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Using heart rate and acceleration biologgers to estimate winter activity costs in free-swimming largemouth bass

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ABSTRACT

Winter is a critical period for largemouth bass (*Micropterus nigricans*) with winter severity and duration limiting their population growth at northern latitudes. Unfortunately, we have an incomplete understanding of their winter behaviour and energy use in the wild. More winter-focused research is needed to better understand their annual energy budget, improve bioenergetics models, and establish baselines to assess the impacts of climate warming; however, winter research is challenging due to ice cover. Implantable tags show promise for winter-focused research as they can be deployed prior to ice formation. Here, using swim tunnel respirometry, we calibrated heart rate and acceleration biologgers to enable estimations of metabolic rate ($\dot{M}O_2$) and swimming speed in free-swimming largemouth bass across a range of winter-relevant temperatures. In addition, we assessed their aerobic and swim performance. Calculated group thermal sensitivities of most performance metrics indicated the passive physicochemical effects of temperature, suggesting little compensation in the cold; however, resting metabolic rate and critical swimming speed showed partial compensation. We found strong relationships between acceleration and swimming speed, as well as between $\dot{M}O_2$ and heart rate, acceleration, or swimming speed. Jackknife validations indicated that these modeled relationships accurately estimate swimming speed and $\dot{M}O_2$ from biologger recordings. However, there were relatively few reliable heart rate recordings to model the $\dot{M}O_2$ relationship. Recordings of heart rate were high-quality during holding but dropped during experimentation, potentially due to interference from aerobic muscles during swimming. The models informed by acceleration or swimming speed appear to be best suited for field applications.

1. Introduction

The onset of winter brings about significant seasonal changes for aquatic organisms including annual temperature minimums throughout the water column, shorter photoperiod, the potential for reduced oxygen (mainly in freshwater environments), and a reduced density of food resources (Shuter et al., 2012; Studd et al., 2021). In fish, these intra-annual variations are ecologically important drivers of physiological and behavioural changes that can promote species coexistence, influence competitive interactions and population dynamics, and often alter many aspects of their biology and life-history (Hurst, 2007; McMeans et al., 2020). For instance, winter can be a particularly stressful season for many fish species, which results in overwinter mortality, especially at the poleward edge of a species range (Hurst, 2007). Despite the biological and ecological significance of winter for fish, this period remains understudied (Marsden et al., 2021; Sutton et al., 2021). Problematically, climate warming is rapidly modifying historic winter norms (e.g., reductions in duration and severity; IPCC, 2013). Greater winter-relevant research is needed to establish baselines so that we may better understand the impacts of climate warming on fish (e.g., Farmer et al., 2015).

Our understanding of fish's responses to winter is limited in part because conducting winter research can be challenging as cold water and ice cover add technical and logistical obstacles (Marsden et al., 2021). Sensor-equipped biotelemetry or biologging tags can circumvent these challenges by being deployed prior to the onset of cold conditions

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and ice formation, and then continuously record fine-scale measurements over the winter. These tags can be equipped with accelerometers (i.e., activity sensors) and/or heart rate sensors which provide useful information on the individual's locomotor activity or physiological state (Cooke et al., 2016). Moreover, when standardized laboratory calibrations are performed, tag recordings of heart rate or acceleration can be used to estimate energy expenditure (e.g., Clark et al., 2010; Wright et al., 2014; Cruz-Font et al., 2016; Brownscombe et al., 2017; Lear et al. 2017).

Heart rate correlates well with energy expenditure since increased tissue oxygen demand must be supported by increased cardiac output, in accordance with Fick's principle (Fick, 1870). Heart rate calibrations rely on the assumption that heart rate has predominance over cardiac output, but many fish species are known to alter stroke volume independent of heart rate to modulate their cardiac output (Thorarensen et al., 1996; Shiels et al., 2006). Nevertheless, there is a growing body of evidence to suggest that heart rate remains an important regulator in energy linked cardiac output in fish (e.g., Lucas, 1994; Altimiras and Larsen, 2000; Cooke et al., 2003; Clark et al., 2010). Measurements of acceleration are useful to approximate swimming activity in fish since their locomotion relies on undulating tail beats which manifest in continual acceleration forces. Acceleration correlates well with energy use, as activity is often the major and most variable modulator of metabolism in fish (Gleiss et al., 2011). However, measurements of acceleration cannot portray changes in metabolic rate that do not result from activity (e.g., stress, digestion, etc.) which may be captured in heart rate recordings (Clark et al., 2013; Hvas et al., 2020).

Largemouth bass (*Micropterus nigricans*) is an economically important warm-water centrarchid fish species native to eastern and central United States, south-eastern Canada, and northern parts of Mexico (Warren, 2009), and invasive in many regions around the world (Kim et al., 2022; Long and Seguy, 2024). Since winter represents the primary constraint on their growth and distribution at northern latitudes, northern populations of largemouth bass are expected to proliferate and expand northward in response to climate warming (Hansen et al., 2017; Wu et al., 2023). Wintertime research on free-swimming largemouth bass is needed to better understand how climate warming will impact these northern populations and communities. Exemplified by winter-specific inaccuracies in their existing bioenergetics model (e.g., Wright et al., 1999), there is currently a coarse understanding of their winter behaviour and energy use in the wild. For instance, largemouth bass have long been considered a winter-dormant fish species, that presumably is inactive and non-feeding over the winter (Lemons and Crawshaw, 1985; Suski and Ridgway, 2009). As a result, their current model assumes that their metabolic costs of activity are zero (i.e., their metabolic costs equate to resting metabolism) below 10 °C (using the Trebitz model; Trebitz, 1991; Wright et al., 1999). However, field studies in North Carolina and Idaho, USA have demonstrated sustained winter activity in some largemouth bass (Woodward and Noble, 1999; Karchesky and Bennett, 2004). By deploying largemouth bass with calibrated sensor-equipped tags, one could assess their winter behaviour, activity, and energy use in fine detail which may be used to determine their overwintering strategy and improve their bioenergetics model.

This study aimed to generate heart rate and acceleration calibrations to estimate swimming speed and energy expenditure across a range of winter-relevant temperatures in free-swimming largemouth bass using heart rate and tri-axial acceleration biologgers. In doing so, this research will also support future field research on largemouth bass, bettering our ability to assess how they respond to the winter period.

2. Methods

Experimental methods and data analyses for calibration were established in Reeve et al. (In Review) on a study of lake trout (*Salvelinus namaycush*) but adapted here for use in largemouth bass.

