Effects of ontogeny, season, and temperature on the swimming performance of juvenile green sturgeon (Acipenser medirostris)

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Effects of ontogeny, season, and temperature on the swimming performance of juvenile green sturgeon (*Acipenser medirostris*)

Peter J. Allen, Brian Hodge, Inge Werner, and Joseph J. Cech, Jr.

Abstract: Because some salmonids show decreased swimming performance (U_{crit}) during their parr–smolt transformation, we tested the hypothesis that juvenile anadromous green sturgeon (*Acipenser medirostris*) decrease U_{crit} during their analogous ontogenetic stage. Juvenile green sturgeon (mean age: 98 days) that had not reached seawater tolerance had a positive relationship of U_{crit} ($cm \cdot s^{-1}$) with total length (TL), whereas seawater-tolerant sturgeon (mean age: 150 days) had a negative relationship of U_{crit} with TL. This U_{crit} decrease was presumably seasonal because a similar-sized group of fish tested later (mean age: 288 days) showed a linear increase in U_{crit} with TL. Smaller sturgeon displayed both morphological (larger relative pectoral fin surface areas) and behavioral (rostrum wedging and pectoral fin holding) attributes for station holding in a riverine environment. In a second experiment to test the effects of increased river temperature near the predicted time of downstream migration, U_{crit} and heat-shock protein concentrations increased at 24 °C compared with at 19 °C (mean age: 155 days). Thus, although there was evidence for cellular stress, the swimming ability of the fish was not compromised. Therefore, water velocity, temperature, and time of year should be considered in life-stage-specific efforts to manage or protect green sturgeon.

Résumé : Parce que certains salmonidés accusent une baisse de performance natatoire (U_{crit}) durant leur transformation de tacon en saumoneau, nous avons évalué l'hypothèse qui veut que les jeunes esturgeons verts (*Acipenser medirostris*) anadromes réduisent leur U_{crit} durant leur stade ontologique analogue. Les jeunes esturgeons verts (âge moyen de 98 jours) qui n'ont pas encore atteint leur tolérance à l'eau de mer montrent une relation positive entre U_{crit} ($cm \cdot s^{-1}$) et la longueur totale (TL), alors que les esturgeons tolérants à l'eau de mer (âge moyen de 150 jours) ont une relation négative entre U_{crit} et TL. Cette réduction d'U_{crit} est sans doute saisonnière puisque qu'un groupe de taille semblable testé plus tard (âge moyen de 288 jours) montre une augmentation linéaire d'U_{crit} avec TL. Les esturgeons plus petits possèdent des caractéristiques morphologiques (surface relative plus grande des nageoires pectorales) et comportementales (insertion du rostre et position des nageoires pectorales) pour se maintenir sur place dans un environnement de rivière. Dans une seconde expérience d'évaluation des effets d'une augmentation de la température de la rivière près du moment prédit de l'émigration vers l'aval, U_{crit} et les concentrations de protéines du choc thermique sont plus élevées à 24 °C qu'à 19 °C (âge moyen de 155 jours). Ainsi, bien qu'il y ait des indices d'un stress cellulaire, la capacité de nage des poissons n'est pas compromise. Il faut donc prendre en considération la vitesse du courant, la température de l'eau et le moment de l'année dans les efforts reliés au stade de vie que l'on fait pour aménager ou protéger l'esturgeon vert.

[Traduit par la Rédaction]

Introduction

Maximum aerobic swimming performance of fish has been widely measured as critical swimming velocity (U_{crit}). Typically determined in a water flume or tunnel, U_{crit} can be described as sustainable swimming in stepped water velocity increases until fatigue (Brett 1964; Beamish 1978; Hammer 1995). Despite some inherent limitations in simulating natural environments, this laboratory-based measurement has correlates with ecological performance and relationships to swimming abilities in a fish's natural environment (reviewed by Plaut 2001; Wolter and Arlinghaus 2003). U_{crit} has been studied extensively in juvenile salmonids, and some of these studies have directly compared freshwater parr with seawater-tolerant smolts. Whereas most fishes increase U_{crit} as they grow and develop (Beamish 1978; Hammer 1995), several studies have reported decreased U_{crit}, increased tail beat frequency (TBF), and increased refusal to swim during the

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parr–smolt transformation (PST; Thorpe and Morgan 1978; Flagg and Smith 1982). A recent study shows evidence of locomotory muscle restructuring (including thyroid hormone induced restructuring) during the PST, affecting muscle contractility and fiber type, and decreasing U_{crit} (Katzman and Cech 2001). Thus, the downstream movements of these juveniles is facilitated by a decrease in aerobic, red muscle fibers and the associated ability to maintain position in stream currents (Katzman and Cech 2001). However, questions remain concerning the swimming performance and downstream migration in nonsalmonid anadromous fishes, including sturgeon.

There have been several studies on swimming performance in juvenile sturgeons (McKenzie et al. 2001; Peake 2004). Most of the sturgeon swimming studies used limited size and age ranges of fish (McKenzie et al. 2001; Adams et al. 2003) or did not study anadromous species (Peake et al. 1995; Adams et al. 1999). Therefore, the potential age- and size-related changes in swimming performance have not been elucidated for anadromous species of sturgeon. Green sturgeon (*Acipenser medirostris*) are anadromous and are known to spawn in three river systems: the Sacramento and Klamath in northern California and the Rogue in southern Oregon. Adults range from Ensenada, Mexico, to the Bering Sea (Moyle 2002), but there is little information on their early life stages, particularly on size and age of juvenile seawater entry. Populations appear to be declining (Moyle 1994, 2002), and their natal rivers are modified by anthropogenic changes such as dams and water diversions, which in turn have increased summer water temperatures over historic levels (Bartholow 2005).

