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Article

Understanding the energy use of cultured juvenile catfishes at low temperatures

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ABSTRACT

Objective: Cultured catfish are subjected to cold temperatures during winter, as aquaculture ponds are relatively shallow (<1.5 m) and experience seasonal thermal fluctuations. Cold temperatures reduce metabolic processes; however, little is known about comparative differences in metabolic rates, swimming performance, and blood metabolites among principal types of cultured catfish. Therefore, the objective of this study was to address this knowledge gap for catfish types used in the U.S. aquaculture industry.

Methods: Standard metabolic rate, maximum metabolic rate, metabolic scope, critical swimming speed (U_{crit}), and blood metabolites were analyzed at 10°C and 20°C in juvenile Channel Catfish *Ictalurus punctatus*, Blue Catfish *I. furcatus*, and hybrid catfish (Channel Catfish × Blue Catfish).

Results: It was hypothesized that hybrid catfish would have greater metabolic and swimming performance than Channel and Blue catfishes across experimental temperatures due to heterosis. However, metabolic scope and U_{crit} did not vary among fish types, but U_{crit} was reduced among all fish types at 10°C. Lactate and glucose concentrations were higher and blood pH was lower in fatigued catfish, with Channel Catfish generally differing in blood metabolites from Blue and hybrid catfishes.

Conclusions: Results indicate that prolonged exposure to cold temperatures limits metabolic processes and swimming capacity, ultimately requiring catfish to allocate energetic resources to maintenance metabolic requirements. Although no distinct comparative advantage was found for any of the catfish types at low temperature, long-term health and survival likely relate to energy stores accrued prior to and during exposure to cold temperatures. These findings provide useful comparative metrics to direct future efforts into investigating the physiological and environmental mechanisms affecting the catfish aquaculture industry.

KEYWORDS: aquaculture, hematology, heterosis, metabolism, respirometry, swim flume

LAY SUMMARY

Low physiological performance at cool temperatures was documented across catfish types commonly used in the U.S. aquaculture industry. Results provide important information for developing bioenergetic models that can guide future management efforts in the catfish aquaculture industry.

INTRODUCTION

In ectothermic fishes, water temperature is the most important abiotic factor affecting physiological processes, including overall metabolism (Brett, 1971; Clarke & Johnston, 1999; Fry, 1947, 1971; Jensen et al., 1993). There is a direct relationship between temperature and metabolic rate (Clarke & Johnston, 1999; Di Santo & Bennett, 2011; Johnston & Dunn, 1987; Schmidt-Nielsen, 1997), with metabolic rate generally increasing or decreasing two- to threefold with every 10°C change in temperature (Di Santo & Bennett, 2011; Jensen et al., 1993; Schmidt-Nielsen, 1997).

The relationship between metabolic rate and temperature has been an active field of research in fishes (Clarke & Johnston, 1999; Fry & Hochachka, 1970; Rosewarne et al., 2016; Schulte,

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2015); however, less investigation has been focused on the effects of cool to cold temperatures. When exposed to cold temperatures, many warmwater fish become inactive, stop feeding, consume less oxygen, and experience a decrease in metabolic rate (De Silva et al., 1986; Fernandes & McMeans, 2019; Johnston & Dunn, 1987). Cold temperature effects on metabolic rates are of particular interest with regard to temperate fish inhabiting modified natural habitats and outdoor aquaculture systems, including commercially cultured catfishes.

The catfish aquaculture industry is a valuable economic component in the southeastern United States, with sales surpassing US$400 million in 2023 (U.S. Department of Agriculture, 2024). Aquaculture systems for catfish production predominantly use shallow ponds (3–5 surface hectares; <1.5 m deep), where water temperature changes seasonally and may dramatically fluctuate daily with changes in air temperature (Arnold et al., 2013; Steeby & Avery, 2002). For instance, Burger et al. (2018) found daily temperature changes up to 7°C in small (0.04-ha) earthen ponds in Mississippi. Although the catfish aquaculture industry is confined mostly to the southeastern United States, seasonal pond temperatures can range from 4°C in winter up to 38°C in summer (Bly & Clem, 1992). In winter, pond temperatures typically fluctuate from 6°C to 23°C, with extreme cold fronts causing rapid temperature changes of up to 9°C in 12 h (Bly & Clem, 1992). Extremely low temperatures and abrupt decreases in water temperature can lead to substantial mortality in commercial catfish ponds (Bly & Clem, 1992). In northwestern Mississippi, the principal location for commercial catfish production in the United States, catfish ponds have an average temperature below 15°C for about 90 d annually (Tucker & Hargreaves, 2004). These low temperatures lead to reduced feed intake, food conversion efficiency, and growth in Channel Catfish *Ictalurus punctatus* (Andrews & Stickney, 1972; Robinson et al., 2001; Suja et al., 2009; Weber & Bosworth, 2005). Notably, many fish species preferring temperatures from 19°C to 30°C are believed to lack both the physiological and behavioral mechanisms necessary for sustained activity and energy acquisition during prolonged winter conditions (Coker et al., 2001; Kolok, 1991; Fernandes & McMeans, 2019; Shuter et al., 2012).

The catfish aquaculture industry has rapidly increased the use of hybrid catfish (Channel Catfish × Blue Catfish *I. furcatus*) to improve performance through heterosis by selecting preferred culture traits from the female Channel Catfish and male Blue Catfish parental strains (Bosworth & Waldbieser, 2014). Rapid growth is among these preferred traits (Dunham et al., 1987, 1990; Li et al., 2004), which may be due in part to greater metabolic capabilities (Gerhart et al., 2024). Despite prolonged cold temperature exposure during winter, comparative metabolic responses in Channel, Blue, and hybrid catfishes are not well understood. However, cold temperature effects on metabolism are important for understanding growth and optimizing productivity (Claireaux & Lefrançois, 2007; Fitzgibbon et al., 2007; Neill & Bryan, 1991).

Standard metabolic rate (SMR), maximum metabolic rate (MMR), and metabolic scope (the difference between MMR and SMR) are metrics commonly used to aid in understanding overall metabolic responses when fish are exposed to changing environments. For most organisms, physiological functions become impaired and life cannot be sustained if the metabolic rate falls below the SMR (Chabot et al., 2016; Claireaux & Chabot, 2016; Job, 1957; Priede, 1985; Smit, 1965). Maximum metabolic rate (typically measured as critical swimming speed [U_{crit}]; Brett, 1964; Kolok, 1999; Rubio-Gracia et al., 2020) and metabolic scope frequently exhibit bell-shaped curves, with maximized performance at the thermal optimum and diminished performance at extreme temperatures (Brett, 1971; Brett & Glass, 1973; McKenzie & Claireaux, 2010). Notably, red muscle power production decreases at low temperatures, requiring compensation from white muscle, which results in poor swimming performance (McKenzie & Claireaux, 2010).

In addition to overall metabolic rate, blood metabolite measurements further the understanding of temperature effects on metabolism (Lurman et al., 2007). Blood pH, lactate, and glucose are indicative of exhaustive exercise (Seibel et al., 2021; Woodward & Smith, 1985), while red blood cell (RBC) concentration, hematocrit (Hct), and hemoglobin (Hb) reflect aerobic capacity. Hematology is helpful for determining how various fishes meet metabolic requirements and provides important insight for comparisons among Channel, Blue, and hybrid catfishes for understanding physiological performance in cool to cold environments.

