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REGULAR ARTICLE

Calibrating acceleration transmitters to quantify the seasonal energetic costs of activity in lake trout

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Abstract

Bioenergetics models are powerful tools used to address a range of questions in fish biology. However, these models are rarely informed by free-swimming activity data, introducing error. To quantify the costs of activity in free-swimming fish, calibrations produced from standardized laboratory trials can be applied to estimate energy expenditure from sensor data for specific tags and species. Using swim tunnel respirometry, we calibrated acceleration sensor-equipped transmitting tags to estimate the aerobic metabolic rates ($\dot{M}O_2$) of lake trout (*Salvelinus namaycush*) at three environmentally relevant temperatures. Aerobic and swim performance were also assessed. Like other calibrations, we found strong relationships between $\dot{M}O_2$ and acceleration or swimming speed, and jackknife validations and data simulations suggest that our models accurately predict metabolic costs of activity in adult lake trout (~5% algebraic error and ~20% absolute error). Aerobic and swim performance metrics were similar to those reported in other studies, but their critical swimming speed was lower than expected. Additionally, lake trout exhibited a wide aerobic scope, suggesting that the avoidance of waters ≥15°C may be related to selection for optimal growing temperatures. The ability to quantify the free-swimming energetic costs of activity will advance our understanding of lake trout ecology and may yield improvements to bioenergetics model.

KEYWORDS
acceleration, bioenergetics, calibration, Lake trout, metabolic rate

1 | INTRODUCTION

Bioenergetics models are powerful analytical tools that can be used to address a broad range of questions related to physiology, ecology, aquaculture, and fisheries management (Armstrong & Schindler, 2011; Bevelhimer & Breck 2009; Brownscombe et al., 2022; Canale et al., 2013; Chipps & Wahl, 2008; Deslauriers et al., 2017; Hartman & Hayward, 2007; Madenjian, 2011). To date, estimates of the respiration component in bioenergetics models (note that here and elsewhere we refer specifically to the Wisconsin model; Kitchell et al., 1977) are often based on standard or resting metabolic rate, with an arbitrary activity multiplier that is rarely informed by actual activity values (Boisclair & Leggett, 1989; Deslauriers et al., 2017; Jørgensen et al., 2016). Traditional approaches such as these fail to

address the major yet variable impact that activity can have on fish bioenergetics. In natural ecosystems, wild fishes exhibit highly variable activity patterns. This is reflected in the broad range of energetic costs associated with activity, ranging from 0% to 40%, that fish may allocate to activity in their energy budgets (Boisclair & Leggett, 1989). Therefore, in applying bioenergetics models to real-world ecological scenarios, there is a major need to acquire more accurate estimates of activity-related metabolic costs.

In fish, metabolic rate is usually quantified using oxygen consumption as a proxy (i.e., $\dot{M}O_2$; Chabot et al., 2016). Currently, there is no device that can directly measure free-swimming metabolic rates in wild fish. However, because activity is often the major (and most variable) factor in modulating energy expenditure in fish (Boisclair & Leggett, 1989), measurements of activity can be used to estimate metabolic rate (Gleiss et al., 2011; Halsey et al., 2008). Over the past few decades, attempts have been made to use electronic tags equipped with various sensors to collect high-resolution measurements of activity from free-swimming fish (e.g., acceleration biologgers, Ropert-Coudert et al., 2012; electromyogram radio telemetry, Cooke et al., 2004; acoustic acceleration transmitters, Lennox et al., 2023). Prior to field deployment, calibrations must be conducted to produce models that permit the estimation of $\dot{M}O_2$ from sensor data for specific tag types and target species (Halsey & Bryce, 2021; Økland et al., 1997; Treberg et al., 2016; Weatherley et al., 1982). Ideally, these calibrations should incorporate an environmentally relevant range of temperatures, swimming speeds, and consider the range of fish size that will be tagged to improve their capacity to estimate changes in $\dot{M}O_2$ over time, between individuals, and across ecosystems (Treberg et al., 2016).

Calibrations between acceleration and $\dot{M}O_2$ have been produced for a number of fish species, including, but not limited to, sockeye salmon (*Oncorhynchus nerka*; Clark et al., 2010; Wilson et al., 2013), lake trout (*Salvelinus namaycush*; Cruz-Font et al., 2016), European and Japanese seabass (*Dicentrarchus labrax* and *Latealabrax japonicus*, respectively; Wright et al., 2014; Mori et al., 2015), bonefish (*Albula vulpes*; Nowell et al., 2015), as well as several species of shark (Gleiss et al., 2010; Lear et al., 2017, 2020, 2021). However, many calibrations have limited field utility, as relatively few have collected measurements of $\dot{M}O_2$ across a range of environmentally relevant temperatures (e.g., Brownscombe et al., 2017; Lear et al., 2017; Wilson et al., 2013; Wright et al., 2014) or used acoustic transmitters (e.g., Brownscombe et al., 2017; Cruz-Font et al., 2016; Lear et al., 2017, 2020, 2021; Wilson et al., 2013). Several other studies have calibrated heart rate to measurements of $\dot{M}O_2$ (e.g., Clark et al., 2010; Doherty et al., 2021; Lucas, 1994; Priede & Tytler, 1977); however, heart rate calibrations can be more challenging for field deployment, as there are no commercially available transmitting tags (i.e., only data-loggers are currently available for purchase), meaning fish must be recaptured to acquire the data. Moreover, using heart rates to estimate metabolic rate relies on the assumption that heart rate is the main factor controlling energy-linked blood flow, but some fish species are known to alter stroke volume to modulate cardiac output (e.g., Cooke et al., 2003; Thorarensen et al., 1996).

Lake trout are an ecologically and commercially important large, cold-water adapted, stenothermal species native to deep oligotrophic lakes in Canada and northern USA (Nieland et al., 2008; Scott & Crossman, 1973). Lake trout are particularly sensitive to climate warming due to a limited capacity for thermal acclimation, increased competition, and thermal exclusion from productive foraging areas (Ficke et al., 2007; Guzzo & Blanchfield, 2017; Kelly et al., 2014; Sharma et al., 2009). Metabolic rate measurements from wild lake tout will improve our understanding of their ecology, shedding light on how their energetic demands influence their movements and habitat use (e.g., see Cruz-Font et al., 2019; Hlina et al., 2024). Additionally, considering that the current lake trout bioenergetics model (i.e., Stewart et al., 1983) lacks information on their free-swimming costs of activity, incorporating free-swimming metabolic rate measurements in bioenergetics models could improve our ability to accurately predict how lake trout populations and lake trout–dominated systems respond to environmental change.

Cruz-Font et al. (2016) developed initial calibrations for accelerometer transmitters to estimate the energy expenditure in free-swimming lake trout in summer. In their study, $\dot{M}O_2$ measurements were collected for a single temperature (~12°C) and across a few swimming speeds, limiting their model's ability to accurately predict metabolic rate across seasons. Here, we seek to expand on the work of Cruz-Font et al. (2016) and produce functional models to predict energy expenditure across a range of temperatures and swimming speeds in lake trout using acceleration acoustic transmitters, expanding the predictive scope. This study is a fundamental part of a larger project that seeks to examine the behavioral and energetic costs associated with changing habitat availability and use within lakes as a result of climate warming. The goal of this project is to better inform projections on the anticipated impacts to lake trout and other cold-water fishes, improving our ability to adaptively manage lake trout systems.

