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Winter behaviour and energetics of free-swimming largemouth bass

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Abstract

Bioenergetics models have many valuable applications for fishes, but often lack ecological realism due to limited data from free-living wild animals. Here we used heart rate loggers and accelerometers in wild largemouth bass (LMB; *Micropterus nigricans*) to characterize their bioenergetics during the winter (fall to late-spring) in a small lake. Activity, heart rate, and metabolic rate decreased over the fall, remained low over the winter, and peaked in the late-spring coinciding with spawning. Interestingly, LMB exhibited continued slow swimming over the winter period. Growth rates were predominately negative over the winter period; however, mass change was highly variable. Using an updated Wisconsin bioenergetics model, estimates of consumption indicated that overwinter feeding was likely occurring and simulations of winter fasting predicted greater mass lost than observed for most LMB; however, if fasting results in a reduction in metabolic rate, predicted losses suggest that some LMB may be able to fast through the winter. This study provides insights into ecologically realistic bioenergetics parameters for LMB and furthers our understanding of LMB winter behaviour and energy use.

Key words: largemouth bass, biologging, metabolism, bioenergetics, winter

Introduction

Largemouth bass (LMB; *Micropterus nigricans*) are one of the most popular sportfish worldwide (Quinn and Paukert 2009) as well as a notable invasive species in many regions (Long and Seguy 2023).Although LMB prefer warm water (thermal optima: 25–28 °C; (Niimi and Beamish 1974; Coutant and Cox 1976; Díaz et al. 2007), LMB must tolerate cold winter conditions across most of their native and invaded ranges. Winter then represents a critical bottleneck for juvenile LMB, wherein year-class strength is shaped by size-selective winter mortality (Garvey et al. 1998; Fullerton et al. 2000). Despite reduced energetic costs due to cold-induced reductions in whole-animal metabolism, reduced winter forage and foraging capacity at low temperatures can result in negative growth in warm- and cool-water fishes, increasing the risk of mortality (Block et al. 2020). Size selective mortality in primarily juvenile LMB is largely influenced by winter duration and temperature (Garvey et al. 1998; Wright et al. 1999) and fall energy density (Sullivan 1986; Miranda and Hubbard 1994; Ludsin and DeVries 1997). In short, juvenile LMB must attain a minimum size (or energy content) prior to the onset of winter to persist until the following spring, with longer and colder winters requiring a larger minimum size (Shuter et al. 1980; Fullerton et al. 2000; Garvey et al. 2004). As annual growth rates of LMB are also reduced at higher latitudes with a shorter growing season, winter conditions impose limits on their population distribution and abundance (Niimi and Beamish 1974; Shuter and Post 1990; Díaz et al. 2007). Interestingly, climate warming is altering winter phenology, reducing winter duration and severity (IPCC 2013). Thus, it is anticipated that climate warming will facilitate a northern expansion of LMB populations and increase their abundances in their current northern range (Hansen et al. 2017*b*; Wu et al. 2023).

LMB, being voracious predators, often play a large role in shaping fish communities (e.g., Cazelles et al. 2019); thus, fisheries managers would benefit from a better understanding of these populations shifts to adaptively manage changes in fish community structure. Bioenergetics models, based on the energy inputs and outputs of an organism, are a mechanistic approach to estimate the energy requirements of fishes and may be useful to understand demographic changes in northern fish community structure (Deslauriers et al. 2017). Although other forms exist, the Wisconsin bioenergetics model (Kitchell et al. 1974, 1977) is the most widely used framework for fish. This framework relies on the theory of energy-balance, balancing energy consumed with the energetics costs associated with growth, metabolism, reproduction, and wastes. These models are often used to predict growth or consumption but may be broadly applied to predict species distributions based on suitability to environmental conditions (i.e., temperature, prey availability), as has been done for smallmouth bass (*Micropterus dolomieu*) and yellow perch (*Perca flavescens*) at larger scales (Shuter and Post 1990). Notably, our limited understanding of LMB physiology and feeding behavior during the winter impedes our ability to accurately predict their responses to warming environments with bioenergetics models.

Historically, LMB have been considered winter-dormant, implying overwinter inactivity and fasting (Lemons and Crawshaw 1985). Yet, sustained winter activity and positive growth rates have been observed in some studies, challenging the idea that LMB exhibit winter dormancy (Woodward and Noble 1999; Garvey et al. 2004; Karchesky and Bennett 2004). Nevertheless, dormancy assumptions have permeated existing bioenergetics models which assume inactivity of LMB below 10 °C (Trebitz 1991; Wright et al. 1999). A winter-specific evaluation of these models concluded that the parameters characterizing activity and metabolism were inadequate in describing responses of LMB to winter (Wright et al. 1999). Accurately assessing the contribution of activity is a fundamental challenge in bioenergetics modeling as, in natural systems, fish often exhibit highly variable activity patterns (for example, activity costs may range from 0% to 40% of their energy budget; Boisclair and Leggett 1989).

Sensor-equipped biologging or biotelemetry tags that store or transmit behavioural and/or physiological data show promise for winter-specific bioenergetics research on free-swimming fish (Cooke et al. 2016; Marsden et al. 2021). These tags can be deployed prior to the onset of cold conditions and ice formation, and continuously record fine-scale measurements of fish behaviour and/or physiology throughout the winter, avoiding many of the difficulties associated with winter field work. In addition, these tags can also be calibrated to estimate the free-swimming metabolic rates from recordings of heart rate or acceleration (Gleiss et al. 2011; Clark et al. 2013). Calibrations for these devices were recently produced by Reeve et al. (2024) which now allow us to make novel estimates of overwinter activity and energy use for LMB using these technologies.

Here, we sought to expand the current body of knowledge on the winter behaviour and energetics of free-swimming LMB using heart rate and acceleration biologgers, and the previously established calibrations from Reeve et al. (2024). Specifically, we sought to better describe their patterns of activity and depth use, and estimate their energy expenditure between fall and late spring. Using this information we also aspired to update their bioenergetics model with free-swimming activity data to improve the winter-accuracy of their model and to better understand overwinter feeding patterns in LMB.

Methods

Study site

Warner Lake (Elgin, Ontario; 44°31′N, 76°22′W) is a small, private research lake (18.2 ha surface area) operated by Queens University Biological Station possessing one shallow (max. depth ≈ 3 m) and one deep basin (max. depth ≈ 7 m; lake bathymetry can be found at https://qubs.ca/resources/bathymetry). This lake is a closed system, making it suitable for the recapture of tagged LMB. LMB are the top predators of this system, with yellow perch (*Perca flavescens*), pumpkinseed sunfish (*Lepomis gibbosus*), brown bullhead (*Ameiurus nebulosus*), golden shiner (*Notemigonus crysoleucas*), and white sucker (*Catostomus commersonii*) also being documented within the lake. Warner Lake has also been a notable research location for studying LMB ecology (e.g., Hanson et al. 2007*a*, 2007*b*; Hasler et al. 2009*a*, 2009*b*), which adds useful background to this study.

Fish collection and surgical implantation

LMB were collected with rod and reel from Warner Lake in the fall or winter between 2020 and 2023 (Table S1). Once angled, morphometrics were recorded (mass in mg and total length in mm) and LMB were tagged with a 12 mm passive integrated transponder. Fish deemed appropriate for tagging based on body size (min. total length = 300 mm to reduce tag burden) were surgically implanted with either a TechnoSmArt Axy-5 acceleration, depth, and temperature biologger (22 mm × 45 mm × 8 mm, 11 g in air; TechnoSmArt, Guidonia Monticello, Italy) or a Star Oddi milli-HRT heart rate and temperature biologger (hereinafter referred to as HRT; length = 39.5 mm, diameter = 13 mm, mass in air = 12 g; Star Oddi, Gardabaer, Iceland). A total of 63 LMB were tagged with Axy-5 ($n = 31$) and HRT ($n = 32$) biologgers over three winter seasons. During surgery, LMB were immobilized through electrosedation using a transcutaneous electrical nerve stimulation unit (TENS 3000; Roscoe Medical, Ohio, USA) and a constant flow of lake water was maintained across the gills of the fish (see Reid et al. 2019). The surgical implantation of Axy-5 biologgers required a 3–4 cm incision made off-centre on the LMBs ventral side, between their anus and pectoral girdle. Because of the relatively wider and rectangular profile of the Axy-5 biologger, the off-centre cut permitted easier insertion into the body cavity and more accurate placement once inside. The Axy-5 was inserted charging port facing posteriorly with the flat side facing the body wall. A suture tied around the midline of the biologger was passed through the body wall, just posterior of the pelvic girdle, then tied to anchor the tag in place. The incision was then closed with 4–5 interrupted stitches (EthiconTM 3–0 PDS II Violet Monofilament FS-1 needle; Fig. S1). HRT implantation required a 2–3 cm incision made off-centre, anterior of the pelvic girdle. The off-centre incision functioned to prevent damage to the pelvic girdle during surgery. Tags were then inserted with the blunt end facing anteriorly and the electrodes facing the body wall. To anchor the biologger, suture material was tied around the midline of the tag then passed through the body wall. The biologger was pulled forward so that it was near the pericardium then the suture material was tied to the body wall just posterior of the pericardium (Fig. S1). Following surgery, LMB were then released back into Warner Lake. In all but a few cases, tag burden was <2% (average tag burden ± standard deviation (s.d.) = 1.46 ± 0.36%; max. tag burden = 2.54%; for details on the effects of tag size see Smircich and Kelly 2014; note that all averages are ± standard error of the mean unless otherwise noted).

