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Critical thermal maxima and hematology for juvenile Atlantic (*Acipenser oxyrinchus* Mitchill 1815) and shortnose (*Acipenser brevirostrum* Lesueur, 1818) sturgeons

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Summary

The critical thermal maximum (CTmax) and the associated hematological response of juvenile (~145 g, n = 8 for both species) Atlantic *Acipenser oxyrinchus* and shortnose *Acipenser brevirostrum* sturgeons acclimated to 15°C were determined using a heating rate of 8°C h^{-1}. The critical thermal maximum averaged 30.8°C and 31.6°C for Atlantic and shortnose sturgeon, respectively, and values fell within the range noted for other sturgeon species. Oxygen-carrying capacity (hemoglobin and hematocrit) measures were generally unaffected by thermal stress. Plasma lactate levels increased from 0.5 mM to 4 mM following temperature stress in both species. Both plasma glucose and potassium levels increased following CTmax, however, these levels were about double in the shortnose sturgeon. Lastly, plasma sodium and chloride levels were significantly depressed (by more than 10%) following thermal stress in shortnose sturgeon, whereas only chloride levels decreased in Atlantic sturgeon. Taken together, while CTmax values were similar, thermal stress resulted in different hematological profiles; these differences are consistent when compared to other stressors, and may be related to the phylogenetic position and thus could reflect the evolutionary history of these two species.

Introduction

All sturgeon species are found only in the northern hemisphere, and many species have a broad geographical range (Gilbert, 1989). For example, shortnose *Acipenser brevirostrum* sturgeon are distributed as far south as the St. John's River, Florida (USA) and as far north as the Saint John River, New Brunswick (Canada) (Gilbert, 1989). Atlantic *A. oxyrinchus* sturgeon can be found from the Hamilton River, Labrador (Canada) and as far south as the St. John's River, Florida (USA) (Gilbert, 1989). Most sturgeon species inhabit a wide variety of waterways, including estuaries, rivers, lakes and oceans (Beamesderfer and Farr, 1997). Both shortnose and Atlantic sturgeon can tolerate a variety of salinities (Gilbert, 1989; Penny and Kieffer, 2014), and as such can travel between fresh and brackish water. This lifestyle exposes sturgeon to many environmental conditions, including changes in salinity, turbidity, flow/current speed, and temperature (Beamesderfer and Farr, 1997). Temperature is considered one of the most important factors influencing the survival, distribution, ecology, behaviour and physiology of fishes (Fry, 1947; Brett, 1956; Beitinger et al., 2000; Beitinger and Lutterschmidt, 2011). Dredging, damming and effluent runoff from refineries and factories (Rajaguru, 2002) have greatly influenced temperature profiles in aquatic environments (Beamesderfer and Farr, 1997).

Throughout their lifespan many sturgeon species will encounter highly variable environmental conditions, both annually and seasonally (Beamesderfer and Farr, 1997). While research has focused on the effects of acute and chronic temperature changes on oxygen consumption rates (i.e. metabolism) in various sturgeon species (Secor and Gunderson, 1998; Mayfield and Cech, 2004; Patterson et al., 2013; Kieffer et al., 2014), less is generally known about the thermal tolerance of this group of animals (summarized in Zhang and Kieffer, 2014). Quantifying a species' upper thermal tolerance has become increasingly important for the understanding of this critical aspect of fish ecology (Murchie et al., 2011) as well as the potential impacts of climate change (Beitinger and Lutterschmidt, 2011). Thermal tolerance in animals can be studied using various approaches; of these, the critical thermal maximum test (CTmax) is the most relevant (Beitinger et al., 2000) and is often used to provide an ecologically and physiologically valuable reference point that can signal an early sign of thermal stress (Stewart and Allen, 2014). The CTmax method exposes fish to a gradual, linear increase in water temperature over time (Beitinger et al., 2000). The CTmax procedure does not rely on sacrificing the fish as an endpoint (Becker and Genoway, 1979; Lutterschmidt and Hutchison, 1997; Beitinger et al., 2000), and thus this may be more preferable for working with endangered/threatened species.