2 | METHODS

2.1 | Experiment

Lake trout ($n = 15$, mean mass = 536 ± 36 g, ranging from 153 to 978 g; all values are mean ± SE of the mean unless otherwise noted) were collected from Big Turkey Lake (Algoma, Ontario, Canada) using ice angling between February 8 and 10, 2022, and transported to the Aquatic Life Research Facility at the Canadian Centre for Inland Waters (Burlington, Ontario, Canada). Big Turkey Lake contains populations of both natural and stocked lake trout, denoted with a fin clip (for this study: $n = 8$ wild and $n = 7$ stocked). On their arrival, lake trout were subjected to a prophylactic 0.7% salt treatment for 7 days and were maintained at ~5°C in a recirculating aquaculture system. During this period, fish underwent a surgical procedure. Lake trout were anaesthetized using 5°C water mixed with tricaine methanosulfate (MS-222) at 120 mg L^{-1} buffered with sodium bicarbonate at 2:1. During surgery, a maintenance dose of MS-222 (60 mg L^{-1}),

buffered with bicarbonate, was pumped over the fish's gills during the surgery to maintain appropriate sedation. A 3–4-cm incision was made 3 cm anterior of the anus on their ventral side, which permitted the insertion of a V9A Vemco accelerometer acoustic transmitter (length = 24 mm, mass in air = 3.6 g, mass in water = 2 g, recording frequency = 10 Hz, nominal delay = 55–65 s, sampling window = 27 s, ± 4.9 m s^2 sensitivity, tailbeat [2D] algorithm; InnovaSea, Canada). The tag was anchored to the body wall, just anterior to the opening, before closing the incision using three interrupted sutures (EthiconTM 3–0 PDS II Violet Monofilament CT-1 needle). Mean tag burden ± SD was 0.73% ± 0.37% (range = 0.33%–3.27%; for more details on the impacts of tag burden see Smircich & Kelly, 2014). After the surgery, morphometrics were recorded (i.e., mass, total length, width, and body depth). Fish were transferred into an aerated water-bath for recovery and then transferred back into their holding tanks. Fish had a minimum of 7 days to recover from the surgery before experimentation began (see Hvas et al., 2020; Zrini et al., 2021). Two days after the surgery, lake trout were offered food (San Francisco Bay Brand Sally's Frozen Bloodworms; 8239 Enterprise Drive, Newark, CA, USA, 94560). Food was withheld 48 h prior to experimentation.

After their recovery and acclimation period, lake trout were transferred into a 185-L acrylic swim tunnel respirometer (water-bath dimensions = 1735 × 850 × 375 cm, test section dimensions = 88 × 25 × 25 cm, inner length × width × height, respectively; Loligo Systems Inc., Viborg, Denmark, https://www.loligosystems.com) maintained at their holding temperature (i.e., 5°C; average temperature ± SD = 5.01 ± 0.35°C). A hydrophone (VR100 Acoustic Receiver; Innovasea, Canada) was placed within the water-bath next to the swim tunnel that collected and recorded acoustic transmissions of acceleration (m s^{-2}; V9A tags record and transmit the root mean square of acceleration averaged over the sampling window) during the swim trial.

Aerobic metabolic rate was estimated by measuring oxygen consumption (i.e., $\dot{M}O_2$, mgO_2 kg^{-1} h^{-1}) using intermittent-closed optical respirometry. The swim tunnel respirometer was fitted with two optodes and a temperature probe to measure the within-tunnel temperature-compensated oxygen concentration using a four-channel Firesting (PyroScience, Aachen, Germany). The swim tunnel was cleaned prior to experimentation to reduce microbial growth, and two blank measurements were recorded at each temperature to correct for background respiration that occurred within the tunnel. During the open period (i.e., flushing), oxygenated water was pumped into the swim tunnel from its surrounding water-bath using an Sicce Syncra 2.0 water pump (1250 L/h; Sicce, Pozzoleone, Italy; i.e., the flush pump) to ensure that the water within the tunnel was sufficiently saturated with oxygen.

Once in the swim tunnel, fish had 15 min to habituate to the new environment followed by a practice swim (to help habituate fish to swimming within the chamber; Jain et al., 1997) during which the flow was slowly increased to 30 cm s^{-1}. Once the desired flow was reached, the flush pump was turned off, and the fish continued to swim at this speed for 12 min. After 12 min had elapsed, the flow was decreased to 10 cm s^{-1}, and the flush pump was turned back on to reoxygenate the swim tunnel. If a fish did not complete the practice swim, it was returned to its holding tank and given a minimum of 24 h to recover before being tested again. After a successful practice swim, the fish were given 45 min to recover before being subjected to a modified ramp-U_{crit} protocol (Jain et al., 1997), where the flow was initially increased to 30 cm s^{-1} over 2 min and then increased by 10 cm s^{-1} every 30 min until the fish became exhausted and could no longer orient themselves into the flow. At the start of each 30-min interval, the flush pump was turned off, and the decline in within-tunnel oxygen was recorded over a 20-min period. After 20 min had elapsed, the flush pump was turned back on, replenishing within-tunnel oxygen levels before the next incremental increase in flow. Dissolved oxygen concentrations were always maintained in excess of 9 mgO_2 L^{-1}. In cases where fish did not swim to maintain position in the tunnel, an electric shock was administered using an electric grid (8 V; BK Precision DC Regulated Power Supply, model 1621A; BK Precision, USA) at the back of the swim tunnel to motivate the fish to swim. Swim trials ended once the fish had been shocked consecutively thrice with <5 s off the grid between shocks, after which they were transferred back into their holding tank (similar to the methods used in Jain and Farrell [2003] and Tudorache et al. [2007]).

Once all fish had been subjected to the modified U_{crit} protocol, the temperature in the holding tank was increased to ~15°C over 5 days (~2°C day^{-1}). Fish were acclimated to 15°C for 3 days; however, some fish responded poorly to this temperature, resulting in increased mortality for a subset of our sample (n = 7; 3 stocked and 4 wild). It is unclear why mortality occurred when water temperatures were raised, as other studies have successfully acclimated lake trout to much warmer temperatures using similar rates of warming (e.g., Kelly et al., 2014 and Hébert & Dunlop, 2020 were able to acclimate lake trout to 19°C). It's possible that lake trout of larger size may be more thermally sensitive to warming (Recsetar et al., 2012; Audzijonyte et al., 2020; e.g., our fish were ~ 600 g, whereas the fish used in their studies were ~ 100–250 g in size) or that lake trout can only tolerate a small temperature change using this rate of warming. To reduce stress, we lowered the temperature to 12°C over 3 days (~1°C day^{-1}). The fish were left to acclimate to 12°C for a minimum of 4 days. After this acclimation period, fish were transferred into a swim tunnel maintained at 15°C (average temperature ± SD = 15.08 ± 0.14°C) and were then subjected to the U_{crit} protocol described earlier. Fish had 1 h to acclimate to the elevated temperature prior to collecting measurements of swim performance and $\dot{M}O_2$. This acute change in temperature is not uncommon in wild lake trout and is somewhat representative of short littoral foraging events above the thermocline in the summer (Guzzo et al., 2017; Morbey et al., 2006). Once fish completed the U_{crit} protocol, they were transferred back into their holding tank and maintained at 12°C for a minimum of 7 days. After this period, fish were transferred into the swim tunnel, which was maintained at 12°C (average temperature ± SD = 12.08 ± 0.11°C), and once again subjected to the U_{crit} protocol.

To increase our sample size at 12 and 15°C, we collected additional lake trout from Kennisis Lake (n = 5, mean mass = 801

± 183 g, ranging from 510 to 1522 g; Haliburton, Ontario, Canada) using ice angling on February 28, 2023. These fish experienced the same methods as described above with respect to surgery, acclimation, and measurement of swim performance and $\dot{M}O_2$.

Fish collections were approved by Fisheries and Oceans Canada, and experimental work was approved by the Animal Care Committee (OPA-ACC-2022-15), following the standards and guidelines outlined by the Canadian Council on Animal Care.