Although important for maximizing aquaculture production and understanding environmental influences, little is known of cold temperature effects on different commercial catfish types, particularly regarding physiological performance. Therefore, the objective of this study was to examine the effects of low temperature on SMR, MMR, metabolic scope, swimming performance, and hematological variables in Channel, Blue, and hybrid catfishes. It was hypothesized that due to heterosis, hybrid catfish would have greater swimming performance and a larger metabolic scope than Channel and Blue catfishes at low (10°C) and moderate (20°C) temperatures.

METHODS

Fish rearing

Juvenile Channel, Blue, and hybrid catfishes were spawned during the same time of the year and reared by the U.S. Department of Agriculture's Agricultural Research Service at the Thad Cochran National Warmwater Aquaculture Center (Stoneville, Mississippi); they were then transported to Mississippi State University's South Farm Aquaculture Facility. Channel Catfish were from the Delta Select strain, Blue Catfish were from the Delta Elite strain, and hybrid catfish were produced from the same parental strains. Established in 2006 by the U.S. Department of Agriculture's Warmwater Aquaculture Research Unit, the Delta Select strain was derived from select catfish farms to improve growth and carcass yield (Bosworth et al., 2020). The Delta Elite strain was developed by crossbreeding the four highest-performing strains of Blue Catfish evaluated by the Warmwater Aquaculture Research Unit (Bosworth & Waldbieser, 2020).

Pond temperatures typically fluctuate from 6°C to 23°C during the winter (Bly & Clem, 1992), with averages below 15°C for about 90 d annually (Tucker & Hargreaves, 2004). Bosworth (2012) reported a mean water temperature of 10.8°C during a

14-week pond study in the Mississippi Delta; therefore, 10°C and 20°C were considered average cold and mild temperatures, respectively, and served as the two treatment temperatures for this study. Fish were gradually acclimated for 2 weeks from 27°C at the Thad Cochran National Warmwater Aquaculture Center to 20°C at the South Farm Aquaculture Facility. After the 2-week acclimation, fish were measured (nearest mm), weighed (nearest 0.01 g), and equally distributed into eighteen 355-L tanks, with 50 catfish/tank, across two independent recirculating aquaculture systems (RASs). Each RAS consisted of 10 tanks, a sump tank, a header tank, a chilling reservoir, a biofilter, and an ultraviolet sterilizer.

Temperature was gradually decreased in one RAS by 1°C per day until 10°C was reached. Each RAS was maintained at either 10°C or 20°C and consisted of three tanks of each fish type (randomly distributed) and one empty tank that served as a holding tank for experiments. All tanks were supplied with well water and forced air via air stones. Salinity was maintained at 1‰ with marine salt (Instant Ocean; Spectrum Brands, Inc., Blacksburg, Virginia) to reduce disease potential.

Fish were held at a 12 h light : 12 h dark photoperiod. Temperature, dissolved oxygen, salinity, and pH were measured daily with a dissolved oxygen meter (Pro 2030; YSI, Inc., Yellow Springs, Ohio) and a pH probe (EcoSense pH100A; YSI, Inc.). Alkalinity (titration), nitrite (diazotization method), and total ammonia nitrogen (salicylate method) were measured twice weekly with a colorimeter (DR/850; Hach Company, Loveland, Colorado). Water quality was maintained appropriately for Channel Catfish (Tucker & Robinson, 1990) across all tanks and treatments (Table 1). Biofilters were backwashed daily, and tanks were siphoned and/or scrubbed weekly. All tanks were observed daily, and any dead fish were removed immediately. Feeding to satiation occurred daily with a commercial diet (Fry/Fingerling Catfish Food; Fishbelt Feeds, Inc., Moorhead, Mississippi) consisting of 35% crude protein, 2.5% crude fat, 7% crude fiber, and 0.4% phosphorus. Tanks were monitored for 30 min, and additional pellets were added as needed until feed consumption ceased, determined by pellets remaining at the surface. The remaining pellets were removed from the tanks after feeding. All fish were fed an unrestricted ration to prevent potential bias among fish types for those that may have been feeding optimally and those that were ration restricted. This led to some of the fish types growing faster than others. Allowing for a sufficient time of temperature acclimation also resulted in different fish sizes. This was an inevitable outcome but allowed for the evaluation of fish at their optimal physiological performance levels at each temperature, which was preferred for evaluating metabolic measurements.

Standard metabolic rate

The SMRs were measured using intermittent respirometry. Four 2.24-L respirometers (Loligo Systems, Viborg, Denmark) were used to simultaneously measure the SMRs of four fish. The respirometers were held in a rectangular, insulated tank filled with 470 L of well water. To reduce external stimuli, a plastic mesh cover allowing for visual observations of fish movement was placed over the tank during all respirometer runs. Inside the tank, the two treatment temperatures (10°C and 20°C) were maintained by chillers (Cyclone Drop-In, 373 W [0.5 hp]; Aqua Logic, Inc., San Diego, California). All fish were thermally acclimated to the treatment temperatures for at least 2 weeks and were approximately equally distributed from the three holding tanks for each temperature. Ten fish of each type from the 10°C temperature treatment were randomly sampled, and 15 fish of each type were randomly sampled from the 20°C treatment, for 75 total samples. More fish from the 20°C treatment were sampled than from the 10°C treatment due to greater variation in SMR measurements.

In fish, SMR is typically measured after acclimation to the experimental temperature when the fish is in a resting, postabsorptive state (Chabot et al., 2016; Rosenfeld et al., 2015). Therefore, food was withheld for 48 h by isolating the selected fish in an identical holding tank within the RAS to ensure a postabsorptive state before the fish were placed into the respirometers. A low level of buffered anesthetic solution (200-mg/L concentration of Syncaine [tricaine methanesulfonate; Syndel, Ferndale, Washington] with 400-mg/L $NaHCO_3$) was used to sedate the fish and minimize the stress associated with handling (Prystay et al., 2017; Trushenski et al., 2012). Although the fish recovered shortly after being placed in respirometers, the first several hours in the respirometers were considered acclimation and were not used for selection of SMR measurements. Individual fish were sedated in a buffered anesthetic solution, weighed, and measured. Oxygen consumption was measured with a fiber optic oxygen microsensor and T-shaped flow-through cell (PreSens Precision Sensing GmbH, Regensburg, Germany), a temperature probe (Pt1000; Loligo Systems), a connected meter (Witrox 1/Witrox 4; Loligo Systems), and associated computer software (AutoResp version 2.3.0; Loligo Systems). Oxygen probes were calibrated at 0% oxygen saturation with sodium sulfite (Na_2SO_3) and at 100% oxygen saturation with air-saturated water before each run. Respirometer cycles for both 10°C and 20°C consisted of a 9-min flush, a 1-min wait, and a 15-min measuring period, with each cycle lasting 25 min. For each fish, the three lowest measurements of metabolic rate (MO_2; mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) over 21–24 h were recorded, and the average was calculated to obtain the SMR (Coffill-Rivera, Neal, & Allen, 2023; Cutts et al., 2002; McKenzie, 2001; Roche et al., 2013). A fin clip was taken from the anal fin of each fish used in the respirometer to indicate that it had been sampled before returning the fish to the RAS.