Relative to other groups of fish, there is a general lack of information on the thermal tolerance of sturgeon species (Lutterschmidt and Hutchison, 1997; Ziegeweid et al., 2008; Zhang and Kieffer, 2014) and the hematological response to thermal stress in sturgeon (Zhang and Kieffer, 2014). Hematological studies can provide additional information about the overall magnitude and physiological limits of thermal stress on a species. Efforts to conserve shortnose and Atlantic sturgeon populations require, among other things,

knowledge of their thermal tolerance and thermal physiology, which currently is not elaborate. As sturgeon are the focus of intensive aquaculture in North America and abroad, an understanding of the thermal tolerance of individual sturgeon species is necessary.

The objective of this study was to determine the CTmax values for two sturgeon species in order to compile a thermal background for these animals. This study also aims to quantify the stress response (i.e. measurements of hematological stress indices such as lactate, glucose, ions; Barton et al., 2000) of the sturgeon species through examination of their hematological values pre- and post-CTmax testing. Given that these groups of animals have an identical acclimation temperature, similar thermal histories, and can be found within similar habitats under natural settings, it was hypothesized that the CTmax values for the two species would be similar.

Methods

Fish culture

Shortnose and Atlantic sturgeon were obtained from Acadian Sturgeon and Caviar (Carter's Point, Kingston, New Brunswick, Canada). Insulated containers filled with 10°C water supplemented with air were used for the 30-min transport from the hatchery to the university. Atlantic and shortnose sturgeon were the progeny of wild brood-stocks originating from the Saint John River, New Brunswick. Fish were fed twice daily to satiation (Corey Aquafeed: 1.5 mm optimum, 52% protein: http://www.coreyaqua.ca), and fasted for 24 h prior to experimentation. Fish were held in two, 1 m diameter (160-L) cylindrical flow-through tanks (one tank for each species, 30 fish per tank) continuously supplied with fresh, well-aerated, 15°C dechlorinated Saint John city water at a rate of $1 L min^{-1}$. A 12 h light: 12 h dark photoperiod was maintained throughout the study. At the time of the experiment the fish were approx. 145 g and 35 cm (see Table 1, for specifics). Overall, shortnose sturgeon were shorter (two-way ANOVA; d.f., = 1.31; $F = 5.93$; $P = 0.02$) and lighter (two-way ANOVA: d.f., = 1.31; $F = 4.8$; $P = 0.037$) than Atlantic sturgeon.

Experimental design

Critical thermal maximum tests were performed in a rectangular insulated tank (test tank) (41.9 × 24.8 × 29.8 cm) filled with approx. 30-L fresh, de-chlorinated water (Zhang and Kieffer, 2014). A 90-L rectangular heating tank (approx. 45 × 56 cm) was located above the test tank equipped with a 1000-W heater (Pentaire Aquatic Ecosystems) and multiple 10 cm air diffusers. The water from the heating tank flowed to the test tank by gravity and returned to the heating tank using a submersible pump (Loligo Systems, Denmark), which was isolated from the test arena by a perforated black plexiglass shield. Electronic thermometers (Loligo Systems, Denmark) were placed at each end of the test tank to record the temperature. The heater was calibrated and set to heat the water at a constant rate of 1.3°C every 10 min (~$8°C\ h^{-1}$) and maintained throughout the study.

CTmax testing

Shortnose or Atlantic sturgeons were randomly selected from one of the holding tanks (i.e. shortnose or Atlantic) and placed in the test arena at 15°C 1 h prior to the start of the test (individual testing, n = 8 per species; Zhang and Kieffer, 2014). Fish were thereafter exposed to thermal stress or not (control). For the control fish, the individuals were removed from the test tank following the 1 h recovery period and anaesthetized with a buffered TMS solution (250 mg L^{-1} tricaine methanesulfonate buffered in $NaHCO_3$). Once fully anaesthetized (indicated by a loss of equilibrium, no response to touch, and lack of ventilation), the fish were removed from the tank, quickly weighed, and total length measured. Approx. 1 ml of blood was removed from the caudal vasculature and placed in a 1.5 ml centrifuge tube using a lithium heparinized needle and syringe.