Starting the following spring, efforts to retrieve tagged LMB via angling began. Most LMB from their respective cohort were collected the following spring, but others were collected in later years' angling events given the inherent challenges with recapturing wild fish (Table S1). When recaptured, LMB were weighed then subjected to surgery to remove their biologger. As before, LMB were electrosedated and a constant flow of lake water was maintained over their gills. The previous incision was reopened, the biologger was removed, and the incision was closed, again using 4–5 interrupted stitches if implanted with an Axy-5 biologger or 3–4 interrupted stitches if implanted with an HRT biologger. The LMB were then released back into the lake. Fish were never tagged more than once. Recapture rates were relatively high with 81% of Axy-5 ($n = 25$) and 66% of HRT ($n = 21$) biologgers being recovered.

Axy-5 biologgers were programmed to record tri-axial acceleration at 10 Hz, while depth and temperature were recorded at a rate of 0.2 Hz, between 06:00 and 17:00 and 22:00 and 02:00. This programming was selected to extend battery life (based on recommendations from TechnoSmArt) and to prioritize daytime activity measurements since LMB are a diurnal fish species (Binder et al. 2012). The 2020/2021 cohort of HRT biologgers were programmed to record heart rate (at 125 Hz over 15 s) every 20 min on every third day (i.e., high resolution of recording, skip 2 days, repeat). Three electrocardiograms (ECGs) were saved every 6 h to corroborate heart rate recordings. Like Axy-5 biologgers, this sampling regime was designed to maximize recordings while prolonging battery life. Unfortunately, these heart rate recordings were of mostly poor quality (discussed in greater detail below) so to ensure heart rates were correct, in the 2022/2023 cohort, HRT biologgers were programmed to record heart rate and save the associated ECG every 6 h. Additionally, since these LMB were tagged slightly earlier in the year, to extend battery life, these biologgers were programmed to start recording 1 month after deployment.

Several dissolved oxygen and temperature loggers (aquaMeasure DOT, InnovaSea, Canada) were deployed each year in the fall or winter and retrieved following spring or summer to record seasonal environmental changes. These loggers were programmed to record dissolved oxygen (percent saturation) and temperature once every 2 h. In 2020, 2 loggers were placed in the shallow basin and 2 loggers were placed in the deep basin at intermediate depths (~1.5 and 2.5 m deep) to assess environmental changes in both areas of the lake. However, following data collection from the first winter, it was apparent from depth distributions and through visual observations during ice fishing excursions, that LMB did not overwinter in the shallow basin. Therefore, in the latter two winters, we deployed a single vertical string of loggers in the centre of the deep basin. Details on the logger's depth strata and deployment dates are shown in Fig. S2.

Fish collections and experimentation were conducted under the approval of the Canadian Council on Animal Care as administered by Fisheries and Oceans Canada (for the laboratory aspects; (OPA-ACC-2022-15) and Carleton University (for the field aspects; CU-Tagging Umbrella Protocol). In addition, a scientific collection permit was obtained from the Ontario Ministry of Natural Resources and Forestry.

Data analysis

Axy-5 tri-axial acceleration data were used to calculate overall dynamic body acceleration (ODBA) as the absolute sum of dynamic acceleration from all three axes, after removal of static acceleration using weighted smoothing at an interval of 2 s (see Gleiss et al. 2011). Due to the vast amount of data collected from the Axy-5 biologgers (~250 million data points in total), ODBA, depth, and temperature were then averaged to the minute. Due to the poor quality of heart rate recordings collected from most HRT tags, only manually calculated heart rates from ECGs were accepted. Heart rates were calculated using the Star-Oddi HRT Analyzer (see https://www.star-oddi.com/support/software for details). Using the following formulas derived from standardized laboratory biologger calibrations (see Reeve et al. 2024), we estimated swimming and aerobic metabolic rate (i.e., $\dot{M}O_2$, mgO$_2$ kg^{-1} h^{-1}) using recordings of ODBA and heart rate.

$$(1)\quad \log_{10}\left(\dot{M}\,O_2\right) = 4.449 + 0.043 \cdot (T) - 1.145 \cdot \log_{10}(L) + 0.332 \cdot \log_{10}(A)$$

$$(2)\quad \log_{10}\left(\dot{M}\,O_2\right) = 9.437 - 3.437 \cdot \log_{10}(L) + 0.912 \cdot \log_{10}(HR)$$

$$(3)\quad \log_{10}(\mathrm{SS}) = 1.316 + 0.028 \cdot (T) - 0.651 \cdot \log_{10}(L) + 0.342 \cdot \log_{10}(A)$$

where SS is swimming speed (body lengths s^{-1}; hereinafter BL s^{-1}), T is temperature (°C), M is mass (g), A is acceleration (i.e., ODBA; m·s^{-2}), and L is total length (mm). As per recommendations in Reeve et al. (2024), MO$_2$ was not extrapolated to ODBA values below 0.1 m·s^{-2} (i.e., values below 0.1 m·s^{-2} were converted to 0.1 m·s^{-2} to prevent overextrapolations of MO$_2$). In addition, we estimated the amount of time LMB spent swimming at critical swimming speeds using the formula

$$(4)\quad \log_{10}(U_{\mathrm{crit}}) = 2.035 + 0.0276 \cdot T - 0.914 \cdot \log10(L)$$

The amount of time LMB were inactive or engaging in burst swimming was also assessed. Inactivity was defined as ODBA values < 0.1 m s^2, as Reeve et al. (2024) found that these values typically corresponded with LMB at rest. Burst swimming was defined as ODBA values > 1.5 m·s^{-2} as values above this range typically corresponded with burst swimming behaviour in the Reeve et al. (2024) calibrations.

To predict the dissolved oxygen concentrations experienced by LMB, we produced a random forests regression tree model (using the "randomForests" package; Liaw 2022). This model was informed by temperature and dissolved oxygen measurements collected from the lake. Data were split into training and testing datasets (70% training, 30% testing). The model was trained using the following predictors: Julian day, depth, and temperature. The model explained 98.22% of the variance in the training dataset (mean of squared residuals = 28.93) and when applied to the test dataset, absolute average error rate ± s.d. was 3.59 ± 4.19% (see Fig. S2 for visual example of model predictions versus observed values). This model was then used to predict the dissolved oxygen concentrations experienced by Axy-5 implanted LMB using biologger recorded depth and temperature measurements. Some Axy-5 tags had issues with their temperature ($n = 4$) or depth sensors ($n = 5$). In such cases, these values were informed by averages from the other fish at that time. To facilitate comparisons of dissolved oxygen concentrations with other studies, we converted dissolved oxygen concentrations to units of mg L^{-1} using the equations outlined in Mortimer (1981).

To determine the effect of temperature and dissolved oxygen on swimming activity (ODBA and predicted swimming speeds), depth use, and heart rate, linear mixed-effects models (LMMs; "lme4" package; Bates et al. 2023) were produced with individual being treated as a random effect to account for repeated measures. Log-transformations were used to attain linear and normalized data for certain models and models were tried with and without mass as an explanatory variable. Final models were selected based on Akaike information criterion (AIC; with the lowest AIC being selected (Zuur et al. 2009)) and visual observation of the predicted relationships.

Using LMM we investigated whether activity (ODBA and predicted swimming speed) and depth use were impacted by surgery and release. Specifically, we determined whether there were significant changes in individual average daily activity and depth use over time. Changes were assessed over 3 weeks as surgical recovery has been shown to take up several weeks for some fish (see Hvas et al. 2020; Zrini and Gamperl 2021). Changes in heart rate following surgery could not be assessed due to the quality of the recordings in the 2020/2021 cohort and due to the recording delay used in the 2022/2023 cohort. We also investigated their overall and monthly diel cycles of activity (ODBA and predicted swimming speeds) and depth use using LMM. For these analyses, data were averaged to the hour (e.g., hour 6 represents average data between 06:00:00 and 06:59:59) for each fish.

Significant effects were calculated using Analysis of variance (ANOVA; *anova* function) and, when appropriate, differences between groups were determined using post hoc multiple comparisons tests with a Bonferroni based adjustment (alpha = 0.05; "emmeans" package; Lenth 2023). When employing LMM, individuals were included in all models 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).

All analyses were conducted in Rstudio (R Version 4.2.1; R Core Team 2019).

