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Publication Date
2018-08-01

DOI
10.1016/j.jtherbio.2018.07.015

Peer reviewed

Plastic responses to diel thermal variation in juvenile green sturgeon, *Acipenser medirostris*

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ABSTRACT

Human-induced thermal variability can disrupt energy balance and performance in ectotherms; however, phenotypic plasticity may play a pivotal protective role. Ectotherm performance can be maintained in thermally heterogeneous habitats by reducing the thermal sensitivity of physiological processes and concomitant performance. We examined the capacity of juvenile green sturgeon (*Acipenser medirostris*) to respond to daily thermal variation. Juveniles (47 days post-hatch) were exposed to either stable ($15 \pm 0.5\,°C$) or variable (narrowly variable: $13–17\,°C\,day^{-1}$ or widely variable $11–21\,°C\,day^{-1}$) thermoperiod treatments, with equivalent mean temperatures ($15 \pm 0.5\,°C$), for 21 days. Growth (relative growth rate, % body mass gain), upper thermal tolerance (critical thermal maxima, CTMax) and the thermal sensitivity of swimming performance (critical swimming speed, U_{crit}) were assessed in fish from all treatments. Accelerated growth was observed in fish maintained under widely variable temperatures compared to narrowly variable and stable temperatures. No significant variation in CTMax was observed among thermoperiod treatments, suggesting all treatment groups acclimated to the mean temperature rather than daily maximums. The widely variable treatment induced a plastic response in swimming performance, where U_{crit} was insensitive to temperature and performance was maintained across a widened thermal breadth. Maximum U_{crit} attained was similar among thermoperiod treatments, but performance was maximised at different test temperatures (stable: $4.62 \pm 0.44\,BL\,s^{-1}$ at $15\,°C$; narrowly variable: $4.52 \pm 0.23\,BL\,s^{-1}$ at $21\,°C$; widely variable: $3.90 \pm 0.24\,BL\,s^{-1}$ at $11\,°C$, mean $\pm$ s.e.m.). In combination, these findings suggest juvenile *A. medirostris* are resilient to daily fluctuations in temperature, within the temperature range tested here.

1. Introduction

Aquatic ectotherms must contend with increasing thermal variability as habitat temperatures are continually modified by anthropogenic activities (Thome et al., 2016; Verones et al., 2010). Riverine thermal regimes have been extensively altered by channelization, flow regulation, and the installation of instream structures (Caissie, 2006; Casado et al., 2013). The operation of waterway infrastructure can abruptly raise or lower daily and seasonal water temperatures by 5–15 °C, with alterations often persisting for hundreds of kilometres downstream (Lugg and Copeland, 2014; Raptis et al., 2016; Thome et al., 2016). The major sources of thermal pollution are injections of heated effluent from thermoelectric power plants and inputs of cold,

hypolimnetic water from dams (Caissie, 2006). Additionally, ongoing climate change compounds the issue of rising environmental thermal variability (Rahmstorf and Coumou, 2011; Wang and Dillon, 2014). The frequency and intensity of extreme weather events, such as drought and heat waves, are forecast to increase and create increasingly stochastic environments (Hansen et al., 2012).

Thermal variability may be particularly threatening to ectothermic species where body temperature is largely dictated by environmental temperature and performance is optimised within a limited range of body temperatures (Hochachka, 1967; Huey and Stevenson, 1979). Consequently, inhabiting thermally polluted waters may increase exposure to suboptimal temperatures and lead to corresponding declines in organismal performance and fitness (Bartheld et al., 2017).

Ectotherms exposed to thermally variable conditions are theorised to incur higher energetic costs compared to stable environments with equivalent mean temperatures (Ruel and Ayres, 1999; Williams et al., 2012). Under fluctuating thermal regimes an ectotherm's metabolic rate may rise and fall as temperatures shift above and below the mean, respectively; but increases in energetic demands at elevated temperatures are not offset by equivalent decreases in temperature, due to the non-linear, but exponential relationship between metabolism and body temperature (Ruel and Ayres, 1999). Raised energetic demands can reduce somatic growth rates (Jobling, 1997). Depressed growth rates have been observed in a wide range of fishes exposed to daily thermal variation including: walleye (*Sander vitrus*; Coulter et al., 2016), brown trout (*Salmo trutta*; Spigarelli et al., 1982), Japanese medaka (*Oryzias latipes*; Dhillon and Fox, 2007) and zebrafish (*Danio rerio;* Schaefer and Ryan, 2006). Daily thermal variation has also been seen to induce sex reversal in fathead minnows (*Pimephales promelas*), cause skin ulcers in yellow perch (*Perca flavescens*) and increase disease susceptibility in an aquatic invertebrate (Ben-Horin et al., 2013; Coulter et al., 2015, 2016). Exposure to high magnitudes of daily thermal variability can also directly affect fish fitness by lowering egg production and fertilisation rates, and increasing mortality rates (Coulter et al., 2016; Podrabsky et al., 2008).