2.2 | Data analysis

$\dot{M}O_2$ was measured from the slope of the decline in water oxygen content during the closed period. The first and last minutes of each closed period were excluded from the slope calculation to ensure that equilibrium was achieved in the chamber. If the slope of the decline in water oxygen content had an *r*-squared (R^2) value <0.9, $\dot{M}O_2$ was not calculated. Several fish displayed signs of stress during the first swimming speed (evidenced by irregular swimming and associated elevated acceleration values and $\dot{M}O_2$); therefore, we chose to exclude measurements of $\dot{M}O_2$ from the first swimming speed (i.e., 30 cm s^{-1}). Several irregularly high $\dot{M}O_2$ measurements ($n = 9$) were also identified and selectively removed from our analyses to reduce error caused by stress or irregular swimming behavior (corroborated by video observations; for more details see Table S1).

Swimming speed was corrected for body size (i.e., body lengths per second using total length; BL s^{-1}), as well as the solid blocking effect (Bell & Terhune, 1970). U_{crit} was calculated using the formula outlined by Brett (1964): $U_{crit} = U + (T/T_i \times U_i)$, where U is the penultimate speed, U_i is the velocity increment, T is the total time spent on swimming at the final velocity increment, and T_i is time interval for each increment.

We used linear mixed effects modeling (LMM; "lme4" package; Bates et al., 2023) to produce predictive models for the estimation of swimming speed from acceleration (and vice versa; see details below regarding the inclusion of Cruz-Font et al., 2016 data) and $\dot{M}O_2$ from acceleration or swimming speed with respect to fish size and temperature. Using the package "MuMIn" (Bartoń, 2023), we tested all possible model combinations, including two-way interactions with the following covariates: temperature, mass or total length, population (e.g., Turkey Lake, Kennisis Lake), stocked/wild, and depending on the model, swimming speed, or acceleration (see Table S2). It is known that $\dot{M}O_2$ scales exponentially with temperature and mass (White et al., 2005), and $\dot{M}O_2$ and acceleration have been shown to increase exponentially with swimming speed (e.g., Cruz-Font et al., 2016); therefore, these variables (i.e., $\dot{M}O_2$, mass, and acceleration) were log transformed to obtain linear and normalized data. Previous studies have described the relationship between $\dot{M}O_2$ and swimming speed using both semi-log and log–log equations (e.g., Brodie et al., 2016; Cruz-Font et al., 2016); therefore, we tested both methods to determine the best fit. Models were selected based on their AIC, with the lowest AIC being selected (Zuur et al., 2009).

The final reduced models (i.e., following single term deletions) were validated using a jackknife approach (e.g., Halsey et al., 2009; Lear et al., 2017). This involved excluding an individual fish's data from the total dataset, rebuilding the final model without said fish, then testing the new model on the excluded fish's data. Percentage error was calculated for each prediction post-jackknife as $[(\text{predicted} - \text{observed})/\text{observed}] \times 100$, and mean algebraic and absolute error (%) was calculated for each model (see Halsey et al., 2007, 2009). We also estimated prediction error by calculating the coefficient of variation (COV), using the bootstrap validation technique described by Byrnes et al. (2021).

Measurements from Cruz-Font et al. (2016; $n = 16$, mean mass = 1505 ± 58 g, ranging from 1002 to 1926 g) were included in our $\dot{M}O_2$ modeling as they followed a similar protocol and were tested at a similar temperature (11.76 ± 1.26°C). The fish used in the Cruz-Font et al. trials were first-generation hatchery lake trout from wild spawn collections taken from lakes Opeongo and Louisa (Algonquin Provincial Park, Ontario, Canada) in 2003 and 2004. Individual total lengths were estimated from recorded fork lengths using the conversion for Ontario lake trout populations described by Shuter et al. (1998). Cruz-Font et al. (2016) did not collect simultaneous measurements of acceleration and $\dot{M}O_2$ but instead used both the relationship between swimming speed and acceleration and between swimming speed and $\dot{M}O_2$ to estimate metabolic rate (see Figure 3 in Cruz-Font et al., 2016). Although we could use their predicted acceleration values (i.e., derived from their equation), we chose to use our own equation to predict acceleration from their recorded swimming speeds (Figure 1), as tag type and tag placement can impact acceleration values (e.g., see Figure 2 in Cruz-Font et al., 2016). Generally, estimations of acceleration were similar at lower swimming speeds, but, at higher swimming speeds, the Cruz-Font et al. (2016) equation estimated higher acceleration values. To assess the impact of these data on $\dot{M}O_2$ predictive models, models were produced both with and without the addition of Cruz-Font et al. (2016) data using the methods described earlier to determine if different variables were selected or if variable estimates were considerably different.

Cost of transport (COT) was calculated as $\dot{M}O_2$/swimming speed (in BL s^{-1}). For each individual, estimates of resting metabolic rate (RMR) were calculated using relationships between swimming speed (in BL s^{-1}) and log-transformed $\dot{M}O_{2\ 1kg}$. The equations followed the format: $\dot{M}O_{2\ 1kg} = a \cdot e^{b \cdot (\text{swimming speed})}$, where a equates to RMR (i.e., extrapolated $\dot{M}O_{2\ 1kg}$ at zero activity; Brett, 1964; Korsmeyer et al., 2002; Reeve et al., 2022), and b is the slope of the relationship between $\dot{M}O_{2\ 1kg}$ and swimming speed. RMR was not calculated for individuals that had fewer than three measurements of $\dot{M}O_2$ at a given temperature to reduce uncertainty in exponential relationships. We report RMR instead of standard metabolic rate (SMR), because SMR can only be attained when the fish are in an inactive, nongrowing, postabsorptive, non-stressed state (Chabot et al., 2016). Because we observed some signs of elevated $\dot{M}O_2$ in earlier swimming speeds, RMR is a more appropriate metric to report. For each individual, maximum metabolic rate (MMR) was determined as the highest recording of $\dot{M}O_2$. Aerobic scope (AS) was calculated as MMR − RMR. Cruz-Font et al. (2016) did not measure $\dot{M}O_2$ at critical swimming speeds, and most fish only swam at two swimming speeds (~30 and ~50–60 cm s^{-1}, respectively; $n = 10$). For these reasons, U_{crit},

MMR, and AS could not be calculated for these individuals, and RMR could not be calculated for most of them.

We investigated the effect of test temperature (i.e., 5, 12, and 15°C as categorical variables) and swimming speed (i.e., 40, 50, 60 cm s^{-1}, and so on as categorical variables) on metabolic and swim performance. To compare $\dot{M}O_2$ between acclimation temperatures and swimming speeds, which often included fish of various sizes, we calculated mass-adjusted $\dot{M}O_2$ for a 1-kg fish ($\dot{M}O_{2\ 1\ kg}$) using an allometric mass exponent of 0.85, following the equation outlined in Steffensen et al. (1994): $\dot{M}O_{2\,1kg} = \dot{M}O_2 \cdot \left(\frac{m}{1000}\right)^{(1-A)}$, where A is the mass exponent, and m is the fish's mass in grams (Beamish et al., 1989; Cruz-Font et al., 2016; Job, 1955). The effect of test temperature and swimming speed on metabolic and swim performance metrics (i.e., $\dot{M}O_{2\ 1kg}$, RMR_{1kg}, MMR_{1kg}, AS_{1kg}, COT_{1kg}, and U_{crit}) was determined using LMM. Metrics were assessed for normality, and $\dot{M}O_{2\ 1kg}$, RMR_{1kg}, MMR_{1kg}, and AS_{1kg} were log transformed.

We also produced temperature performance curves for MMR, RMR, and U_{crit} using LMM. MMR and U_{crit} were fit to quadratic equations, and RMR was fit to an exponential equation (Kraskura et al., 2023; Lee et al., 2003). Model combinations were tested with the following covariates: temperature, mass, length, population, and stocked/wild (note that if mass was not included, $\dot{M}O_{2\ 1kg}$ was used, i.e., MMR_{1kg}). Final models were selected based on AIC and visual observation of the predicted relationships.

In all models, individuals were included as a random effect to account for lack of independence in the data. Model assumptions were checked through visual inspection of residual plots. Conditional and marginal R^2 values were calculated using the function *r.squaredGLMM* ("MuMIn" package; Bartoń, 2023). Significant effects were calculated using ANOVA (*anova* function), and differences between groups were determined using post hoc multiple comparison tests with a Bonferroni-based adjustment (alpha = 0.05; "emmeans" package; Lenth, 2023).