Bioenergetics modeling: model building

Bioenergetics modeling followed the structrure of the Wisconsin bioenergetics model (Kitchell et al. 1974; Deslaurier et al. 2017). Using LMM and data collected in calibration experiments from Reeve et al. (2024), we derived the respiration parameter coefficients *RA*, *RB*, *RQ*, and *RTO* by modeling the relationship between metabolism, mass, and swimming speed using the format, $R = RA \cdot M^{RB} \cdot e^{(RQ \cdot T)} \cdot e^{(RTO \cdot U)}$, where R is metabolic rate (g O_2 g^{-1} day^{-1}), M is mass (g), T is temperature (°C), and U is swimming speed (cm·s^{-1}) (see Fish Bioenergetics 4.0; Deslauriers et al. 2017). Coefficients *RB*, *RQ*, and *RTO* describe the effect of mass, temperature, and swimming speed on metabolic rate, respectively, and *RA* is the intercept of this relationship, effectively highlighting the metabolic rate for a non-moving 1 g fish at 0 °C. The resulting equation explained the data well ($R^2_{\text{Conditional}} = 0.82$, $R^2_{\text{Marginal}} = 0.64$), but the mass effect on metabolism (explained using the parameter coefficient *RB*) was insignificant and data simulations indicated poorer performance (likely due to the relatively narrow size range used in Reeve et al. (2024)). Thus, in our bioenergetics simulations we continued to use the original *RB* coefficient (−0.355). Additionally, we determined the parameter coefficients *ACT*, *RK4*, and *BACT* using predicted swimming speeds from Axy-5 implanted LMB using LMM; modeling the data using the format, $U = ACT \cdot M^{RK4} \cdot e^{(BACT \cdot T)}$ (note that relative swimming speed was converted to absolute swimming speed by multiplying by total length; average total length ± s.d. = 37.8 ± 2.5 cm). In this form, *RK4* and *BACT* describe the mass and temperature dependence of swimming speed, and *ACT* is the intercept of this equation. This equation explained the data well ($R^2_{\text{Conditional}} = 0.81$, $R^2_{\text{Marginal}} = 0.81$; see Fig. S3). To effectively apply these relationships, *RTL*, the cutoff temperature at which the activity relationship changes, and *RK1*, the intercept for routine swimming speed when water temperature > *RTL*, must also be defined. We defined *RTL* as 20 °C, with the assumption that their activity rates are similar within a narrow range of their optimal temperature (i.e., their *pejus* temperatures; LMB thermal optimum = 25–28 °C; Niimi and Beamish 1974; Coutant and Cox 1976; Díaz et al. 2007). *RK1* was calculated by solving the equation $U = RK1 \cdot M^{RK4}$ using predicted swimming speeds at 20 °C. Bioenergetic modeling coefficients can be found in Table 1.

Bioenergetics modeling: estimating overwinter consumption

Using Fish Bioenergetics 4.0 formulations (Deslaurier et al. 2017), we calculated overwinter consumption from observed growth rates using the Rice et al. (1983) bioenergetics model and compared these values to those calculated using a model which included the updated metabolism and activity coefficients we derived here (but otherwise included the same parameter coefficients for consumption, egestion, excretion, and specific dynamic action as those reported in Rice et al. (1983)). Additionally, we calculated consumption using a model that was informed using biologger derived estimates of metabolic rate rather than predicting metabolic costs using bioenergetics equations. Hereinafter, these models will be referred to as the original model, the updated model, and the biologger-informed model. For these analyses, we assumed a prey energy density of 4000 J·g^{-1} (the estimated energy density of prey fish; Kershner 1998; Deslaurier et al. 2017) and only included individuals that (1) were recaptured within 30 days of their final biologger recording and (2) had com-

Table 1. Updated bioenergetic parameter coefficients derived from my field data and from calibrations conducted in Reeve et al. (In review).

Parameter coefficient	Parameter description	Calculated value	95% CI	p-value	Original value
RA	Intercept for metabolism	0.0035	0.0003, 0.0315	<0.0001	0.008352
RB	Coefficient for metabolism vs. weight	**−0.292***	−0.622, 0.058	0.1096	**−0.355***
RQ	Coefficient for metabolism vs. temperature	0.0529	0.0394, 0.0663	<0.0001	0.0313
RTO	Coefficient for metabolism vs. swimming speed	0.0217	0.0175, 0.0260	<0.0001	0.0196
ACT	Intercept for routine swimming speed	1.4343	0.4132, 4.9804	0.5767	1
BACT	Coefficient for routine swimming speed vs. temperature	0.0690	0.0686, 0.0695	<0.0001	0
RK4	Coefficient for routine swimming speed vs. weight	0.3162	0.1075, 0.5248	0.0070	0
RK1	Intercept for routine swimming speed when water temperature > RTL	5.7058	NA	NA	0
RTL	The cutoff temperature at which the activity relationship changes	20	NA	NA	0

Note: Parameter descriptions adapted from Stewart et al. (1983). Values within the "original value" column are the parameter coefficients included in the Rice et al. (1983) model. Note that in our bioenergetics analyses the "original value" for the *RB* coefficient was used (i.e., −0.355; swapped values are bolded and highlighted using "*").

plete metabolic rate data (i.e., no days were missed) ($n = 10$ Axy-5 tagged fish, $n = 1$ HRT tagged fish). The proportion of max consumption ($p_{\text{consumption}}$) was compared between models (which is a single value calculated from observed mass changes) as well as their average daily consumption rates over the winter period. This period was defined as the interval in which average daily water temperatures remained below 10 °C as LMB appear to exhibit changes in feeding and behaviour above this temperature (Markus 1932; Johnson and Charlton 1960; Lemons and Crawshaw 1985).

Bioenergetics modeling: effects of winter fasting

Using these same models, we also estimated how much mass would be lost if LMB did not feed over the winter (i.e., the period in which average daily water temperature remained <10 °C). The proportion of max consumption ($p_{\text{consumption}}$) was set to zero for these individuals and mass loss was calculated. Additionally, we estimated mass loss assuming a fasting induced reduction in the predicted metabolic rates included in the biologger-informed model. Ranney et al. (2024) reported 38% lower resting metabolic rates in LMB fed maintenance rations and Gingerich et al. (2010) reported 75% lower resting metabolic rates in fasted LMB when compared to fish fed ad libitum. Since the effects of fasting on LMB active metabolism are unclear, and because it is unlikely that wild LMB fed at rates similar to laboratory ad libitum, we conservatively simulated a 30% reduction in winter metabolic rates after 2 weeks of fasting and calculated their predicted mass loss.

To determine if patterns of wintertime consumption and mass loss were influenced by body size or energetic status, we performed linear regression analyses to examine the relationships between fall mass or fall condition and the proportional change in mass for individuals that were released in the fall (between mid-September and early November) and recaptured the following spring (between early May and mid-June). Linear regressions were also performed to assess the relationships between fall mass, fall condition, or proportional change in mass and estimates of consumption produced from the bioenergetics models. Fall condition was calculated using the formula $\text{condition} = 100 \cdot \left(\frac{\text{mass}}{\text{TotalLength}^3}\right)$.

Results

Growth

Most LMB had lost mass upon recapture (average mass ± s.d. at release and upon recapture were 825 ± 174 g and 788 ± 146 g, respectively). For their respective year, on average (±s.d.), LMB were released on 11 November ± 73 days and recaptured on 8 June ± 30 days. There was considerable individual variation in mass change (range = −18% body mass to +15% body mass). On average, LMB lost 3.56 ± 1.35% body mass between release and recapture (Table S1). However, if only LMB that were released in the fall (between mid-September and early November) and recaptured the following spring (between early May and mid-June) are considered, LMB lost 5.3 ± 1.8% body mass (ranging from −18.3% to 7.6% change in body mass). On average, Axy-5 biologgers recorded measurements for 168 days (range = 82–208 days) and HRT biologgers recorded measurements for 196 days (range = 97–264 days; Table S1). However, due to the poor quality of heart rate recordings from HRT biologgers, the number of calculated heart rates per individual ranged from 46 to 1072 (average number of heart rates recorded = 293 ± 51; successful proportion of heart rates calculated from ECGs = 30.5 ± 3.4%; Table 2).

Swimming activity and depth use

Swimming activity and depth use showed no change in their daily behaviour in the 3 weeks following release ($p = 0.15$ and $p = 0.42$, respectively; Fig. S4). Overall diel patterns of activity or depth use were marginal (Fig. S5). The strength of diel patterns changed over the winter, appearing dampened in the mid-winter but becoming more obvi-

Table 2. Average monthly measurements (± s.e.m.) collected from HRT implanted largemouth bass from the winter 2020/2021 and winter 2022/2023 cohort.

