

# The effect of temperature on the resting and post-exercise metabolic rates and aerobic metabolic scope in shortnose sturgeon *Acipenser brevirostrum*

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**Abstract** The effects of acclimation temperature (15, 20, 25 °C) on routine oxygen consumption and post-exercise maximal oxygen consumption rates ( $MO_2$ ) were measured in juvenile shortnose sturgeon (*Acipenser brevirostrum* LeSueur, 1818). The routine  $MO_2$  of shortnose sturgeon increased significantly from 126.75 mg  $O_2$   $h^{-1}$   $kg^{-1}$  at 15 °C to 253.13 mg  $O_2$   $h^{-1}$   $kg^{-1}$  at 25 °C. The temperature coefficient ( $Q_{10}$ ) values of the routine metabolic rates ranged between 1.61 and 2.46, with the largest  $Q_{10}$  values occurring between 15 and 20 °C. The average post-exercise  $MO_2$  of all temperature groups increased to a peak value immediately following the exercise, with levels increasing about 2-fold among all temperature groups. The  $Q_{10}$  values for post-exercise  $MO_2$  ranged from 1.21 to 2.12, with the highest difference occurring between 15 and

20 °C. Post-exercise  $MO_2$  values of shortnose sturgeon in different temperature groups all decreased exponentially and statistically returned to pre-exercise (resting) levels by 30 min at 15 and 20 °C and by 60 min at 25 °C. The aerobic metabolic scope (post-exercise maximal  $MO_2$ -routine  $MO_2$ ) increased to a maximum value ~156 mg  $O_2$   $h^{-1}$   $kg^{-1}$  at intermediate experimental temperatures (i.e., 20 °C) and then decreased as the temperature increased to 25 °C. However, this trend was not significant. The results suggest that juvenile shortnose sturgeon show flexibility in their ability to adapt to various temperature environments and in their responses to exhaustive exercise.

**Keywords** Temperature · Exhaustive exercise · Aerobic metabolic scope · Shortnose sturgeon · Metabolic rate

## What is already known

Acclimation temperature has significant impacts on the routine oxygen consumption rate in teleost fish. It also affects the post-exercise maximal oxygen consumption rate and exercise/stress response.

## What this study adds

The current study shows that acclimation temperature significantly increases the routine oxygen consumption rate and post-exercise oxygen consumption rate in shortnose sturgeon.

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## Introduction

The physiological response to exhaustive exercise in fish has been well studied for more than 50 years with an emphasis on salmonid species (for reviews, see Wood 1991; Milligan 1996; Kieffer 2000, 2010). It has been shown that various abiotic and biotic factors (e.g., temperature, body size, and training) influence the process of and the recovery from exhaustive exercise in fish (Kieffer 2000). It is generally agreed upon that temperature is among the most important abiotic factors affecting an ectothermic animal's biology, ranging from modifying their distribution to their physiology (Brett 1971; Beitinger and Lutterschmidt 2011). Exhaustive

exercise results in marked disturbances to acid-base, osmotic, and electrolyte balance, and increases in oxygen consumption rates in fish (Wood 1991, Kieffer 2000, for reviews), and that these processes and the recovery rate are affected by temperature (e.g., Kieffer et al. 1994; Galloway and Kieffer 2003; Zeng et al. 2010; Kieffer 2010).