Despite the costs generally associated with exposure to fluctuating temperatures, some species appear resilient and exhibit accelerated growth rates, improved locomotor performance and higher reproductive success (Biette and Geen, 1980; Cooke et al., 2003; Niehaus et al., 2006). Species resilience to thermally variable environments may depend on the efficacy of compensatory responses. Unfavourable temperatures may be avoided by actively relocating to maintain body temperature within a preferred range (Golovanov, 2006; Jobling, 1981). Alternatively, modified thermal regimes may induce physiological remodelling, where the thermal effects on biochemical processes are blunted (Williams et al., 2012). The capacity to responsively alter underlying physiology to changes in environmental temperature, so that performance is maintained or optimised, is termed thermal acclimation when observed under experimental conditions, or thermal acclimatisation when observed in free-ranging animals (Prosser, 1991). Several ectothermic species can compensate for gradual thermal changes by remodelling underlying physiology to express seasonal phenotypes (Seebacher et al., 2003; Taylor et al., 1996). However, human-induced thermal changes are generally more pronounced and rapid (Lugg and Copeland, 2014; Raptis et al., 2016). Ectotherms exposed to high magnitudes of thermal variation may benefit from lowering thermodynamic effects on rate processes so that performance is maintained across a wider breadth of temperatures (Huey and Hertz, 1984; Gabriel et al., 2005). For example, alpine newt larvae (*Triturus alpestris*) exposed to large daily thermal fluctuations lowered the thermal sensitivity of maximal swimming capacity, resulting in performance being maintained over a wider thermal range compared to animals held at a constant temperature (Měráková and Gvoždík, 2009).

Several factors can modulate the effects of thermal variation and the induction of plastic responses, including the rate and magnitude of thermal variability and the proximity of temperature variations from a species' optimum temperature (Angilletta, 2009; Gabriel et al., 2005). Under a constant thermal signal, ectotherms are predicted to adopt a specialist strategy where performance is optimised at temperatures matching mean conditions. In contrast, ectotherms exposed to thermal variation may benefit from adopting a generalist strategy, where the thermal sensitivity of physiological processes is reduced, and performance is maintained across a widened thermal range (Angilletta et al., 2003; Kingslover and Gomulkiewicz, 2003). Plastic responses may be triggered at specific thresholds of thermal variation. For example, a fluctuating thermal regime with a daily amplitude of 5 °C did not elicit compensatory responses in *T. alpestris*, but a wider daily amplitude of 9 °C induced a new phenotypic optimum. Thermal variability may also induce changes in organismal thermal tolerance. For example, upper

thermal tolerance, measured as critical thermal maxima (CTMax), increased by 0.4 °C in zebrafish (*D. rerio*) and by 0.89–1.6 °C in frog larvae following exposure to cycling thermal regimes (Kern et al., 2015; Schaefer and Ryan, 2006). Increased thermal tolerance may be beneficial because the likelihood of experiencing temperatures surpassing physiological limits is lowered (Gunderson et al., 2017).

Anadromous fishes provide an ideal model to investigate responses to human-induced thermal variation. Early life-history stages of anadromous species are generally restricted to highly regulated watersheds and can experience exacerbated daily thermal fluctuations (Caissie, 2006). We examined the effect of diel thermal variation on a range of physiological traits in juvenile green sturgeon (*Acipenser medirostris*). *Acipenser medirostris* spawn in river systems subject to extensive flow regulation and modified thermal regimes (Moyle, 1994; Moyle, 2002). The Northern distinct population segment (DPS) spawns in the Klamath (California, USA) and Rogue (Oregon, USA) rivers, and the Southern DPS spawns in the Sacramento River (California, USA) (Beamesderfer et al., 2007; Israel et al., 2009) The Northern DPS is listed as a species of concern by NOAA Fisheries, and the Southern DPS is listed as threatened under the U.S. Endangered Species Act (Adams et al., 2007). Water reservoir operations can result large temperature fluctuations from of 10 to 23 °C in spring- the peak spawning period for *A. medirostris* (Moyle, 2002; Van Eenennaam et al., 2005; Pike et al., 2013).