Month, year	*N*	Temp. (°C)	Heart rate (bpm)	% ECGs calculated	MO_2 ($mgO_2\ kg^{-1}\ h^{-1}$)
September 2020	1	20.9	36.3	8.2	117.2
October 2020	1	17.5	29.8	7.5	98.0
November 2020	6	6.0 ± 0.2	17.3 ± 2.4	38.6 ± 16.2	55.3 ± 5.1
December 2020	6	4.1 ± 0.1	14.9 ± 2.2	16.9 ± 8.4	47.3 ± 6.9
January 2021	9	4.7 ± 0.0	16.4 ± 1.7	13.6 ± 4.5	58.6 ± 9.5
February 2021	14	4.5 ± 0.0	16.0 ± 0.9	10.1 ± 3.5	56.6 ± 6.2
March 2021	14	5.3 ± 0.0	20.3 ± 0.9	15.5 ± 4.0	68.1 ± 5.9
April 2021	14	12.5 ± 0.0	32.6 ± 1.1	48.2 ± 5.9	102.8 ± 8.1
May 2021	14	17.7 ± 0.1	38.5 ± 1.2	34.5 ± 5.0	119.3 ± 8.7
June 2021	14	21.8 ± 0.4	40.8 ± 1.7	37.7 ± 6.5	132.8 ± 11.9
October 2022	7	11.8 ± 0.1	16.1 ± 1.3	68.1 ± 2.7	47.9 ± 4.7
November 2022	7	7.9 ± 0.0	13.2 ± 1.0	50.0 ± 6.7	39.4 ± 3.1
December 2022	7	4.1 ± 0.1	10.7 ± 1.5	24.3 ± 9.4	31.9 ± 3.4
January 2023	7	4.5 ± 0.1	11.5 ± 1.5	23.7 ± 9.9	35.0 ± 3.4
February 2023	7	4.7 ± 0.0	11.6 ± 1.7	21.3 ± 9.7	34.6 ± 4.0
March 2023	7	4.7 ± 0.0	11.0 ± 1.3	23.6 ± 10.3	33.3 ± 3.4
April 2023	7	11.3 ± 0.1	29.4 ± 1.5	47.4 ± 6.4	82.1 ± 6.2
May 2023	7	16.3 ± 0.5	31.8 ± 3.0	53.1 ± 7.3	88.3 ± 9.0

ous with spring warming (see Fig. S6). Generally, LMB were most active in the early morning (~06:00) and least active overnight (Fig. S5). Diel cycles of depth use were largely unapparent; however, statistical testing indicated that LMB moved marginally shallower in the night (~0.2 m shallower at night; see Figs. S5 and S7).

LMB showed seasonal trends in activity and depth use. Generally, LMB displayed low levels of activity during the winter which increased once water temperatures began to rise in the spring (Figs. 1 and 2). Though activity levels were low, the proportion of time spent inactive peaked in the fall; spending on average ~2% of their day inactive (Fig. 2). Activity peaked in the late spring (late May/early June). Burst and critical swimming (i.e., swimming at predicted U_{crit} speeds) was rarely observed over the study period (~0.1% of time spent burst swimming or critical swimming; see Table 3); however, burst swimming behaviour also exhibited seasonality, peaking in the spring (Fig. 2). Predictably, heart rate followed similar seasonal trends to activity, with low heart and metabolic rates over the winter, increasing as temperatures rose in the spring (Figs. 2 and 3). Overwinter heart rates ranged from 4 to 26 bpm. It is possible that LMB exhibited lower minimum heart rates; however, we could not calculate heart rates lower than 4 bpm with the sampling interval used (i.e., 15 s). Metabolic rates informed using heart rate and ODBA were similar with respect to seasonal change; however, ODBA informed metabolic rates appeared to be elevated in June when compared to heart rate informed metabolic rates (Fig. 2, Fig. S8). Over the winter, LMB sought deeper waters, moving shallower with spring warming. LMB were shallowest in June, which may coincide with reproductive activity (Fig. 2).

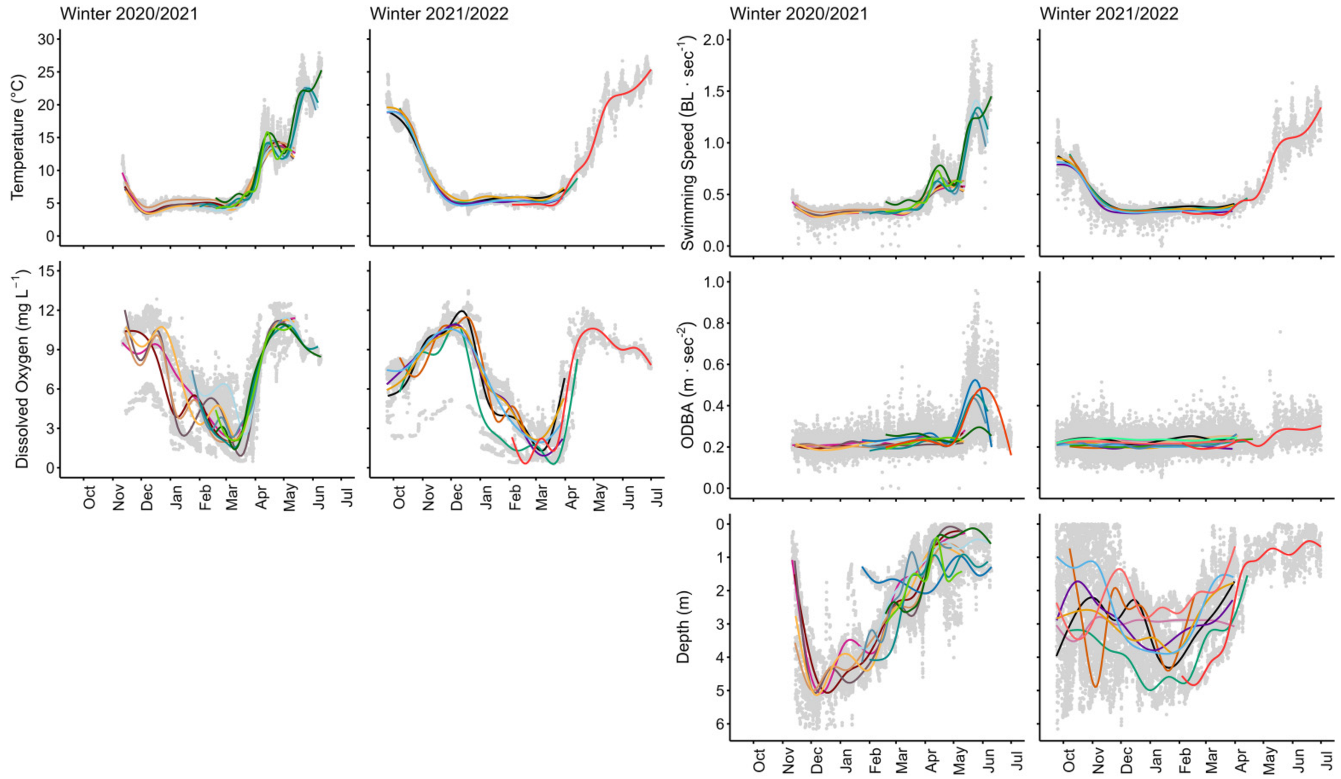
ODBA, swimming speed, depth use, and heart rate increased significantly with temperature ($p < 0.0001$ in all instances; Table S2). Heart rate and activity increased exponentially with increasing water temperature, whereas depth decreased (i.e., fish moved shallower) with increasing water temperature (Fig. S9). Activity and depth use were also significantly correlated to dissolved oxygen concentrations ($p < 0.0001$ in all instances); however, R^2 values suggest that LMB behaviour was more influenced by temperature (Table S2; Fig. S9).

Bioenergetics modeling

We compared the estimated consumption values calculated from the original, updated, and biologger-informed models. The original model routinely predicted greater consumption when compared to the updated model ($p_{consumption} = 0.62 \pm 0.04$ and 0.53 ± 0.02, respectively). The biologger-informed model estimated the lowest rates of overwinter consumption; however, these rates were more variable ($p_{consumption} = 0.37 \pm 0.04$). Converting these units to grams of fish consumed, the original model, the updated model, and the biologger-informed models predicted that LMB consumed 1.9 ± 0.2, 1.7 ± 0.1, and 1.1 ± 0.1 g of fish day^{-1}, respectively. Assuming a winter duration of 150 days (which was approximately the length observed), LMB consumed between 168 and 278 g of fish (18.8%–28.7% of pre-winter body mass) over the winter period. After simulated winter fasting, the original model estimated the greatest loss in body mass over the winter period (27.9 ± 2.8% body mass loss), whereas the updated model and biologger-informed model estimated considerably lower losses (18.8 ± 2.4% and 15.9 ± 3.3%, respectively). After simulating a fasting-induced reduction in metabolic rate (30% reduction), mass loss was predicted to be 11.9 ± 2.5% body mass.