Maximum metabolic rate

To measure MMR, a 98-L, Blazka-style swim flume with a cylindrical swimming chamber (100.3 cm long, 15.2 cm in diameter) was used following Gerhart et al. (2024) and Vaughn et al. (2024). The swim flume was covered on the observer's side with a dark plastic covering to reduce external stimuli. A flow meter and probe (Flo-Mate 2000; Marsh McBirney, Inc., Frederick, Maryland) were used to determine the water velocity (cm/s) and calibrate to revolutions per minute in a tachometer display box. The measurements of revolutions per minute for each water velocity were an average of measurements at the bottom, middle, and top of the swim flume fish chamber. During the swimming tests, oxygen

Table 1. Mean ± SE water quality variables from juvenile Channel Catfish, Blue Catfish, and hybrid catfish tanks. Dissolved oxygen (DO), pH, and salinity were recorded daily. Total ammonia nitrogen (TAN), un-ionized ammonia (NH_3), nitrite (NO_2), and alkalinity were recorded twice weekly. Different letters indicate significant differences among fish types, and an asterisk indicates a significant difference between the two temperatures (two-way ANOVA: $P < 0.05$).

	10°C			20°C		
Variable	**Channel**	**Blue**	**Hybrid**	**Channel**	**Blue**	**Hybrid**
DO (mg/L)	11.15 ± 0.12* x	11.12 ± 0.16* y	11.02 ± 0.09* y	7.75 ± 0.15 z	8.12 ± 0.11 z	8.42 ± 0.05 z
pH	7.89 ± 0.04* y	7.89 ± 0.01* y	7.96 ± 0.01* z	7.43 ± 0.06 y	7.39 ± 0.01 y	7.53 ± 0.03 z
Salinity (ppt)	0.8 ± 0.0*	0.8 ± 0.0*	0.8 ± 0.0*	0.9 ± 0.0	0.9 ± 0.0	0.9 ± 0.0
TAN (mg/L)	0.20 ± 0.00 w	0.20 ± 0.01 w	0.18 ± 0.00 v	0.36 ± 0.02 z	0.32 ± 0.03 y	0.24 ± 0.01 x
NH_3 (mg/L)	0.003 ± 0.000*	0.003 ± 0.000*	0.009 ± 0.003*	0.004 ± 0.001	0.004 ± 0.001	0.004 ± 0.000
NO_2 (mg/L)	0.040 ± 0.004*	0.042 ± 0.002*	0.034 ± 0.002*	0.112 ± 0.022	0.100 ± 0.017	0.081 ± 0.009
Alkalinity (mg/L)	97 ± 4*	101 ± 2*	95 ± 4*	75 ± 4	79 ± 2	80 ± 5

consumption was measured with a fiber optic oxygen probe (Oxygen Dipping Probe; PreSens), a connected meter (OXY-1 SMA; PreSens), and associated computer software (PreSens Measurement Studio 2, version 3.0.3.1703). The oxygen probe was calibrated at 0% and 100% oxygen saturation before placing each fish into the swim flume.

Six to seven fish of each type were randomly sampled from an approximately equal distribution of tanks within both the 10°C and 20°C temperature treatments. To ensure a postabsorptive state, a fish was selected and placed in an identical holding tank within the RAS, where food was withheld for 36 h before placing it in the swim flume and 48 h before the swimming test. Fish were acclimated to the swim flume overnight at 10 cm/s at the given treatment temperature. During acclimation, water was continuously recirculated to the flume from an adjacent circular, 200-L tank, where temperature was maintained by a chiller (Cyclone Drop-In, 373 W [0.5 hp]; Aqua Logic, Inc.) and oxygen was maintained by air stones. After overnight acclimation (~12–15 h) and before oxygen measurements, the water velocity was increased by 10 cm/s (i.e., to 20 cm/s) for 5 min. After 5 min, the water velocity was increased again to 30 cm/s. At this point, oxygen measurements began and the recirculating pump connecting the swim flume to the adjacent 200-L tank was turned off to prevent oxygenated water from flowing into the swim flume during the 30-min measurement period. After 30 min, an 11-min flush followed, allowing oxygenated water from the adjacent 200-L tank to pump into the swim flume at 9 L/min to complete one water turnover. After the 11-min flush, this 41-min procedure was repeated with increasing water velocities of 10 cm/s. The swim test was concluded once the fish fatigued, which was determined by three uninterrupted, 10-s impingements of the fish on the back screen of the swim flume (Allen et al., 2021). After each impingement, the timer was paused, and water velocity was reduced to 0 cm/s to allow the fish to remove itself from the back screen. The water velocity was increased to the designated velocity and the timer was resumed immediately after the fish removed itself from the back screen.

After completing the swimming test, the fish was sedated in a buffered anesthetic solution, weighed, and measured. Axis lengths (nearest mm) were obtained from the widest points of the body with calipers, a fin clip was taken from the anal fin to indicate that the fish had been sampled, and a blood sample was taken from the caudal vein. The U_{crit} was calculated following Brett (1964):

$$U_{crit} = V_f + V_i\left(T_f / T_i\right),$$

where V_f is the final water velocity at which the fish swam the entire 41 min; V_i is the increment of water velocity increase (10 cm/s); T_f is the time swam at the water velocity of fatigue; and T_i is the time increment for each water velocity (41 min). To determine whether a solid-blocking correction was needed for U_{crit} calculations, cross-sectional areas of fish were compared with the flume. For the fish, cross-sectional area was determined using an equation for the area of an ellipse:

$$\text{Area} = \pi \times A \times B,$$

where A is the radius of the vertical axis and B is the radius of the horizontal axis. Because the maximum cross sections of fish did not exceed 10% of the cross-sectional flume area, no solid-blocking corrections were required (Bell & Terhune, 1970).

Using measures of oxygen consumption and fish weight, MO_2 was calculated for each fish at each water velocity following Behrens et al. (2006) and Khan and Herbert (2012):

$$MO_2 = \alpha \times V_{resp} \times \beta \times M^{-1},$$

where MO_2 is the oxygen consumption (mg $O_2 \cdot kg^{-1} \cdot h^{-1}$), α is derived from the oxygen consumption rate over the 30-min measurement period, V_{resp} is the difference between the full flume volume (98 L) and the fish volume (converted from g to mL), β is oxygen's solubility in water (0.542 and 0.439 mg $O_2 \cdot L^{-1} \cdot kPa^{-1}$ for 10°C and 20°C, respectively), and M is the fish's mass (nearest 0.01 g). The highest metabolic rate before fatigue for each fish served as the MMR for that sample.

Metabolic scope for activity

To determine the metabolic scope for each treatment, the SMRs and MMRs for each treatment and fish type were averaged, and the difference between the average SMR and the average MMR was then used to calculate the metabolic scope (Clark et al., 2013).