The effects of these temperature increases on early life stages of green sturgeon, including the life stages during which seawater adaptation occurs, are not fully understood. In salmonids, temperature is known to influence endogenous changes that occur during the PST (McCormick et al. 2002; Handeland et al. 2004; Marine and Cech 2004), as well as affect swimming performance (Johnston and Ball 1997; Taylor et al. 1997). In green sturgeon, embryos and larger, older (yearling) juveniles have been found to be negatively impacted by warm temperatures (Mayfield and Cech 2004; Van Eenennaam et al. 2005), which has included depressed swimming abilities (Mayfield and Cech 2004), although smaller, younger (~1–2 months old) juveniles may not be adversely affected (Allen et al. 2006). Heat-shock protein (hsp) expression, a cellular measure of temperature-related stress, may show complementary changes with swimming performance. Although hsps have not been shown to be directly linked to many measures of physiological performance (a tertiary physiological stress response), this has been primarily due to a paucity of studies (Iwama et al. 2004). Therefore, measurements of swimming performance and hsp expression can provide an integrated whole-organism and cellular evaluation of the effects that temperature may have on juvenile green sturgeon during the critical period of seawater adaptation.

There were two main objectives of this study. The first was to measure changes in U_{crit} with ontogeny in juvenile green sturgeon. Because of their anadromy, we hypothesized that they would display a "smolt-like" temporary decrease in U_{crit} when they reached seawater tolerance. To aid in the comparisons of swimming performance with increasing sizes of fish, a concurrent study was carried out on the ontogeny of salinity tolerance in green sturgeon with size and age (Allen 2005). The second objective was to measure temperature-related effects on juvenile green sturgeon swimming performance and hsp expression. Larger (yearling) juvenile green sturgeon show decreased swimming performance at 24 °C (Mayfield and Cech 2004). Because of this we hypothesized that U_{crit} would decrease at 24 °C compared with at 19 °C and that hsp expression would increase.

Materials and methods

Fish rearing and holding

Green sturgeon were hatched according to the methods described by Van Eenennaam et al. (2001). Briefly, adult wild fish were obtained from the Klamath River and were artificially induced to spawn, and first generation fish (73–288 days posthatch (dph) or 2.5–9.5 months old) were used in experiments. Larval to juvenile fish were reared, under natural (springtime) photoperiods, in circular (1 m diameter) fiberglass tanks with continuous flows of nonchlorinated well water at 18.6 ± 0.3 °C (mean ± standard deviation, SD). Inflowing water was oriented with a spray bar to provide a very slight current in the tank. Ad libitum rations of commercial diet (Silver Cup Soft-Moist Trout Diet; Nelson & Sons, Inc., Murray, Utah) and small amounts of tubifex were added once the fish started exogenous feeding. Currents in holding tanks were gradually increased as the fish grew larger and were better able to hold position. Before experiments, fish were transferred into a 1 m diameter tank similar to the holding tanks except that water currents were increased throughout the tank. Increased flows from a small, submersible pump better simulated currents found in the fishes' natal river environment. Fish were always acclimated to the stronger currents (6–12 $\text{cm}\cdot\text{s}^{-1}$) for 3–14 days before experimentation. Fish were fed commercial diet according to the optimal growth feeding chart derived for white sturgeon (S.I. Doroshov, Department of Animal Science, University of California at Davis, Davis, CA 95616, unpublished data). Experimental tanks were measured daily for temperature (19.2 ± 0.02 °C), pH (7.78 ± 0.02), dissolved oxygen (always >7.75 $\text{mg}\cdot\text{L}^{-1}$ or 84.4% saturation; mean 8.33 ± 0.04 $\text{mg}\cdot\text{L}^{-1}$ or 90.4 ± 0.5%), and dissolved total ammonia (unionized ammonia always <11.0 $\mu\text{g}\cdot\text{L}^{-1}$; mean 5.5 ± 0.3 $\mu\text{g}\cdot\text{L}^{-1}$).

Experiment 1: changes in swimming performance (U_{crit}) with ontogeny

We measured ontogenetic changes in swimming performance (weekly U_{crit} tests) with increasing age (73–177 dph or 2.5–6 months old; July–October) and total length (TL) from fish of the same cohort. The experiment was conducted until fish had far surpassed a length and age threshold at which all fish were surviving in seawater, based on concurrent salinity-tolerance experiments with the same cohort. Fish in all U_{crit} experiments were used only once.

A Brett-type swim chamber (Brett 1964) that generated rectilinear flow was used to measure U_{crit}. Fish were individually netted, placed in a water-filled plastic container, and transferred (3.3 m distance) to the cylindrical swimming chamber (65 cm length, 15 cm diameter). Each fish was acclimated for 30–60 min at a low water velocity (5 $\mathrm{cm \cdot s^{-1}}$) to orient it to the current and chamber. Fish were shielded from observers by black plastic or opaque plastic sheets, and swimming was observed via a mirror oriented at an angle over the top of the swimming chamber. After acclimation, water velocity was increased in increments of 10 $\mathrm{cm \cdot s^{-1}}$ at 20 min intervals. U_{crit}, as a measure of the maximum aerobic swimming ability (Beamish 1978), was calculated from Brett (1964):

$$(1) \qquad U_{\mathrm{crit}} = V_{\mathrm{f}} + V_{\mathrm{i}}(T_{\mathrm{f}}/T_{\mathrm{i}})$$

where V_{f} is the final velocity at which the fish swam for the entire 20 min period, V_{i} is the increment of water velocity increase (10 $\mathrm{cm \cdot s^{-1}}$), T_{f} is the time swum at the water velocity of fatigue, and T_{i} is the time increment for each water velocity (20 min). The swimming chamber was maintained at a constant temperature by a thermostat-controlled water bath, and its water was partially exchanged with fresh, air-equilibrated well water between experiments to ensure dissolved oxygen levels near air saturation. No solid blocking corrections were used, because the maximum cross-sectional area of the fish was always <10% of the cross-sectional area of the swimming chamber (Bell and Terhune 1970).