Fish belonging to the thermal stress group were exposed to increases in temperature immediately following the 1 h recovery period. CTmax testing involved increasing the temperature of the water in the test arena by ~$8°C\ h^{-1}$ at a constant rate (determined through pilot studies) until loss of equilibrium (LOE) occurred. Loss of equilibrium as an endpoint is indicated when the fish rolls dorso-ventrally and is unable to right itself within 10 s (Ziegeweid et al., 2008; Zhang and Kieffer, 2014). To ensure that each fish reached its CTmax, individuals were righted manually a total of three times. Following the third incidence of LOE, the fish were removed from the tank, anaesthetized and measured. The water temperature in the test arena was recorded at 10 min intervals throughout the trials

Table 1
Total length and mass (ranges, means, standard deviation, sample size) of shortnose and Atlantic sturgeon used in experiments

Species and condition	Variable	Mean	SD	Range	Sample size (n)
Shortnose sturgeon (no thermal stress)	Total length (cm)	34.2	2.2	31–37	8
	Mass (g)	139.5	8.4	130–155	8
Shortnose sturgeon (thermal stress)	Total length (cm)	36.3	1.1	34–37	8
	Mass (g)	142.6	7.2	130–152	8
Atlantic sturgeon (no thermal stress)	Total length (cm)	36.5	1.4	34–38	8
	Mass (g)	147.1	9.6	134–160	8
Atlantic sturgeon (thermal stress)	Total length (cm)	36.5	0.9	35–38	8
	Mass (g)	149.4	11.4	140–173	8

Control fish = not exposed to thermal stress; Critical thermal maximum = fish exposed to thermal stress; SD = standard deviation.

until the third incidence of LOE, at which point the CTmax for the fish was recorded. Blood samples were removed from the fish using procedures identical to control fish. Both control and experimental fish were sacrificed by an overdose in buffered ($NaHCO_3$; 2 g L^{-1}) MS-222 (1 g L^{-1}) following blood sampling. The test tank was emptied and cleaned following each individual trial.

Whole blood and plasma analysis

A portion of whole blood was used to determine hematocrit (HCt) and hemoglobin concentrations (Hb) following standard procedures (Baker et al., 2005a; Penny and Kieffer, 2014; Zhang and Kieffer, 2014). The mean erythrocytic hemoglobin content (MEHC) was calculated = 100 × (hemoglobin/hematocrit) (Houston, 1990). The remaining blood was centrifuged (10 000 **g** for 2 min); the resultant plasma was drawn off, then frozen at −20°C for later analysis. Plasma sodium, chloride and potassium concentrations were measured using a SmartLyte ion analyzer (Diamond Diagnostics; www.diamonddiagnostics.com). Plasma glucose levels were measured using a blood glucose meter (OneTouch Ultra 2; Code 25 test strips; www.onetouch.ca). Total plasma lactate concentrations were measured using a standard colorimetric assay and appropriate standards (lactate reagent: 735-10; lactate standard: 735-11; TrinityBiotech).

Statistical analysis

Statistics were analyzed using SIGMASTAT 3.5 software (www.sigmaplot.com). Normality for all variables was evaluated using the Shapiro-Wilks test. Critical thermal maximum values were compared between species using a *t*-test. The mean blood parameters were compared between conditions (thermal stress vs no thermal stress) and species (Atlantic and shortnose) using two-way ANOVAS. Tukey *post hoc* tests were used to compare mean hematological variables between species. Significance was determined at $\alpha = 0.05$.

Results

CTmax

Mean (±SE) CTmax values were not different between Atlantic and shortnose sturgeon (*t*-test; $P > 0.05$). Atlantic and shortnose sturgeon had CTmax values of 30.8 (±0.31) and 31.6°C (±0.22), respectively.