Linear regressions indicated that there was a near-significant negative relationship between fall mass or fall condition and post-winter mass loss; however model fit

Fig. 1. Data collected from Axy-5 biologger implanted largemouth bass (LMB) over two winter seasons. Different coloured solid lines correspond to different individual LMB, created using a generalized additive model (GAM) smoother.



was low ($p = 0.079$, $R^2 = 0.12$, $F = 3.34$; and $p = 0.052$, $R^2 = 0.14$, $F = 4.19$, respectively; Fig. S10). When assessing the relationships between fall mass, fall condition, or proportional change in mass and estimates of consumption produced from the bioenergetics models, relationships were consistently strongest when examining estimates of consumption from the biologger-informed model. Generally, the updated model and the biologger-informed model showed similar trends, albeit with different magnitude and strength, whereas the original model showed more varied responses (Fig. S11). Estimates of consumption from the biologger-informed model had a significant negative relationship with fall mass ($p = 0.01$, $R^2 = 0.55$, $F = 13.03$), a significant positive relationship with the post-winter proportional change in mass ($p = 0.03$, $R^2 = 0.36$; $F = 6.61$), and a near-significant negative relationship with fall condition ($p = 0.058$, $R^2 = 0.27$; $F = 4.74$). Estimates of consumption from the updated model were only significantly related to the post-winter proportional change in mass ($p < 0.001$, $R^2 = 0.75$, $F = 30.67$; Fig. S11).

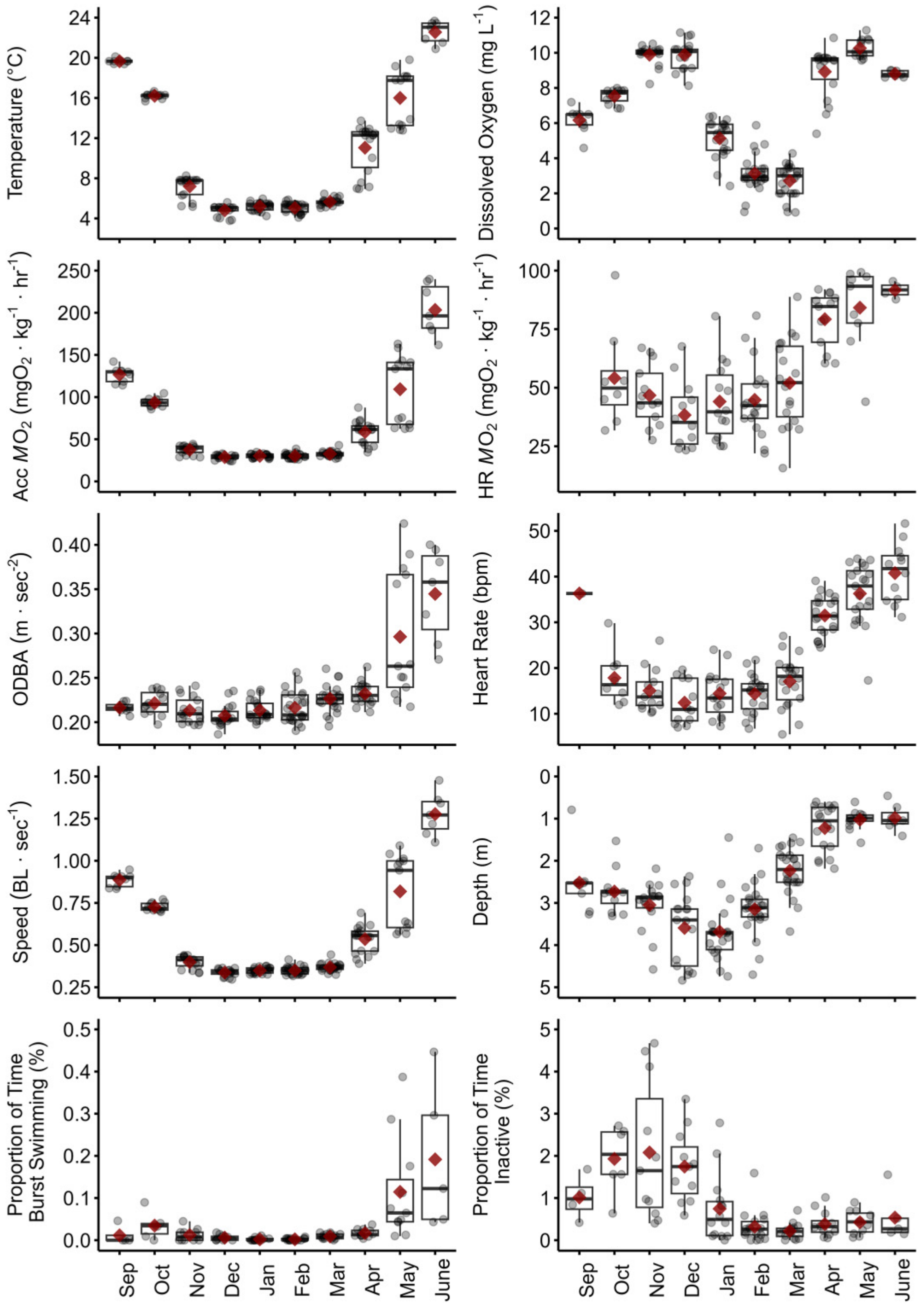
Discussion

Our monitoring of LMB over several winters highlights trends in seasonal and diel patterns of activity and depth use, and elucidates overwinter energy expenditure and consumption in LMB. Generally, LMB showed similar seasonal and diel cycles to those described in previous studies which were largely influenced by changes in temperature (Demers et al. 1996; Karchesky and Bennett 2004; Hanson et al. 2007*a*; Binder et al. 2012). Although patterns of activity were similar to previous reports, our estimates of activity were several orders of magnitude greater than previously described when using acceleration-informed estimates versus telemetry-informed estimates (e.g., Hanson et al. 2007*a*) LMB typically lost mass over the winter; however, assessments of their consumption rates estimated from bioenergetics modeling suggest that LMB likely engage in low levels of feeding over the winter. Moreover, we found evidence that such overwinter feeding behaviour may be influenced by size or energetic status. In total, these results challenge the putatively winter-dormant LMB and instead suggest that LMB exhibit winter-lethargy punctuated by low levels of activity and feeding over the winter period.

Diel and seasonal patterns of activity

LMB exhibited subtle diurnal or crepuscular patterns of activity; however, these patterns were observably dampened over the course of the winter period (see Fig. S6). Cold-induced dampening of diel activity cycles has been reported in a number of species including LMB (e.g., Demers et al. 1996; Hanson et al. 2007*a*) and appears to be a common phenomenon in winter-lethargic or winter-dormant fish species (Reeve et al. 2022). Changes in activity and depth use were largely explained by changes in temperature with their swimming activity being positively correlated, and depth use being negatively correlated with water temperature (Hanson et al. 2008*b*; Hasler et al. 2009*a*) Activity and depth use were similarly correlated with dissolved oxygen concentrations, but R^2

Fig. 2. Monthly trends in largemouth bass activity and physiology. *Acc* and *HR* MO_2 refer to metabolic rates predicted from Axy-5 and HRT recordings, respectively. Grey dots represent average individual values. Red triangles are group averages.



values suggest that temperature had a greater influence on their behaviour and it is likely that relationships between activity or depth use and dissolved oxygen were confounded by seasonal temperature changes.

Accordingly, LMB exhibited reductions in activity and moved deeper in response to fall cooling (average speed decreased from 0.89 to 0.34 BL s^{-1} and average depth increased from 2.52 to 3.59 m between September and December). Their activity remained low over the winter period (between December and March), but LMB were rarely inactive despite previous reports (e.g., Lemons and Crawshaw 1985; see Fig. 2). Instead, the proportion of time spent inactive peaked in the late fall but declined as winter progressed indicating some acclimation to winter temperatures. Average activity and heart rate also increased over this period, but the change was marginal (average speed increased from 0.34 to 0.36 BL s^{-1} and average heart rate increased from 12.4 to 17.1 bpm between December and March). These results add to the growing body of literature which suggests that LMB are not a winter dormant fish species (Garvey et al. 2004; Karchesky and Bennett 2004; Hanson et al. 2007*a*) and may be more appropriately considered winter lethargic (Reeve et al. 2022).

With spring warming, LMB became increasingly active and moved shallower. LMB were most active and inhabited the shallowest water in June when water temperatures were highest. LMB also exhibited greater individual variation in activity during the spring which may reflect sex-specific differences in spawning behaviour. During the spawning period (mid-May to mid-June) male LMB engage in energetically expensive nest guarding and nest maintenance activities. For example, Cooke et al. (2002) found that nest guarding males exhibited activity rates approximately twice that of non-nesting conspecifics. Burst swimming behaviour also peaked in May/June with similarly high individual variability, likely representative of nest guarding behaviours by male LMB. In a few instances during spring recapture efforts, we observed tagged LMB engaging in nesting behaviours, supporting this assumption. We were unable to determine the sex of tagged LMB as they were released once biologgers were recovered and external sexing of LMB is challenging and often unreliable (Benz and Jacobs 1986). Hasler et al. (2009*b*) reported year-round sex specific differences in activity and depth use; thus, sex-specific differences may also explain some of the variability observed outside of the spawning period.