Physiological responses to changes in mean temperature are well documented in larval and juvenile *A. medirostris* (e.g. Allen et al., 2006a; Lankford et al., 2003; Van Eenennaam et al., 2005). Based on the thermal sensitivity of growth rates, food conversion efficiency, oxygen uptake rates and swimming performance, optimal bioenergetic performance in juvenile *A. medirostris* is predicted to occur between 15 and 19 °C and decline at temperatures outside this range (Mayfield and Cech, 2004). Comparatively little is known regarding the effects of daily thermal variation on physiological processes in early life-history stages of *A. medirostris*. Allen et al. (2006b) compared specific growth rates between fish (15–65 days post hatch, dph) maintained under constant temperatures (19 °C or 24 °C) and a cycling regime (19–24 °C day^{-1}) and found no adverse effects of thermal variability. However, the independent effects of thermal variability and mean temperature were indistinguishable, as both factors differed among treatment groups (Allen et al., 2006b). Here we offer a robust examination of the effects of diel thermal variation on the physiological performance of juvenile *A. medirostris*, by controlling mean temperatures and varying only the magnitude of thermal variation. Fish were either exposed to a narrowly variable thermoperiod (13–17 °C day^{-1}) or a widely variable thermoperiod treatment (11–21 °C day^{-1}). A control group of fish were also maintained at a stable temperature of 15 ± 0.5 °C. We predicted that: (P$_1$) fish maintained in variable thermoperiods would widen their thermal performance breadth by reducing the thermal sensitivity of swimming performance, (P$_2$) growth would decline in fish maintained under variable thermoperiods compared to stable temperatures, and (P$_3$) upper thermal limits would increase in fish exposed to variable thermoperiods.

2. Materials and methods

2.1. Study species and maintenance

Acipenser medirostris larvae were obtained from an artificial tank spawning of captive F1 broodstock, at the Center for Aquatic Biology and Aquaculture (CABA) at the University of California, Davis, CA, USA. The captive F1 broodstock originated from wild-caught Klamath River Northern DPS sturgeon and were maintained at a mean annual temperature of 18.5 ± 1.3 °C (mean ± s.d.). Spawning was artificially induced at 15 ± 0.5 °C in one female (age = 10 y, body mass, BM = 37 kg) and three males (age range = 6–17 y, BM range = 16–26 kg) using methodologies described in Van Eenennaam et al. (2012). Fertilised eggs were incubated at 15 ± 0.5 °C in Macdonald-type hatching

jars and then held in crystallising dishes sitting within 194.3-L circular, fibreglass flow-through tanks (*ID x h* = 94 × 42 cm, filled to 28 cm, flow rate ~15-L min^{-1}) continuously supplied with non-chlorinated, degassed well water. Following hatching, crystallising dishes were removed and larvae remained in flow-through tanks where they were maintained in an environment aimed at optimising healthy growth prior to experimentation (water temperature = 15 ± 0.5 °C with a natural photoperiod). Exogenous feeding initiated at 7 dph and fish were continuously supplied with commercial soft-moist, starter feed (Rangen Inc, Buhl, USA) using 24-h automatic feeders (AA-100, Double 'A' Brand, Dallas, USA). Fish were fed ad libitum during development and throughout the experiment as a continuous food supply was necessary to ensure optimal growth (Cui et al., 1997). Excess food and solid wastes were siphoned from tanks twice daily. Experimental and animal care procedures were approved by the University of California Davis Institutional Animal Care and Use Committee (protocols #18767; #19928).

2.2. Experimental design and thermoperiod treatments

Juvenile fish (47 dph) were randomly assigned to one of three thermoperiod treatments (*N* = 50 fish tank^{-1}, 3 replicate tanks treatment^{-1}, 150 fish treatment^{-1}). Thermoperiod treatments had equivalent mean daily temperatures of 15 ± 0.5 °C, but daily minimum and maximum temperatures differed (Fig. 1). Thermoperiod treatments were as follows:

(i) Stable thermoperiod (15 ± 0.5): Water temperatures were held constant at 15 °C, with minimal fluctuation (± 0.5 °C).
(ii) Narrowly variable thermoperiod (13–17 °C day^{-1}): Water temperatures cycled between the daily minimum (13 ± 0.5 °C between 0200 and 0600) and maximum (17 ± 0.5 °C between 1400 and 1800) temperatures. Temperature increased and decreased by 0.5 °C h^{-1} during the rising phase and falling phases of the cycle.
(iii) Widely variable thermoperiod (11–21 °C day^{-1}): Water temperatures cycled between the daily minimum (11 ± 0.5 °C between 0400 and 0500) and maximum (21 ± 0.5 °C between 1600 and 1700) temperature. Temperature increased and decreased by 0.9 °C h^{-1} during the rising phase and falling phases of the cycle.