U_{crit} swimming tests were concluded when fish impinged three times at the same water velocity. Impingement was determined as either impingement (one-third or greater of body in contact with the rear screen) or fatigue (sustained contact with the rear screen for 60 s). After the initial impingement, the water velocity was decreased for <60 s until the fish came off the rear screen. If the fish did not come off the rear screen within 60 s, the experiment was ended. If the fish did come off the rear screen, the water velocity was increased until it was at the same velocity of impingement. Usually, the second and third impingements occurred in rapid succession at the water velocity of the first impingement. In contrast, 23% of fish were excluded from analyses because of either tail propping (caudal fin supporting fish on rear screen despite rapid increases and decreases in water velocity to coax the fish into swimming) or rostrum wedging (rostrum thrust into front screen holding nonswimming fish in the current). Fish would occasionally use their pectoral fins to help brace against the currents on the bottom of the swimming chamber. This bracing was usually very temporary, because fish were unable to hold their position without swimming for more than a few seconds because of the cylindrical shape of the swimming chamber. Fish were not touched, prodded, or shocked during the experiment.

During experiment 1, TBF and ventilation frequency (VF) were also measured. Both measurements were means from watching the fish for 30 s periods three times at every water velocity interval: 5, 10, and 15 min after water velocity increases. Data from water velocities >45 $\mathrm{cm \cdot s^{-1}}$ were not used because of the difficulty in accurately observing TBF and VF.

The possible effects of flume size on swimming performance in larger juvenile green sturgeon (330–450 mm TL) were tested using a larger-sized flume (91 cm long × 25.4 cm diameter, cylindrical) and found not to be significantly different from the flume size used above (t test, $p < 0.05$, $n = 6$ per flume, 54.49 ± 1.19 $\mathrm{cm \cdot s^{-1}}$ vs. 55.03 ± 2.14 $\mathrm{cm \cdot s^{-1}}$). These fish were from a different cohort, were swum in winter (February) instead of in late summer – early autumn (August–October), and were older (287–288 dph or 9.5 months old) than the other comparably sized experiment 1 fish (3.5–6 months old).

After experiment 1, fish were immediately euthanized in 500 $\mathrm{mg \cdot L^{-1}}$ tricaine methanesulfonate (MS 222) and pectoral fin dimensions, TL, and wet mass were measured (for pectoral fin dimensions, $n = 47$, with 29 of the smallest fish, out of the total 76 fish, not measured). Each pectoral fin (right and left) was measured for length (anterior to posterior) and width (insertion to fin tip). Relative pectoral fin surface area was estimated by the following equation:

$$(2) \qquad \text{surface area} = (\text{length} \cdot \text{width})/\mathrm{TL}^2$$

Experiment 2: elevated temperature effects

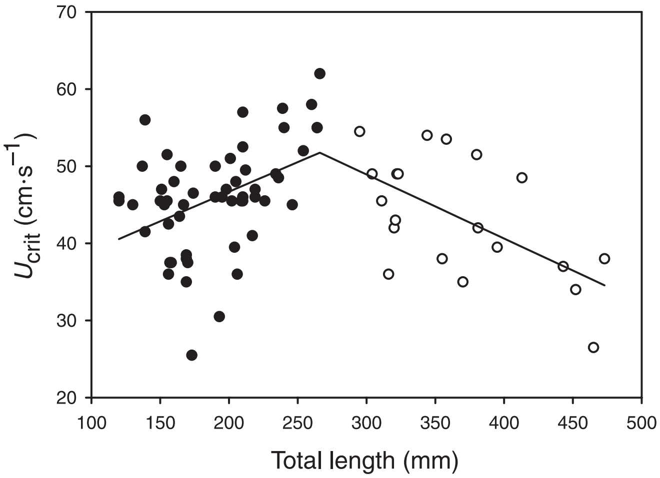
Twenty fish were placed in a tank with water flows and feeding regimes similar to those in the 19 °C pre-experimental tank. These fish were acclimated to 24 °C (1 $\mathrm{°C \cdot day^{-1}}$) and were held at 24 °C for 2.5–5 weeks before swimming performance experiments. The experimental tank was measured daily for temperature (24.3 ± 0.08 °C), pH (8.21 ± 0.03), dissolved oxygen (always >6.43 $\mathrm{mg \cdot L^{-1}}$ or 77.3% saturation; mean 7.21 ± 0.09 $\mathrm{mg \cdot L^{-1}}$ or 86.4 ± 1.0%), and dissolved total ammonia (unionized ammonia always <44.1 $\mathrm{\mu g \cdot L^{-1}}$; mean 22.2 ± 1.1 $\mathrm{\mu g \cdot L^{-1}}$). Experimental parameters were the same as those previously described, and fish were from the same cohort as those used in experiment 1. These experiments were conducted during the late summer to early autumn period (September–October) when sturgeon were 123–177 dph (4–6 months old). The 24 °C level was chosen because it is a high summer water temperature in their natal rivers (Erickson et al. 2002; US Geological Survey (USGS) 2004).

Following TL and wet mass measurements in experiment 2, dorsal muscle samples (1 $\mathrm{cm^2}$ section from the right side adjacent to the third and fourth dorsal scutes) were removed by scalpel and forceps for hsp analyses. For pelvic fin samples, a 1 $\mathrm{cm^2}$ section of the right pelvic fin was removed. All samples were placed into individual frozen-sample vials, frozen on dry ice, and stored at –80 °C until hsp analyses (<3 months). Fish acclimated to 24 °C for 2.5–5 weeks ($n = 16$) and fish of the same age and size ($n = 15$) held at 19 °C were sampled regardless of whether they cooperated during swimming trials or not. Hsp60, hsp70, and hsp90 were analyzed using Western blotting techniques as described by Werner et al. (2001) and Viant et al. (2003), with protein bands being quantified by densitometry (Bio-Rad GS710; Bio-Rad Laboratories, Hercules, California).

Statistical analyses

For the relationship of swimming performance with TL, two separate linear regressions were used (Sall et al. 2001): one for TLs of fish from 120 to 266 mm and another for TLs of fish from 267 to 475 mm because of the results of the concurrent salinity-tolerance experiment, which found that 100% salinity tolerance was achieved in an experimental group of fish with a mean ± standard error (SE) TL of 266 ± 24 mm (Allen 2005). After both relationships were found to be significant ($p < 0.05$), a piecewise regression (Neter et al.