All analyses were conducted using RStudio (version 4.2.1; R Core Team, 2019).

3 | RESULTS

3.1 | Predictive models

The following predictive models were produced:

1) $\log_{10}(A) = -0.346 + 1.997 \cdot \log_{10}(SS)$

2) $\log_{10}(SS) = 0.154 + 0.368 \cdot \log_{10}(A)$

3) $\log_{10}(\dot{M}O_2) = 2.113 + 0.019 \cdot T + 0.296 \cdot \log_{10}(A) + 0.021 \cdot [\log_{10}(A) \cdot T]$

4) $\log_{10}(\dot{M}O_2) = 5.499 + 0.010 \cdot T - 3.140 \cdot SS - 1.485 \cdot \log_{10}(L) + 1.347 \cdot [SS \cdot \log_{10}(L)]$

where SS is swimming speed (in BL s^{-1}), A is acceleration (in m s^{-2}), T is temperature (°C), and L is total length (in millimeters). We found that a semi-log relationship best explained the relationships between $\dot{M}O_2$ and swimming speed (when a log–log relationship $\Delta AIC = 198$ was used), whereas log–log relationships were used in all other models. Temperature had a significant influence on predictions of $\dot{M}O_2$ but was not selected as an explanatory variable in the predictive models for acceleration or swimming speed (i.e., models 1 and 2). Population or stocked/wild origins were not selected as covariates in any model, indicating little effect. The addition of data from Cruz-Font et al. (2016) appeared to have little impact on covariate selection and effect estimates when $\dot{M}O_2$ was predicted from acceleration (i.e., model 3; see Table 1); however, after these data were added, we found that predictions of $\dot{M}O_2$ were significantly affected by an interaction between swimming speed and total length, which was not noted previously (i.e., model 4; $p < 0.0001$; Tables 1 and S3). There was also a significant interactive effect between acceleration and temperature on predictions of $\dot{M}O_2$ in model 3 ($p < 0.0001$; Table S3). Variance was well explained by all models ($R^2_{Condional}$ ranged from 0.82 to 0.91; $R^2_{Marginal}$ ranged from 0.58 to 0.83; Table 2). Model 1 predicted acceleration from swimming speed with mean algebraic and absolute error rates of 6.6% ± 8.3% and 35.8% ± 3.1%, and a COV of 42.2% (Figure S1). Interestingly, the inverse of this equation (i.e., model 2) predicted swimming speed from acceleration with lower error (mean algebraic error = 2.2% ± 3.8%, mean absolute error = 14.8% ± 1.8%, COV = 10.9%; Figure S1). $\dot{M}O_2$ was predicted with mean algebraic and absolute error rates of 2.7% ± 2.8% and 15.2% ± 1.5% when acceleration was used and 7.2% ± 4.4% and 22.3% ± 2.7% when swimming speed was used (i.e., models 3 and 4, respectively; Figure S2). COV for these models were similar (~20%; Table 1).

3.2 | Temperature effects on performance

Test temperature significantly affected all metabolic and swim performance metrics, excluding RMR_{1kg}, although this effect did approach significance ($p = 0.088$; see Table S4). $\dot{M}O_{2\ 1kg}$ and acceleration significantly increased with swimming speed (see Table 2; Figure S3). MMR and AS increased significantly between 5 and 12°C, but there was no difference between 12 and 15°C (see Figure 2; Table S4). Temperature performance curves of RMR and MMR highlight these trends (Figure 3). RMR was best described when both temperature and mass, as well as their interaction were used, whereas MMR was best described using only temperature (see Tables S3 and S5). For this reason, we chose to model MMR using mass-adjusted metabolic rate (i.e., MMR_{1kg}) to permit more accurate extrapolation across sizes by applying the allometric mass exponent (i.e., 0.85) and following the equation outlined by Steffensen et al. (1994). MMR_{1kg} was significantly affected by temperature ($p = 0.003$), whereas RMR was not ($p = 0.093$). Additionally, RMR was not significantly affected by mass or its interaction with temperature, although these approached significance ($p = 0.055$ and 0.09, respectively; see Table S3). There was

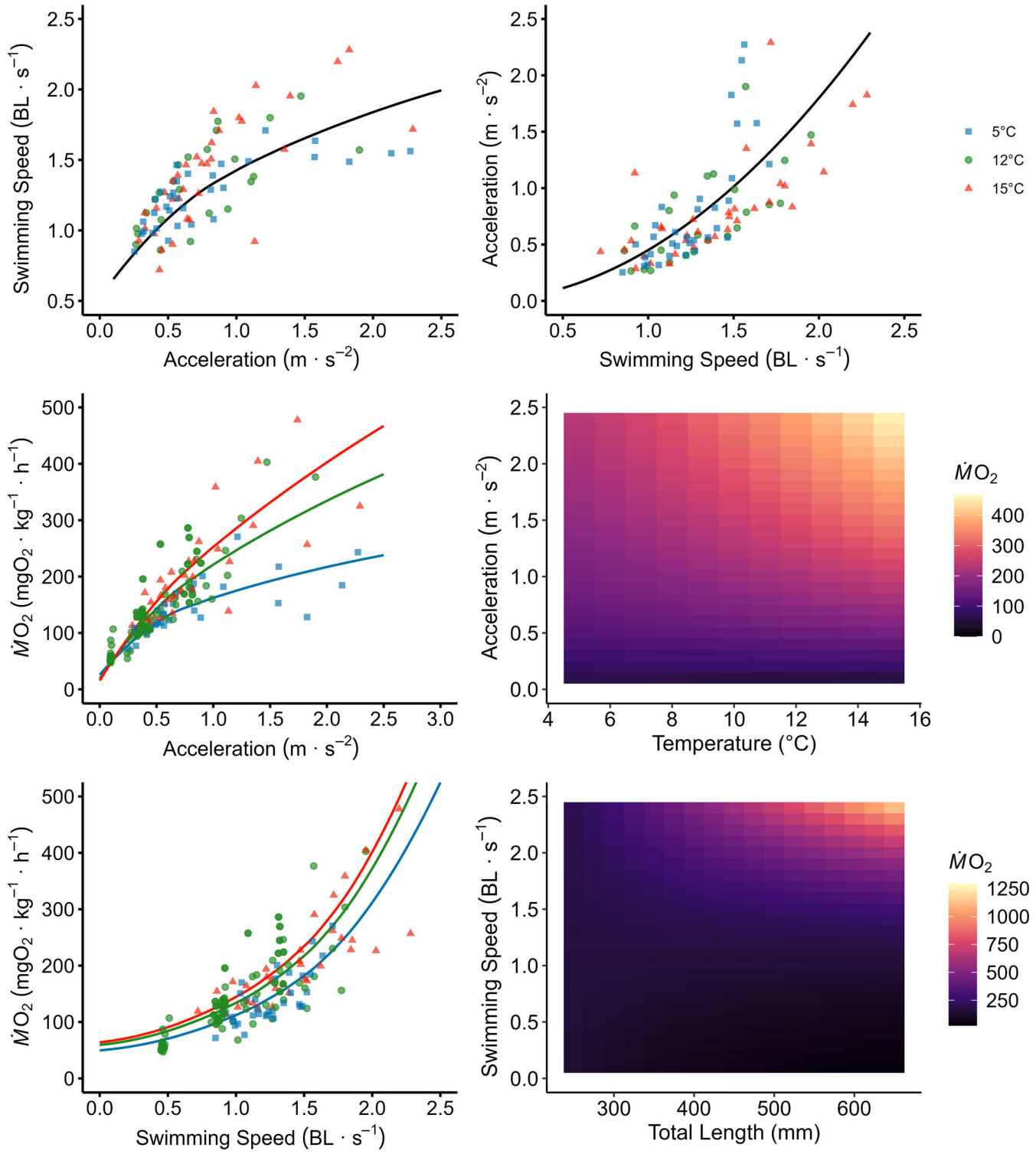

FIGURE 1 The relationships between temperature, swimming speed, acceleration, and $\dot{M}O_2$. Modeled relationships (predicted using models 1 to 4) are shown using solid lines, with different colors reflecting the different test temperatures. A black line was used when there was no effect of temperature. Different colored and shaped points reflect the measured values at each test temperature. Heatmaps demonstrate interactive effects on $\dot{M}O_2$.

considerable individual variation in measurements of MMR and RMR, and thus these performance curves only weakly explained the observed variance (Table S5). Nevertheless, these curves indicate minor narrowing of aerobic scope at 15°C (see Figure 2).