Blood metabolites

Blood samples were simultaneously collected from fatigued and nonfatigued fish in postabsorptive states (e.g., not fed for 48 h). For each temperature treatment, six or seven fatigued and nonfatigued fish of each type were randomly sampled, for 78 total samples. Immediately after a fish had fatigued in the swimming flume, it was removed and sedated in a buffered anesthetic solution, and a nonfatigued fish was sampled from the holding tank in the same manner. After losing equilibrium, fish were placed into a supine position on a wet sponge and the caudal peduncle was dried. Blood samples (~0.5 mL) were collected from the caudal vein with two different methodologies depending on the temperature treatment due to smaller sizes and quicker blood clotting in fish acclimated to 10°C. A heparinized syringe or Vacutainer and a 22–25-gauge hypodermic needle were used to collect blood samples from fish acclimated to 20°C. In fish acclimated to 10°C, the caudal fin was severed posterior to the anal fin and blood was collected with a heparinized Hct tube directed into a 1.5-mL microcentrifuge tube. Immediately after sampling, blood was placed on ice and fish were weighed and measured; for fish at 20°C, a fin clip was taken from the anal fin to indicate that the fish had been sampled.

Immediately after collection, pH was measured in whole blood with a microelectrode (Accumet AB15; Fisher Scientific, Hampton, New Hampshire) and a water bath set at the treatment temperature. Hematocrit, Hb, RBC, mean corpuscular volume (MCV), mean corpuscular Hb (MCH), and mean corpuscular Hb concentration (MCHC) were also measured from whole blood. Hemoglobin was analyzed with Drabkin's reagent (Sigma-Aldrich, St. Louis, Missouri), and RBC counts were determined with a hemocytometer (1:200 dilution with saline). From the whole blood samples, a 50–200-µL quantity was transferred to a 0.6-mL microcentrifuge tube and centrifuged for 3 min at 2,795 × *g*. Plasma was collected, stored at −80°C, and used later to measure lactate and glucose. Lactate was analyzed with an L-Lactate Assay Kit (A-108S/L; Biomedical Research Service & Clinical Application, Buffalo, New York), and glucose was analyzed with a QuantiChrom Glucose Assay Kit (DIGL-100; BioAssay Systems, Hayward, California).

Statistical analysis

All statistical analyses were performed with SAS version 9.4 (SAS Institute, Inc., Cary, North Carolina). Dixon's *Q*-tests at 95% CIs were used to test for outliers, with no more than one outlier removed from each treatment combination group. Acclimation tanks were analyzed for a tank effect on SMR, MMR, and U_{crit}. No differences were found, so each fish was considered a replicate in analyses. To determine whether fish weights for each treatment combination within and between SMR and MMR/U_{crit} experiments were similar, a three-way ANOVA was used. Although there were significant differences in fish weight (Table 2), SMR and MMR data were adjusted to fish weight. A two-way ANOVA with temperature (10°C or 20°C) and fish type (Channel Catfish, Blue Catfish, or hybrid catfish) as fixed factors was used to analyze SMR and MMR. A two-way ANCOVA with temperature and fish type as fixed factors and weight as a covariate was used to analyze U_{crit} since data were not adjusted for differences in fish weight. A three-way ANOVA with temperature, fish type, and exercise (fatigued or nonfatigued) as fixed factors was used to analyze blood pH, lactate, glucose, and hematological variables. If the overall ANOVA or ANCOVA was significant, Tukey's honestly significant difference post hoc tests were used to determine treatment-level differences between factors. In all cases, significance was determined at $P \leq 0.05$. Data are reported as mean ± SE unless noted otherwise.

RESULTS

Standard metabolic rate

For SMR, the interaction between temperature and fish type was not significant (ANOVA: $F_{2, 68} = 1.79$, $P = 0.1755$), whereas the two main effects of temperature (ANOVA: $F_{1, 68} = 208.09$, $P < 0.0001$) and fish type (ANOVA: $F_{2, 68} = 5.54$, $P = 0.0059$) were significant. The SMR was greater at 20°C than at 10°C, and hybrid catfish had greater SMRs than Channel and Blue catfishes (Figure 1A).

Maximum metabolic rate

For MMR, the interaction between temperature and fish type was significant (ANOVA: $F_{2, 31} = 5.01$, $P = 0.0130$). Both Channel and Blue catfishes had significantly lower MMRs at 10°C than at 20°C. However, hybrid catfish MMRs were not different between the two temperatures (Figure 1B).

Metabolic scope

At 10°C, hybrid catfish had the largest numerical metabolic scope, Channel Catfish had an intermediate numerical metabolic scope, and Blue Catfish had the smallest numerical metabolic scope (Figure 1C). At 20°C, Channel Catfish had the largest numerical metabolic scope, hybrid catfish had an intermediate numerical metabolic scope, and Blue Catfish had the smallest numerical metabolic scope (Figure 1C).

Critical swimming speed

For U_{crit}, the interaction between temperature and fish type was not significant (ANCOVA: $F_{2, 31} = 0.08$, $P = 0.9263$), and the main effect of fish type was also not significant (ANCOVA: $F_{2, 31} = 0.10$, $P = 0.9084$). However, the main effect of temperature was significant (ANCOVA: $F_{1, 31} = 128.34$, $P < 0.0001$), with U_{crit} greater at 20°C than at 10°C (Figure 1D). The covariate of weight was not significant (ANCOVA: $F_{1, 31} = 0.00$, $P = 0.9478$).

Blood metabolites

For pH, the interaction among temperature, fish type, and exercise was not significant (ANOVA: $F_{2, 65} = 0.47$, $P = 0.6254$) and the interaction between temperature and exercise was not significant (ANOVA: $F_{1, 65} = 3.49$, $P = 0.0663$). However, the interaction between fish type and exercise was significant (ANOVA: $F_{2, 65} = 3.65$, $P = 0.0315$), with nonfatigued Blue and hybrid catfishes having higher blood pH and fatigued Channel and hybrid catfishes having lower blood pH (Figure 2A). The interaction between temperature and fish type was also significant (ANOVA: $F_{2, 65} = 10.62$, $P = 0.0001$), with Channel Catfish acclimated at 20°C having the lowest blood pH (Figure 2B).

Table 2. Mean ± SE weight (g) of juvenile Channel, Blue, and hybrid catfishes within different experiments. Different letters indicate significant differences among fish types, and an asterisk indicates a significant difference between the two temperatures (three-way ANOVA: $P < 0.05$). Abbreviations are as follows: SMR = standard metabolic rate, MMR = maximum metabolic rate, and U_{crit} = critical swimming velocity.