Hematological response

Mean hemoglobin concentrations (g dl^{-1}) were not significantly different amongst the control groups or thermal stress groups in Atlantic and shortnose sturgeon (Table 2; Fig. 1a). Similarly, mean hematocrit values did not differ between the control and thermal stress group in Atlantic sturgeon and shortnose sturgeon (Table 2; Fig. 1b). Mean erythrocytic hemoglobin (MEHC) (g dl^{-1}) levels were similar under control conditions in both species (Fig. 1c), but decreased significantly in Atlantic sturgeon following thermal stress (Fig. 1c; Table 2). Mean glucose concentrations (mM) were similar amongst the control groups for both species (Fig. 2a). Plasma glucose levels increased in both species following thermal stress (Table 2), however this response was only significant for shortnose sturgeon ($P < 0.05$). Mean control lactate concentrations (mM) were similar between species (Fig. 2b). Thermal stress caused lactate to increase significantly (from about 0.5 mM to 4 mM) in both species ($P < 0.001$; Fig. 2b; Table 2). Mean sodium ion (Na^+) concentrations (mequiv L^{-1}) were influenced by both thermal stress ($P < 0.001$) and species ($P < 0.02$) (Table 2; Fig. 3a). Control sodium levels were similar between species, and thermal stress caused Na^+ to decrease in both species; however, this pattern was only significant for shortnose sturgeon (Fig. 3a). Similar patterns were noted for chloride levels, however in this case, thermal stress caused these levels to decrease significantly in both species (Table 2; Fig. 3b), particularly in shortnose sturgeon. Mean potassium ion (K^+) concentrations were influenced by thermal stress ($P < 0.001$) and species ($P < 0.001$) (Fig. 3c). In control fish, potassium levels were higher in shortnose (~3 (mequiv L^{-1}) compared to Atlantic sturgeon (~2 mequiv L^{-1}); Fig. 3b). Thermal stress caused significant increases in K^+ levels in all sturgeon, however the increase was larger in shortnose sturgeon (Fig. 3c).

Table 2
Two-way ANOVA results for blood chemistry values following laboratory determination of CTmax for juvenile shortnose and Atlantic sturgeon

Response variable	Factor	SS	F	P
Hemoglobin	Condition	0.164	0.214	0.647
	Species	0.113	0.147	0.704
	Condition × Species	0.315	0.411	0.527
Hematocrit	Condition	49.444	3.276	0.081
	Species	2.834	0.188	0.668
	Condition × Species	0.093	0.006	0.938
Mean erythrocytic Hemoglobin (MEHC)	Condition	52.14	5.404	0.028*
	Species	0.366	0.038	0.847
	Condition × Species	7.329	0.760	0.391
Glucose	Condition	199.750	14.600	<0.001*
	Species	139.654	10.207	0.003
	Condition × Species	45.482	3.324	0.079
Lactate	Condition	109.600	50.971	<0.001*
	Species	0.032	0.015	0.903
	Condition × Species	0.356	0.166	0.687
Sodium	Condition	1800.000	12.683	0.001*
	Species	861.125	6.068	0.020*
	Condition × Species	128.000	0.902	0.350
Potassium	Condition	39.383	41.260	<0.001*
	Species	21.615	22.645	<0.001*
	Condition × Species	2.050	2.148	0.154
Chloride	Condition	1352.000	14.169	<0.001*
	Species	1128.125	11.823	0.002
	Condition × Species	66.125	0.693	0.412

All significant values designated with an asterisk (*); n = 8 for controls (no thermal stress) for each species; n = 8 for thermal stress for each species; Condition (two levels): (i) control, no thermal stress and (ii) thermal stress Species (two levels): (i) shortnose sturgeon and (ii) Atlantic sturgeon.