Fig. 1. Experiment 1 relationship between U_{crit} and total length (TL) for juvenile green sturgeon (*Acipenser medirostris*) during summer and early autumn: ●, fish that were less than 100% seawater (SW) tolerant; ○, fish that were 100% SW tolerant based on a concurrent experiment. The regression line represents the linear relationship $y = 0.077x_1 + 31.348 - 0.160(x_1 - 266)x_2$, where x_1 = TL and $x_2 = 1$ if $x_1 > 266$, otherwise $x_2 = 0$ ($r^2 = 0.26$, $n = 76$).



1996) was used to combine the two regressions at the TL that accounted for the maximum amount of variance, which happened to be 266 mm. Regressions also characterized the relationships between pectoral fin dimensions and TL. All regressions were found to be significant ($p < 0.05$). For TBF and VF, data were divided into four groups (10–20, 20–30, 30–40, and 40–50 cm) to analyze size effects at each water velocity using analyses of variance. No differences were found, so data from all sizes of fish were combined and analyzed for water velocity. Multiple comparison tests (Tukey's honestly significant difference test) were used only if the overall one-way analysis of variance (ANOVA) was found to be significant. Student's *t* tests were used to compare 24 °C and 19 °C groups for U_{crit} and hsp results. In all cases, differences were considered significant at $p < 0.05$. All statistical values for measurements are reported as means ± SE.

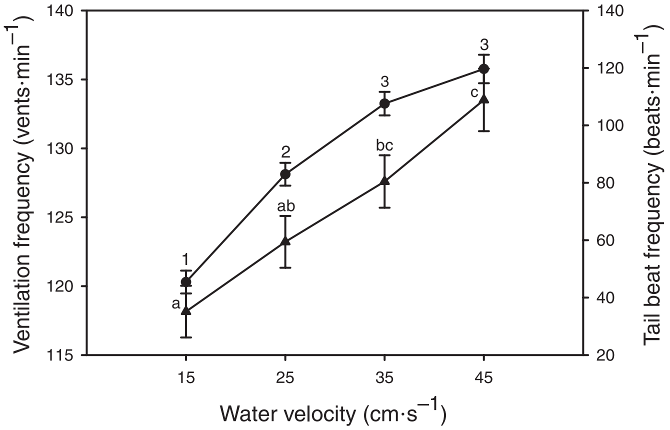
Results

Experiment 1: changes in swimming performance (U_{crit}) with ontogeny

U_{crit} increased in fish with TLs from 120 to 266 mm ($n = 56$) and decreased in fish with TLs from 267 to 475 mm ($n = 20$; $y = 0.077x_1 + 31.348 - 0.160(x_1 - 266)x_2$, where x_1 = TL and $x_2 = 1$ if $x_1 > 266$, otherwise $x_2 = 0$, $r^2 = 0.26$; Fig. 1). The change from increasing to decreasing U_{crit} with increasing fish size also corresponded with the mean TL (266 ± 24 mm) of fish achieving full-strength seawater tolerance in a concurrent experiment (Allen 2005), supporting our hypothesis.

There were no differences in TBF or VF among the four size groups; therefore, all the size groups were combined and TBF and VF were analyzed between water velocities. TBF and VF both increased with water velocity (Fig. 2).

Fig. 2. Mean (± standard error) juvenile green sturgeon (*Acipenser medirostris*) gill ventilation (n = 50–73, ▲) and tail beat frequencies (n = 49–76, ●) with swimming velocity, experiment 1, summer to early autumn fish. Different letters and numbers represent significant differences in gill ventilation and tail beat frequency, respectively (analysis of variance, $p < 0.05$).



As fish TL increased, pectoral fin length ($y = 0.664x - 0.046$, $r^2 = 0.86$, $n = 47$; Fig. 3*a*), width ($y = 0.882x - 0.743$, $r^2 = 0.89$, $n = 47$; Fig. 3*b*), and surface area ($y = 1.546x - 0.789$, $r^2 = 0.896$, $n = 47$; Fig. 3*c*) all had negative allometric relationships (slope <1 for length and width, slope <2 for surface area).

Experiment 2: elevated temperature effects

U_{crit} was 14.9% greater in fish acclimated to 24 °C (U_{crit} = 51.77 ± 1.93 cm·s^{-1}, TL = 357 ± 12 mm, wet weight = 203.6 ± 19.0 g, $n = 11$) compared with fish at 19 °C (U_{crit} = 45.14 ± 2.03 cm·s^{-1}, TL = 355 ± 11 mm, wet weight = 197.2 ± 17.6 g, $n = 11$, $p = 0.028$), rejecting our hypothesis of decreased swimming ability at 24 °C.