	10°C			20°C		
Experiment	**Channel**	**Blue**	**Hybrid**	**Channel**	**Blue**	**Hybrid**
SMR	42.34 ± 2.27 x	66.46 ± 4.79 y	30.60 ± 3.44 x	87.27 ± 5.59 z	81.33 ± 6.54 zy	67.42 ± 5.15 y
MMR/U_{crit}	68.34 ± 4.63* z	74.16 ± 6.68* z	40.58 ± 6.55* y	119.33 ± 5.37 z	121.56 ± 11.18 z	64.42 ± 5.56 y

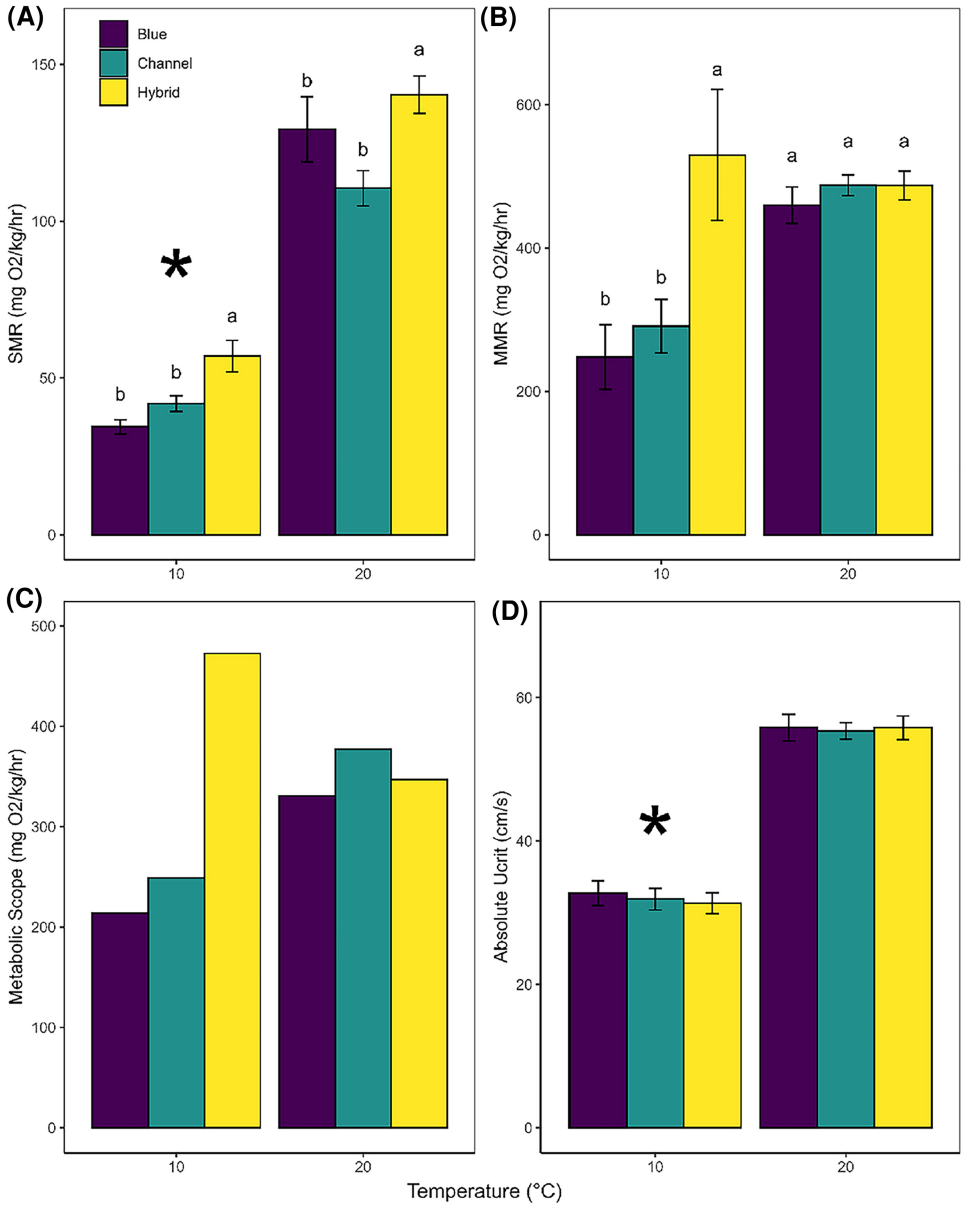

Figure 1. Mean ± SE of (A) standard metabolic rate (SMR), (B) maximum metabolic rate (MMR), (C) metabolic scope, and (D) absolute critical swimming velocity (U_{crit}) of juvenile Channel, Blue, and hybrid catfishes. Different lowercase letters indicate significant differences among the three fish types, and an asterisk indicates a significant difference between the two temperatures (panels A and B: two-way ANOVA, Tukey's honestly significant difference post hoc test: $P < 0.05$; panel D: two-way ANCOVA, covariate = weight: $P < 0.05$).

For lactate, none of the interactions were significant. However, the main effects of temperature (ANOVA: $F_{1,\ 61} = 15.40$, $P = 0.0002$), fish type (ANOVA: $F_{2,\ 61} = 7.27$, $P = 0.0015$), and exercise (ANOVA: $F_{1,\ 61} = 84.01$, $P < 0.0001$) were significant. Lactate concentrations were higher in catfish acclimated at 20°C (130%) than in catfish acclimated at 10°C

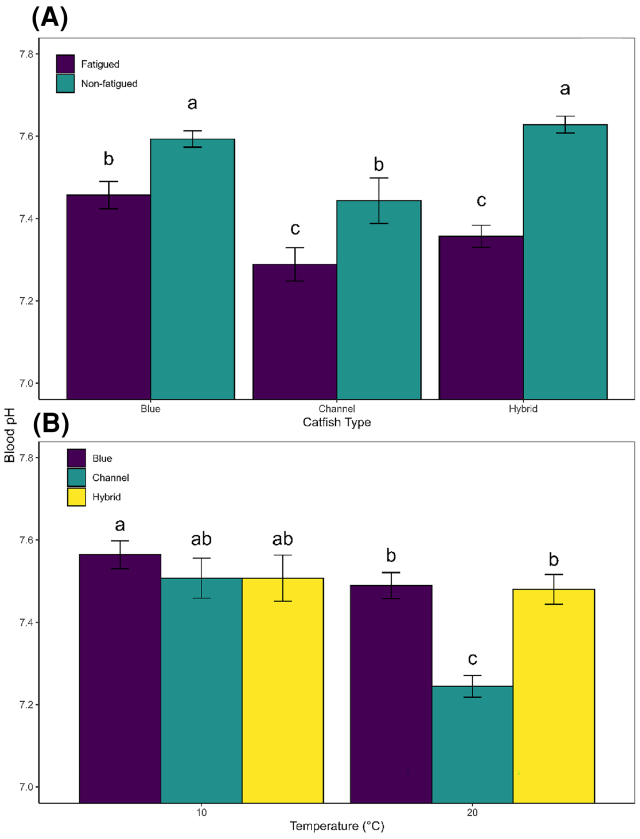

Figure 2. Mean ± SE blood pH of (A) fatigued and nonfatigued juvenile Channel, Blue, and hybrid catfishes; and (B) juvenile Channel, Blue, and hybrid catfishes acclimated at 10°C and 20°C. Different lowercase letters indicate significant differences among the three fish types (three-way ANOVA, Tukey's honestly significant difference post hoc test: $P < 0.05$).