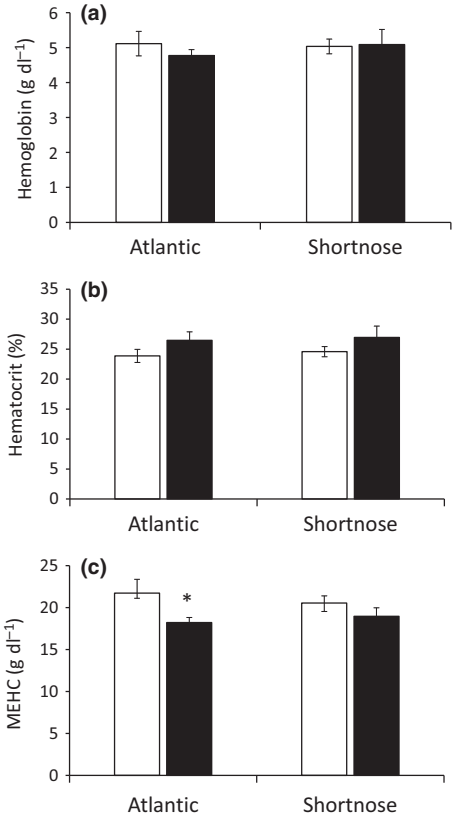

Figure 1. Mean (±SE) Hemoglobin (a), Hematocrit (b) and Mean Erythocytic Hemoglobin concentration (MEHC) (c) concentrations of Atlantic and shortnose sturgeon for control (no thermal stress; open bars, n = 8 for each species) and thermal stress (black bars, n = 8 for each species). * indicates that the physiological parameter is significantly different between the thermally stressed group and the control (no thermal stress) ($P < 0.05$)

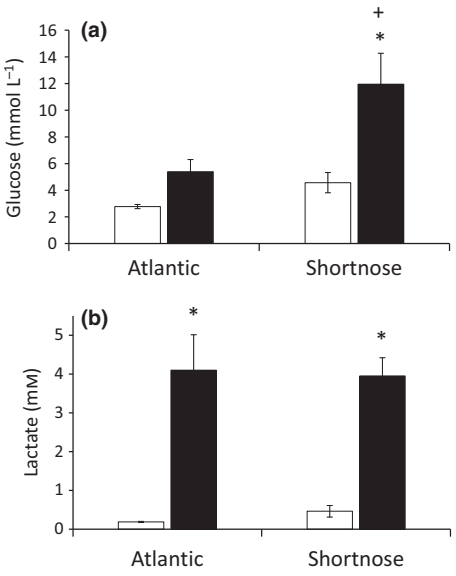

Figure 2. Mean (±SE) plasma glucose (a) and lactate (b) concentrations of Atlantic (*Acipenser oxyrinchus*) and shortnose (*A. brevirostrum*) sturgeons for control (no thermal stress; open bars, n = 8 for each species) and thermal stress (black bars, n = 8 for each species). * = physiological parameter significantly different between thermally stressed group and control (no thermal stress) ($P < 0.05$). + = significant difference between Atlantic and shortnose sturgeon ($P < 0.05$)

Discussion

CTmax

Surprisingly, little research has been performed on the critical thermal maximum and physiological consequences of thermal stress in sturgeon species. This is perplexing since most sturgeon species are protected under legislation due to human-made disturbances that might involve water temperature alterations (Pikitch et al., 2005). The critical thermal maximum values for Atlantic and shortnose sturgeon noted in the present study were found to be similar to those in other studies using pallid (*Scaphirhynchus albus*), Lake (*Acipenser fulvescens*), shortnose, shovelnose (*Scaphirhynchus platorynchus*) and green (*Acipenser medirostris*) sturgeons (Sardella et al., 2008; Zhang and Kieffer, 2014; D. Deslauriers, unpubl. data; Table 3). Values for CTmax in sturgeon appear relatively uniform across acclimation temperatures and heating rates (Table 3). The similarity between the CTmax values for Atlantic and shortnose sturgeon examined in the current study was likely influenced by the shared thermal history and identical acclimation temperatures and rearing conditions. Factors such as body size (Ziegeweid et al., 2008; Zhang and Kieffer, 2014) and acclimation temperature are known to influence CTmax (Lutterschmidt and Hutchison, 1997). Thus, our study is important, as the body size and acclimation temperature were held constant, allowing for direct comparison of the results. As these findings are only for a single acclimation temperature and heating rate, future and more detailed studies are needed to determine how other factors (e.g. salinity, toxicants, heating rate, acclimation temperature) influence thermal tolerance in different species of sturgeon. In particular, experiments with multiple acclimation temperatures might provide insight into the ecological and physiological flexibility of a species across seasons.