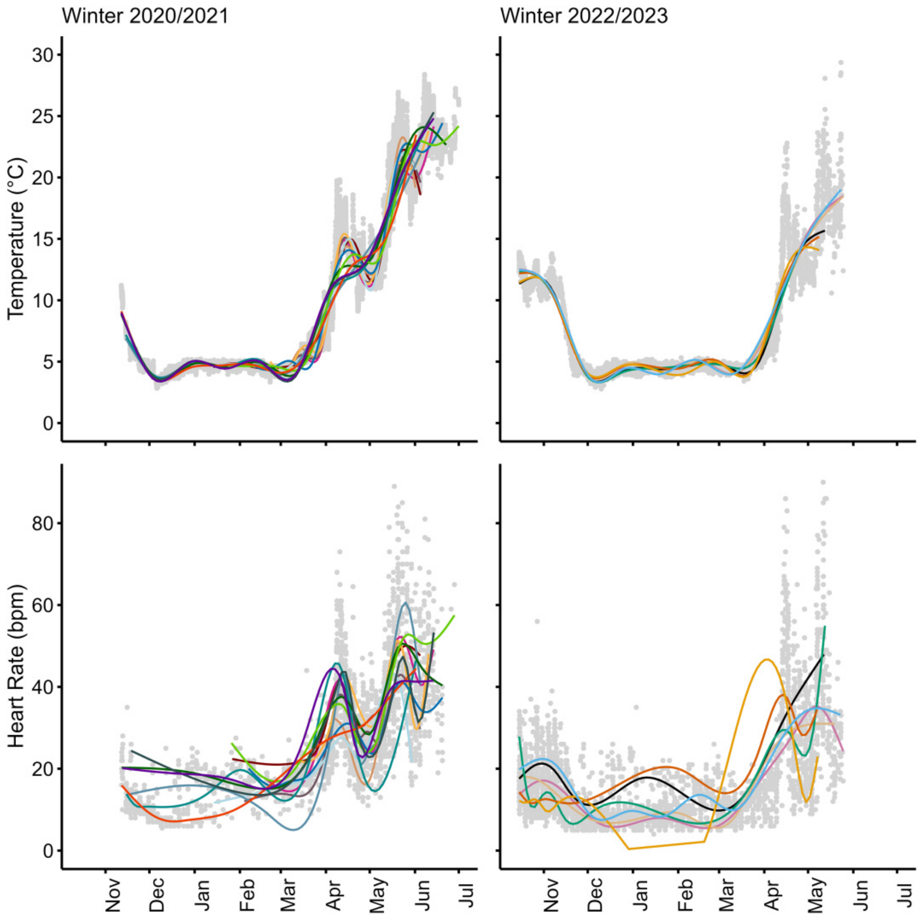
Table 3. Average monthly measurements (±s.e.m.) collected from Axy-5 implanted largemouth bass from the winter 2020/2021 and winter 2021/2022 cohort.

Month, year	*N*	Temp. (°C)	Dissolved oxygen (mg L^{-1})	Depth (m)	Speed (BL s^{-1})	ODBA ($m{\cdot}s^{-2}$)	Time inactive (%)	Time U_{Crit} (%)	Time bursting (%)	MO_2 (mgO_2 kg^{-1} h^{-1})
November 2020	5	5.7 ± 0.3	9.6 ± 0.4	3.5 ± 0.3	0.35 ± 0.01	0.20 ± 0.00	0.98 ± 0.27	0.00 ± 0.00	0.00 ± 0.00	30.5 ± 1.1
December 2020	5	4.1 ± 0.2	9.0 ± 0.3	4.7 ± 0.1	0.31 ± 0.01	0.20 ± 0.00	1.64 ± 0.26	0.02 ± 0.00	0.01 ± 0.01	25.7 ± 1.0
January 2021	9	4.8 ± 0.1	5.1 ± 0.5	3.7 ± 0.3	0.34 ± 0.01	0.21 ± 0.00	0.46 ± 0.20	0.01 ± 0.00	0.00 ± 0.00	28.6 ± 0.9
February 2021	12	4.7 ± 0.1	3.7 ± 0.5	3.0 ± 0.2	0.34 ± 0.01	0.21 ± 0.01	0.35 ± 0.21	0.00 ± 0.00	0.00 ± 0.00	29.0 ± 1.5
March 2021	12	5.7 ± 0.1	3.4 ± 0.2	2.0 ± 0.1	0.37 ± 0.01	0.23 ± 0.00	0.18 ± 0.06	0.01 ± 0.00	0.01 ± 0.00	33.2 ± 1.7
April 2021	12	12.6 ± 0.1	9.8 ± 0.2	0.9 ± 0.1	0.59 ± 0.02	0.23 ± 0.00	0.35 ± 0.13	0.03 ± 0.00	0.02 ± 0.00	67.0 ± 3.5
May 2021	12	15.7 ± 0.8	10.3 ± 0.2	1.0 ± 0.1	0.81 ± 0.10	0.30 ± 0.02	0.38 ± 0.11	0.19 ± 0.10	0.13 ± 0.01	107.3 ± 18.9
June 2021	6	22.5 ± 0.5	8.8 ± 0.1	1.0 ± 0.2	1.30 ± 0.06	0.31 ± 0.02	0.60 ± 0.29	0.31 ± 0.12	0.21 ± 0.08	207.3 ± 14.1
September 2021	9	19.7 ± 0.1	6.2 ± 0.3	2.5 ± 0.3	0.89 ± 0.01	0.22 ± 0.00	1.01 ± 0.24	0.02 ± 0.01	0.02 ± 0.00	126.6 ± 4.1
October 2021	12	16.2 ± 0.1	7.5 ± 0.2	2.7 ± 0.2	0.73 ± 0.01	0.22 ± 0.00	1.93 ± 0.36	0.07 ± 0.02	0.03 ± 0.00	93.6 ± 2.3
November 2021	12	8.1 ± 0.1	10.0 ± 0.1	2.8 ± 0.1	0.42 ± 0.01	0.22 ± 0.00	3.00 ± 0.77	0.04 ± 0.01	0.02 ± 0.00	40.4 ± 1.1
December 2021	12	5.2 ± 0.1	10.3 ± 0.3	3.1 ± 0.2	0.35 ± 0.01	0.21 ± 0.00	1.83 ± 0.48	0.01 ± 0.01	0.00 ± 0.00	30.2 ± 0.8
January 2022	12	5.5 ± 0.1	5.1 ± 0.5	3.7 ± 0.2	0.36 ± 0.01	0.22 ± 0.00	1.12 ± 0.47	0.01 ± 0.01	0.00 ± 0.00	31.5 ± 0.8
February 2022	13	5.4 ± 0.1	2.6 ± 0.3	3.3 ± 0.2	0.36 ± 0.01	0.22 ± 0.00	0.28 ± 0.11	0.01 ± 0.00	0.00 ± 0.00	31.2 ± 1.0
March 2022	12	5.6 ± 0.1	2.1 ± 0.3	2.5 ± 0.2	0.36 ± 0.01	0.22 ± 0.00	0.28 ± 0.10	0.02 ± 0.00	0.01 ± 0.00	32.0 ± 1.2
April 2022	6	7.9 ± 0.5	7.2 ± 0.6	1.9 ± 0.2	0.44 ± 0.01	0.24 ± 0.01	0.52 ± 0.19	0.01 ± 0.00	0.01 ± 0.00	41.8 ± 2.1
May 2022	1	19.8	9.6	0.9	0.94	0.27	0.90	0.26	0.11	133.5
June 2022	1	23.1	8.8	0.7	1.16	0.29	0.27	0.22	0.12	179.6

Interestingly, Warner Lake once had a functioning whole-lake telemetry array which boasted sub-meter accuracy. Using that array, several studies assessed LMB habitat use and seasonal movements using temperature and depth sensing acoustic transmitter tags (e.g., Hanson et al. 2007*a*; Hasler et al. 2009*a*, 2009*b*). Generally, these studies reported similar seasonal trends in activity; however, our estimates of activity were consistently higher. For example, Hanson et al. (2007*a*) reports daily distances traveled ranging from ∼0.75 to 2.5 km between November and April whereas average swimming speeds in this study suggest that LMB traveled ∼10–18 km day^{-1} over the same period whilst experiencing similar temperatures. There is little reason to believe that LMB engage in significant interannual variability in activity; thus, these findings suggest that even high-resolution telemetry (e.g., Lennox et al. 2023) may miss ecologically important and energetically costly fine-scale movements. This may be especially important during the spawning season when males engage in localized but highly active nest guarding behaviours (Cooke et al. 2002). Our estimates of swimming activity appear to be more in-line with those reported by Cooke et al. (2002). Using electromyogram transmitting tags, Cooke et al. (2002) estimated that nesting male LMB move 37–58 km day^{-1} over the spawning period (15 May to 9 June). Over roughly the same period, we estimated LMB moved ∼26–42 km day^{-1}; however, our dataset presumably includes nesting and non-nesting LMB (males and females). It should be noted that although acceleration provides a coarse measure of activity (i.e., overall body acceleration generated from movement), Reeve et al. (2024) showed that the acceleration-swimming speed relationship is also influenced by temperature in LMB. Thus, the use of acceleration alone may impair observations of locomotor activity for some species and prior acceleration-swimming speed calibrations may be necessary to accurately assess fine scale activity rates in certain free-swimming fish.