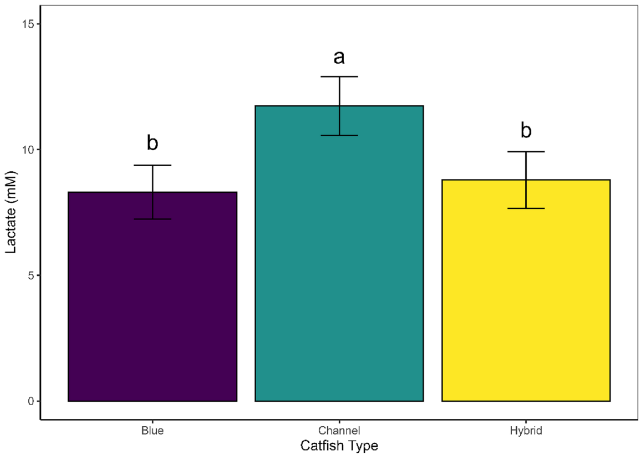

Figure 3. Mean ± SE lactate of juvenile Channel, Blue, and hybrid catfishes. Different lowercase letters indicate significant differences among the three fish types (three-way ANOVA, Tukey's honestly significant difference post hoc test: $P < 0.05$).

and were higher in fatigued fish (41%) than in nonfatigued fish. Channel Catfish had higher lactate concentrations than Blue and hybrid catfishes (Figure 3).

For glucose, the interaction among temperature, fish type, and exercise was significant (ANOVA: $F_{2,63} = 5.50$, $P = 0.0063$). Fatigued Channel Catfish that were acclimated at 20°C had the highest glucose concentrations (Figure 4).

For Hct, the interaction among temperature, fish type, and exercise was not significant (ANOVA: $F_{2,63} = 0.71$, $P = 0.4968$). However, the interaction between fish type and exercise was significant (ANOVA: $F_{2,63} = 3.45$, $P = 0.0378$), with fatigued Channel Catfish having the highest Hct values (Table 3). The interaction between temperature and exercise was also significant (ANOVA: $F_{1,63} = 7.53$, $P = 0.0079$), where fatigued catfish acclimated at 20°C had higher Hct, nonfatigued catfish acclimated at 20°C had moderate Hct, and both fatigued and nonfatigued catfish acclimated at 10°C had lower Hct (Table 3). The interaction between temperature and fish type was also significant (ANOVA: $F_{2,63} = 6.46$, $P = 0.0028$), with Channel Catfish acclimated at 20°C having the highest Hct (Table 3).

For RBC counts, the interaction among temperature, fish type, and exercise was not significant (ANOVA: $F_{2,63} = 1.35$, $P = 0.2668$); likewise, the interaction between fish type and exercise (ANOVA: $F_{2,63} = 2.88$, $P = 0.0635$) and the interaction between temperature and fish type (ANOVA: $F_{2,63} = 5.99$, $P = 0.0932$) were not significant. However, the interaction between temperature and exercise was significant (ANOVA: $F_{1,63} = 4.32$, $P = 0.0417$), as fatigued catfish acclimated at 20°C had the highest RBC counts, nonfatigued catfish acclimated at 20°C had intermediate RBC counts, and both fatigued and nonfatigued catfish acclimated at 10°C had the lowest RBC counts (Table 3). The main effect of fish type was also significant (ANOVA: $F_{2,63} = 5.99$, $P = 0.0041$), with hybrid catfish having lower RBC counts than Channel and Blue catfishes (Table 3).

For Hb, the interaction among temperature, fish type, and exercise was not significant (ANOVA: $F_{2,62} = 0.80$, $P = 0.4521$). However, the interaction between fish type and exercise was significant (ANOVA: $F_{2,62} = 3.76$, $P = 0.0288$), with fatigued Channel Catfish having the highest Hb (Table 3). The interaction between temperature and exercise was also significant (ANOVA: $F_{1,62} = 6.49$, $P = 0.0133$), as fatigued catfish acclimated at 20°C had the highest Hb, nonfatigued catfish acclimated at 20°C had intermediate Hb, and both fatigued and nonfatigued catfish acclimated at 10°C had the lowest Hb (Table 3). The interaction between temperature and fish type was also significant (ANOVA: $F_{2,62} = 4.08$, $P = 0.0217$), with Channel Catfish acclimated at 20°C having the highest Hb and hybrid catfish acclimated at 10°C having the lowest Hb (Table 3).

For MCV and MCHC, there were no significant interaction effects or main effects. For MCH, no interaction effects were significant, but the main effect of temperature was significant (ANOVA: $F_{1,61} = 14.53$, $P = 0.0003$): Catfish acclimated at 20°C had higher MCH than catfish acclimated at 10°C (Table 3).

DISCUSSION

Cold water influences many physiological processes in ectothermic fish, including feed intake, growth, and metabolic

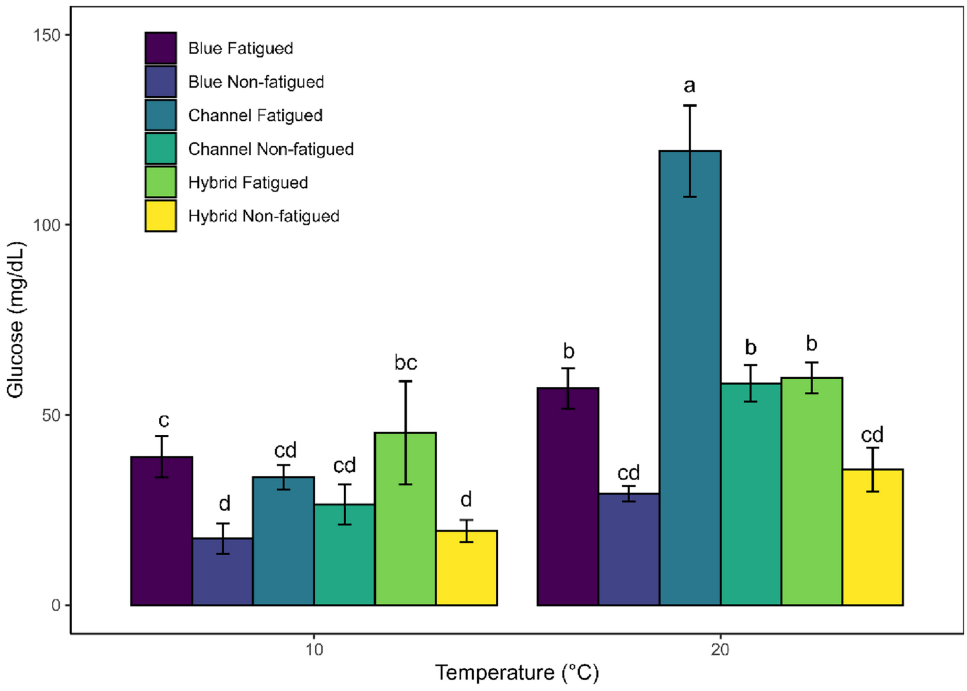

Figure 4. Mean ± SE glucose of fatigued and nonfatigued juvenile Channel, Blue, and hybrid catfishes acclimated at 10°C and 20°C. Different lowercase letters indicate significant differences among the three fish types (three-way ANOVA, Tukey's honestly significant difference post hoc test: $P < 0.05$).