Lake trout attained higher U_{crit} at higher test temperatures ($p = 0.0158$; Table S4). However, there was considerable individual variation in U_{crit}, in particular, at 15°C (see Figure 3). Post hoc multiple comparisons revealed no significant differences in U_{crit} between test

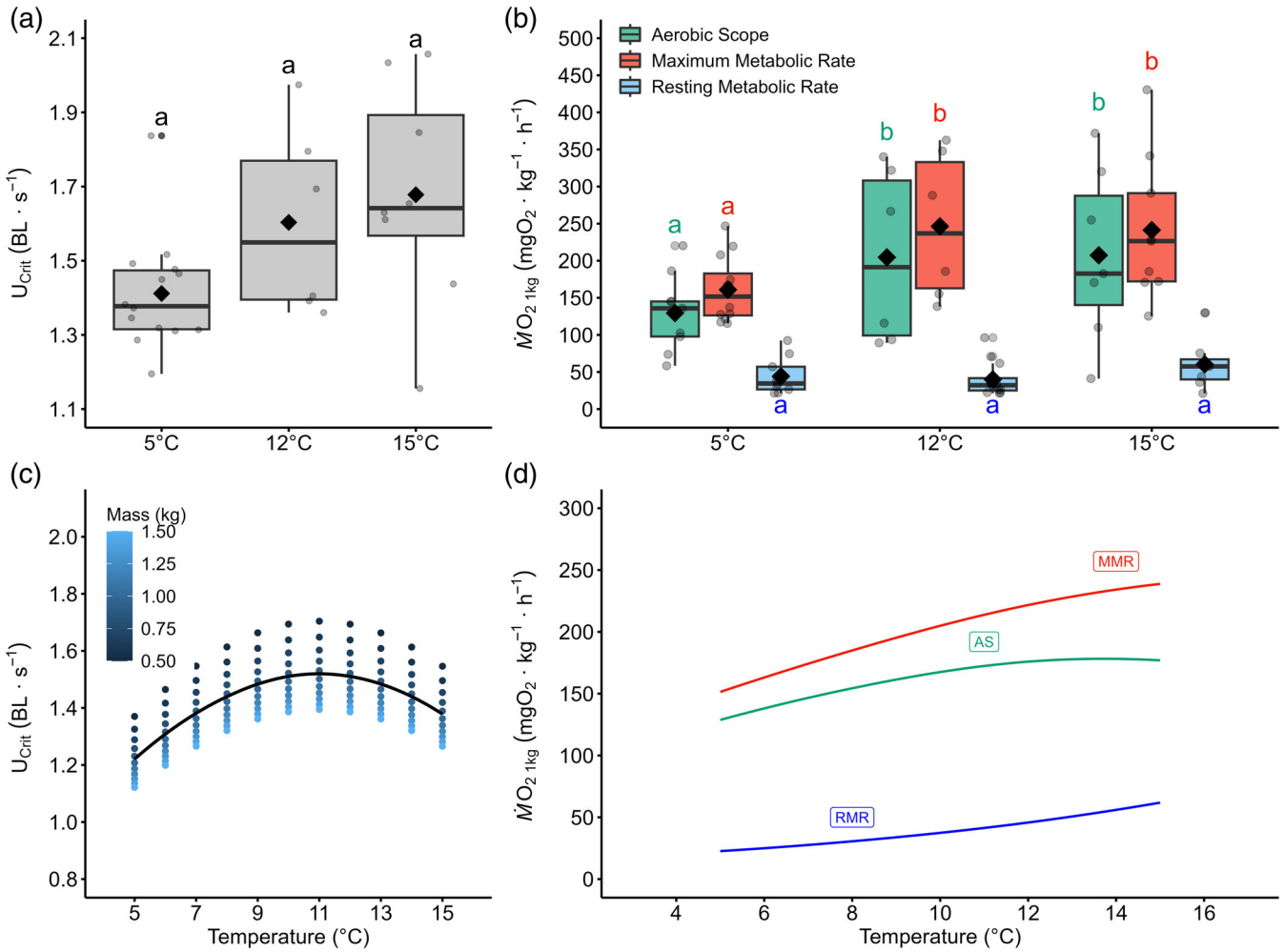

FIGURE 2 Temperature effects on aerobic and swim performance metrics. Panels A and B highlight measurements of U_{crit} (a) and aerobic scope (AS), maximum metabolic rate (MMR), and resting metabolic rate (RMR) (b) for each temperature treatment. Panels C and D highlight the temperature performance curves for U_{crit} (c) and AS, MMR, and standard metabolic rate (SMR) (d). Boxplots show the interquartile range, with whisker denoting the 95% CI. Black dots above or below the whiskers highlight outliers. Gray circles are observed measurements. Black diamonds reflect the mean value at each temperature. Letters denote significant differences between groups within a variable (differences determined using linear mixed effects models with Bonferroni-adjusted post hoc multiple comparisons tests; ANOVA outputs in Table S4). Temperature performance curves are summarized in Table S5 (ANOVA outputs in Table S3).

temperatures, although there was a near-significant difference between 5 and 12°C ($p = 0.0595$) and 5 and 15°C ($p = 0.0827$). The temperature performance curve of U_{Crit} suggests that optimal swim performance occurs at ~11°C; however like MMR_{1kg} and RMR performance curves, due to large individual variation in U_{crit}, this relationship weakly explained the observed variance (Figure 3; Table S5).

COT increased with increasing test temperatures but differed by swimming speed (see Table 2, Table S4). In general, lake trout displayed a higher COT at low or high speeds and a lower COT at intermediate speeds (e.g., 50 or 60 cm s^{-1}); however, COT at 50 cm s^{-1} and 12°C was elevated (see Figure S3).

4 | DISCUSSION

The ability to measure the energetic costs of activity in free-swimming lake trout will advance our understanding of their ecology and may yield improvements to their bioenergetics model. Here, we present modeled relationships that can be used to accurately estimate the $\dot{M}O_2$ of lake trout from recordings of acceleration or swimming speed. These models can be readily applied to similarly tagged lake trout to estimate free-swimming energy expenditure and swimming speed. As our ability to accurately track fish movements and estimate swimming activity improves (e.g., Kraft et al., 2023; Kraus et al., 2018), researchers may be able to approximate lake trout energy expenditure using swimming speed alone (i.e., they may not need accelerometer-equipped acoustic transmitters and could rely on acoustic transmissions alone). However, positioning error and the lack of signal at low speeds would have to be accounted for; thus, acceleration-based models appear to be the most accurate method for estimating the $\dot{M}O_2$ of free-swimming fish (e.g., Cruz-Font et al., 2016; Pereñíguez et al., 2022).