Most work to date has focused on the physiological response to exhaustive exercise in teleost fish (e.g., Kieffer 2000; Kieffer and Cooke 2009), and less has focused on ancient fish, such as sturgeon and paddlefish (Barton et al. 2000; Kieffer et al. 2001; Beyea et al. 2005; Baker et al. 2005). The sturgeon (genus *Acipenser*) are freshwater chondrosteian fish that have existed since the Jurassic period (approximately 200 million years ago). Sturgeon have retained many ancestral body characteristics and ways of living that distinguish them as relict fishes (Bemis et al. 1997). Almost all acipenserids are listed as threatened, vulnerable, and endangered throughout their ranges (Birstein and Bemis 1997). Thus, there has been an increased demand for information on all aspects of sturgeon biology, physiology, and evolutionary history (Billard and Lecointre 2001). It has been shown that the physiological response to exhaustive exercise and other forms of acute stressors (e.g., air emersion, hypoxia, confinement) is reduced in sturgeon compared with teleosts (Barton et al. 2000; Kieffer et al. 2001; Baker et al. 2005). In particular, blood and muscle lactate and plasma cortisol levels are not elevated greatly following exhaustive chasing/exercise (Barton et al. 2000; Kieffer et al. 2001; Beyea et al. 2005; Baker et al. 2005, Baker et al. 2008). Oxygen consumption rates increase rapidly and remain elevated for about 30 min following exercise in juvenile shortnose (*Acipenser brevirostrum*) and Atlantic (*Acipenser oxyrinchus*) (Kieffer et al. 2001) and Amur (*Acipenser schrenckii*) sturgeon (Cai et al. 2013). Of the available research on the effects of temperature on the exercise/stress response in sturgeon and paddlefish, studies have focused on critical swimming (Mayfield and Cech 2004; Deslauriers and Kieffer 2012; Aboagye and Allen 2014) and blood parameters following exercise/handling stress (Cataldi et al. 1998; Lankford et al. 2003). In general, a paucity of information exists on the effects of acclimation temperature on the post-exercise metabolic rate changes in sturgeon, yet some recent work exists for routine metabolic rates at various temperatures (Mayfield and Cech 2004; Kieffer et al. 2014). As such, the purpose of this study was to

investigate the effects of acclimation temperature (15, 20, and 25 °C) on the routine (routine metabolic rate (RMR)) and post-exercise maximal (maximum metabolic rate (MMR)) metabolic rates and aerobic scope in juvenile shortnose sturgeon. We chose to measure oxygen consumption rates because these are non-lethal measurements and multiple calculations (e.g., routine metabolic rate, maximal metabolic rate, metabolic scope) can be made. Assessing the maximum aerobic metabolic rate and aerobic scope of fish helps in understanding the capacity for performing oxygen consuming physiological capacities (Killen et al. 2016). Previous research has shown that maximum metabolic rate can be influenced by abiotic factors, such as temperature (Norin and Clark 2016). In addition, the metabolic recovery can be easily assessed using relatively low sample sizes. It is important to understand whether temperature affects recovery processes as it has been suggested that a fast recovery process could facilitate the speed at which subsequent exercise bouts could take place (Milligan 1996, for a review). Moreover, the production of sturgeon in intensive aquaculture settings has increased worldwide because of the high market value of caviar (Feshalami et al. 2016). Assessing the potential effects of aquaculture practices, such as exercise/handling stress, on the physiology of sturgeon can help to understand the metabolic costs associated with these events.

## Materials and methods

Young-of-the-year shortnose sturgeon were obtained from Acadian Sturgeon and Caviar, Inc. (New Brunswick, Canada; <http://www.acadian-sturgeon.com>). Groups of fish were assigned to one of three acclimation temperatures: 15, 20, or 25 °C. The tanks were supplied with a flow-through of fresh, aerated, dechlorinated, municipal tap water at 10 °C. To achieve the required temperatures, the incoming water was heated at a rate of 1 °C/day until the required temperature was attained. Once the desired temperature was achieved, the fish were held at that temperature (i.e., 15, 20, or 25 °C) for 4 weeks prior to the beginning of the experiment (see in the following). Fish were fed twice daily to satiation (Corey Aquafeed: 1.5 mm optimum, 52% protein), but fish were fasted for 24 h prior to the experiments. A 12-h light: 12-h dark photoperiod was maintained throughout the study.