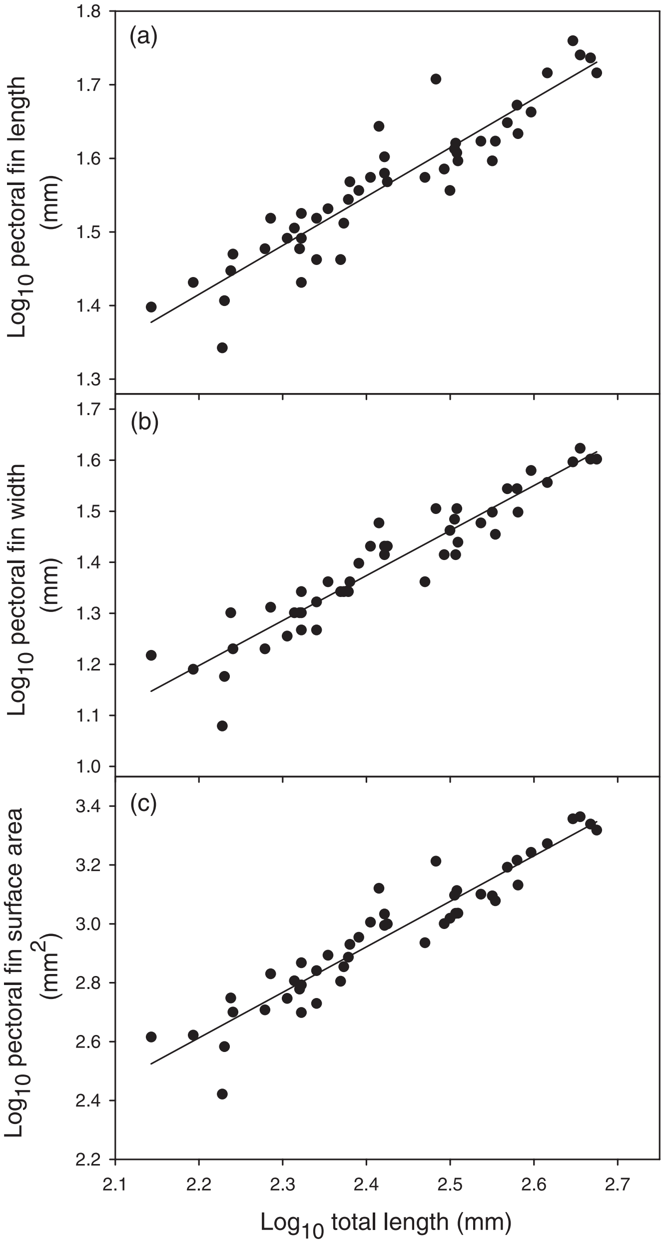
Chronically elevated temperatures (24 °C) caused an increase in hsp expression, a measure of the temperature-induced cellular stress response, in both muscle and fin tissue (representative gels shown in Allen 2005). Soluble dorsal muscle tissue samples from fish acclimated to 24 °C had significantly elevated hsp72, hsp78, and hsp90 levels, but not hsp60 (Fig. 4*a*). The membrane-associated portions of the dorsal muscle tissue samples had significantly elevated hsp72 levels, but not hsp90. Soluble pelvic fin tissue samples from fish acclimated to 24 °C had significantly elevated hsp72 and hsp78 levels, but not hsp60 and hsp90 (Fig. 4*b*). The membrane-associated portions of the pelvic fin tissue samples had significantly elevated hsp72, hsp78, and hsp90 levels.

Discussion

Changes in swimming performance (U_{crit}) with ontogeny

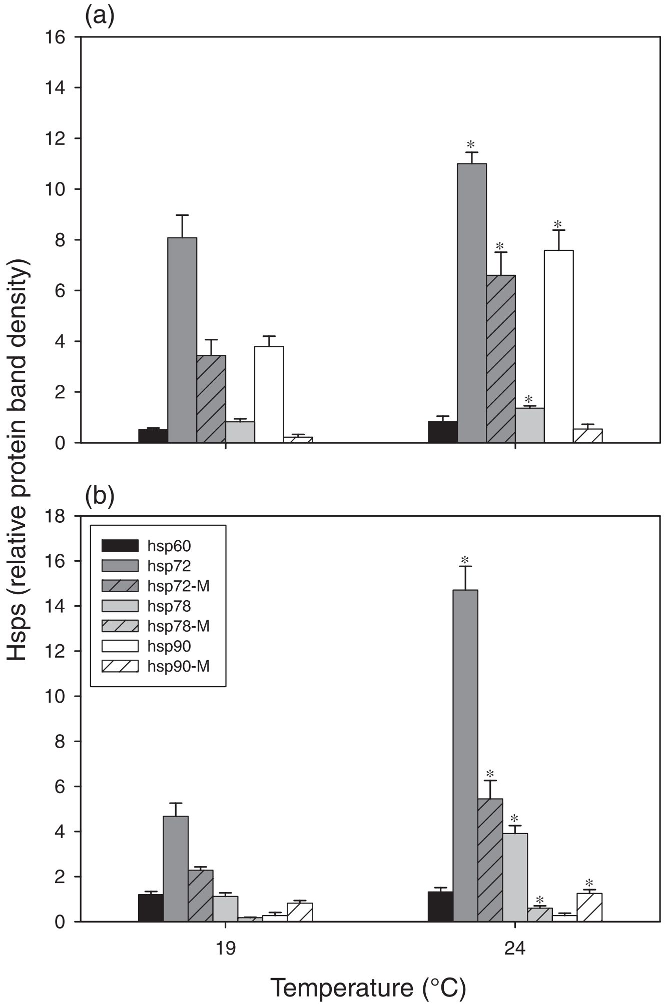
Most studies of swimming performance in juvenile sturgeons did not investigate changes in swimming performance with body length (Adams et al. 1999, 2003; McKenzie et al. 2001), assess anadromous species (Peake et al. 1995), or incorporate fish sizes smaller than those typifying seawater tolerance (Mayfield and Cech 2004). Our study provides the

Fig. 3. Relationships between juvenile green sturgeon (*Acipenser medirostris*) pectoral fin dimensions and total length (TL; mm), experiment 1, summer to early autumn fish. (*a*) For pectoral fin length (mm) to TL, the regression line represents the linear relationship $y = 0.664x - 0.046$ ($r^2 = 0.86$, $n = 47$ fish). (*b*) For pectoral fin width (mm) to TL, the regression line represents the linear relationship $y = 0.882x - 0.743$ ($r^2 = 0.89$, $n = 47$ fish). (*c*) For pectoral fin surface area (length × width; mm^2) to TL, the regression line represents the linear relationship $y = 1.546x - 0.789$ ($r^2 = 0.896$, $n = 47$ fish).