We found strong relationships between acceleration and swimming speed and between $\dot{M}O_2$ and acceleration or swimming speed

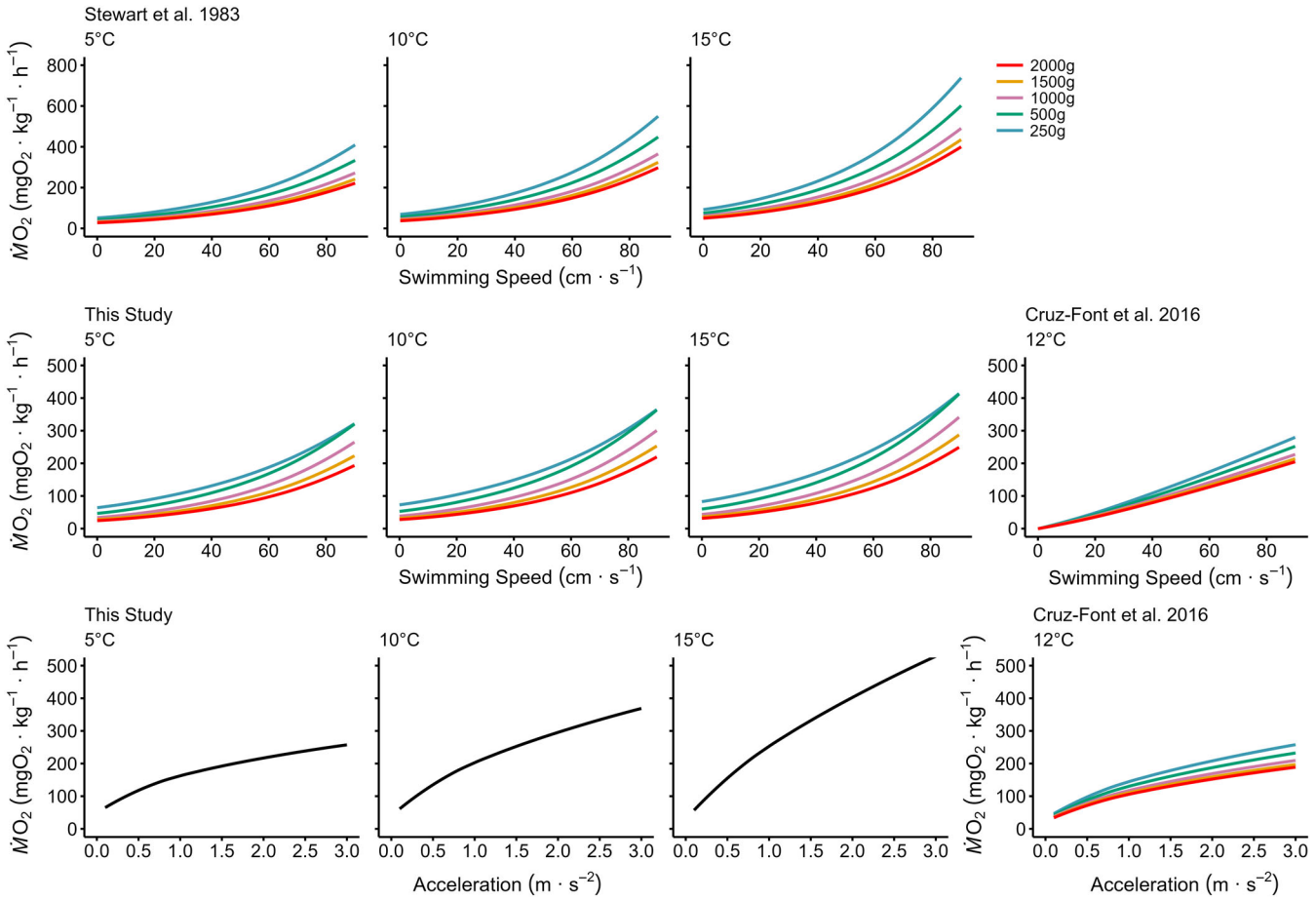

FIGURE 3 Predicted values of $\dot{M}O_2$ simulated for different-sized lake trout (mass classes shown using different colored lines) across a range of acceleration values or swimming speeds at three different temperatures. A black line was used when there was no effect of fish size. Predicted values of $\dot{M}O_2$ were generated using models 3 and 4, models developed by Cruz-Font et al. (2016), and the model developed by Stewart et al. (1983). Note that, because the Cruz-Font et al. (2016) and Stewart et al. (1983) models required speed in centimeters per seconds (cm s^{-1}) we needed to convert prediction values generated from model 4 to centimeters per seconds (cm s^{-1}). See Supplemental Material for more details on methods used for model comparisons.

similar to those reported in other calibration studies (e.g., Clark et al., 2010; Cruz-Font et al., 2016; Gleiss et al., 2010; Lear et al., 2017; Wilson et al., 2013; Wright et al., 2014). Error rates for predicting $\dot{M}O_2$ are similar to those reported in similar calibration studies (e.g., Byrnes et al., 2021; Halsey et al., 2009; Lear et al., 2017). To our knowledge, error rates have not been reported for predictions of acceleration from swimming speed or vice versa (i.e., models 1 and 2); however, our models demonstrated a similarly strong model fit compared to other calibrations (e.g., Brownscombe et al., 2017; Cruz-Font et al., 2016; Wright et al., 2014). Interestingly, despite explaining similar variance, error rates were noticeably higher when predicting acceleration from swimming speed than when predicting swimming speed from acceleration. It is likely that this occurred due to the larger variation in acceleration recordings. Generally, these models are accurate to estimate the mean energy expenditure of a group but are less accurate when estimating the specific energy expenditure of an individual (i.e., low algebraic error but higher absolute error; see Halsey et al., 2007). Considering the natural intraspecific variation in metabolic rate, these trends in prediction error make sense (e.g., Metcalfe et al., 2015). Although individual error rates were highly variable, error was typically lower at lower relative swimming speeds, which may translate to reduced individual error when applied to field data (e.g., Blanchfield et al. [2023] report daily swimming speeds <1 BL s^{-1}).

We found that total length interacts with swimming speed, significantly affecting predictions of $\dot{M}O_2$ such that an increase in relative swimming speed results in a proportionally greater increase in $\dot{M}O_2$ for longer lake trout. This interactive effect between swimming speed and total length likely results from the increasing drag forces associated with larger fish size, resulting in more laborious swimming (Webb et al., 1984). Interestingly, this interactive effect was not present in our model until the addition of Cruz-Font et al.'s (2016) data, demonstrating the importance of including a range of fish sizes in calibrations (i.e., lake trout in Cruz-Font et al. [2016] were ~ 1500 g). We also found an interactive effect between acceleration and temperature when predicting $\dot{M}O_2$, indicating that vigorous swimming (resulting in

TABLE 1 Predictive model summaries.

Response	Covariates	Estimates	Estimated 95% CI	$R^2_{Cond.}$, $R^2_{Marg.}$	COV	Algebraic error (%)	Absolute error (%)
$\log_{10}(A)$	Intercept	−0.3458	−0.4183, −0.2734	0.82, 0.60	42.2	6.6 ± 8.3	35.7 ± 3.1
	$\log_{10}$(SS)	1.9966	1.7343, 2.2462				
$\log_{10}$(SS)	Intercept	0.1535	0.1226, 0.1840	0.82, 0.58	10.9	2.2 ± 3.8	14.8 ± 1.8
	$\log_{10}(A)$	0.3679	0.3206, 0.4136				
$\log_{10}(\dot{M}O_2)$	Intercept	2.1007	2.0490, 2.1518	0.89, 0.80	17.5	1.4 ± 3.6	14.4 ± 1.7
	T	0.0188	0.0147, 0.0228				
	$\log_{10}(A)$	0.3053	0.1706, 0.4449				
	$\log_{10}(A)$:T	0.0257	0.0135, 0.0378				
***$\log_{10}(\dot{M}O_2)$**	Intercept	2.1130	2.0592, 2.1659	0.91, 0.83	19.3	2.7 ± 2.8	15.2 ± 1.5
	T	0.0193	0.0150, 0.0235				
	$\log_{10}(A)$	0.2962	0.1533, 0.4415				
	$\log_{10}(A)$:T	0.0212	0.0125, 0.0376				
$\log_{10}(\dot{M}O_2)$	Intercept	1.5666	1.4787, 1.6546	0.83, 0.64	21.3	7.1 ± 6.1	22.7 ± 3.6
	T	0.0101	0.3555, 0.4677				
	SS	0.4119	0.0053, 0.0148				
***$\log_{10}(\dot{M}O_2)$**	Intercept	5.4992	3.1181, 7.8594	0.88, 0.76	21.6	7.2 ± 4.4	22.3 ± 2.7
	T	0.0110	0.0063, 0.0156				
	SS	−3.1400	−4.7896, −1.4675				
	$\log_{10}(L)$	−1.4853	−2.3611, −0.6017				
	SS:$\log_{10}(L)$	1.3474	0.7249, 1.9611				

Note: Response variables with '*' indicate when Cruz-Font et al. (2016) data were included. Bolded response variables highlight correspond to the final models (i.e., models 1 to 4). Letters T, SS, A, L, P, and SW refer to temperature, swimming speed, acceleration, mass, total length, population, and stocked/wild.