The evening before trials began, an individual sturgeon (~100 g) was removed from its holding tank (at one of the acclimation temperatures), weighed in water, and placed into a custom-made clear respirometer in fresh water (Loligo® Systems, Denmark; <http://www.loligosystems.com>; see in the following) held at the acclimation temperature ( $N = 8$  fish at each acclimation temperature). The following morning, baseline measurements of  $\text{MO}_2$  ( $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ ) were taken over 2 h (the mean of this time period was used as the routine metabolic rate) before the exercise. Following this, each fish was removed from the respirometer and exercised to exhaustion via 5-min manual chasing (Kieffer et al. 2001; Baker et al. 2005). Chasing was performed at the same temperature as the experimental exposure. Following exercise, fish were quickly (within a minute) placed back in the respirometer at the same temperature, and  $\text{MO}_2$  was measured for a further 8 h.

#### Respirometer setup and oxygen consumption measurement

Custom-made 3.5L respirometers (Loligo® Systems, Denmark; <http://www.loligosystems.com>) were submerged in a water table with a constant supply of fresh, aerated water at the appropriate acclimation temperature (either 15, 20, or 25 °C). Using a series of pumps, the respirometers were set up to allow for either (i) flow-through from the water table (during flushing) or (ii) recirculation of water within the respirometer (during measurement). An oxygen electrode (Loligo® Systems, Denmark) was located within the recirculation pump circuit tubing to allow for direct measurements of system oxygen levels. All respirometers were set up with visual barriers according to Penny and Kieffer (2014). All measurements of oxygen consumption were calculated using an automated intermittent respirometry program (RESP\_EDU, Loligo® Systems, Denmark). Flush/recirculation periods were adjusted for each fish to optimize  $R^2$  values ( $>0.9$ ) while insuring oxygen concentrations were maintained at or above 75% saturation (400–500 s).

#### Data handling and analysis

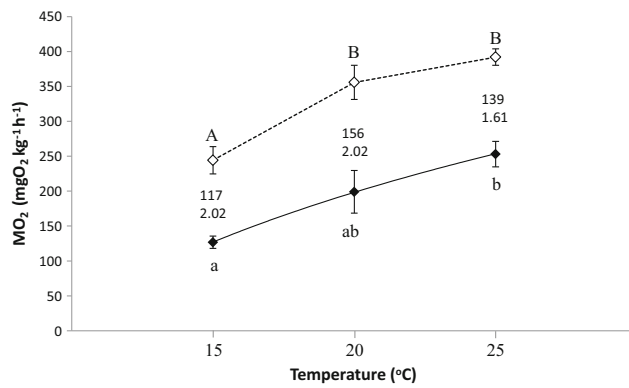
RMR was defined as the post-absorptive  $\text{MO}_2$  value for a given fish. MMR was defined as the  $\text{MO}_2$  value immediately following exercise. From these two values,

the absolute (MMR – RMR) aerobic and factorial (MMR/RMR) metabolic scopes were determined for each fish. To determine the effects of acclimation temperature on RMR, and the absolute metabolic scopes, a one-way ANOVA was used. Linear regressions were also carried out to determine the relationship between temperature and the endpoint (e.g., RMR, MMR). Temperature quotients ( $Q_{10}$ ) were calculated using the formula provided by Prosser (1991):  $Q_{10} = (k_2/k_1)^{10/(t_2 - t_1)}$ , where  $k_1$  and  $k_2$  are the rates of reaction (rate constants) at temperatures  $t_1$  and  $t_2$ , respectively. All values are presented as mean  $\pm$  SEM ( $N = 8$  fish per group). When the ANOVA revealed significance ( $P < 0.05$ ), Tukey's tests were used to test for where these differences between pairs of temperatures occurred. Alpha in all cases was 5% ( $P < 0.05$ ).

In addition to the previously mentioned, a repeated measures ANOVA followed by a Dunnett's multiple comparison test was used to compare post-exercise (MMR) values with their respective routine (RMR) values at each acclimation temperature. To test whether differences in the rate of recovery of oxygen consumption ( $\text{MO}_2$ ) between fish at the various acclimation temperatures, a two-way repeated measure analysis of variance was used (factors: acclimation temperature and time). A Tukey post hoc test was used if significant differences were found. Values are presented as means  $\pm$  standard error of the means (SEM). In all cases,  $P < 0.05$  was the accepted level of significance.

