter
Aerobic Scope
Scope for Activity
Metabolic Rate ($mgO_2\ kg^{-1}\ h^{-1}$)
160
140
120
100
80
60
40
20
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Date

◂**Fig. 5** Generalized additive mixed effects models and their 95% confidence intervals (**a**) were used to determine daily mean standard, active, and maximum metabolism (**b**) and aerobic scope and scope-for-activity for Lake Trout in Lake Papineau. The daily mean regardless of basin is denoted by the colored points for each metric. Unshaded regions represent spring and fall. Data were collected from May 2019 to April 2020

in Lake Papineau might have greater flexibility in scope-for-activity (Auer et al. 2016). This flexibility might provide Lake Trout the ability to respond quickly to altered thermal habitats, changes in prey resources, and other anthropogenic disturbances.

Fish behaviorally thermoregulate by actively seeking preferred thermal habitats (Beitinger and Fitzpatrick 1979; Amat-Trigo et al. 2023). Metabolic thermal optimum (T_{opt}) for Lake Trout has been reported within a narrow thermal range of 10 ± 2 °C (McCauley and Tait 1970; Stewart et al. 1983; Magnuson et al. 1990). Several studies, however, have shown wild populations of Lake Trout will occupy thermal habitats at or below T_{opt} (Bergstedt et al. 2003; Mackenzie-Grieve and Post 2006; Blanchfield et al. 2009; Guzzo et al. 2016). Our observations of daily thermal habitat use were consistently below the historically reported T_{opt} of 10 °C and ranged from 2.8 °C ± 0.01 in winter to 8.2 °C ± 0.05 in summer (Fig. 3). Our findings add to the growing evidence that wild populations of Lake Trout often use colder thermal habitats than previously hypothesized or observed (Elrod et al. 1996; Bergstedt et al. 2012; Raby et al. 2019). Cold-water fisheries management often relies on historically derived laboratory observations of thermal ranges for Lake Trout, yet those observations might be unsuitable as the basis of management decisions because they do not accurately capture thermal habitats used by wild populations (Plumb and Blanchfield 2009). If fish are behaviorally thermoregulating by actively seeking colder thermal habitats as our results suggest, then there might be increased energy expenditures resulting in an individual having less energy for growth and reproduction (Fig. 5). Our results are further supported by similar observations by others, particularly when thermal habitats become seasonally limited (e.g., summer; Plumb et al. 2014; Cruz-Font et al. 2019). This evidence suggests that as cold-water habitats are reduced by changes in climatic conditions and/or other anthropogenic stressors, populations of Lake Trout might experience unaccounted increases in energy expenditures (RMR), that could result in limited allocation of energy into survival, somatic growth, and reproductive potential.

In freshwater ecosystems with complex geomorphology (e.g., multibasin lakes; Fig. 1), thermal habitats can be discontinuous during parts of the year (e.g., summer; Fig. 2), and might affect the ability of Lake Trout (and other cold-water fishes) to behaviorally thermoregulate (Kraemer et al. 2015; Guzzo and Blanchfield 2017; Ridgway et al. 2022). In southern populations, thermal preferences typically result in the seasonal use of deep hypolimnetic zones (Dillon et al. 2003) or metalimnetic and shallow hypolimnetic zones (Christie and Regier 1988). Changes in access to thermal habitats within a lake, however, could cause an individual to expend more energy foraging and seeking habitats compared to in systems where prey and/or habitats are more concentrated (e.g., small basins and/or lakes with less complex geomorphology; Brett 1971; Tunney et al. 2012; McMeans et al. 2016; Rodrigues et al. 2022). Shifts in season duration (e.g., extended springs) have already been shown to change Lake Trout phenologies, causing reduced spatial occupancy of spring littoral habitats, influencing prey consumption and growth (Guzzo et al. 2017). Cold-water habitats are particularly susceptible to anthropogenic stressors that are vital for cold-water fishes (e.g., Lake Trout; Tunney et al. 2014; Hansen et al. 2022) and our study provides direct evidence of how important thermal habitats are in the context of bioenergetics and metabolism for this cold-water fish.

In the wild, aerobic scope and active metabolism are driven simultaneously by multiple factors, making them difficult to accurately predict when using laboratory-derived single variable models (Brownscombe et al. 2022). Our approach further extends bioenergetics modeling by measuring multiple metrics simultaneously in situ (i.e., temperature use and activity) to estimate metabolic costs for wild populations. This approach can provide more accurate and ecologically-relevant information on fish metabolism and bioenergetics to scientists and fisheries managers.

Our study estimated metabolic costs for wild Lake Trout throughout an entire year. The ability to estimate multiple parameters associated with metabolism for the species in the wild has been a gap in the literature and our work sheds light on how thermal habitats affect energy expenditures. In freshwater ecosystems of moderate size (surface area ≤ ~5,000 ha), where cold-water habitats will likely be reduced by climatic changes (Jane et al. 2021; Kraemer et al. 2021), metabolic costs for cold-water species will likely increase, affecting population health (i.e., survival, growth, and reproduction) and possibly resulting in extirpation from systems (Sharma et al. 2007; Schulte 2015). To successfully manage cold-water fisheries for ecological resiliency, insight into thermal habitat use and the metabolic costs of movement will be vital (Hansen et al. 2022). Future studies should continue to focus on how multiple factors affect Lake Trout metabolic costs (and those of other fishes) because this information will further facilitate the sustainable management of Lake Trout fisheries.

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Author contributions All authors contributed to the design of the study. Field work and sampling were conducted by all authors except M.P. Data analyses and figures were done by B.L.H. The manuscript was written by B.L.H with all authors contributing to revisions. Study design was conceived by B.L.H., J.E.C., D.P.P, J.E.M., M.P., and S.J.C.

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Data availability Data is available at the following GitHub repository.

Declarations

Conflict of interest All authors declare that they have no conflicts of interest.

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