rate (De Silva et al., 1986; Fernandes & McMeans, 2019; Johnston & Dunn, 1987). Despite cold temperatures in catfish aquaculture systems, little is known regarding their comparative effects on the metabolic processes and hematology of Channel, Blue, and hybrid catfishes. As hypothesized, temperature had a direct effect on metabolism and physiological performance, with reduced SMR and U_{crit} for all fish types at 10°C compared with 20°C. Similarly, MMR and metabolic scope declined at 10°C in Channel and Blue catfishes. In contrast to the hypothesis of heterosis, hybrid catfish did not demonstrate greater metabolic capabilities at 20°C, with similar MMR, metabolic scope, and swimming performance despite the elevated SMR. Although hybrid catfish had greater MMR and metabolic scope at 10°C, the differences are likely attributable to smaller body size (Fernandes & McMeans, 2019). In terms of blood comparisons, interestingly, Channel Catfish generally differed from Blue and hybrid catfishes, as observed in greater lactate and glucose and lower blood pH. There was also a temperature effect for all catfish types, where fish at 20°C tended to have greater Hct, RBC, and Hb concentrations than fish at 10°C.

In fish, SMR exponentially increases with increasing temperature, whereas MMR increases with temperature until it plateaus or decreases near upper tolerance limits (Brett, 1971; Farrell et al., 2007; Fry, 1971; McKenzie & Claireaux, 2010; Taylor et al., 1997). Similarly, in this study, cold temperature (10°C) reduced the SMR and generally the MMR and metabolic scope in catfish. The exception was in hybrid catfish at 10°C, which may have been influenced by smaller body size (Fernandes & McMeans, 2019). As temperature increased (20°C), SMR, MMR, and metabolic scope increased, with MMR and metabolic scope being generally similar among catfish types. These findings indicate no clear metabolic advantages at low temperatures for any of the catfish types. In contrast, at warmer temperatures (23°C and 33°C), hybrid catfish have been found to exhibit a greater MMR and metabolic scope (Gerhart et al., 2024).

Similar to metabolism findings, swimming performance was directly related to temperature, with U_{crit} reduced at 10°C compared with 20°C in all fish types. Swimming performance is usually maximized at an optimum temperature for a given species and decreases as the temperature rises above or falls below the optimum (Beamish, 1978; Clark et al., 2013; Heuer et al., 2021; Hocutt, 1973; Pörtner, 2010; Pörtner & Farrell, 2008; Pörtner & Knust, 2007). Furthermore, swimming performance and metabolic scope are closely related (Brett, 1964; Claireaux et al., 2006; McKenzie & Claireaux, 2010; Reidy et al., 2000), with swimming performance increasing at increased temperatures due to greater metabolic scopes (Beamish, 1978; Clark et al., 2013; Heuer et al., 2021; Hocutt, 1973; Pörtner, 2010; Pörtner & Farrell, 2008; Pörtner & Knust, 2007). Therefore, reduced metabolic scopes at 10°C presumably resulted in poor swimming performance in the current study, which likely stemmed from reduced feed intake, energy stores, and body size (Kieffer, 2000; Rubio-Gracia et al., 2020), as were observed in fish acclimated at 10°C (Vaughn, 2022).

In this study, there were no differences in swimming performance among the different catfish types at 10°C or 20°C. At 20°C, U_{crit} ranged from 50.89 to 62.28 cm/s among Channel, Blue, and hybrid catfishes with an average weight of approximately 100 g and an average total length of about 222 mm. These values are comparable to those reported in previous studies on Channel and Blue catfishes. Hocutt (1973) found that 140–154-mm Channel Catfish at 30°C had a U_{crit} of

61.27 cm/s, but when the fish were exposed to a rapid 10°C temperature decline to 20°C, U_{crit} decreased to 48.77 cm/s. A more recent study indicated that ~100-g Channel Catfish had an average U_{crit} of 59.3 cm/s, while Blue Catfish had an average U_{crit} of 51.6 cm/s from 19°C to 21°C (Beecham, 2004).

Exhaustive exercise requires fish to use both aerobic and anaerobic metabolic resources (Kieffer, 2000; Lurman et al., 2007). Understanding how blood metabolites respond to exercise and temperature in different catfishes is important for understanding energy use. Results from the current study indicate acidosis after exercise based on increased blood lactate and decreased pH (Black et al., 1959; Cameron & Cech, 1990; Wood, 1991). In fish, lactate rapidly increases after exercise, peaking 2–4 h later, and then returns to normal 12–24 h later (Beecham et al., 2007; Black et al., 1959, 1962; Cameron & Cech, 1990; Rees et al., 2009). As expected, blood lactate was higher in fatigued fish than in nonfatigued fish in the current study, but interestingly, blood lactate was highest in Channel Catfish. Correspondingly, blood pH was lowest in fatigued and nonfatigued Channel Catfish at 20°C, suggesting that Channel Catfish may use more anaerobic energy to sustain swimming. Moreover, among fatigued fish, Channel and hybrid catfishes across both 10°C and 20°C had lower blood pH than Blue Catfish. Caillouet (1967) showed that lactic acid in unexercised Channel Catfish acclimated to 14–15°C ranged from 0.26 to 0.84 mM, increased to 2.34–4.90 mM after 5 min of exercise, and increased to 6.56–7.50 mM after 15 min of exercise. Similarly, Beecham et al. (2007) reported that lactate concentrations were higher after exercise and gradually declined to pre-exercise levels after 4 h in Channel and Blue catfishes. In the current study, lactate was also higher at 20°C than at 10°C. Caillouet (1967) found similar results whereby lactate was generally higher in juvenile Channel Catfish at warmer temperatures (19°C) compared with cooler temperatures (15°C).

Like lactate, glucose concentrations were higher in fatigued catfish than in nonfatigued catfish. Similar to the current study, Beecham et al. (2007) concluded that glucose increased after exhaustive exercise and then returned to pre-exercise levels after 4 h in Channel and Blue Catfish fingerlings acclimated to 18–22°C. Increased glucose occurs after exercise due to the breakdown of glycogen through glycogenolysis (Wendelaar Bonga, 1997). In our study, fatigued Channel Catfish at 20°C had the highest glucose concentrations. Similarly, Beecham et al. (2007) reported that Channel Catfish generally had higher glucose concentrations than Blue Catfish, although they never differed statistically.

Hematocrit, RBC abundance, and Hb concentration also showed a similar pattern: Fatigued catfish acclimated at 20°C had the highest values, nonfatigued catfish acclimated at 20°C had moderate levels, and both fatigued and nonfatigued catfish acclimated at 10°C had the lowest values. These results suggest that temperature and exercise resulted in hematological differences. Water temperature is the primary factor affecting physiological processes in fish (Brett, 1971; Clarke & Johnston, 1999; Fry, 1947, 1971; Jensen et al., 1993) and has been shown to influence these hematological variables (Ashaf-Ud-Doulah et al., 2020; Coffill-Rivera, Paez Mendez, et al., 2023; Sambraus et al., 2017; Seibel et al., 2021; Zhang & Kieffer, 2014). In this study, condition factor was reduced at 10°C (Vaughn, 2022),

Table 3. Mean ± SE blood metabolites and hematological variables of nonfatigued (N) and fatigued (F) juvenile Channel, Blue, and hybrid catfishes acclimated to 10°C and 20°C. Abbreviations are as follows: Hct = hematocrit, RBC = red blood cell concentration, Hb = hemoglobin, MCV = mean corpuscular volume, MCH = mean corpuscular Hb, and MCHC = mean corpuscular Hb concentration.