## Results

The routine and post-exercise maximal  $\text{MO}_2$  of *A. brevirostrum* was affected by acclimation temperature (Fig. 1). The routine  $\text{MO}_2$  of *A. brevirostrum* increased significantly from 126.75  $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$  at 15 °C to 253.13  $\text{mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$  at 25 °C (Fig. 1a; one-way ANOVA,  $df$  2,23,  $F = 8.9$ ,  $P < 0.002$ ; linear regression:  $\text{MO}_2 = (12.6 \times \text{temperature}) - 59.8$ ;  $R^2 = 0.46$ ,  $P < 0.001$ ). The  $Q_{10}$  values of the resting  $\text{MO}_2$  ranged between 1.61 and 2.46, with the largest  $Q_{10}$  values occurring between 15 and 20 °C (Table 1). Following exercise, the average post-exercise maximal  $\text{MO}_2$  of all temperature groups increased to a peak value immediately following the exercise (Fig. 1; one-way ANOVA,  $df$  2,23,  $F = 15.8$ ,  $P < 0.001$ ; linear regression:  $\text{MO}_2 = (14.8 \times \text{temperature}) + 35.2$ ;  $R^2 = 0.554$ ,  $P < 0.001$ ), with levels increasing about 2-fold among

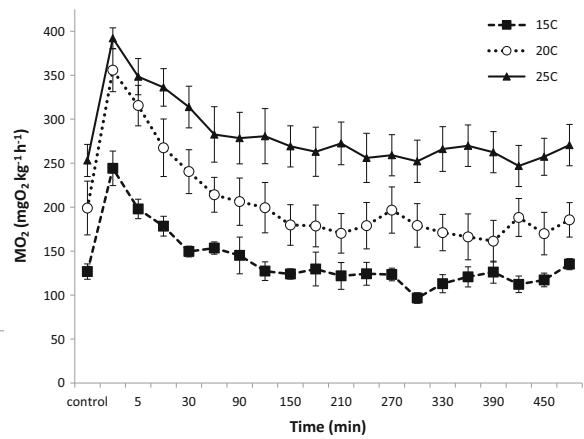


**Fig. 1** The relationships between temperature and post-exercise maximal  $MO_2$  (MMR; indicated by open symbols with a dashed line) and routine  $MO_2$  (RMR; indicated by closed symbols with a solid line) in juvenile shortnose sturgeon (*A. brevirostrum*). The larger number between the two lines represents the aerobic metabolic scope (MMR-RMR), and the smaller number represents the factorial metabolic scope (MMR/SMR). Different lowercase letters indicate significant differences ( $P < 0.05$ ) between temperature groups for RMR. Different uppercase letters indicate significant differences ( $P < 0.05$ ) between temperature groups for MMR. The data represent means  $\pm$  SEM at specific temperatures

all temperature groups. The  $Q_{10}$  values for post-exercise maximal  $MO_2$  ranged from 1.21 to 2.12, with the highest difference occurring between 15 and 20 °C (Table 1). The results of a two-way repeated measures ANOVA indicate that acclimation temperature ( $P < 0.001$ ) and time following exercise ( $P < 0.001$ ) had an overall effect on metabolic rate of shortnose sturgeon. Post-exercise maximal  $MO_2$  values of *A. brevirostrum* in different temperature groups all decreased exponentially and returned to pre-exercise (resting) levels by 30 min at 15 and 20 °C and by 60 min at 25 °C ( $P < 0.05$ ) (Fig. 2). The aerobic metabolic scope (post-exercise  $MO_2$ - routine  $MO_2$ ) increased to a maximum value  $\sim 156 \text{ mg O}_2 \text{ h}^{-1} \text{ kg}^{-1}$  at intermediate experimental temperatures (i.e., 20 °C) and then decreased as the temperature increased to 25 °C (Fig. 1). However, this trend was not significant