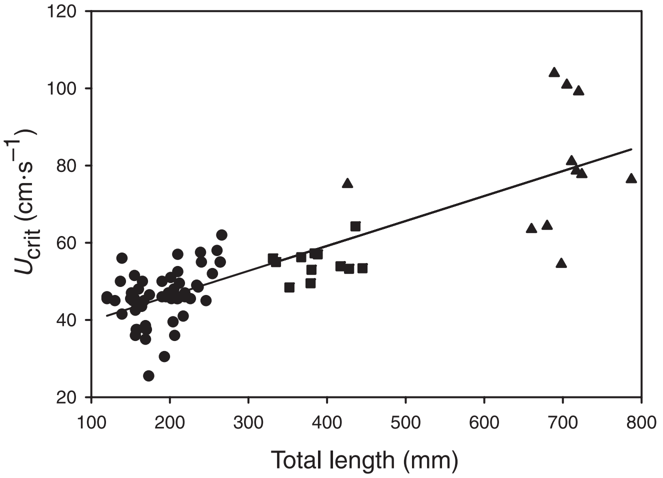
first information on the relationship between ontogeny interval and swimming ability in an anadromous sturgeon species. The relationship between U_{crit} and body size in juvenile green sturgeon is remarkable in how closely it parallels the onset of seawater tolerance (based on concurrent studies on the same cohort of fish). The positive relationship of U_{crit} with body size in smaller fish that could not tolerate seawater changed to a negative one at the same size at which fish were able to tolerate full-strength seawater (based on mean size of a group of fish with 100% survival in 34‰ seawater). Interestingly, Kynard et al. (2005) found that green sturgeon show a behavioral preference for downstream movement at 110–181 dph, which is similar to the ages (106–177 dph) of seawater-tolerant fish in our study.

Fig. 4. Juvenile green sturgeon (*Acipenser medirostris*) soluble and membrane-bound (M) (*a*) muscle and (*b*) pelvic fin heat-shock proteins (hsps) with temperature, experiment 2. Data represent means + standard error (n = 15–16 for each hsp and temperature); asterisks represent significant differences (t test, $p < 0.05$) between temperatures, with each hsp analyzed separately.



In experiment 1, pooled mean U_{crit} (54.8 ± 1.9 cm·s^{-1}, n = 12) of winter fish was significantly greater than late summer – early autumn data for fish >266 mm TL (43.3 ± 1.5 cm·s^{-1}, n = 20). When plotted along with data from experiment 1 for fish ≤266 mm TL and with U_{crit} data for larger green sturgeon (Mayfield and Cech 2004), a steady increase in U_{crit} with TL ($y = 0.065x + 33.320$, $r^2 = 0.67$, $n = 79$) is apparent (Fig. 5). The comparatively greater swimming abilities of this winter group of fish fit much better with data from Mayfield and Cech (2004) on larger juvenile green sturgeon and with linear relationships seen in swimming abilities of other sturgeon (Peake et al. 1995) and salmonid species (Glova and McInerney 1977; Peake and McKinley 1998).

Fig. 5. Juvenile green sturgeon (*Acipenser medirostris*) relationship between U_{crit} and total length, excluding fish that are newly tolerant to seawater from the late summer to early autumn period: ●, summer fish with <100% seawater (SW) tolerance; ■, winter fish with 100% SW tolerance; ▲, fish from Mayfield and Cech (2004). The regression line represents the linear relationship $y = 0.065x + 33.320$ ($r^2 = 0.67$, $n = 79$).



Katzman and Cech (2001) discussed a potential mechanism leading to changes in swimming performance related to endogenous changes during the PST. They found a thyroid hormone mediated developmental shift in mosaic locomotory muscle kinetics and a resulting depression in swimming performance in coho salmon (*Oncorhynchus kisutch*) smolts compared with parr. In fish of the same size, thyroid hormone (tri-iodothyronine, T_3) implanted smolts decreased U_{crit}, increased muscle twitch and tetanic contraction forces, and increased muscle contraction and relaxation rates compared with sham-implanted or control fish. They pointed out that the increased contraction and relaxation rates indicate an upregulation of fast-type fiber contractile proteins, which would probably promote burst swimming over sustained swimming and may be an adaptation for downstream migration in escaping cataracts or predators.

Although sustainable swimming ability is suggested to decrease during the PST based on these muscle tissue changes, evidence in wild or hatchery populations is lacking (Table 1). Smith (1982) proposed that a decrease in swimming performance aids in downstream migration by the inability to hold station in strong currents. However, the early studies used in support of this hypothesis by Thorpe and Morgan (1978) and Flagg and Smith (1982) were limited in that they did not demonstrate statistically significant decreases in swimming performance during the PST, based on studies on both parr and smolts. Furthermore, although several studies have suggested a plateau (Graham et al. 1996) or slight decrease in swimming or holding abilities associated with the time of smolting (Virtanen and Forsman 1987; Castleberry et al. 1991; Taylor and Foote 1991), none of these studies demonstrated statistically significant decreases in swimming ability. In contrast, there have been several studies that have shown a statistically significant increase in swimming ability during the time of the PST (Glova and McInerney 1977; Peake and McKinley 1998). These results support Hammer (1995), who in a review of swimming experiments found that the absolute (cm·s^{-1}) swimming ability of fish generally increases with length. Other studies on swimming during the PST have been designed for other purposes (Moore et al. 1990) and therefore did not compare parr–smolt swimming differences or had concurrent changes in temperature (Muir et al. 1994).

Likewise, studies contrasting the swimming ability of anadromous or downstream-migrating fishes with freshwater forms have generally found improved, not decreased, swimming performance. Taylor and Foote (1991) found that the anadromous form of sockeye salmon (*Oncorhynchus nerka*) had better swimming performance (U_{crit}) than the freshwater form (kokanee) at the same body sizes. Taylor and McPhail (1986) found that anadromous threespine sticklebacks (*Gasterosteus aculeatus*) had greater prolonged swimming abilities but slower maximum and mean burst swimming velocities than freshwater sticklebacks. Ellerby et al. (2001) found that catadromous, silver-phase (migrate to seawater) European eels (*Anguilla anguilla*) have a greater mass-specific power output of slow-twitch aerobic muscle fibers than similar-sized freshwater, yellow-phase eels, yielding more efficient swimming capabilities.

In our study, three factors were different between the late summer – early autumn fish and winter fish of experiment 1: cohort, age, and time of year. Any one of these differences could contribute to the observed U_{crit} differences, such as through endogenous thyroid hormone levels, as suggested by Katzman and Cech (2001). Age and time of year (seasonal cues) are known to influence thyroid hormone levels and migration propensity (reviews by Folmar and Dickhoff 1980; Hoar 1988; Hogasen 1998) in juvenile salmonids. Thyroid hormone levels were measured in the same cohort of fish concurrently with experiment 1 summer – early autumn fish, and a peak in plasma T_3 concentration was observed near the time of the depression in swimming performance (P.J. Allen and J.J. Cech, Jr., unpublished data). However, thyroid hormones were not measured during the winter runs. Late summer – early autumn experiment 1 fish may represent migrating fish and winter fish may represent nonmigratory fish based on the times of year when the two experiments were conducted and the juveniles' respective ages.