Cycling thermal regimes were achieved by inputting heated or chilled water into tanks at specific timepoints by irrigation valves (700B-0.75 Irritol, Riverside, USA) operated by programmable timers (Apollo 9, Titan Controls, Vancouver, USA). Water was heated using two natural gas-powered heaters (Takagi T-K4, Irvine, USA) attached to
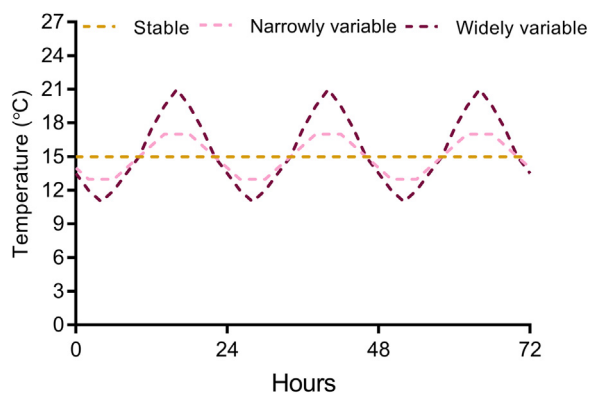

Fig. 1. Daily thermal variation experienced in each thermoperiod treatment over a sample of 3 days. Juvenile green sturgeon (*Acipenser medirostris*) were randomly assigned to a stable (15 ± 0.5 °C), narrowly variable (13–17 °C day^{-1}) or widely variable (11–21 °C day^{-1}) thermoperiod treatment for 21 days.

Omrom E5ak controllers (Omron, Chicago, USA) with a proportional control actuator (Belimo ARB24-SR, Danbury, USA). Temperatures were reduced using a 30 tonne chiller (Trane, Sacramento, USA) controlled using Omrom E5ak controllers and a linear stroke actuator (Honeywell ML7984A4009, Sacramento, USA). Actuators mixed the facility's ambient water source with the chilled or heated water to dampen the effect of the thermal (heating or cooling) processes to maintain constant supplies of water within a tenth of degree of a target point. Water temperatures were recorded every 2 min using calibrated optic shuttle temperatures loggers (Onset Computer Corporation, Bourne, USA). Mortality (%) was recorded daily and was negligible in all treatments (≤ 4% in all treatments over the course of the experiment).

2.3. Thermal sensitivity of swimming performance

Swimming performance trials were conducted in a 1.5-L flow-controlled swim tunnel with a modified Blazka design (Loligo Systems, Tjele, Denmark; swim chamber dimensions: *ID x L* = 5.5 × 20 cm). Water speeds were controlled by a variable speed frequency drive motor attached to the swim tunnel propeller and calibrated using a digital particle tracking velocimetry system and software (DPTV, Loligo Systems, Tjele, Denmark). The swim tunnel water bath was constantly aerated, and water temperature was maintained using an air-cooled heat pump attached to a digital thermostat (Ranco, Chattanooga, USA). Water was continuously exchanged between the swim tunnel and water bath using a 1.8 W water pump (LightObject EWP-2502HT6V, Sacramento, USA) to maintain oxygenation and temperature. The thermal sensitivity of prolonged swimming performance was assessed in fish from all three thermoperiod treatments at five test temperatures selected to mirror the minimum, maximum and mean temperatures of each thermoperiod treatment (11, 13, 15, 17 and 21 °C, *N* = 5–6 for each treatment group at each test temperature; dph range: 86–105; BM: 3.7 ± 1.2 g, mean ± s.d.). Fish were tested individually in a post-absorptive state (fasted 24 h) and swum only once to avoid training effects (Davison, 1997). Water temperatures were raised or lowered to test temperatures at a rate of 2 °C h^{-1}, after which fish were transferred to the swim tunnel and allowed a 30-min habituation period before a trial commenced. Swimming trials were run between 0630 and 1900 and test temperature order was randomised. Swimming performance trials began at a water speed of 0.05 m s^{-1} and water speed was increased at a rate of 0.05 m s^{-1} every 5 min until fish fatigued (Verhille et al., 2014). Total swimming time until fatigue and water speed at fatigue were recorded to calculate critical swimming speed (*U*crit, m s^{-1}), using Brett's (1964) equation:

$$U_{crit} = Uf + [Ui(T_f/T_i)] \qquad (1)$$

Where *Uf* is the highest water speed maintained for an entire 5 min interval (m s^{-1}), *Ui* is the water speed increment (0.05 m s^{-1}), T_f is the amount of time swum in the final increment (s) and T_i is the time interval (300 s). Fish were considered fatigued when at least one third of their body became impinged on the back wall of the swim chamber for ≥ 3 s (Kern et al., 2017). Absolute *U*crit values were converted to relative swimming speeds in terms of body lengths per second (BL s^{-1}) by dividing absolute values by the total length of each fish. Following the completion of swimming trials, fish were blot-dried and weighed to the nearest 0.0001 g using an electronic balance (A-200DS Denver Instrument Company, Bohemia, USA). Fish were photographed atop laminated grid-paper (0.5 × 0.5 cm) and total length (TL), fork length (FL), body depth and body width were measured using ImageJ (1.x, Schneider et al., 2012). The maximum cross-sectional area (CSA) was calculated for each fish, assuming an ellipsoid shape. Cross-sectional areas of all individuals were < 10% of the swim tunnel CSA and corrections for the solid-blocking effect were unnecessary (Bell and Terhune, 1970; Kline et al., 2015). Fish were kept in individual, flow-through chambers to track post-trial survival for 24-h, after which fish

were euthanised with an overdose of MS-222. Post-U_{crit} trial survival was 100% for all treatments.

2.4. Growth rates

Body mass (wet mass, g) and body length (TL and FL, mm) were measured at the start and end of the growth experiment (i.e. 46 dph and 67 dph). To minimise handling stress, fish were batch-weighed (10 batch^{-1}, $N = 50$ tank^{-1}, 150 treatment^{-1}) using an electronic balance (A-200DS Denver Instrument Company, Bohemia, USA) and immediately returned to an aerated recovery tank (Haller et al., 2014; Lee et al., 2015, 2016). Length measurements (TL and FL) were recorded in a subset of fish in each replicate tank ($N = 10$ tank^{-1}, 30 fish treatment^{-1}). Relative growth rates (RGR, % BM gain) were calculated as the percentage increase in BM (Eq. (2)) for each tank (Hopkins, 1992):

$$RGR = 100((BM_f - BM_i)/BM_i) \qquad (2)$$

Where BM_f and BM_i are mean final and initial body mass (g) per fish. Fish were fasted for 24 h prior to all measurements.

2.5. Critical thermal maxima

Upper thermal tolerance (i.e. critical thermal maxima, CTMax) was assessed in fish from all three thermoperiod treatments at the end of the exposure period ($N = 8$–9 treatment^{-1}; dph range: 82–109; BM: 5.6 $\pm$ 1.5 g, mean $\pm$ s.d.), between 0900 and 1000. The CTMax test chamber was an insulated, glass aquarium ($l \times w \times h = 50.5 \times 26.0 \times 30.0$ cm) where water temperature was manipulated using a YSI 74 Proportional Temperature Controller (YSI, Yellow Springs, USA). Water mixing was maintained using a submersible 5.3 W pump (Rio Plus, model: Rio$^+$ 50, TAAM, Camarillo, USA). Following a 24 h fasting period, fish were individually placed within one of four cylindrical, opaque glass chambers ($ID \times h = 8.0 \times 16.0$ cm), filled with 600 ml of water matching the lowest temperature in each respective thermoperiod treatment (i.e. stable = 15 °C, narrowly variable = 13 °C and widely variable = 11 °C). Water within chambers was constantly aerated by running airlines attached to pipette tips (10 µl, Thermo Fisher Scientific, Waltham, USA) into each chamber. Fish were allowed a 1 h adjustment period before water temperature was increased at a rate of 0.3 °C min^{-1} (Sardella et al., 2008; Verhille et al., 2015). Chamber water temperatures were monitored and recorded using alcohol thermometers calibrated against a certified standard mercury thermometer (Thermo Fisher Scientific, Waltham, USA), and a calibrated optic shuttle temperature logger (Onset Computer Corporation, Bourne, USA) also recorded temperature every 15 s. Fish were observed throughout the trials and loss of equilibrium (LOE) for 10 s was used as an endpoint (Lee et al., 2016). Following LOE, fish were immediately placed in an aerated, recovery tank matching the lowest temperature in each respective thermoperiod treatment. Once equilibrium was regained, TL, FL and BM measurements were recorded for each fish. Post-trial survival was monitored by keeping fish inside individual, flow-through chambers for 24 h, and survival was 100% for all treatments.