Hematological responses to thermal stress

There is a paucity of information on the thermal tolerance (CTmax) and its associated hematology in any fish species (Zaragoza et al., 2008; Murchie et al., 2011; Ellis et al., 2013; Zhang and Kieffer, 2014). CTmax led to a marked change in a number of blood parameters across sturgeon species, which is indicative of increased stress in the animal (Wedemeyer et al., 1990; Barton et al., 2000). Lactate concentrations increased in Atlantic and shortnose sturgeon during the thermal stress and at levels comparable to previous research on shortnose sturgeon (Zhang and Kieffer, 2014; Y. Zhang and J. D. Kieffer, unpubl. data). These elevated lactate levels suggest that anaerobic pathways were activated in the fish (Zhang and Kieffer, 2014). Anaerobic metabolism was likely required and increased during the CTmax test because of (i) increased activity as water temperature

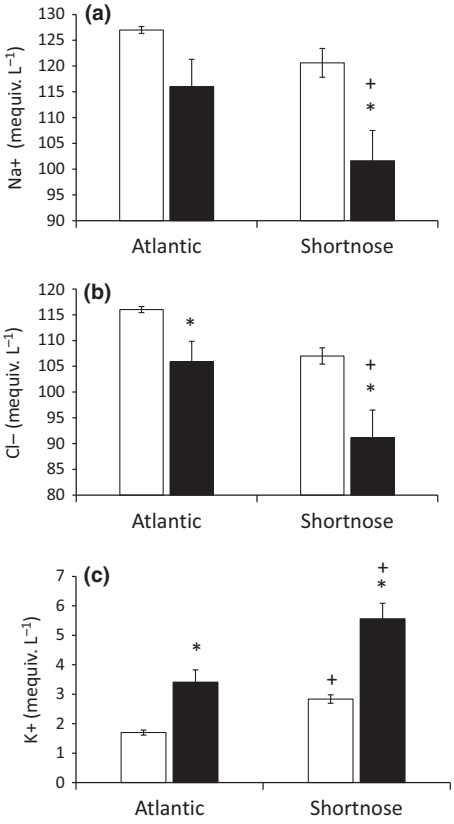

Figure 3. Mean (±SE) plasma sodium (a), chloride (b) and potassium (c) concentrations of Atlantic and shortnose sturgeons for control (no thermal stress; open bars, n = 8 for each species) and thermal stress (black bars, n = 8 for each species). * = physiological parameter significantly different between thermally stressed group and the control (no thermal stress) ($P < 0.05$). + = significant difference between Atlantic and shortnose sturgeons ($P < 0.05$)

increased, (ii) decreased oxygen in the experimental chamber with increases in temperature, and (iii) no major changes in the oxygen carrying capacity of blood (e.g. hematocrit and hemoglobin) following thermal stress in either species. As fish approached their CTmax, many became agitated and increased their activity that ranged from slow movement to rapid, burst-type activity. Burst type activity has been shown to activate anaerobic metabolism (reviewed in Kieffer, 2000), likely contributing to the associated hematological changes (e.g. changes in glucose, ions) noted in the present study. In addition, oxygen levels (although not monitored) likely decreased during the CTmax trials (as noted by Murchie et al., 2011; Ellis et al., 2013). Thus, combining the increased activity with (potential) hypoxic conditions during the tests could have heightened the lactate response in the sturgeons. Additional research should investigate the combination of high temperature and oxygen levels on the physiological responses in sturgeons (see Ellis et al., 2013).

Although the CTmax values were nearly identical between the two species, it was noted that many of the secondary indicators changed as a result of thermal stress. In particular, glucose, lactate, and potassium all increased, whereas sodium and chloride decreased. These changes are similar to those noted in another study using shortnose sturgeon (Zhang and Kieffer, 2014). Of interest, however, was the consistent and larger physiological disturbance following thermal stress in shortnose sturgeon relative to Atlantic sturgeon. The underlying mechanism surrounding these differences is difficult to glean from the current data, but there are examples from our lab that support these differences. For example, Baker et al. (2005a,b) found that cortisol levels (primary stress response) were significantly larger (up to 4-fold higher) and more variable in shortnose sturgeon following both exercise and hypoxia stress (Baker et al., 2005b). While there is still some controversy around the role of cortisol in fishes (Mommsen