A second point of interest is the relationship of TBF with the PST. Webb et al. (1984) found that TBF increases linearly with water velocity and decreases with increasing TL at the same water velocity in rainbow trout (*Oncorhynchus mykiss*). However, Flagg and Smith (1982) found an increase in TBF (relative to body length) in coho salmon during the smolt stage, which decreased in postsmolts. Coughlin et al. (2001*a*) found decreased TBF (relative to body length) in older rainbow trout juveniles compared with parr that was related to a change in muscle fiber type and could be induced by the administration of thyroxine (T_4; Coughlin et al. 2001*b*). Ellerby et al. (2001) found that TBF increased in nonmigratory yellow-phase eels, compared with migratory silver-phase eels, to maintain the same swimming speeds by changes in muscle power output.

In our study, TBF increased with water velocity, which is similar to studies on juvenile Adriatic sturgeon (*A. naccarii*; McKenzie et al. 2001), juvenile lake sturgeon (*A. fulvescens*; Webb 1986), and shovelnose sturgeon (*Scaphirhynchus*

Table 1. Swimming ability during the parr–smolt transformation (PST).

Study	Species, source	Temperature (°C)	Swimming methods
Virtanen and Forsman 1987	Atlantic salmon (*Salmo salar*), W	10–12	50 cm·s^{-1}, 8 h
Moore et al. 1990	Atlantic salmon (*S. salar*), H	11–13.5	5 cm·s^{-1} every 10 min
Graham et al. 1996[a]	Atlantic salmon (*S. salar*), H	2–15	1 BL·s^{-1} every 60 min
Peake and McKinley 1998	Atlantic salmon (*S. salar*), W	12–20	Parr, 3 cm·s^{-1}; smolts, 6 cm·s^{-1} for 2, 5, or 10 min
Peake and McKinley 1998	Atlantic salmon (*S. salar*), W	12–20	Fixed velocity: 200 min
Glova and McInerney 1977	Coho salmon (*Oncorhynchus kisutch*), W	3–23	~6 cm·s^{-1} every 60 min
Katzman and Cech 2001[b]	Coho salmon (*O. kisutch*), H	19	10 cm·s^{-1} every 20 min
Castleberry et al. 1991[c]	Chinook salmon (*O. tshawytscha*), W	10–25	10 cm·s^{-1} every 5 min
Muir et al. 1994[d]	Chinook salmon (*O. tshawytscha*), H	4–12	15–26 cm·s^{-1} every 15 min
Taylor and Foote 1991	Sockeye salmon (*O. nerka*), 1G	10	~8–9 cm·s^{-1} every 60 min
This study (exp. 1, summer – early autumn)	Green sturgeon (*Acipenser medirostris*), 1G	19	10 cm·s^{-1} every 20 min
This study (exp. 1, summer and winter) and Mayfield and Cech 2004	Green sturgeon (*A. medirostris*), 1G	19	10 cm·s^{-1} every 20 min

Note: Data are either means ± standard error or a range based on information provided in the study. Abbreviations: W, wild; H, hatchery; 1G, first

[a] Graham et al. (1996) made holding not swimming measurements, data are for parr and smolts.

[b] Katzman and Cech (2001) "smolts" = parr + T_3 implant.

[c] Castleberry et al. (1991) data are for parr and smolts.

[d] Muir et al. (1994) results are not independent of temperature (parr, 4–5 °C; smolts, 10–12 °C).

platorynchus; Parsons et al. 2003). Our results did not support the findings of Flagg and Smith (1982) in relation to changes in TBF before and after seawater tolerance. Tail beat amplitude and body curvature has been noted to relate to swimming speed in sturgeon (Webb 1986; Long 1995); however, this was not investigated in our study.

McKenzie et al. (2001) found a decrease in Adriatic sturgeon VF at high water velocities, reflecting a partial shift to ram ventilation. We did not find this result in green sturgeon, possibly because we were only able to conduct measurements reliably up to a swimming velocity of 45 cm·s^{-1}.

Sturgeon actively use the posterior portions of their pectoral fins to control their body angle and initiate maneuvering movements in the water column (Wilga and Lauder 1999). Therefore, the larger pectoral fins, relative to TL, of the smaller juvenile green sturgeon should confer better station-holding ability in riverine life. Similarly, Pelis and McCormick (2003) found larger pectoral fins in parr compared with similar-sized smolts. In our experiments, the smaller fish used their pectoral fins to hold station (including propping) against water currents more often than did the larger fish. Several other sturgeon (Adams et al. 1997, 1999) and salmonid species (Arnold et al. 1991; Peake and McKinley 1998) have shown similar behavioral use of pectoral fins. As juvenile green sturgeon grow larger and move into seawater, large pectoral fins would presumably be less useful for station holding in currents. During steady horizontal swimming in sturgeon, pectoral fins are not used to generate lift (Wilga and Lauder 1999). Therefore, because green sturgeon from the San Francisco Estuary are known to migrate long distances (Miller 1972), large pectoral fins might be disadvantageous for extensive marine migratory movements because of increased drag. Webb (1986) noted that lake sturgeon have 3.5 times more drag per unit area than rainbow trout, and 18% less overall thrust. Thus, small decreases in drag from smaller (relative to fish TL) pectoral fins may improve swimming efficiencies, particularly when available thrust may be less than that of other migratory species. Our data supported this with negative allometric relationships with increasing TL for pectoral fin length, width, and surface area.

The most interesting behavior that was observed in small juvenile green sturgeon was rostral wedging. Fish would wedge their rostrum into the wire mesh in the front of the swim chamber to avoid swimming. Then they would tilt their bodies downward slightly using their pectoral fins to lever their rostrum into the mesh. Rostrally wedged fish (n = 11) were able to withstand water velocities far above their U_{crit}, as they were immediately impinged after losing their hold and, therefore, were not included in the data analyses. Perhaps the small green sturgeon have a behavioral propensity for wedging their rostrum into crevices or under rocks or debris in strong currents to avoid being swept downstream.