2.1. Fish collection

Largemouth bass were collected from Stoney Lake (Peterborough County, Ontario; *n* = 11, total length = 429.6 ± 9.4 mm, mass = 882.9 ± 66.2 g; all values are mean ± standard error of the mean unless otherwise noted) in July 2022. Later, several largemouth bass were collected from Stoney Lake and Longpoint Bay, Lake Erie (Port Rowan, Ontario) in May 2023 to increase our sample sizes at 10 °C and 5 °C as several bass lacked the motivation to swim at these temperatures (e.g., 5 fish from the initial cohort refused to swim at 5 °C). Largemouth bass were collected based on size, with larger largemouth bass being selected to reduce tag burden (see details below). Bass were transported in aerated coolers filled with lake water to the Aquatic Life Research Facility at the Canadian Centre for Inland Waters (Burlington, Ontario, Canada) where they were held in circular fiberglass tanks (1600 L, 170x172cm). Upon their arrival largemouth bass were transitioned to their holding temperature (at a rate of 2 °C day^{-1}) and subjected to a prophylactic 0.7% salt (NaCl) treatment for 7 days in a recirculating system. The administration of NaCl has been shown to reduce stress and treat fungal, bacterial, and ectoparasites in freshwater fishes (Selosse and Rowland, 1990; Tavares-Dias, 2021). Largemouth bass from the July 2022 cohort were initially held at ~15 °C whereas the bass from the May 2023 cohort were initially held at ~10 °C. Shortly after their arrival, several bass from the May 2023 cohort developed an aggressive fungal infection resulting in the use of only 6 fish (*n* = 1 Stoney; *n* = 5 Longpoint Bay; total length = 391.2 ± 16.5 mm, mass = 762.8 ± 98.2 g). Thus, in total, 17 fish (total length = 413.6 ± 13.4 mm, mass = 836.9 ± 87.2 g, length range = 345–565 mm, mass range = 454–2010 g) were used in the swim performance trials; however, samples sizes varied by temperature (e.g., some fish refused to swim at 10 °C and 5 °C and the July 2023 cohort were only tested at 10 °C and 5 °C; sample sizes reported in Table 1).

2.2. Tag implantation

After their salt treatment, bass underwent surgery where either a TechnoSmArt Axy-5 (herein after referred to as Axy-5; length = 45 mm, width = 22 mm, height = 8 mm, mass in air = 11 g; TechnoSmArt, Guidonia Monticello, Italy) biologger or a Star Oddi centi-HRT-ACT G2 (herein after referred to as HRT-ACT; length = 46 mm, diameter = 15 mm, mass in air = 19 g, mass in water = 12 g; Star Oddi, Gardabaer, Iceland) biologger was implanted. Axy-5 s were programmed to record tri-axial acceleration at 10 Hz continuously and HRT-ACTs were programmed to record heart rate (at 125 Hz for 12 s), its associated electrocardiogram (ECG), and tri-axial acceleration (at 5 Hz for 60s) every 5 min. This sampling regime represented the maximum number of measurements that could be recorded while still saving the associated ECGs which we believed were necessary based on personal experience and the relatively low proportion of high-quality heart rates collected in similar studies (e.g., Doherty et al. 2022). To maximize the quantity of data that could be recorded during experimentation, HRT-ACT tags were progamed to begin recording within two days of experimentation.

Bass were anesthetized using 15 °C water mixed with tricaine methanesulfonate (MS-222; 120 mg L^{-1}) buffered with bicarbonate and during surgery a maintenance dose (60 mg L^{-1}) was pumped over their gills to ensure continued sedation. Prior to surgery, bass morphometrics were recorded (total length, width, height, and mass). To implant the Axy-5 tags a ~ 4–5 cm incision was made ~1 cm off-center on the bass' ventral side, between their anus and pectoral girdle (Fig. 1). A suture was tied around the midline of the tag with a slip knot, then the tag was inserted with the charging port oriented posteriorly and the flat side facing the body wall. The tied-on suture was passed through the body wall just posterior to the pelvic girdle and tied, anchoring the tag (EthiconTM 3–0 PDS II Violet Monofilament CT-1 needle). The incision was closed using 4–5 interrupted stitches. To implant the HRT-ACT tags, a ~ 3 cm incision was made off-center, just in front of the pectoral girdle

Table 1

Average overall dynamic body acceleration (ODBA), heart rate, $\dot{M}O_{2\ 1kg}$ and COT values, as well as their respective sample size for each swimming speed and temperature (shown as average ± s.e.m.; sample size). Swimming speed is shown as the ramp speed and the corrected speed (i.e., considering the blocking effect) in body lengths per *se*cond (BL sec^{-1}).

Temp.	Speed (cm sec^{-1})	Corrected Speed (BL sec^{-1})	ODBA (m sec^{-2})	Heart Rate (bpm)	$\dot{M}O_{2\ 1kg}$ (mgO_2 kg^{-1} h^{-1})	COT $_{1kg}$ (mgO_2 kg^{-1} h^{-1}) / (BL sec^{-1})
5 °C	15	0.39 ± 0.01; 9	0.62 ± 0.05; 9	21.0; 1	34.3 ± 6.8; 7	88.8 ± 11.7; 7
	20	0.53 ± 0.01; 9	1.16 ± 0.24; 9	20.0; 1	39.2 ± 7.9; 6	76.9 ± 16.4; 6
	25	0.66 ± 0.02; 7	1.19 ± 0.22; 7	21.0; 1	45.0 ± 9.7; 5	70.2 ± 15.9; 5
	30	0.78 ± 0.02; 4	2.06 ± 0.76; 4	43.0; 1	66.0 ± 8.9; 2	88.7 ± 16.0; 2
	35	0.88 ± 0.04; 2	0.93 ± 0.15; 2	NA	76.9 ± 5.4; 2	87.8 ± 2.2; 2
	40	1.05; 1	1.21	NA	NA	NA
10 °C	20	0.53 ± 0.01; 17	0.57 ± 0.06; 16	29.3 ± 2.5; 4	54.4 ± 7.5; 13	102.0 ± 9.0; 13
	30	0.80 ± 0.02; 17	0.84 ± 0.16; 16	30.4 ± 1.9; 4	66.9 ± 6.5; 15	85.1 ± 5.8; 15
	40	1.08 ± 0.02; 12	1.71 ± 0.30; 12	32.8 ± 2.6; 3	85.0 ± 8.3; 9	79.6 ± 7.0; 9
	50	1.32 ± 0.05; 4	1.62 ± 0.17; 4	40.5; 1	113.3 ± 11.5; 3	89.5 ± 10.2; 3
15 °C	20	0.53 ± 0.01; 9	0.35 ± 0.04; 9	43.7 ± 3.8; 5	71.6 ± 11.1; 8	132.6 ± 13.3; 8
	30	0.78 ± 0.02; 11	0.48 ± 0.04; 11	48.5 ± 1.6; 4	86.5 ± 8.8; 10	109.6 ± 10.1; 10
	40	1.04 ± 0.02; 11	0.99 ± 0.16; 11	51.6 ± 1.4; 4	109.4 ± 7.1; 9	104.4 ± 6.3; 9
	50	1.29 ± 0.03; 7	1.46 ± 0.33; 6	53.7; 1	132.3 ± 10.8; 5	101.0 ± 6.0; 5
	60	1.56 ± 0.04; 3	1.06 ± 0.17; 3	NA	127.6; 1	81.3; 1
	70	1.83; 1	3.68; 1	NA	NA	NA