**Table 1** Temperature coefficient ( $Q_{10}$ ) values for routine (RMR) and post-exercise maximal (MMR) metabolic rates for juvenile shortnose sturgeon acclimated to various temperatures

	Temperature comparisons (°C)		
	25 versus 15	25 versus 20	20 versus 15
$Q_{10}$ routine	2.0	1.61	2.46
$Q_{10}$ post-exercise	1.61	1.21	2.12

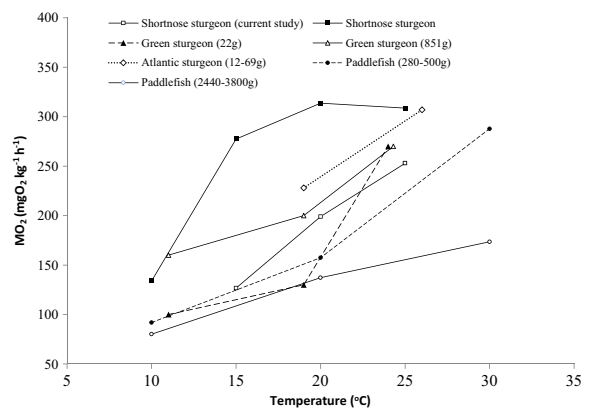


**Fig. 2** Oxygen consumption rates (means  $\pm$  SE) in juvenile shortnose sturgeon before (control) and after forced activity at 15 (closed squares), 20 (open circles), or 25 °C (closed triangles)

( $P > 0.05$ ). Factorial metabolic scope was consistent (2.02) at 15 and 20 °C but decreased slightly (to 1.61) at 25 °C (Fig. 1).

### Discussion

While there have been several studies that have examined the effects of temperature on the routine metabolic rates of sturgeon (see Fig. 3), few studies have examined the effects of temperature on post-exercise responses. It has been suggested that the mean global surface temperature has increased by 0.7 °C over the past 100 years (IPCC 2007, in Lassalle et al. 2010). These temperatures are expected to increase which could have significant effects



**Fig. 3** The relationship between routine oxygen consumption and temperature variation that exists for various sturgeon and paddlefish species (e.g., green sturgeon, Mayfield and Cech 2004; shortnose sturgeon, Kieffer et al. 2014; Atlantic sturgeon, Secor and Gunderson 1998; paddlefish, Patterson et al. 2013)

on the distribution and survival of many species (Lassalle et al. 2010). Thus, the findings from the present study are important from both biological and applied perspectives (e.g., aquaculture) and can provide the foundation and some of the parameters to guide future experiments examining the thermal tolerance of sturgeon species.

#### Routine metabolic rates

The overall mean RMR of the shortnose sturgeon increased with increases in acclimation temperature (Figs. 1 and 3). This pattern is similar (although the absolute values lower) to our previous study using ~10 g shortnose sturgeon (Kieffer et al. 2014). Despite these parallels, studies for other species of sturgeon and paddlefish report rates of routine metabolism that were quite dissimilar to the present study (Fig. 3). For example, the mass-specific metabolic rate of 22-g green sturgeon (*Acipenser medirostris*) was lower than shortnose sturgeon at cooler temperatures (Kieffer et al. 2014). In addition, the relationship between metabolic rate and temperature appears to vary between species of sturgeon. Mayfield and Cech (2004) showed that metabolic rates increased exponentially with increases in temperature in both 22- and 851-g green sturgeon; a similar trend is noted for small (280–500 g) and larger (11–12 kg) paddlefish (*Polyodon spathula*), but not medium (2.4–