Elevated temperature effects

The effects of elevated temperatures during the time period when juvenile green sturgeon may be moving downriver are generally contrary to what was hypothesized. Green sturgeon exposed to a chronically elevated temperature (24 °C) actually increased in swimming performance compared with sturgeon acclimated to a lower temperature (19 °C). However, hsp expression did increase with temperature, showing a possible indirect relationship between these two measurements representing the whole-organism and cellular levels, respectively.

The increases in swimming speeds at 24 °C in juvenile green sturgeon are likely due to a complex interaction of fac-

Parr / pre-SW tolerant		Smolt / SW tolerant		
Length (cm)	Swimming ability (cm·s^{-1})	Length (cm)	Swimming ability (cm·s^{-1})	PST swimming relationship
13.3±1.5	All lasted 8 h	16.1±0.9	10 of 14 lasted 8h	Possibly decreasing
12.7–17.2	~69–108	12.2–18.9	~66–105	Not compared
5.7–12.5	~20–60			Possible plateau in smolts
4.8–13 FL	44–90	12.4–18 FL	76–164	Increasing
5–13.1 FL	53–86	13–17 FL	99–126	Increasing
Mean ~9.5 FL	~35–59	Mean ~11.5 FL	~40–63	Increasing
10.53±0.14 FL	Mean 77.7	10.23±1.6 FL	Mean 61.8	Decreasing
3–9 SL	~30–55			Plateau or decrease: 5–9 cm
10.2–17.6 FL	~24–80			Increasing
7.0–8.5 FL	60.1±0.52	8.6–10.0 FL	58.5±0.56	Plateau or slight decrease
12–26.6 TL	25.5–62	26.7–47.3 TL	54.5–26.5	Decreasing
12–26.6 TL	25.5–62	26.7–78.7 TL	48.3–103.9	Increasing

generation that is reared in captivity; SW, seawater; T$_3$, tri-iodothyronine; SL, standard length; FL, fork length; TL, total length; BL, body length.

tors (Taylor et al. 1997). Johnston and Ball (1997) noted that swimming speeds usually increase with temperature up to a species' thermal tolerance limit, at which performance declines. Therefore, juvenile green sturgeon of the ages and sizes studied clearly tolerate 24 °C. This conclusion is supported by increased growth rates at 24 °C compared with at 19 °C in post-yolk-sac juvenile green sturgeon that were fed ad libitum, showing that the fish were not overly stressed (Allen et al. 2006). In juvenile shovelnose and pallid (*Scaphirhynchus albus*) sturgeons, Adams et al. (2003) found increased U_{crit} at 20 °C compared with at 10 °C. Interestingly, Mayfield and Cech (2004) found that swimming performance in older (age-1) juvenile green sturgeon decreased at 24 °C and that fish were severely stressed at these temperatures. They also found that metabolic costs (MO_2) increased between 19 and 24 °C but not between 11 and 19 °C. It is possible that juvenile green sturgeon of the ages and sizes studied in this experiment can perform at an increased level at warm summer river temperatures compared with larger fish, despite the increase in energy costs, if ample rations are available.

The increased metabolic costs that Mayfield and Cech (2004) found between 24 and 19 °C may be partly accounted for by increases in hsp production. In our experiment, the increased hsps in both muscle and pelvic fin tissues indicated that the chronically high temperature (24 °C) caused some temperature-related cellular stress (Iwama et al. 1998, 1999). It is interesting that hsp levels were elevated after the long-term (2.5–5 weeks) 24 °C temperature exposure, as compared with the more typical acute temperature exposures used in most hsp studies. Viant et al. (2003) observed a transient (3 day) increase of hsp72 in steelhead trout parr exposed for several weeks to 20 °C, a temperature that is not acutely stressful, and concluded that hsp72 remained elevated until other temperature adaptation mechanisms could be activated. Podrabsky and Somero (2004) found that hsp70 and hsp90 tended to be more responsive to longer-term temperature elevations, whereas smaller hsps tended to be more responsive to fluctuating temperatures. Perhaps the difference in hsp levels between the temperature treatments is more reflective of an hsp expression Q_{10} between temperatures. Because hsps remained elevated throughout the exposure period, this may indicate that juvenile green sturgeon are unable to adapt, needing increased hsp synthesis to counteract the damaging effects of high temperature. Finally, because the temperature-related differences in hsps were comparable between muscle tissue and pelvic fin clips, our results suggest that hsp studies could be incorporated into field sampling using the much less invasive pelvic fin clips, provided immediate and rapid freezing of samples is accomplished (i.e., dry ice or liquid N_2).

In conclusion, U_{crit} studies are most relevant in simulating conditions that riverine fishes might experience (Plaut 2001). As juvenile green sturgeon develop, U_{crit} increases until fish reach the size at which they can tolerate seawater. Once fish reach this size, U_{crit} either decreases or continues to increase, depending on time of year, age, and related thyroid hormone levels. Decreases in U_{crit} during this time may facilitate downstream movements, although juvenile green sturgeon movements have not been investigated in relation to seasonally peaking flow rates or freshets. Comparison with swimming abilities in developing anadromous salmonids during the PST reveals that some studies have only demonstrated trends for decreasing U_{crit}, whereas others have shown a steady increase in swimming abilities during this developmental period. The evidence from recent studies on thyroid hormone effects on muscle development and swimming abilities during these life stages indicates that further research on both salmonid and nonsalmonid anadromous species is needed.

Juvenile green sturgeon clearly have morphological and behavioral adaptations to riverine life, with relative pectoral fin surface areas decreasing as fish grow larger and the presence of behaviors such as rostral wedging. Juvenile green sturgeon responded to warmed (24 °C) conditions with increased U_{crit}, despite increased hsp production. Management or protection efforts for green sturgeon should thus consider effects of changing seasonal flow rates and water temperature.

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