2.6. Statistical analyses

Data analyses were performed using R studio (version 3.2.5; http://www.R-project.org/) using the *nlme* (Linear and Non-linear Mixed Effects Models; https://CRAN.R-project.org/package=nlme), *lsmeans* (Least-Squares Means; https://cran.r-project.org/web/packages/lsmeans/index.html) and *multcomp* (Simultaneous Inference in General Parametric Models; https://cran.r-project.org/web/packages/multcomp/index.html) packages. A series of linear mixed-effects models were run to examine the effects of thermoperiod treatment (3-level factor) on RGR, CTMax and U_{crit}. Relative growth rate was modelled as a function of thermoperiod treatment (fixed factor) and holding tank identification number (ID) was included as a random effect.

Similarly, a single model was run to determine the effect of thermoperiod treatment on CTMax, where fish BM and CTMax chamber number were included as covariates and holding tank ID was a random effect. Minimal adequate models were determined using maximum likelihood simplification. Assumptions of homoscedasticity and normality of errors were graphically checked, and response variables were log$_{10}$-transformed where necessary. Tukey's *post hoc* tests were run to discern statistical differences among thermoperiod treatments with respect to RGR and CTMax. Separate thermal sensitivity mixed-effects models were run for each thermoperiod treatment to examine the effect of test temperature on U_{crit}. Test temperature was included as a 5-level fixed factor, TL as a covariate, and holding tank ID as a random effect. The least-squares means *post hoc* function was used to discern statistical differences among test temperatures. A series of linear and non-linear mixed-effects models were also run to examine the effects of thermoperiod treatment (3-level factor) at each test temperature. Tukey's *post hoc* tests were run to discern statistical differences among thermoperiod treatments with respect to U_{crit}. Thermal performance curves were fitted to U_{crit} data using TableCurve 2D (v. 5.01) and Akaike information criterion (AIC) values were used for model selection (Angilletta, 2006). The AIC values provided a measure of fit whilst correcting for model complexity to avoid 'over-fitting' data, and were calculated as:

$$AIC = -2L + 2K + 2K(K+1)/N - K - 1 \qquad (3)$$

where L is the maximised log-likelihood value, K is the number of model parameters (including the error term), and N is the sample size. The maximized log-likelihood value (L) was calculated as:

$$L = \log(RSS/N)\frac{-N}{2} \qquad (4)$$

where RSS is the model's residual sum of squares. Temperature coefficients (Q_{10} values) were calculated for U_{crit} measurements in each thermoperiod treatment, to provide a measure of thermal sensitivity over a 10 °C range. Eq. 5(5) was used to calculate Q_{10} values:

$$Q_{10} = (U_{crit2}/U_{crit1})^{10/T2 - T1} \qquad (5)$$

where U_{crit2} is mean critical swimming speed measured at test temperature 2($T2$) and U_{crit1} is the mean critical swimming speed measured at test temperature 1($T1$); and $T2 > T1$. Statistical significance was accepted at $p < 0.05$.