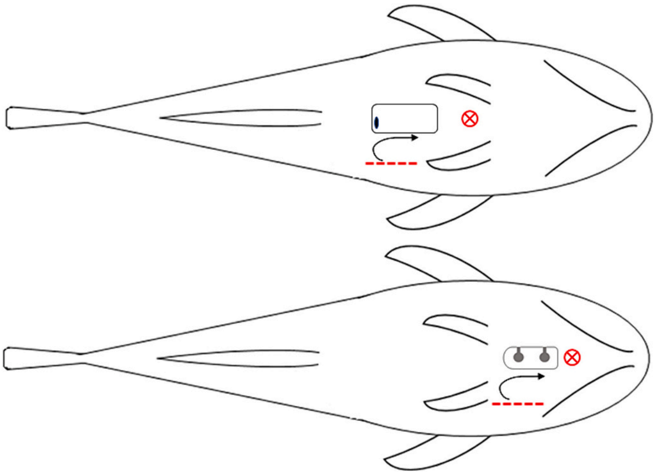

Fig. 1. Simple schematic illustrating the surgical implantation of the TechnoSmArt Axy-5(A) and Star Oddi centi-HRT-ACT (B) biologgers in largemouth bass. Shown is the ventral side of the bass. Red dotted lines signify the location of the incision, and the red crosses show where the anchors sutures were placed. The arrow highlights how the tag is inserted then oriented into the correction position. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

on their ventral side (Fig. 1). Two sutures were tied to the HRT-ACT (one through the attachment hole and one roughly midline around the biologger) then inserted blunt end towards the heart with the electrodes facing the body wall. The tied-on sutures were then passed through the body wall just posterior of the pericardium and just posterior of the pectoral girdle then tied to hold the tag in place. Tags were pulled forward so that they would be lightly pressed against the pericardium. Postmortem dissections indicated that HRT-ACT biologgers moved very little and were all within ~5 mm of the pericardium. An earlier exploration of different orientations in two bass indicated that this orientation and anchoring method yielded high quality heart rates (other orientations attempted included: a vertical orientation (e.g., see Doherty et al., 2022) and the round end towards to the heart). After the tag was inserted and anchored to the body wall, the incision was closed using 3–4 interrupted stitches. PIT tags (12 mm HDX) were also placed in the body cavity to aid with fish identification. The average tag burden ± s.d. for the Axy-5 and HRT-ACT biologgers were 1.32 ± 0.45% body mass (max = 1.92%, min = 0.59%) and 2.38 ± 0.51% body mass (max = 3.48%, min = 1.53%), respectively (see the 2% rule; Smircich and Kelly, 2014). After surgery, bass were transferred back to their holding tanks where they had a minimum of 10 days to recover prior to experimentation. The majority of surgical recovery is thought to occur within the first week following implantation. Following tag implantation, fish heart rates begin to stabilize after ~4 days but may remain marginally elevated for 2–3 weeks potentially due to a prolonged immune response to the tag (Semple et al., 2018; Brijs et al., 2018, 2019; Hvas et al., 2020; Zrini and Gamperl, 2021). Two days after surgery, bass were offered food (San Francisco Bay Brand® Sally's Frozen Bloodworms; 8239 Enterprise Drive, Newark, CA, 94560). Food was withheld 48 h prior to experimentation.

2.3. *Experiment*

Largemouth bass were tested at three temperatures (15 °C, 10 °C, and 5 °C; average temperatures ± s.d. = 15.01 ± 0.38 °C, 10.02 ± 0.28 °C, and 4.90 ± 0.36 °C), which represented the range of temperatures bass would experience between fall and spring in their northern range (e.g., see Wright et al., 1999). Bass had a minimum of 7 days to acclimate to each temperature (plus a 3-day cooling period following the completion of the previous temperature trial; holding tanks cooled at a rate of ~1.5 °C day^{-1}). We used a truncated acclimation period to reduce the amount of time the bass spent in laboratory since wild fish are more likely to develop infections when confined (Kent et al., 2009). Ideally, a > 3-week acclimation period would be used as this is typically the required period for full thermal acclimation (Sandblom et al., 2014; Nyboer and Chapman, 2017; Gilbert et al., 2022); however, it appears that most thermal acclimation of heart and metabolic rates occurs within 2–5 days with more gradual acclimation occurring over the following weeks (e.g., Klicka, 1965; Hanson and Stanley, 1970; Gilbert et al., 2022). For example, Reeve et al. (2022) found no difference in the standard metabolic rates of acutely cooled and 4–6 week acclimated pumpkinseed sunfish (*Lepomis gibbosus*; a similar species to largemouth bass).

Following their acclimation period, bass were moved to 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 and at a flow rate of 10 cm sec^{-1} (to ensure appropriate distribution of oxygen within the tunnel). Bass were allotted 15 min to acclimate to the new environment then subjected to a practice swim (to help habituate bass to swimming within the chamber; Jain and Farrell, 2003). The flow was slowly increased to an low swimming speed (30 cm sec^{-1} at 15 °C, and 20 cm sec^{-1} at 10 °C and 5 °C) and, once the desired flow was reached, bass swam for 12 min. If a fish did not complete the practice swim, they were returned to their holding tank and given a minimum of

24 h to recover prior to being tried again. Following a successful practice swim, bass were given a minimum of 45 mins to recover before being subjected to the swim performance trial. Ideally, an overnight acclimation period would be used (e.g., Norin and Clark, 2015); however, due to logistical challenges (e.g., maintaining healthy adult fish in a laboratory over a prolonged period or dealing with temperamental fish that refuse swimming) a shorter period was necessary to attain the desired sample size. The swim performance trial consisted of a modified ramp-U_{crit} protocol (Jain and Farrell, 2003) where, at 15 °C and 10 °C, the flow was initially increased to 20 cm sec^{-1} then increased by 10 cm sec^{-1} every 30 min until the bass became exhausted and could no longer orient themselves into the flow. Due to poorer swimming performance at 5 °C, the flow was initially increased to 15 cm sec^{-1} then increased by 5 cm sec^{-1} every 30 min until exhaustion. To prevent resting and ensure that bass continued swimming, an electric grid was placed at the back of the swim tunnel which could administer an electric shock (8 V; BK Precision DC Regulated Power Supply, model 1621 A; BK Precision, USA) to motivate swimming. Swim trials ended once bass had been shocked 3 times consecutively with <5 s off the grid between shocks (similar to the methods used in Jain and Farrell (2003) and Tudorache et al. (2007)). Afterwards, they were transferred back into their holding tank.

At the start of each 30 min interval, the flush pump (Sicce Syncra 2.0 waterpump, 1250 L hr^{-1}; Sicce, Pozzoleone, Italy) was turned off, and the decline in within-tunnel oxygen was recorded over a 20 min period. After 20 mins had elapsed, the flush pump was turned back on, replenishing within-tunnel oxygen levels before the next incremental increase in flow. Metabolic rate was estimated by measuring oxygen consumption ($\dot{M}O_2$, $mgO_2\ kg^{-1}\ h^{-1}$) using intermittent-closed optical respirometry. The swim tunnel respirometer was fitted with two optodes (OXROB10; PyroScience, Aachen, Germany) and a temperature probe to measure the within-tunnel temperature-compensated oxygen concentration, using a 4-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 (at approximately the half-way point and at the end of the trials) to correct for background respiration that occurred within the tunnel.

All fish collection, transport, and experimental procedures were approved by the Fisheries and Oceans Canada Ontario & Prairies Region Animal Care Committee (OPA-ACC-2022-15), following the standards and guidelines outlined by the Canadian Council on Animal Care.

2.4. *Data analysis*

$\dot{M}O_2$ ($mg\ O_2\ kg^{-1}\ h^{-1}$) was measured from the slope of the decline in water oxygen content during the closed period. The first and last minute of each closed period were excluded from slope calculation to ensure equilibrium was achieved in the chamber. Overall dynamic body acceleration (ODBA) was calculated as the absolute sum of dynamic acceleration from all three axes (static and dynamic acceleration were separated using weighted smoothing at an interval of 2 s; Wilson et al., 2006; Shepard et al., 2008). All HRT-ACT recordings of heart rate were corroborated using Star Oddi's quality index metric (determined by an on-board algorithm which grades the quality of heart rate recordings; high quality corresponds to QI = 0 and QI = 1–3 represent decreasing quality) and through visual inspection of ECGs. If QI >0 or a heart rate appeared irregular, the associated ECGs were assessed using the Star-Oddi HRT Analyzer (see https://www.star-oddi.com/support/software for details). Poor quality heart rates typically resulted from increased noise in ECG recordings which can interfere with heart rate calculations. If the R-R interval (i.e., the successive peaks of the QRS waveform produced during depolarization of the ventricles) was observable amongst the noise, heart rates were manually calculated to reduce data loss. If the R-R interval could not be differentiated from the background noise, the associated heart rate was removed.