Heart rate was also positively correlated with temperature and followed a similar trend to locomotor activity, decreasing in response to fall cooling, remaining low over the winter, then increasing in response to spring warming. As

Fig. 3. Data collected from HRT biologger implanted largemouth bass (LMB) over two winter seasons. Different coloured solid lines correspond to different individual LMB, created using a GAM smoother.



metabolic rates were informed by heart rate and ODBA, estimates of free-swimming metabolism also reflected that seasonal trend. Winter estimates of metabolism informed by heart rates and ODBA were similar; however, due to individual variability in winter heart rates, there was greater variability in metabolic rate estimates informed by heart rate. Elevated winter heart rates were observed in some fish which may represent periods of opportunistic feeding which would likely not be captured using recordings of acceleration. Heart rate has been used to predict feeding events in several species since heart rate is elevated to support increased postprandial oxygen demand (e.g., Clark et al. 2013; Shen et al. 2023). Molnár and Tölg (1962) found that LMB digestion rates were dependent on water temperature, and that digestion in the cold could elapse several days (they report 110 h to digest a meal at 5 °C). Therefore, if LMB did engage in winter feeding events, heart rate and associated metabolic rates may be elevated for several days post-feeding.

Bioenergetics modeling and estimates of winter consumption

When comparing the outputs of the original and updated models, the updated model predicted lower wintertime costs, but considerably higher summertime costs (see Figs. 4 and 5). However, it should be noted that when applying the original model to summer conditions, users often, somewhat arbitrarily, modify the activity component (e.g., estimating a routine swimming speed of 5 $cm \cdot s^{-1}$; Rice and Cochran 1984) which would alter this comparison. Wright et al. (1999) noted that the original model overestimated winter costs by more than 20%; thus, it appears that the updated model shows improved performance in the winter. As we lack data on the swimming behaviour of summertime LMB (e.g., in July and August), it is unclear whether our updated model (which assumes optimal swimming performance at >20 °C) will adequately predict summer growth and consumption; however, Hasler et al. (2009*b*) found that LMB exhibited their highest levels of voluntary activity between July and August, which is inline with our model. Nevertheless, further validations will be needed to determine how this model performs in warmer conditions. Additionally, one may note an irregular curvature for larger fish (i.e., >1 kg) when approaching the cutoff temperature at which the activity relationship changes (i.e., *RTL*; see Methods for more details) in the updated model. This is an unfortunate artifact caused by the activity equation used which is based on an exponential equation. This equation was used as it best described the relationships between swimming speed and temperature over the winter period; however, quadratic equations may fit better over a wider range of temperatures

Fig. 4. Visual representation of the inputs and outputs of the original model (i.e., Rice et al. 1983). The effects for largemouth bass of differing size are shown using different colour. Note that this visualisation uses the default activity settings included in Fish Bioenergetics 4.0 (Deslauriers et al. 2017); however, users often alter this setting to meet their expectations of activity.

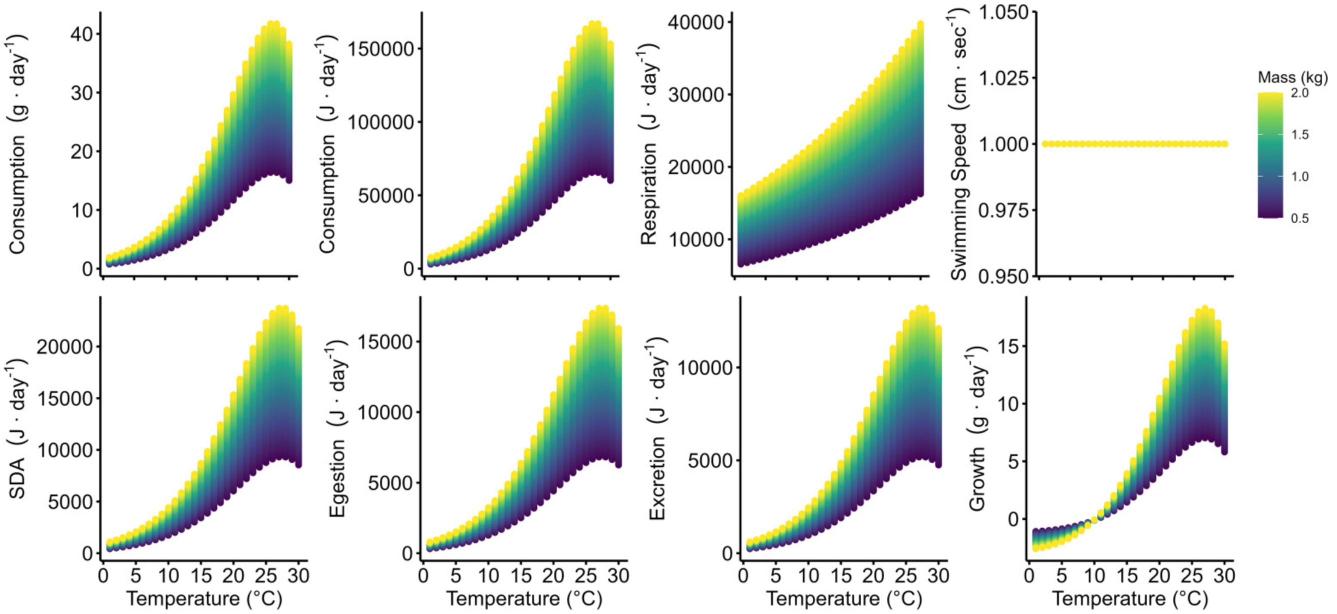
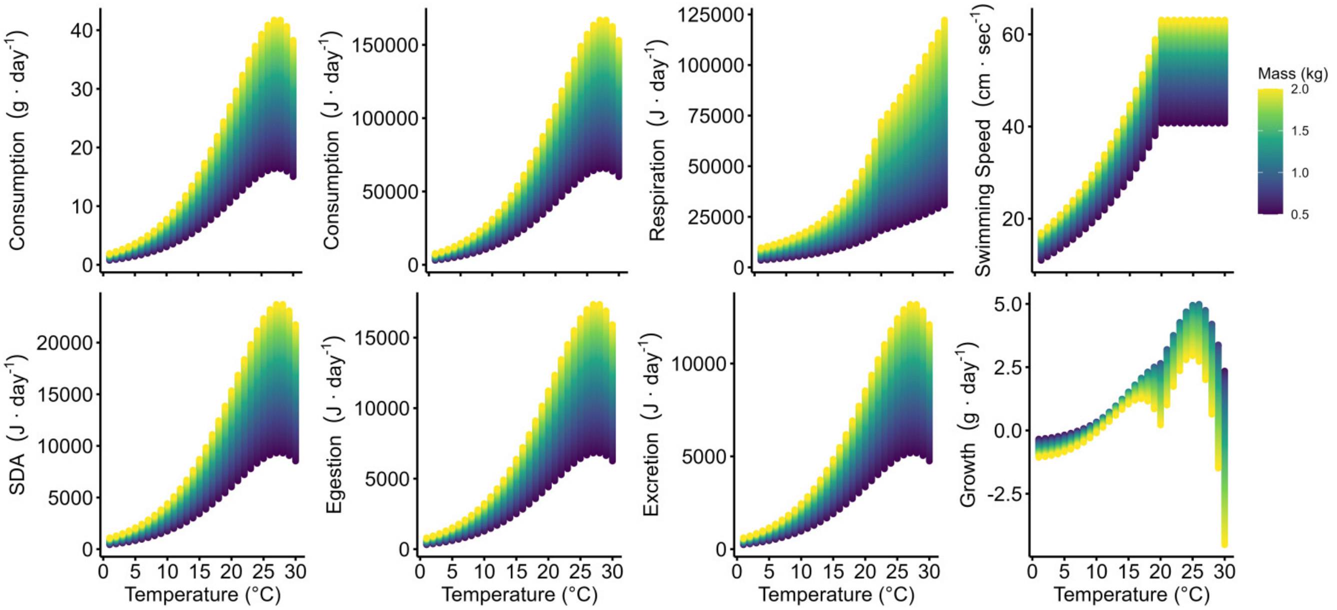


Fig. 5. Visual representation of the inputs and outputs of the updated model (i.e., informed using updated respiration and activity coefficients which were derived from our free-swimming data as data collected from Reeve et al. (2024)).



(e.g., Lee et al. 2003). Nevertheless, future users should consider this artifact when applying the updated model to larger individuals.