Abbreviation: COV, coefficient of variation.

higher acceleration recordings) at higher temperatures results in a greater increase in $\dot{M}O_2$ than at lower temperatures. We believe this interaction highlights temperature effects on the COT in lake trout (discussed in greater detail below). To our knowledge, this interactive effect has not yet been described in other calibrations; however, few calibrations have considered a similarly wide range of temperatures.

We compared the existing models, which relate $\dot{M}O_2$ with swimming speed or acceleration in lake trout (i.e., Stewart et al., 1983; Cruz-Font et al., 2016; see Supplemental Material for details on methods used to compare models). We found that the Stewart et al. (1983) model appears to overestimate $\dot{M}O_2$ with increasing swimming speeds and temperature (see Figure 3). This is concerning considering that this model is used in the derivation of the currently used bioenergetics model for lake trout (e.g., see Deslauriers et al., 2017), potentially confounding its calculations. In contrast, we found that Cruz-Font et al.'s (2016) models underestimate $\dot{M}O_2$ when swimming speed or acceleration approaches zero. Like Cruz-Font et al. (2016), we also found that our acceleration-informed model (i.e., model 3) also underestimates $\dot{M}O_2$ at near-zero acceleration. Cruz-Font et al. (2016) found that acceleration values up to 0.15 m s^{-2} were typically observed in fish at rest, which appears to be consistent with our data (we found that acceleration at zero activity ≈0.12 m s^{-2}). Therefore, we suggest that users not extrapolate $\dot{M}O_2$ <0.1 m s^{-2}, treating these values as resting. In addition, because $\dot{M}O_2$ was related to averaged values of acceleration over the closed period, it is possible that irregularly high acceleration recordings (e.g., caused by quick turning maneuvers or erratic swimming) may result in overestimations of $\dot{M}O_2$. For example, high acceleration values (e.g., >3 m s^{-2}) were occasionally recorded during swim performance trials that did not correspond to high swimming speeds (e.g., see Figure S4). Therefore, future users of these models may consider averaging acceleration recordings over a period of time (e.g., 1 h) if high-resolution recordings are not needed and detection rates are good.

In addition to producing these predictive equations, we were able to record several ecologically important metabolic and swim performance end points, including RMR, MMR, AS, COT, and U_{crit}. After the metabolic rate to a similar sized fish (1-kg), our estimates of RMR were fairly consistent with other previously published reports of RMR or SMR (e.g., Beamish et al., 1989; Cruz-Font et al., 2016; Guzzo et al., 2019; Hébert & Dunlop, 2020). However, our estimates of RMR, MMR, and AS were quite variable, potentially due to the range of fish populations used (e.g., Hébert & Dunlop, 2020; Kelly et al., 2014). Because our model includes data from several different populations, including hatchery reared fish, it will lack specificity in

TABLE 2 Average mass, acceleration, $\dot{M}O_{2\ 1kg}$, and cost of transport (COT) values ± mean SE for each swimming speed and temperature.

Temperature	N	Mass (g)	Speed (cm s^{-1})	Corrected speed (cm s^{-1})	Corrected speed (BL s^{-1})	Acceleration (m s^{-2})	$\dot{M}O_{2\ 1kg}$ ($mgO_2\ kg^{-1}\ h^{-1}$)	COT_{100g} ($mgO_2\ kg^{-1}\ h^{-1}$) / (BL s^{-1})
5°C	10 T	556 ± 56	30	31.41 ± 0.13	0.75 ± 0.02	0.44 ± 0.08	NA	NA
	10 T	556 ± 56	40	41.88 ± 0.18	1.00 ± 0.03	0.52 ± 0.06	107.11 ± 7.98	106.20 ± 6.66
	10 T	556 ± 56	50	52.36 ± 0.23	1.25 ± 0.03	0.77 ± 0.04	116.70 ± 9.62	96.06 ± 6.44
	10 T	556 ± 56	60	62.99 ± 0.26	1.48 ± 0.04	1.28 ± 0.08	147.94 ± 10.85	101.80 ± 6.38
	2 T	612 ± 75	70	73.81 ± 0.62	1.69 ± 0.04	1.37 ± 0.56	227.28 ± 19.50	135.71 ± 8.68
	1 T	759	80	79.86	1.72	1.83	NA	NA
12°C	16CF	1285 ± 116	30	28.40 ± 0.55	0.53 ± 0.03	0.19 ± 0.04	65.86 ± 3.96	140.84 ± 7.50
	3 T; 2 K	604 ± 61	40	42.15 ± 0.18	0.93 ± 0.03	0.42 ± 0.08	97.36 ± 14.63	105.38 ± 16.98
	3 T; 3 K; 15CF	1377 ± 89	50	51.77 ± 0.49	0.94 ± 0.02	0.40 ± 0.03	138.96 ± 7.92	149.09 ± 7.48
	3 T; 3 K; 2CF	865 ± 176	60	62.26 ± 0.92	1.29 ± 0.07	0.68 ± 0.10	152.10 ± 13.37	120.43 ± 11.76
	3 T; 2 K; 3CF	848 ± 114	70	70.58 ± 1.34	1.47 ± 0.07	1.15 ± 0.30	216.89 ± 23.10	152.22 ± 14.46
	2 T; 6CF	1368 ± 144	80	79.65 ± 0.84	1.43 ± 0.07	1.00 ± 0.19	233.18 ± 18.58	167.66 ± 15.31
	1 T	495	90	94.71	2.20	3.19	NA	NA
15°C	4 T; 2 K	633 ± 146	30	31.66 ± 0.35	0.73 ± 0.06	0.42 ± 0.08	NA	NA
	4 T; 2 K	633 ± 146	40	41.82 ± 0.25	1.01 ± 0.08	0.58 ± 0.12	133.13 ± 8.99	132.52 ± 11.71
	6 T; 2 K	647 ± 133	50	51.55 ± 0.90	1.19 ± 0.10	0.73 ± 0.21	143.58 ± 9.16	124.10 ± 10.87
	5 T; 2 K	725 ± 142	60	62.17 ± 0.94	1.34 ± 0.08	0.62 ± 0.04	161.84 ± 9.37	122.19 ± 6.93
	5 T; 2 K	725 ± 142	70	72.80 ± 0.91	1.57 ± 0.09	1.12 ± 0.21	217.62 ± 20.69	138.25 ± 9.53
	4 T; 1 K	756 ± 197	80	82.97 ± 1.08	1.78 ± 0.13	1.07 ± 0.12	263.80 ± 37.17	148.96 ± 17.72
	2 T	476 ± 23	90	94.22 ± 0.49	2.24 ± 0.04	1.78 ± 0.43	329.30 ± 101.15	147.96 ± 47.93

Note: Swimming speed is shown as the ramp speed and the corrected speed (i.e., considering the blocking effect) in both cm s^{-1} and BL s^{-1}. Sample sizes (*N*) are shown for each temperature and swimming speed; letters refer to the different populations included (T = Big Turkey Lake; K = Kennisis Lake; CF = individuals included from Cruz-Font et al., 2016).
Abbreviation: COT, cost of transport; NA, not available.

predicting the metabolic responses of any one population but may be more broadly applicable to the lake trout populations within Ontario. Variability in RMR (and AS) could also result from the method used to estimate RMR (i.e., an extrapolation to zero activity), which is sensitive to error (e.g., elevated $\dot{M}O_2$ due to stress), especially because only a few measurements were used for each individual (i.e., three to six measurements of $\dot{M}O_2$).