In a few instances bass displayed signs of stress or irregular swimming behaviour (evidenced by elevated ODBA values and metabolic rates); therefore, we chose to exclude these measurements from our analyses (for more details see Table S1; sample sizes for included data shown in Table 1). Additionally, $\dot{M}O_2$ was not calculated if the slope of the decline in water oxygen content had an r-squared (R^2) value <0.9 (often resulting from a short period of swimming at their final swimming speed). Swimming speed was corrected for the solid blocking effect (Bell and Terhune, 1970) and standardized by fish length (i.e., body lengths per second using total length; BL sec^{-1}).

All analyses were conducted using RStudio (Version 4.2.1; R Core Team, 2022). In all models, individuals were included as a random effect to account for a lack of independence in the data. Using linear mixed modeling (LMM; 'lme4' package; Bates et al., 2023), we modeled the relationships between ODBA, swimming speed, heart rate, and $\dot{M}O_2$ with respect to fish size and temperature. Several models were produced to predict $\dot{M}O_2$ from heart rate, ODBA, or swimming speed, and to predict swimming speed from ODBA. We tested all possible model combinations (using the package 'MuMIn'; Bartoń, 2023) and their two-way interactions. Covariates included in model testing included temperature, mass or total length, and depending on the model, acceleration, swimming speed, or heart rate. $\dot{M}O_2$, heart rate, ODBA, and mass were $\log_{10}$ transformed. Reeve et al. (In Review) found that the acceleration-swimming speed relationship was best explained using a log-log relationship (i.e., log-transformed ODBA and swimming speed) whereas the swimming speed-$\dot{M}O_2$ relationship was best explained using a semi-log relationship (i.e., only $\dot{M}O_2$ is log-transformed); thus, we modeled our relationships using the same formula. The top models were selected based on Akaike information criterion (AIC; with the lowest AIC being selected; Zuur et al., 2009).

The top five models selected based on AIC were validated using a jackknife approach (Halsey et al., 2009; Lear et al. 2017) which involved excluding an individual fish's data from the total dataset, rebuilding the final model without said fish, then testing the new linear model on the excluded fish's data. This was repeated for each individual. We then determined the percent error of the residuals post-jackknife for each individual using the formula $[(\text{predicted}–\text{observed})/\text{observed}] \times 100$. Using these values, mean algebraic and absolute error rates were then calculated for each model (see Halsey et al., 2007, 2009). In addition, we calculated the coefficient of variation (COV), which explains percent variation in predictions from the observed mean, using the bootstrap validation technique described in Byrnes et al. (2021). Final models were selected based on AIC, error rates, and visual observation of model predictions while prioritizing models with fewer covariables.

U_{crit} was calculated using the formula described in 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 swimming at the final velocity increment and T_i is time interval for each increment. Cost of transport (COT) was calculated as $\dot{M}O_2$ / swimming speed (in BL sec^{-1}). Resting metabolic rate (RMR) was estimated using individual linear relationships between swimming speed (BL sec^{-1}) and log-transformed $\dot{M}O_2$. The equations followed the format: $\dot{M}O_2 = a \bullet e^{b \bullet (\text{swimming speed})}$, where RMR equates to the y-intercept (i.e., extrapolated $\dot{M}O_{2\ 1kg}$ at zero activity; Brett, 1964; Korsmeyer et al., 2002; Reeve et al., 2022). RMR was not calculated for individuals that had less than three measurements of $\dot{M}O_2$ at a given temperature (i.e., the bass failed to complete three or more different swimming speeds, or an erroneous $\dot{M}O_2$ measurement was otherwise removed) to reduce uncertainty in the exponential relationships. We define here RMR rather than standard metabolic rate as we cannot be certain that stress did not contribute to measurements of metabolic rate since we used a shortened acclimation period. Maximum metabolic rate (MMR) was recorded as the highest recording of $\dot{M}O_2$ for each individual. Aerobic scope (AS) was calculated as MMR – RMR.

We produced thermal performance curves of RMR, MMR, AS and U_{crit} using LMM to assess the impact of temperature on largemouth bass aerobic and swim performance. These models were produced and tested with different combinations of the covariates, temperature and mass or total length and their two-way interactions. Additionally, models were tested in the form of exponential and quadratic equations, as both forms have been previously used to describe the effect of temperature on aerobic or swim performance (e.g., Lee et al., 2003; Kraskura et al., 2023). Final models were selected based on AIC and visual observation of the predicted relationships. Additionally, we assessed the effects of acclimation temperature (i.e., 5 °C, 10 °C, and 15 °C as categorical variables) and swimming speed (i.e., 30 cm sec^{-1}, 40 cm sec^{-1}, and so on as categorical variable) on aerobic and swim performance metrics using LMM. Since fish size differed between acclimation temperatures and swimming speeds aerobic performance (i.e., COT, RMR, MMR, etc.) was compared using mass-adjusted metabolic rates for a 1 kg bass ($\dot{M}O_{2\ 1kg}$), calculated using the allometric mass exponent of 0.65 (derived from Beamish (1970)) and following the equation described in Steffensen et al. (1994): $\dot{M}O_{2\ 1kg} = \dot{M}O_2 \bullet \left(\frac{m}{1000}\right)^{(1-A)}$, where A is the mass exponent and m is the fish's mass in g. Therefore, we specifically investigated the effects of acclimation temperature and swimming speed