3. Results

3.1. Thermal sensitivity of swimming performance

The main effect of test temperature on critical swimming speeds differed among thermoperiod treatments, as did Q_{10} values (Fig. 2 A-C and Table 1; stable thermoperiod: $F_{4,21} = 4.15$, $p = 0.01$; narrow thermoperiod: $F_{4,23} = 3.08$, $p = 0.04$; wide thermoperiod: $F_{4,20} = 1.80$, $p = 0.17$, lme). Swimming performance was temperature sensitive in fish acclimated to the stable thermoperiod; performance was highest at 15 °C ($U_{crit} = 0.36 \pm 0.01$ m s^{-1}, 4.62 $\pm$ 0.44 BL s^{-1}, mean $\pm$ s.e.m.) and declined significantly at lower temperatures of 11 °C ($U_{crit} = 0.24 \pm 2.02$ m s^{-1}, 2.78 $\pm$ 0.28 BL s^{-1}) and 13 °C ($U_{crit} = 0.24 \pm 0.03$ m s^{-1}, 2.79 $\pm$ 0.28 BL s^{-1}; $p \leq 0.01$, lme). Q_{10} values calculated between 11 and 15 °C were much higher in fish acclimated to the stable thermoperiod ($Q_{10} = 3.56$) compared to the narrowly ($Q_{10} = 0.91$) and widely variable thermoperiods ($Q_{10} = 0.57$). In fish acclimated to the narrowly variable thermoperiod, swimming performance was greater at 21 °C ($U_{crit} = 0.38 \pm 0.01$ m s^{-1}, 4.5 $\pm$ 0.23 BL s^{-1}), compared to other test temperatures (Fig. 2 B). In contrast, the acute effects of temperature were not present in the widely variable thermoperiod treatment, such that, swimming performance maintained a plateau of temperature independence between 11 and 21 °C ($U_{crit} = 0.31 \pm 0.01$ m s^{-1}, 3.67 $\pm$ 0.18 BL s^{-1}, pooled mean $\pm$ s.e.m., Fig. 2 C). Critical swimming speeds were independent of total length in all
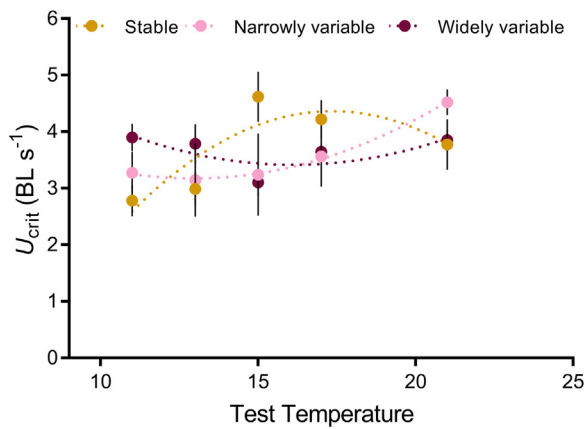
Fig. 2. The thermal sensitivity of size-adjusted critical swimming speed (U_{crit}, body lengths, BL s^{-1}) in juvenile green sturgeon (*Acipenser medirostris*) acclimated to three thermoperiod treatments: a stable thermoperiod ($15 \pm 0.5\,^{\circ}\text{C day}^{-1}$, $y = -8.85 + 1.52x - 0.04x^2$, adjusted [adj.] r^2 = 0.73), a narrowly variable thermoperiod (13–$17\,^{\circ}\text{C day}^{-1}$, $y = 8.67 + 0.029x^2 - 0.805x$, adj. r^2 = 0.86), and a widely variable thermoperiod (11–$21\,^{\circ}\text{C day}^{-1}$, $y = 6.96 + 0.02x^2 - 0.48x$, adj. r^2 = 0.05). Fish maintained in the stable treatment tuned optimal performance to match mean conditions and performance was 37–40% higher at 15 °C compared to fish acclimated to variable thermoperiods. Swimming performance of fish acclimated to the widely variable thermoperiod was temperature insensitive and performance was maintained across the entire range of test temperatures. Thermal performance curves were similar between the variable thermoperiod treatments, but performance was higher at 21 °C in fish maintained in the narrowly variable treatment compared to the widely variable treatment. Values are shown as means ± s.e.m (N = 5–6 test temperature^{-1}).

Table 1
Temperature coefficients (Q_{10}) for critical swimming performance in juvenile green sturgeon, *Acipenser medirostris*, acclimated to stable, narrowly variable and widely variable thermoperiod treatments.

	Stable 15 °C	Narrowly Variable 13–17 °C	Widely Variable 11–21 °C
Q_{10} (11–21 °C)	1.36	1.38	0.99
Q_{10} (11–15 °C)	3.56	0.91	0.57
Q_{10} (15–21 °C)	0.71	1.83	1.43

Fig. 3. Relative growth rates (A, RGR, % body mass gain) and critical thermal maxima (B, CTMax, °C) in juvenile green sturgeon, *Acipenser medirostris*, acclimated to stable ($15 \pm 0.5\,^{\circ}\text{C day}^{-1}$), narrowly variable ($13$–$17\,^{\circ}\text{C day}^{-1}$) or widely variable ($11$–$21\,^{\circ}\text{C day}^{-1}$) thermoperiod treatments. Relative growth rates were higher in the widely variable compared to the stable and narrowly variable treatments ($F_{2,6}$ = 6.39, $p < 0.05$, linear mixed-effects model, lme). Critical thermal maxima were independent of thermoperiod treatment ($F_{2,6}$ = 4.14, $p = 0.07$, lme). Values are shown as raw data points and black lines mark treatment means.