Estimates of consumption and simulations of fasting largely indicate that LMB must engage in some overwinter feeding. Estimates of overwinter consumption were highest when using the original model, followed by the updated model, and the biologger-informed model routinely predicted the lowest rates of winter consumption. Despite the predominately negative growth rates, all models indicated that LMB engaged in supplemental feeding throughout the winter (LMB consumed ∼18%–29% of their body mass over the winter). Simulations of winter fasting also support overwinter feeding, as estimated losses were greater than observed in most instances (averaged predicted losses = 15.9%–27.9% average observed losses = 8.9 ± 1.9%). Interestingly, for a small number of individuals ($n = 3$ when using estimates from the biologger-informed model; $n = 1$ when using estimates from the updated model), observed losses were greater than those predicted from fasting simulations. Adding a simulated fasting-induced reduction in winter metabolic rate resulting in a greater number of these individuals (4 out of the 11 individuals that were tested; average predicted loss = 11.8%). Notably, sex specific differences likely also contribute to differences in overwinter change in mass (Adams et al. 1982). Since the study encapsulated the spawning period for a portion of the LMB collected, nesting male LMB which are believed to fast during spawning may have contributed to greater observed losses in body mass (Heidinger 1975; Miller 1975). We also used a somewhat arbitrary, presumably conservative 30% reduction in metabolic rate, but it is possible that LMB may exhibit a greater drop in their metabolic rate. For example, Gingerich et al. (2010) reported 75% lower resting metabolic rates in fasted LMB when compared to LMB fed ad libitum. Additionally, low dissolved oxygen concentrations may further reduce winter metabolic rates in LMB (Cech et al. 1979; Sullivan 1986). Nevertheless, taken together, these simulations suggest that while most LMB engage in low levels of winter feeding, some LMB fast over the winter period.

Linear regressions of fall mass or condition and post-winter proportional change in mass suggest that larger individuals and individuals with better condition lost proportionally greater mass over the winter period; however, model fit was poor (Fig. S10). These results suggest that overwinter feeding in LMB may be related to energetic status. This notion is further supported by the relationships between fall mass or fall condition and estimates of winter consumption generated from biologger-informed and updated models (Fig. S11). These relationships suggest that smaller individuals and individuals with lower condition consumed proportionally greater food than larger or higher condition counterparts. Therefore, it is possible that the reason studies have found support for both overwinter feeding and fasting (e.g., Lemons and Crawshaw 1985; Wright et al. 1999; Garvey et al. 2004) may be in part due to differences in the size or energetic status of LMB being studied. Nevertheless, it is likely that LMB will still engage in opportunistic overwinter feeding practices considering the presumed benefits of mass maintenance (e.g., greater resources to allocate to post-winter spawning).

Considerations

LMB appeared to respond well to surgical implantation, evidenced by a lack of change in post-release behaviour and high recapture rates. Previous studies have established heart rate as a good indicator of surgical recovery (e.g., Hvas et al. 2020; Zrini and Gamperl 2021); however, post-release changes in heart rate could not be assessed in this study due to the recording delay that was programmed in the 2022/2023 winter cohort to preserve battery, and the poor quality of heart rate recordings in the 2020/2021 winter cohort. Several studies have also noted relatively poor heart rate recordings in LMB (e.g., Doherty et al. 2022; Reeve et al. 2024). Reeve et al. (2024) postulates that the greater density of pectoral musculature present in LMB could cause greater interference in the ECG signal when swimming in comparison to other species like salmonids. Cold-induced low heart rates likely also contributed to reduced success in recording and calculating heart rate (e.g., proportion of heart rates successfully calculated during winter = 19.4 ± 4.5% versus outside the winter season = 44.2 ± 3.8%). The recording interval used could record heart rates as low as 4 bpm but may miss heart rates as high as 7 bpm if the spacing between beats was ill-timed (a minimum of two beats are required to calculate heart rate). Overwinter heart rates were frequently between 4 and 7 bpm (winter range 4–26 bpm), and likely dipped below 4 bpm at times, leaving some calculations not possible causing data loss. Missed heart rates could skew calculations of average winter heart rate and heart rate informed estimates of metabolic rate. This may explain the higher overwinter metabolic rates for heart rate biologger-equipped LMB.

The use of calibrations to estimate free-swimming swimming speed and metabolic rate are also imperfect. For instance, such calibrations can only estimate aerobic metabolic rate and do not consider anaerobic metabolism. There is evidence to suggest that LMB use anaerobic metabolism when environmental dissolved oxygen is <2.0 mg L^{-1} (Gaulke et al. 2015) and, since winter experiences relatively greater hypoxia than other seasons, anaerobic metabolism could contribute to their overwintering energy use. Additionally, these calibrations are only accurate within a narrow range of temperatures and fish sizes that were considered within the study. Although heart rate and ODBA informed metabolic rates were similar across most of the study period, those informed by ODBA were relatively higher at warmer water temperatures (>20 °C). For example, average metabolic rates in June were 132.8 ± 11.5 mg O_2 kg^{-1} h^{-1} when estimated from heart rate and 203.3 ± 11.5 mg O_2 kg^{-1} h^{-1} when estimated from ODBA which approaches estimates of maximum metabolic rate (MMR = ∼215 mg O_2 kg^{-1} h^{-1} at 25 °C after adjusting to a similar mass; Beamish 1970). This is not particularly surprising as the calibrations performed in Reeve et al. (2024) appeared to permit accurate metabolic rate estimation only up to ∼20 °C. Since the ODBA-metabolic rate relationship is affected by temperature, whereas the heart rate-metabolic rate is not, it is likely that ODBA-informed estimates of metabolic rate may be elevated at higher temperatures (i.e., >20 °C). Similarly, the ODBA-swimming speed relationship in LMB is also influenced by temperature, thus it is possible that estimates of swimming speed may also be elevated at higher temperatures. Our results also suggest a noticeable lack of inactive values (i.e., values < 0.1 $m\cdot s^{-1}$) suggesting near-constant movement by LMB, especially at warmer temperatures. While constant activity at warmer temperatures has been observed in other centrarchids (e.g., pumpkinseed sunfish; Reeve et al. 2022), median or paired-fin swimming (which is a common in centrarchids; Higham 2007) and/or body posture changes may have influenced measurements of ODBA and hinder the accurate estimation of inactive measurements and potentially inflating low-activity estimates (in particular in the cold where low levels are activity are more prevalent).

Summary

Few studies have assessed free-swimming fish behaviour and bioenergetics at such fine scales. Accordingly, these results expand our understanding of LMB behaviour, activity, and energy use in the wild. We primarily focused on winter responses; however, as the study period also encapsulated fall and spring. Thus, these results are broadly applicable to most of their annual cycle. Our study also adds to the body of LMB research conducted on Warner Lake (Suski and Philipp 2004; Hanson et al. 2007*a*; Hanson et al. 2008*a*, 2008*b*; Hasler et al. 2009*a*, 2009*b*; Hanson et al. 2010; O'Connor et al. 2010) and builds on the findings of Hanson et al. (2007*a*) and Hasler et al. (2009*a*, 2009*b*). Observed seasonal trends were consistent with other field studies on LMB, exhibiting reductions in activity and depth use over the winter, and largely subtle crepuscular or diurnal patterns of actvity that became dampened with cooling. Like other studies on LMB (Doherty et al. 2022; Reeve et al. 2024), we had difficulty collecting reliable heart rate recordings which may have been exacerbated by low heart rates in the cold. Future winter studies may consider using the longer 18 s sampling interval.

This study also provided a unique opportunity to assess the field performance the acceleration and heart rate informed calibrations produced in Reeve et al. (2024). Our results suggested that heart rate and ODBA provided reasonable estimates of free-swimming metabolism; however, at higher temperatures (>20 °C), ODBA informed metabolic rates appeared to be elevated. To accurately estimate metabolic rates of free-swimming LMB at higher temperatures, warm-water (20–30 °C) biologger calibrations should be conducted. Additionally, our comparisons between activity estimates from accelerometer biologgers and high-resolution telemetry (from Hanson et al. 2007*a*), revealed that telemetry may inadequately measure activity costs for certain species that exhibit more localized activity.

Additionally, few studies have incorporated estimates of free-swimming metabolic rate with bioenergetics modeling to predict growth or consumption (Brodie et al. 2016). Simulations of winter fasting yielded greater than observed mass losses for most individuals, suggesting a necessity for overwinter feeding; however, after simulating a fasting-induced reduction in metabolism, predicted losses were similar to observed changes for some individuals, suggesting that some LMB may engage in fasting whereas others do not. More research is needed to determine the effects of fasting and hypoxia on their winter metabolism to support these findings. Nevertheless, linear regressions suggest that overwinter feeding may be related to LMB size or condition such that smaller, lower conditions individuals are more likely to feed. Considering that overwintering size-selective mortality is a common phenomenon observed in northern LMB populations and that size appears to be related to reproductive success in LMB (Cooke and Philipp 2009), size- or condition-dependent feeding is logical.

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Data availability

Associated data can be found in our online supplement (10.6084/m9.figshare.26863108.v1) and R code is located in our github repository (10.5281/zenodo.14278334).

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Competing interests

We report no conflicts of interest.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2024-0254.

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