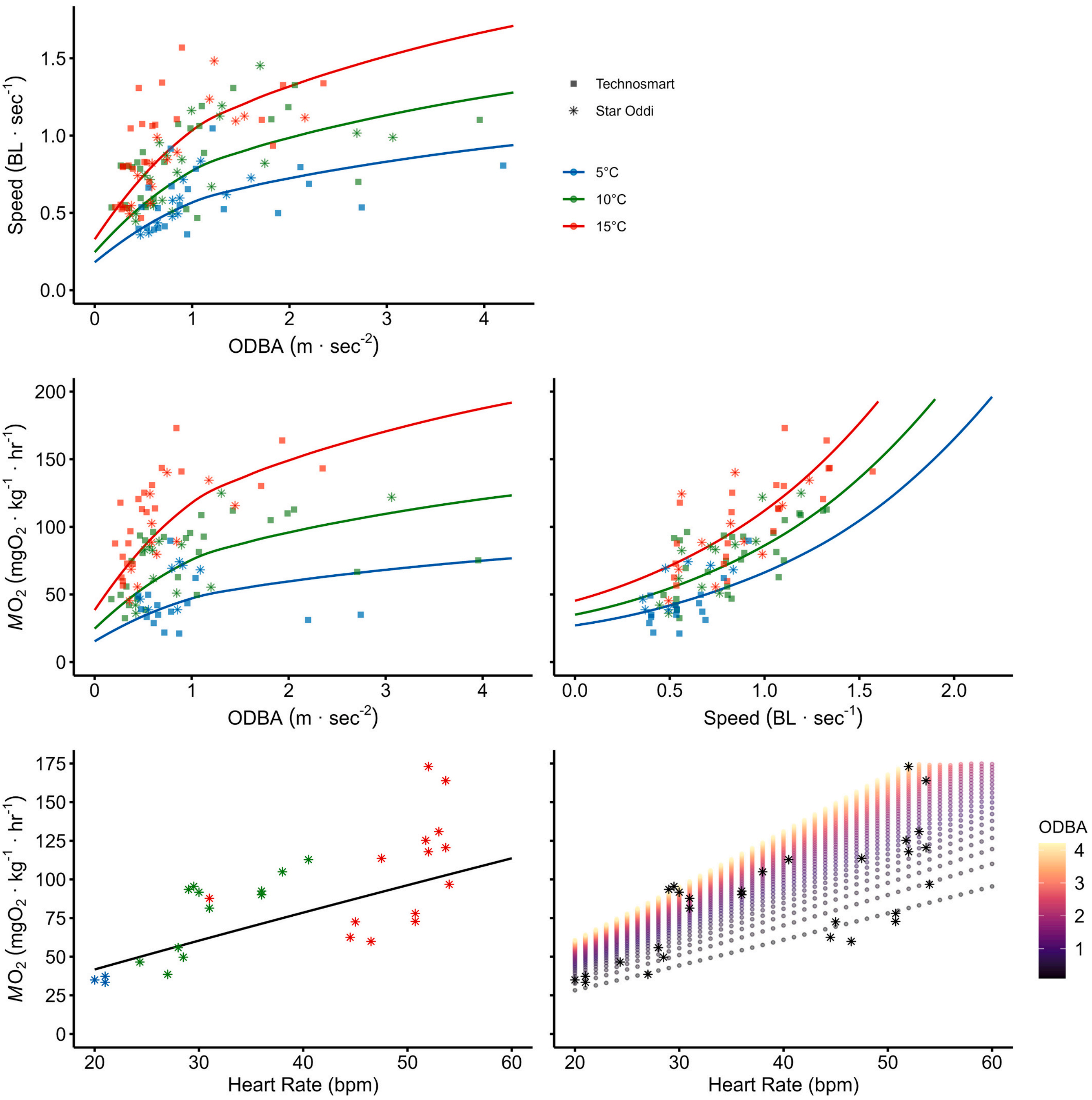

Fig. 2. The relationships between temperature, swimming speed, ODBA, heart rate, and $\dot{M}O_2$. Measurements corresponding to bass implanted with TechnoSmArt Axy-5 and Star Oddi cent-HRT-ACT biologgers are denoted using square and star symbols, respectively. Modeled relationships are shown with solid lines. Colour corresponds to the acclimation temperature. Note that, because the relationship between heart rate and $\dot{M}O_2$ was unaffected by temperature, only a single solid black line was used to illustrate the modeled relationship. To illustrate the combined effects of acceleration and heart rate on predictions of $\dot{M}O_2$, we show the modeled relationship for a range of ODBA values.

on $\dot{M}O_{2\ 1kg}$, COT_{1kg}, RMR_{1kg}, MMR_{1kg}, and AS_{1kg}, as well as ODBA and U_{crit}. Average thermal sensitivities (Q_{10}) were calculated for using average RMR_{1kg}, MMR_{1kg}, AS_{1kg}, U_{crit}, and routine heart rate (i.e., heart rate during holding) over the temperature intervals 5-10 °C, 10-15 °C, and 5–15 °C. Individual Q_{10} could not be calculated since some individuals were not measured at all acclimation temperatures.

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 analysis of variance (ANOVA; *anova* function) and differences between groups were determined using Bonferroni adjusted post hoc multiple comparisons tests (alpha = 0.05; ‘emmeans’ package; Lenth, 2023).

3. Results

Predictions of swimming speed, based on measurements of ODBA, and predictions of $\dot{M}O_2$ based on measurements of ODBA, swimming speed, and heart rate were best explained using the following equations:

$$\log_{10}(SS) = 1.316 + 0.028 \bullet (T) - 0.651 \bullet \log_{10}(L) + 0.342 \bullet \log_{10}(A) \tag{1}$$

$$\log_{10}(\dot{M}O_2) = 4.449 + 0.043 \bullet (T) - 1.145 \bullet \log_{10}(L) + 0.332 \bullet \log_{10}(A) \tag{2}$$

$$\log_{10}(\dot{M}O_2) = 1.314 + 0.394 \bullet (T) + 0.023 \bullet (SS) \tag{3}$$

$$\log_{10}(\dot{M}O_2) = 9.437 - 3.437 \bullet \log_{10}(L) + 0.912 \bullet \log_{10}(HR) \tag{4}$$

$$\log_{10}(\dot{M}O_2) = 10.230 - 3.837 \bullet \log_{10}(L) + 1.108 \bullet \log_{10}(HR) + 0.205 \bullet \log_{10}(A) \tag{5}$$

Where *SS* is swimming speed (BL sec^{-1}), *A* is ODBA (m sec^{-2}), *HR* is heart rate (bpm), *T* is temperature (°C), and *L* is total length (mm). Interestingly, our model selection approach indicated that tag type (i.e., Star Oddi or TechnoSmArt) had little impact on predictions of swimming speed or $\dot{M}O_2$ as tag type was not selected as an explanatory variable in any of the top models (see Table S2). Temperature had a significant effect on swimming speed and $\dot{M}O_2$ in all models except for the models informed by heart rate measurements (see Fig. 2, Table 2, Table S3). Total length was a better predictor than mass, being selected as an explanatory variable in all models excluding model 3, likely because swimming speed was already corrected for body size in this model (i.e., swimming speed is in units of BL sec^{-1}). Using model 1, swimming speed was predicted with a mean algebraic error rate of 4.2 ± 5.5%, a mean absolute error rate of 22.7 ± 3.3% and a COV of 24.8%. Models 2, 3, and 5 predicted $\dot{M}O_2$ with roughly similar mean algebraic and absolute error, and COV (~5%, ~25%, and 25%, respectively; Table 2, Fig. S1). Error rates were relatively higher in model 4 (mean alg. error = 7.3 ± 17.3%, mean abs. error = 36.4 ± 6.3%, COV = 31.6%; Fig. S1, Table 2), likely due to difficulty obtaining reliable heart rate recordings during the swim performance tests. Recordings of heart rate were of high quality during holding but dropped precipitously during experimentation (average quality index ± s.d. during holding = 0.67 ± 0.63 and during experimentation = 1.56 ± 0.47; analysis included all HRT-ACT tagged bass, including those that did not swim at 5 °C; see Fig. S2). Therefore, there were fewer data available for modeling the relationships between heart rate and $\dot{M}O_2$, in particular at 5 °C (see Table 1).

Calculated thermal sensitivities were similar amongst most performance metrics and temperature intervals tested (i.e., 10 °C to 5 °C, 15 °C to 5 °C, and 15 °C to 10 °C; see Table 3). Average thermal sensitivities of MMR_{1kg} and routine heart rate ranged between $Q_{10} = 2$ and 3 across all temperature intervals. Like MMR_{1kg} and routine heart rate, AS_{1kg} was

Table 3
Average performance metrics and routine heart rate at each acclimation temperature, with associated thermal sensitivities across several temperature changes. *N* indicates the sample size. Note that there is a greater number of individuals included in routine heart rate measurements, relative to those included in our modeling or other analyses, as these data also included individuals that refused to swim.