Table 3
Mean Critical Thermal maximum (CTmax) (±SE) for sturgeon species acclimated to varying temperatures (Ta) and at different heating rates

Species	Weight (g)	Ta (°C)	Heating rate (°C min^{-1})	CTmax (°C)	Reference
Atlantic sturgeon, *Acipenser oxyrinchus*	149.38 g	15	0.13	30.9 ± 0.31	Current study
Green sturgeon, *Acipenser medirostris*	58.4	18	0.3	33.7 ± 0.08	Sardella et al., (2008)
Hybrid Sturgeon (♂ Atlantic × ♀ shortnose)	140.00	15	0.13	31.4 ± 0.35	M. C. Spear and J. D. Kieffer, unpubl. data
Pallid Sturgeon, *Scaphirhynchus albus*	14.98	13	0.03	33.14 ± 0.19	D. Deslauriers, unpubl. data
Shortnose Sturgeon, *Acipenser brevirostrum*	142.63	15	0.13	31.6 ± 0.22	Current Study
	~250	10	0.1	27.6 ± 0.12	Zhang and Kieffer, (2014)
	~250	15	0.1	31.5 ± 0.32	Zhang and Kieffer, (2014)
	~250	20	0.1	32.8 ± 0.41	Zhang and Kieffer, (2014)
	0.6–35	19.5	0.1	33.7 ± 0.30	Ziegeweid et al., (2008)
	0.6–35	24.1	0.1	35.1 ± 0.20	Ziegeweid et al., (2008).
	~150	15	0.1	31.06 ± 0.31	Y. Zhang and J. D. Kieffer, unpubl. data
Shovelnose Sturgeon, *Scaphirhynchus platorynchus*	13.85	13	0.03	33.20 ± 0.08	D. Deslauriers, unpubl. data
Lake Sturgeon, *Acipenser fulvescens*	200 dph	18.1	0.1	33.2 ± 0.2	Wilkes, (2011)
	200 dph	24.9	0.1	35.7 ± 0.1	Wilkes, (2011)
	400 dph	18.1	0.1	33.1 ± 0.2	Wilkes, (2011)
	400 dph	24.9	0.1	35.1 ± 0.2	Wilkes, (2011)

et al., 1999), it can promote the mobilization of energy reserves, such as glucose (Donaldson, 1981). The results of the present study support this, as glucose levels were significantly larger following thermal stress in shortnose sturgeon. Although cortisol was not measured in the current study, it is possible that the two species perceive stressors differently or have different cortisol sensitivity (e.g. receptor numbers; Baker et al., 2005a). Additional studies are necessary to ascertain the role of cortisol in sturgeon.

Thermal stress led to significant changes in plasma ion levels (Fig. 3). Similar to that for glucose, the changes in ions following stress were typically larger for shortnose sturgeon. The degree of change in the ions is consistent with our previous research (Zhang and Kieffer, 2014), and may again be related to species differences in the primary stress response. For example, increases in adrenaline (not measured in this study) in response to stress have been linked to decreases in Cl^- and Na^+ concentrations (McDonald and Milligan, 1997). An increase in adrenaline is believed to increase blood pressure in the gills, leading to increased diffusion and ion loss (Gonzalez and McDonald, 1992). Atlantic sturgeon failed to lose sodium and chloride at the same levels as shortnose sturgeon (Fig. 2), which may suggest a muted production rate of adrenaline in response to stress, or an increased ability to maintain regulation of ion diffusion at the surface of the gills.

While the thermal tolerance of sturgeons appears to be similar, the associated stress response may, in fact, vary across species. Understanding the thermal tolerance of fish, including such ancient fish as the sturgeon, might be of importance in future assessments of global climate change (Beitinger and Lutterschmidt, 2011), its effects on fish population sizes and distributions, and recovery efforts. Based on the present results, shortnose and Atlantic sturgeon should be able to tolerate any temperature increase related to climate change. However, understanding the combined effects of low oxygen, high carbon dioxide and elevated temperatures on stress in sturgeons is not well understood, and should be the focus of additional studies.

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