	10°C						20°C					
	Channel		Blue		Hybrid		Channel		Blue		Hybrid	
Variable	N	F	N	F	N	F	N	F	N	F	N	F
pH	7.62 ± 0.05	7.40 ± 0.05	7.65 ± 0.01	7.50 ± 0.04	7.67 ± 0.03	7.35 ± 0.04	7.29 ± 0.03	7.20 ± 0.03	7.55 ± 0.02	7.42 ± 0.05	7.59 ± 0.02	7.37 ± 0.03
Lactate (mM)	5.3 ± 0.6	12.6 ± 2.2	4.4 ± 0.6	9.2 ± 2.5	3.5 ± 0.6	12.5 ± 1.0	12.5 ± 1.3	16.5 ± 2.2	5.6 ± 0.8	14.1 ± 1.6	3.4 ± 0.4	14.8 ± 1.0
Hct (%)	20 ± 1	25 ± 1	22 ± 1	19 ± 2	21 ± 2	19 ± 1	35 ± 2	42 ± 3	29 ± 2	32 ± 1	26 ± 1	31 ± 1
RBC (10^{12} cells/L)	1.1 ± 0.1	1.3 ± 0.1	1.4 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	1.1 ± 0.1	1.9 ± 0.1	2.0 ± 0.1	1.7 ± 0.0	1.8 ± 0.1	1.4 ± 0.1	1.7 ± 0.1
Hb (g/dL)	7.3 ± 0.4	8.5 ± 0.4	8.3 ± 0.4	7.0 ± 0.6	6.9 ± 0.4	6.2 ± 0.4	12.7 ± 0.6	14.4 ± 0.3	11.2 ± 0.7	11.6 ± 0.3	10.1 ± 0.7	11.5 ± 0.4
MCV (fL)	177.1 ± 4.1	193.2 ± 9.1	159.4 ± 4.7	179.5 ± 22.0	211.8 ± 38.2	169.9 ± 19.6	189.6 ± 8.0	211.2 ± 11.0	174.0 ± 6.3	180.6 ± 5.7	188.3 ± 9.5	179.5 ± 10.8
MCH (pg/cell)	63.8 ± 2.0	66.5 ± 3.4	60.2 ± 2.5	63.7 ± 2.0	62.8 ± 4.9	55.1 ± 4.5	68.8 ± 2.1	70.5 ± 2.7	67.9 ± 1.8	65.0 ± 1.5	71.8 ± 2.6	67.4 ± 3.7
MCHC (g/dL)	36.1 ± 1.0	34.5 ± 1.2	37.8 ± 1.1	38.5 ± 5.1	32.5 ± 2.9	33.7 ± 1.9	36.4 ± 0.8	33.1 ± 1.0	38.4 ± 1.0	36.1 ± 0.7	38.4 ± 1.2	37.6 ± 0.8

which may also indicate decreased energy stores that can lead to reduced Hct and Hb (Seibel et al., 2021; Tavares-Dias & Moraes, 2007; Witeska, 2015). Similarly, Tavares-Dias and Moraes (2007) found that well-nourished fingerling Channel Catfish had higher Hct values than poorly fed fingerlings. These hematological variables may also have increased to facilitate greater metabolic output during prolonged exercise in the U_{crit} test (Cech et al., 1996; Groff & Zinkl, 1999; Mendiola et al., 1997). Similar to the temperature effect observed for Hb, MCH was lower in catfish acclimated at 10°C. When catfish types were compared, Channel Catfish generally had higher Hct and Hb than Blue Catfish or hybrid catfish, supporting the observation that Channel Catfish generally differ from Blue and hybrid catfishes in both hematology and blood metabolites.

A number of factors can affect hematological measurements, such as water conditions, fish size, and sampling techniques. Care was taken to standardize these practices when possible. Several, generally minor differences in water quality variables were present between temperature treatments (Table 1). Although all variables were maintained at levels appropriate for catfish health and growth (e.g., dissolved oxygen > 7 mg/L, oxygen saturation > 85%, pH between 7 and 8, NH_3 < 0.15 mg/L, and NO_2 < 1.60 mg/L; Colt & Tchobanoglous, 1978; Colt & Tomasso, 2001; Colt et al., 1981), effects of water quality on hematological variables of fish have been reported (Bhaskar & Rao, 1989; Sahiti et al., 2018). Second, although anesthesia is commonly applied to minimize handling stress and improve animal welfare, it can affect hematological variables in fish (Topic Popovic et al., 2012). Therefore, anesthesia baths were buffered, and concentrations were used to minimize induction times. In this study, blood collection techniques differed between temperature treatments to allow rapid collection within similar time frames, prevent blood clotting, and facilitate comparison.

Prolonged low temperature reduces metabolic rate, physiological performance, blood energy metabolites, and hematological variables in catfish. Based on the results of this study and the study by Gerhart et al. (2024), energetic benefits in Channel, Blue, and hybrid catfishes appear to be temperature dependent, with hybrids outperforming Channel and Blue catfishes at warmer temperatures (≥23°C) but demonstrating no clear advantages at cooler temperatures (≤20°C). Because energy use is minimized during prolonged exposure to cold temperatures, likely benefits would be conferred to the catfish type that minimizes energy use and maximizes food consumption and energy storage prior to and during cold exposure. In this regard, natural distributions of Channel Catfish occur farther north than Blue Catfish (Graham, 1999; Jackson, 2004; McCauley & Beitinger, 1992), presumably exposing them to colder temperatures. Further, Blue Catfish are more migratory than Channel Catfish and may avoid exposure to cold (Graham, 1999). Thus, Channel Catfish would appear to have natural adaptations to tolerate cold temperatures better than Blue and hybrid catfishes. Although the metabolism and swimming performance results of this study did not support a clear advantage, Channel Catfish did differ in exercise-mediated physiological responses, as evidenced by blood metabolites and hematology. Cool to cold temperatures are unfavorable to catfish aquaculture practices; although they are experienced seasonally, they have large implications for production. Future studies evaluating the impacts of rapid cooling would be greatly beneficial for understanding catfish energy use during these events. Additionally, further comparisons in growth and energy storage at cold temperatures would provide important additional insight that may support the benefit of using one type of catfish for pond aquaculture in prolonged cold conditions. This information will be beneficial to guide future management efforts in the catfish aquaculture industry.

DATA AVAILABILITY

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

All experimental work and procedures were conducted in accordance with Mississippi State University Institutional Animal Care and Use Committee guidelines and policies following national animal welfare laws (protocol 20-526).

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CONFLICTS OF INTEREST

The authors report no conflicts of interest.

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