Metric	Temp.	*N*	Average Value	Q_{10} Interval	Q_{10}
RMR_{1kg}	5 °C	7	29.0 ± 5.4	10 °C – 5 °C	1.78
	10 °C	14	38.9 ± 5.6	15 °C – 5 °C	1.82
	15 °C	10	53.0 ± 9.0	15 °C – 10 °C	1.86
MMR_{1kg}	5 °C	7	48.4 ± 8.5	10 °C – 5 °C	2.62
	10 °C	16	79.8 ± 6.3	15 °C – 5 °C	2.63
	15 °C	11	129.6 ± 5.0	15 °C – 10 °C	2.64
AS_{1kg}	5 °C	4	19.4 ± 10.4	10 °C – 5 °C	5.16
	10 °C	6	44.8 ± 7.9	15 °C – 5 °C	3.84
	15 °C	7	75.6 ± 11.6	15 °C – 10 °C	2.84
U_{crit}	5 °C	7	0.68 ± 0.05	10 °C – 5 °C	1.56
	10 °C	16	0.85 ± 0.05	15 °C – 5 °C	1.65
	15 °C	11	1.13 ± 0.08	15 °C – 10 °C	1.75
Routine Heart Rate	5 °C	9	19.1 ± 1.3	10 °C – 5 °C	2.04
	10 °C	9	27.0 ± 1.3	15 °C – 5 °C	2.38
	15 °C	11	41.9 ± 1.8	15 °C – 10 °C	2.86

Table 2
Predictive model summaries. Letters *SS*, *A*, HR, and *L* refer to swimming speed, acceleration (i.e., ODBA), heart rate, and total length. Error was calculated following jackknife validations (see Methods for more details).

Response	Covariates	Est.	Est. 95% CI	$R^2_{Cond.}$, $R^2_{Marg.}$	COV	Alg. Error (%)	Abs. Error (%)
$\log_{10}(SS)$	Intercept	1.3156	−0.2495, 2.8937	0.65, 0.57	24.8	4.2 ± 5.5	22.7 ± 3.3
	T	0.0277	0.0219, 0.0327				
	$\log_{10}(L)$	−0.6505	−1.2565, −0.0515				
	$\log_{10}(A)$	0.3423	0.2713, 0.4074				
$\log_{10}(\dot{M}O_2)$	Intercept	4.4489	1.6248, 7.3087	0.82, 0.62	22.8	5.4 ± 8.1	28.0 ± 5.1
	T	0.0426	0.0369, 0.0482				
	$\log_{10}(L)$	−1.1446	−2.2360, −0.0676				
	$\log_{10}(A)$	0.3321	0.2527, 0.4092				
$\log_{10}(\dot{M}O_2)$	Intercept	1.3139	1.2374, 1.3904	0.82, 0.65	23.7	6.6 ± 6.9	23.8 ± 4.5
	T	0.3942	0.0169, 0.0285				
	SS	0.0227	0.3182, 0.4708				
$\log_{10}(\dot{M}O_2)$	Intercept	9.4369	−4.2095, 23.1840	0.58, 0.49	31.6	7.3 ± 17.3	36.4 ± 6.3
	$\log_{10}(L)$	−3.4368	−8.6837, 1.7889				
	$\log_{10}(HR)$	0.9120	0.6258, 1.372				
$\log_{10}(\dot{M}O_2)$	Intercept	10.2298	0.2864, 20.1682	0.70, 0.70	25.2	0.1 ± 13.8	27.7 ± 5.5
	$\log_{10}(L)$	−3.8374	−7.6299, −0.0443				
	$\log_{10}(HR)$	1.1075	0.8285, 1.3866				
	$\log_{10}(A)$	0.2050	0.0781, 0.3319				

between $Q_{10} = 2$ and 3 between 15 °C and 10 °C, but was elevated between 10 °C and 5 °C, and 15 °C and 5 °C ($Q_{10} = 5.16$ and 3.84, respectively). RMR and U_{crit} thermal sensitivities were lower than the other metrics, ranging between $Q_{10} = 1.5$ and 2 across the tested temperature intervals.

Acclimation temperature and swimming speed significantly affected $\dot{M}O_{2\ 1kg}$, heart rate, ODBA, and COT_{1kg} (see Fig. S3, Table S4 for more details). $\dot{M}O_{2\ 1kg}$, heart rate, and ODBA increased significantly with increasing swimming speed, although the response was more variable in measurements of ODBA such that high ODBA values were often observed when bass approached exhaustion regardless of swimming speed (e.g., see Fig. S3). COT_{1kg} increased with increasing acclimation temperature but differed by swimming speed. Generally, the lowest COT_{1kg} was observed at intermediate swimming speeds (see Fig. S3). Acclimation temperature also significantly affected U_{crit}, MMR_{1kg}, and AS_{1kg}. MMR_{1kg} and U_{crit} significantly increased with increasing acclimation temperature (see Fig. 3; Table S2). AS_{1kg} increased significantly from 5 °C to 10 °C ($p = 0.01$), whereas the increase from 10 °C to 15 °C was not significant ($p = 0.08$; Fig. 3). RMR_{1kg} did not significantly differ between acclimation temperatures ($p = 0.12$; Fig. 3). Temperature performance curves show significant exponential increases in RMR and MMR with increasing temperature (Fig. 3; Table S2, Table S5). Mass was included as a covariate in these models; however, the effect was insignificant likely due to the relatively small sample sizes and mass range (Table S2, Table S5). The U_{crit}-temperature model showed a similar exponential relationship with temperature but was best explained by an interaction between temperature and total length (Table S2, Fig. 3).

4. Discussion

We produced several models that accurately estimate energy expenditure in largemouth bass at winter-relevant temperatures using measurements of acceleration (i.e., ODBA), heart rate, or swimming speed, as well as a model to estimate swimming speed using acceleration. Consistent with other calibration studies we found strong relationships between swimming speed, acceleration, and $\dot{M}O_2$. Error rates for predicting $\dot{M}O_2$ from acceleration or swimming speed were similar to those reported in other calibrations (alg. error ≈ 5%, abs. error ≈ 25%, COV ≈ 25%), albeit marginally higher than reported in some studies (see Halsey et al., 2009; Lear et al. 2017; Byrnes et al., 2021; Reeve et al., In