We found a higher mean RMR at 5°C than at 12°C, which could be a result of the above-mentioned variability. However, Hébert and Dunlop (2020) also found elevated $\dot{M}O_2$ at their coldest test temperature (8°C) in some of their populations tested. Whether these reflect unstressed values, these measurements highlight lake trout's ability to maintain RMR in the cold. Our estimates of MMR are also similar to those reported by Hébert and Dunlop (2020; MMR ≈160 − 260 $mgO_2\ kg^{-1}\ h^{-1}$ from 8 to 15°C) and Kelly et al. (2014; MMR ≈210 − 260 $mgO_2\ kg^{-1}\ h^{-1}$ from 8 to 15°C) after $\dot{M}O_2$ was adjusted to a similar mass (i.e., 1 kg). We found that MMR and AS increased from 5°C but did not change when tested at 12 and 15°C. Hébert and Dunlop (2020) observed a similar response in their AS measurements, but MMR continued to increase with temperature (for most of their populations). This lack of change between 12 and 15°C may result from the acclimation and acute exposure to 15°C that we used or, as suggested by our temperature performance curves (see Figure 3), this lack of change could be due to impaired metabolic performance at higher temperatures. Nevertheless, lake trout appear to maintain a relatively wide aerobic scope over a large range of temperatures.

Evans (2007) aggregated lake trout SMR and MMR measurements from a number of different studies and found that their optimal temperature (T_{opt}) for aerobic scope is ~15°C and appears to remain relatively wide up until the warmest measurements (~22°C). However, although their aerobic performance appears to be maintained, lake trout avoid or limit their exposure to waters ≥15°C in the wild (Blanchfield et al., 2023; Guzzo et al., 2017; Plumb & Blanchfield, 2009). A similar phenomenon has been documented for brook trout (*Salvelinus fontinalis*) where they exhibit eurythermal aerobic performance and a wide aerobic scope at warm temperatures (e.g., ~23°C; Durhack et al., 2021) but avoid or limit exposure to temperatures >20°C in the wild (Bertolo et al., 2011; Petty et al., 2012). These results suggest that thermal habitat use is not driven by aerobic performance; instead these fish may be selecting for optimal growing temperatures (e.g., T_{opt} for growth = ~12°C for lake trout and ~15°C for brook trout; Edsall & Cleland, 2000; Hébert & Dunlop, 2020; Smith & Ridgway, 2019).

Interestingly, our U_{crit} temperature performance curve indicated that lake trout swim performance is optimal at a temperature similar to their T_{opt} for growth (see Figure 3); however, there was considerable individual variation in U_{crit}. Our measurements of U_{crit} were similar to those reported in Beamish et al. (1989) at 10°C (if we convert to absolute U_{crit}, i.e., in cm s^{-1}); however, Beamish et al. (1989) used significantly smaller fish (10–20 g). Previous studies have established that absolute swimming speed increases with size, but relative swimming speed decreases (Beamish, 1978; Hammer, 1995); therefore, we would expect our lake trout to have elicited greater U_{crit}. COT has not been recorded in lake tout; however, the trends observed in COT were similar to those reported for other salmonid species (e.g., sockeye [*Oncorhynchus nerka*] and coho [*Oncorhynchus kisutch*] salmon; Lee et al., 2003). Like Lee et al. (2003), we found that COT increased with temperature, and that the lowest COT was typically observed near 1 BL s^{-1} (average length = 480 ± 70 mm; see Figure S3).

There are some limitations that must be considered when interpreting these results and applying these models to the field (see Cooke et al., 2016). It is likely that the relationships between $\dot{M}O_2$ and acceleration, or swimming speed, are marginally different from those in the wild as a result of unnatural laboratory conditions (e.g., Lear et al., 2018). For instance, swim tunnel respirometry cannot account for energy-saving swimming behaviors (e.g., schooling; Marras et al., 2015), and it can constrain specific swimming gaits (Peake & Farrell, 2004). There is also a gradual increase in the contribution of anaerobic metabolic rate to fuel swimming with increasing swimming speed that cannot be accounted for in our $\dot{M}O_2$ measurements (Norin & Clark, 2016). Notably, our models cannot capture postexercise oxygen consumption (EPOC) that occurs following such anaerobic swimming. Our metabolic rates at 15°C also reflect the metabolic rates following a relatively acute exposure to 15°C rather than the metabolic rates following acclimation (due to difficulties during acclimation to 15°C; see Methods for more details). However, considering the thermal habitat and foraging behaviors used by lake trout (i.e., lake trout tend to reside in waters <10°C and make short forays into warmer littoral areas; Morbey et al., 2006; Guzzo et al., 2017), we believe that our calibrations should be representative of the metabolic rates observed in the wild.

The influence of capture and handling stress on metabolic rate could lead to overestimation of field metabolic rates, which should be considered when applying this model to wild lake trout (e.g., Martins et al., 2011). A longer acclimatory period within the swim tunnel (e.g., several hours or greater) may have helped to alleviate the effects of stress on metabolic rate (Chabot et al., 2016). However, overestimations in $\dot{M}O_2$ may be negated by the complex maneuvers (e.g., quick turning) fish exhibit in the wild, which are energetically costly (Boisclair & Leggett, 1989). Additionally, the potential selection of more thermally tolerant individuals (due to unintended mortality at the highest temperature treatment; see Methods for more details) may have impacted our models as thermal tolerance, and metabolic rates are thought to be linked in fish (e.g., Pörtner, 2010). Moreover, other environmental factors, such as hypoxia, fluctuating temperatures, and lack of food resources, can also influence metabolic rates (Evans, 2007; Gibson & Fry, 1954; Hvas et al., 2020). The incorporation of more environmentally relevant measurements will only improve the accuracy of existing bioenergetics models.

4.1 | Summary

We measured the $\dot{M}O_2$ of lake trout implanted with accelerometer-equipped acoustic transmitters during a modified U_{crit} swim protocol. Measurements of RMR, MMR, AS, and COT were similar to those reported in other studies, but U_{crit} was lower than expected. Lake trout exhibited a wide aerobic scope across the temperatures tested, suggesting that behavioral avoidance of waters ≥15°C in the wild (Guzzo et al., 2017; Plumb & Blanchfield, 2009) may be related to selection for optimal growing temperatures (Edsall & Cleland, 2000; Hébert & Dunlop, 2020), not inhibited aerobic performance. We modeled the relationships between $\dot{M}O_2$, swimming speed, and acceleration in a range of different-sized lake trout across three separate temperatures. Similar to other calibration studies, we observed strong relationships between $\dot{M}O_2$ and acceleration and $\dot{M}O_2$ and swimming speed. Using these relationships, we can accurately predict the $\dot{M}O_2$ of lake trout from measurements of acceleration in tagged individuals or from swimming speed data (e.g., estimated from telemetered movements). These models are useful tools for studying lake trout energy expenditure in the wild, provided that users are aware of the models' limitations and the possible limitations of their field data.

AUTHOR CONTRIBUTIONS

Connor Reeve: Data collection, data analysis, writing, review and editing. **Kurtis A. Smith:** Data collection, review and editing. **Paul A. Bzonek:** Data collection, review and editing. **Steven J. Cooke:** Conceptualization, supervision, review and editing, funding aquisition. **Paul J. Blanchfield:** Conceptualization, review and editing, funding aquisition. **Jacob W. Brownscombe:** Conceptualization, supervision, review and editing, funding aquisition.

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