3.8 kg) paddlefish (Patterson et al. 2013). Evidence for white sturgeon (*Acipenser transmontanus*, Crocker and Cech 1997) and paddlefish (Patterson et al. 2013) shows that an interaction exists between fish size and temperature on the metabolic rate of these species. Relative to some of the other species of sturgeon, however, the pattern for shortnose sturgeon (Kieffer et al. 2014) showed that the routine metabolic rate increased to a large extent at the lower temperatures tested (Kieffer et al. 2014) and then showing a plateau. These findings are supported by the larger  $Q_{10}$  values noted in the present study between 15 and 20 and 15 and 25 °C (Table 1). The relationships between temperature and metabolic rate in sturgeon might reflect the importance of fish size/age, or it may be related to differences in thermal sensitivities (e.g., critical thermal maxima) of the fish species or the range of temperatures used. Thus, future studies are needed to further our understanding of temperature and resting metabolic rate relationships in sturgeon.

#### Post-exercise maximum metabolic rates and recovery patterns

Similar to that for routine metabolism, there was an increase in post-exercise metabolic rates with increases in temperature (Fig. 1) and these rates were about two times higher than routine values across temperatures (see

**Table 2** Various metrics ( $\pm$ SEM) describing the aerobic metabolism of multiple species of sturgeon before and following exhaustive exercise at various temperatures ( $T$ , °C)

Species	$T$ (°C)	RMR	MMR	AAS	Reference
<i>Acipenser brevirostrum</i>	15	127 $\pm$ 8.8	244 $\pm$ 20 <sup>a</sup>	117 $\pm$ 25	Current study
<i>A. brevirostrum</i>	20	199 $\pm$ 30	356 $\pm$ 24 <sup>a</sup>	156 $\pm$ 22	Current study
<i>A. brevirostrum</i>	25	253 $\pm$ 18	392 $\pm$ 12 <sup>a</sup>	139 $\pm$ 20	Current study
<i>A. brevirostrum</i>	12	112	224 <sup>a</sup>	112	Kieffer et al. (2001)
<i>A. oxyrinchus</i>	12	112	240 <sup>a</sup>	128	Kieffer et al. (2001)
<i>A. brevirostrum</i>	15	165 $\pm$ 18	272 $\pm$ 14 <sup>a</sup>	107 $\pm$ 10	Penny and Kieffer, unpublished
<i>A. naccarii</i>	25	216	548 <sup>b</sup>	332	McKenzie et al. (2001)
<i>A. sinensis</i>	20	266	598 <sup>b</sup>	332	Cai et al. (2014)
<i>A. baeri</i>	20	180 <sup>c</sup>	500 <sup>c</sup>	320	Cai et al. (2015)
<i>A. fulvescens</i>	17	88	338	250	Svendsen et al. (2014)
<i>A. schrenckii</i>	20	295	625 <sup>c</sup>	330	Cai et al. (2013)

RMR routine metabolic rate ( $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ ), MMR post-exercise maximal metabolic rate ( $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ ), AAS absolute aerobic metabolic scope (MMR-SMR) ( $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ )

<sup>a</sup> Active metabolic rate following a chasing protocol

<sup>b</sup> Active metabolic rate following a UCrit protocol

<sup>c</sup> Estimated values

Table 2). Compared to routine values, post-exercise metabolic rates were less affected (i.e., lower  $Q_{10}$  values) by temperature. These changes of the routine and post-exercise metabolic rate initially led to an increase in aerobic metabolic scope (between 15 and 20 °C) and then a plateau trend (between 20 and 25 °C). These patterns for *absolute* metabolic scope have been shown in other species of fish, including freshwater and marine species (Tirsgaard et al. 2015; Eliason and Farrell 2016). In contrast, the findings for *factorial* metabolic scope (maximum metabolic rate/routine rate) suggest a slight decrease in factorial scope at the higher temperatures, a pattern also noted for Pacific salmon (*Oncorhynchus* spp.; reviewed in Eliason and Farrell 2016). This may suggest that the ability to do metabolic work at higher temperatures in shortnose sturgeon might be compromised, which has recently been shown by Deslauriers and Kieffer (2012) who showed that critical swimming speed (UCrit) in shortnose sturgeon began to plateau at 15 through 25 °C. From a practical perspective, it is known that maximum metabolic rate determination may be affected by the experimental protocol utilized (see Tirsgaard et al. 2015, Norin and Clark 2016; Killen et al. 2016; for background), such as a chase protocol (as used here) and critical swimming tests (UCrit), specific dynamic action (SDA) test, or critical thermal maximum test (CTmax) to achieve the maximum metabolic rate of the test species. From our experience, the absolute metabolic and factorial scopes following exhaustive exercise in the current study were about 75% of the values noted during a critical thermal maximum test using similar-sized shortnose sturgeon (Zhang and Kieffer, unpublished). However, the burst, chasing stress protocol used within the current study represents a scenario related to exercise responses in fishes and is considered a relevant stressor within the fisheries and aquaculture sectors (e.g., catch-and-release fisheries, commercial fishing throw-back, netting stress, transportation and handling stresses; Wood 1991, Kieffer and Cooke 2009).

Shortnose sturgeon exhibited a physiological stress response to chasing stress as indicated by increases in whole-animal oxygen consumption rates. These responses, however, are considerably lower compared with those previously documented for teleost fishes (Scarabello et al. 1992; Wakefield et al. 2004; Kieffer 2000). Of interest is the fast post-exercise recovery process in shortnose sturgeon. The post-exercise oxygen consumption rates in sturgeon acclimated to 15 and 20 °C return to routine levels within 30 min and

by 60 min at 25 °C. Kieffer et al. (2001) noted a similar return of oxygen consumption rate (i.e., 30 min) following exhaustive exercise in shortnose and Atlantic sturgeon at 12 °C. In the same way, the oxygen consumption rate rapidly decreased after exercise by approximately 50 min in juvenile (32 g) Amur sturgeon (*A. schrenckii*) at 20 °C (Cai et al. 2013). Patterns of metabolic recovery following exhaustive exercise have been shown to be influenced by acclimation temperature in Nile tilapia (*Oreochromis niloticus* McKenzie et al. 1996) and juvenile southern catfish (*Pterygoplichthys anisitsi*; Zeng et al. 2010), also with the slowest recovery occurring at the warmest temperature. Pang et al. (2015) also showed a similar and significant effect of temperature on the post-exercise recovery process in juvenile qingbo (*Spinibarbus sinensis*) following a constant acceleration test. It has been suggested that a fast recovery process could facilitate the speed at which subsequent exercise bouts could take place (Milligan 1996, for a review). Whether this applies to sturgeon is still not entirely clear as little work has been done on multiple exercise bouts in sturgeon (Cai et al. 2014) and at various temperatures. Future work should address whether temperature-related changes in exercise capacity vary with multiple exercise bouts.

In conclusion, the findings from the present study indicate that the routine metabolic rates of shortnose sturgeon, although are impacted by temperature, show a different response compared to documented cases for some other sturgeon species. In addition, while exercise increases metabolic rates in shortnose sturgeon, the magnitude of the response is muted compared with other studied species, such as salmonids (Eliason and Farrell 2016). Lastly, the post-exercise recovery process is relatively fast and affected by temperature in sturgeon. Future research should examine the effects of temperature on the metabolic costs associated with aerobic, sustained swimming in sturgeon, as this is not well known. From a practical perspective, the findings from the present study suggest that recovery from other relevant stressful events (e.g., husbandry practices, hatchery practices, angling, stocking densities) might be relevant and important to understand. As various sturgeon species are being grown in an aquaculture setting, it may be important to understand the impacts of temperature on the stress response (e.g., transport stress, culling of various size classes of fish). However, a more detailed examination of the importance of temperature on

sturgeon biology and physiology (e.g., changes in metabolites, production of heat shock proteins, ion changes, cardiac function, and circulatory physiology) is warranted.

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