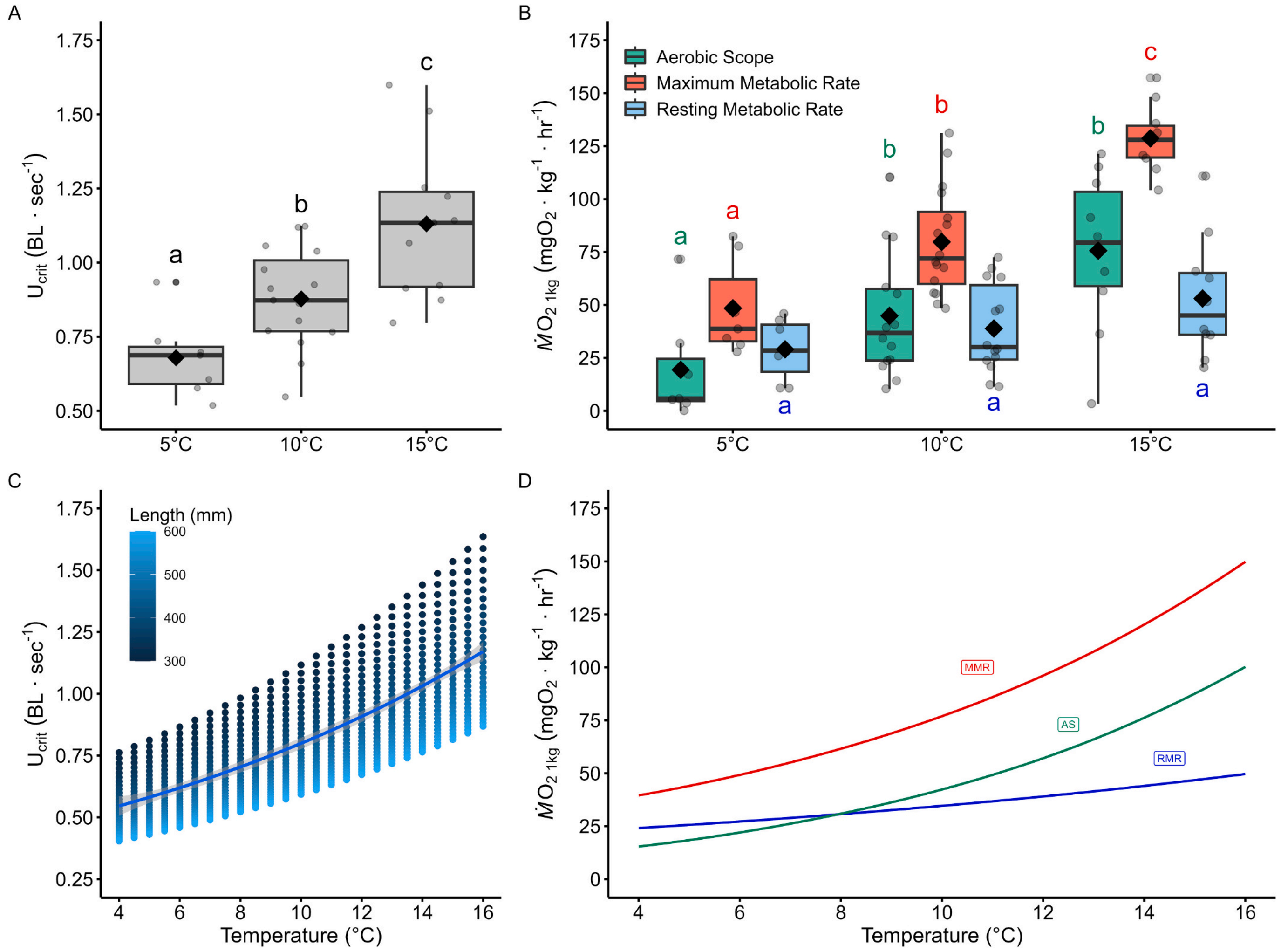

Fig. 3. The effects of temperature on largemouth bass aerobic and swim performance. Measurements of U_{crit} (panel A) and aerobic scope (AS_{1kg}), maximum metabolic rate (MMR_{1kg}), and resting metabolic rate (RMR_{1kg}) (panel B) at each acclimation temperature. Temperature performance curves of U_{crit} with respect to fish size (panel C) and RMR, MMR, and AS (calculated as MMR – RMR) for a 1 kg largemouth bass (panel D). Boxplots show the interquartile range with whiskers denoting the maximum and minimum values. Black dots above or below the whiskers highlight outliers. Grey circles are observed measurements. Black diamonds reflect the mean value at each temperature. Letters denote significant differences between acclimation temperature with their colours corresponding to the metabolic metric (i.e., green = AS, orange = MMR, blue = RMR; linear mixed-effects models with Bonferroni post-hoc multiple comparisons tests; Table S4). Model details corresponding to temperature performance curves are summarised in Table S3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Review). In addition, higher error rates may result from the range of temperatures used in our calibrations (most other calibrations only considered one or two temperatures; e.g., Lear et al. 2017; Byrnes et al., 2021). Nevertheless, given the inherent individual variation in metabolism (Metcalfe et al., 2015), these models accuracies are appropriate for field applications. Moreover, it appears that these models are more accurate at low to moderate acceleration or swimming speeds (see Fig. S1), which are more likely to be observed in free-swimming largemouth bass (Han et al., 2017).

The relationship between heart rate and $\dot{M}O_2$ (i.e., model 4) was also relatively strong and validations revealed similar, albeit higher, error rates when compared to the acceleration and swimming speed informed models (alg. error = 7.3 ± 17.3%, abs. error = 36.4 ± 6.3%, COV = 31.6). Using heart rate and acceleration to predict $\dot{M}O_2$ did improve error rates relative to model 4 (alg. error = 0.1 ± 13.8%, abs. error = 27.7 ± 5.5%, COV = 31.6) but these rates were no different from the model informed by acceleration alone (i.e., model 2; Table 2). Thus, acceleration informed models appear to be better suited for predicting largemouth bass $\dot{M}O_2$. In contrast, Clark et al. (2010) found that heart rate was a better predictor of sockeye salmon (*Oncorhynchus nerka*) $\dot{M}O_2$ than acceleration. However, because of the increased noise in heart rate measurements during largemouth bass swim performance tests, models 4 and 5 were informed using small sample sizes (e.g., see Fig. S2).

It is unclear why heart rate recordings decreased in quality during the swim performance trials. There is evidence to suggest that swimming activity can reduce the quality of heart rates due to interference from aerobic musculature (Altimiras and Larsen, 2000). While this increase in noise is seemingly marginal in salmonids (e.g., see Zrini and Gamperl, 2021), the relatively greater density of pectoral musculature present in largemouth bass could cause greater interference in the ECG signal. Interestingly, Doherty et al. (2022) also found a low percentage of high-quality heart rates (i.e., 56% of heart rates corresponded to QI = 0–1 with only 20.8% deemed reliable). In addition they found that heart rate was only weakly related to largemouth bass $\dot{M}O_2$, suggesting that heart rate may be a poor indicator of $\dot{M}O_2$ in largemouth bass even though largemouth bass are known to be frequency modulators (Cooke et al., 2003). Although the error rates for models 4 and 5 are similar to models 2 and 3, future users should interpret their own results with caution if applying model 4 or 5 to field data. Future users may also want to further experiment with HRT-ACT orientation, considering the poorer quality heart rates collected during swimming; although heart rates were of good quality when bass were at rest.

Interestingly, we found that temperature had a significant effect on the swimming speed-ODBA relationship (i.e., model 1) in largemouth bass which, to our knowledge, has not been found in other calibrations. This may occur because largemouth bass swim performance (e.g., U_{crit}) is greatly impacted by temperature and exhibit earlier onset of burst and coast swimming with decreasing temperature (i.e., since burst swimming elicits higher ODBA values than steady swimming). Such temperature effects on the swimming speed-ODBA relationship may not have been observed in other calibrations since few have used a similarly wide range of temperatures or the target species swim performance is minimally affected by temperature (e.g., Wright et al., 2014; Cruz-Font et al., 2016; Reeve et al., In Review).

Few studies have collected metabolic rate and swim performance measurements at cold temperatures in largemouth bass. To our knowledge, Lemons and Crawshaw (1985) is the only other study that has recorded largemouth bass RMR at similarly low temperatures (measured metabolic rate from 3 °C to 17 °C at 2 °C increments); however, it is difficult to compare results due to a lack of mass data reported in their study. After correcting for the effects of body size on metabolism (calculated for their reported size range = 18–120 g) and converting their units of $\dot{M}O_2$ (from ml O_2 hr^{-1} $kg^{-0.77}$; ml O_2 converted to mg O_2 using the formula outlined in Cech and Brauner, 2011), Lemons and Crawshaw (1985) report much lower estimates of RMR (~ ½ of our estimated values). It is possible that our estimates of RMR were elevated due to stress or could have occurred as a result of our extrapolations (i.e., RMR was calculated by extrapolating swimming speed to zero activity). However, our metabolic rate measurements appear consistent with those of Beamish (1970) across swimming speeds at 15 °C and 10 °C (after adjusting $\dot{M}O_2$ to a similar mass). Additionally, Beamish (1970) measurements of absolute U_{crit} (i.e., cm sec^{-1}) were also similar at 15 °C and 10 °C, however they used smaller bass (total length ≈ 22.5 cm). Therefore, their relative U_{crit} (BL sec^{-1}) was higher, but previous studies have established that relative U_{crit} increases with decreasing body size (e.g., Hammer, 1995). Our measurements of U_{crit} were also similar to those reported in Hasler et al. (2009) at 14 °C and 7.5 °C.

Our temperature model of MMR does not show the characteristic thermal performance curvature, in which performance is curtailed above a certain temperature (e.g., Neubauer and Andersen, 2019). This is likely due to our metabolic rate measurements being well below their thermal optimum (~25 °C; Niimi and Beamish, 1974). Notably, this exponential model is likely to overestimate MMR if extrapolated beyond our temperature range. For instance, our estimate of MMR for a 1 kg largemouth bass at 20 °C (233 mg O_2 kg^{-1} h^{-1}; generated from our temperature model) appear to be relatively close to that of the MMR reported in Beamish (1970) (~180 mg O_2 kg^{-1} h^{-1}; estimated from their Fig. 3 and after adjusting to a similar mass) but begins to overestimate MMR afterwards (e.g., MMR at 25 °C = 407 and ~ 200 mg O_2 kg^{-1} h^{-1} when estimated from our model and Beamish (1970) results, respectively). Our RMR temperature model appears to be more accurate, with estimates of RMR being relatively consistent with those reported in Beamish (1970) and Cech et al. (1979) between 20 °C and 30 °C; however, we recommend that users do not extrapolate far beyond our measured temperature or size ranges.

Generally, group thermal sensitivities of MMR_{1kg}, AS_{1kg}, and routine heart rate highlight the passive physicochemical effects of temperature, indicating little thermal compensation in the cold (i.e., Q_{10} ≈ 2–3; Clarke, 2017). The only exception is the greater thermal sensitivity of AS_{1kg} below 10 °C (Q_{10} = 5.84) which suggests that there may be a cold constraint in their scope for performance. RMR_{1kg} and U_{crit} were relatively less sensitive to temperature change (e.g., Q_{10} = 1.5–2) suggesting partial thermal compensation. This is interesting considering that largemouth bass have historically been considered a winter dormant species (which typically display minimal compensation of RMR; Lemons and Crawshaw, 1985; Reeve et al., 2022). Additionally, partial thermal compensation in U_{crit} also indicates that largemouth bass may maintain some swim performance at cold temperatures. However, their motivation to swim was seemingly reduced in the cold, evidenced by a greater number of largemouth bass that refused to swim at 5°C (n = 5).

Users should understand the limitations of our models when applied to field data. Notably, unnatural laboratory conditions likely impart some error in model estimates when applied to free-swimming largemouth bass. Swim tunnel respirometry constrains specific gaits (e.g., Peake and Farrell, 2004) and cannot account for energy saving swimming behaviours like schooling (Marras et al., 2015). Moreover, handling and unnatural laboratory conditions are known to cause stress in fish, potentially inflating our measurements of $\dot{M}O_2$ relative to those in free-swimming bass (Martins et al., 2011). Therefore, our models may overestimate $\dot{M}O_2$ in free-swimming bass; however, it is also possible that complex swimming behaviours, which are presumably costly, negate these potential overestimations (Boisclair and Leggett, 1989). Our models also cannot capture a number of environmental factors that are known to influence metabolism in fish. For instance, hypoxia and feeding status (e.g., starvation) are known to influence fish metabolism (Pollock et al., 2007; Gingerich et al., 2010). Additionally, like Reeve et al. (In Review) and Cruz-Font et al. (2016), there is a tendency for $\dot{M}O_2$ to be underestimated at low acceleration values. Consistent with their models, acceleration values below 0.1 m sec^{-2} appear to correspond to bass at rest (based on visual assessment of data and calculating acceleration at zero activity using our modeled relationship between swimming speed and acceleration); therefore, we recommend that users do not extrapolate $\dot{M}O_2$ below 0.1 m sec^{-2}; treating these values as resting.

These models can be applied to similarly tagged adult largemouth bass (i.e., using the same biologgers and following the same surgical procedure) to estimate their free-swimming energy expenditure and swimming speeds. These models will also be most accurate if used within or close to the temperature range that was used to inform these calibrations (i.e., 5 °C to 15 °C). Ultimately, these models would be best suited for use in largemouth bass in relatively small, closed systems (e.g., small lakes, ponds, or hatchery/aquaculture systems), since these biologgers must be recollected to acquire their data (i.e., they cannot transmit their data like acoustic transmitter tags). To extend their use, largemouth bass could be deployed with the addition of a radio transmitter to improve recapture rates if released in a larger system (e.g., river or larger lake). Fortunately, largemouth bass typically inhabit specific overwintering areas which may also improve recapture rates (Karchesky and Bennett, 2004). Acoustically tagged largemouth bass may also benefit from our swimming speed informed model, provided that the detection resolution is high enough to reasonably estimate swimming speed; however, the necessary receiver arrays are costly (e.g., Anderson et al., 2022). For most applications, our acceleration-informed model appears to be the most accurate considering the limitations associated with the heart rate model.

5. Conclusions

In summation, our study is one of few to measure largemouth bass metabolic and swim performance metrics at cold temperatures. Our results appear consistent with those reported in Beamish (1970) but are greater than those reported in Lemons and Crawshaw (1985). Group thermal sensitivities of most performance metrics highlight the passive physicochemical effects of temperature, indicating little compensation in the cold; however, resting metabolic rate and critical swimming speed showed partial compensation. Notably, this study found strong relationships between metabolic rate, heart rate, acceleration, and swimming speed which can be used to estimate free-swimming swimming speeds and energy use. These models can be applied to data collected from similarly tagged largemouth bass (i.e., using the same tags, surgical methods, a similar sized individuals) to predict free-swimming swimming speed and energy expenditure. The acceleration-informed model is best suited for most applications and caution should be taken if applying the heart rate informed models to free-swimming fish considering the small sample sizes used to inform these models. Users should be aware of these models' inherent limitations and consider the likelihood of recapture before deployment of biologger implanted bass. These models will advance our ability to remotely measure activity and associated metabolic costs in overwintering largemouth bass, thereby improving our understanding of their winter behaviour and ecology and our ability to predict bass' responses to environmental change.

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CRediT authorship contribution statement

Connor Reeve: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kurtis A. Smith:** Writing – review & editing, Methodology. **Andre Morin:** Writing – review & editing, Methodology. **Paul A. Bzonek:** Writing – review & editing, Methodology. **Steven J. Cooke:** Writing – review & editing, Supervision, Resources, Funding acquisition, Conceptualization. **Jacob W. Brownscombe:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cbpa.2024.111708.

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