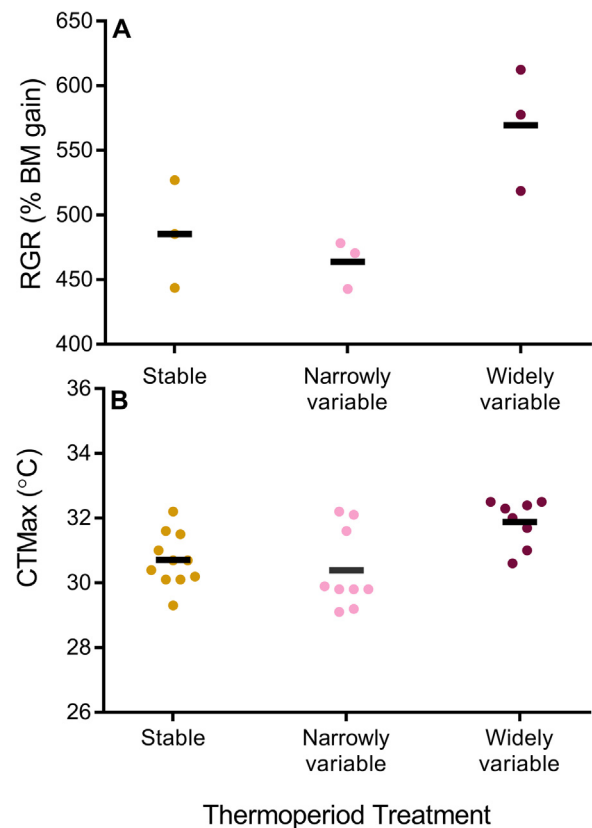treatment groups (stable thermoperiod: $F_{1,21}$ = 1.58, $p = 0.22$; narrow thermoperiod: $F_{1,23}$ = 0.60, $p = 0.45$; wide thermoperiod: $F_{1,20}$ = 3.29, $p = 0.08$, lme).

3.2. Growth

Thermoperiod treatment had a significant effect on RGR (% BM gain; $F_{2,6}$ = 6.39, $p < 0.05$, lme). Relative growth rate was highest in the widely variable thermoperiod ($569.54 \pm 27.38\%$, mean ± s.e.m.; $p < 0.01$, lme) but did not differ between the stable ($485.32 \pm 24.09\%$, mean ± s.e.m.) and narrowly variable thermoperiod treatments ($463.81 \pm 10.76\%$, mean ± s.e.m., $p = 0.65$, lme; Fig. 3A).

3.3. Critical thermal maxima

Critical thermal maxima (CTMax) was independent of thermoperiod treatment ($F_{2,6}$ = 4.14, $p = 0.07$, lme), fish body mass ($F_{1,16}$ = 1.47, $p = 0.24$, lme) and chamber ID ($F_{3,13}$ = 0.86, $p = 0.49$, lme). Fish acclimated to stable, narrowly and widely variable thermoperiod treatments had CTMax values of $30.58 \pm 0.25\,^{\circ}\text{C}$, $30.39 \pm 0.41\,^{\circ}\text{C}$ and $31.89 \pm 0.25\,^{\circ}\text{C}$ (mean ± s.e.m.), respectively (Fig. 3B).

4. Discussion

An organism's capacity for phenotypic plasticity is a key predictor of success in heterogeneous environments (Gabriel et al., 2005; Seebacher et al., 2015b). Here we demonstrated that thermal variability around a tightly controlled mean can elicit beneficial phenotypic alterations in an ectotherm. The thermodynamic effects on swimming performance were blunted in fish exposed to the widely variable treatment and swimming performance was maintained across a broadened thermal performance breadth. No trade-offs were observed in fish which adopted a broadened thermal performance breadth, as maximal swimming performance was similar among thermoperiods treatments. Growth rates were accelerated in fish maintained under widely variable thermoperiods compared to fish maintained under stable thermoperiods, suggesting increased metabolic demands were offset by physiological compensation. Upper thermal tolerance, measured as CTMax, was unaffected by daily thermal variation suggesting thermal tolerance acclimated to mean temperatures and not daily maximums. Together these results highlight disparate responses to daily thermal variation between thermal tolerance and thermal sensitivity of performance and show that phenotypic plasticity can play a pivotal protective role.

4.1. Thermal plasticity in swimming performance

The negative effects of thermal perturbations should be greatest in species with narrow thermal performance breadths and limited

acclimation capacity (Ghalambor et al., 2006; Stillman, 2003). Fish maintained in the stable thermoperiod adopted a thermal specialist strategy and tuned optimal performance to match mean conditions so that swimming performance was highest at 15 °C. However, fish maintained in the widely variable treatment adopted a thermal generalist strategy where swimming performance was temperature insensitive across the entire range of test temperatures (supporting P_1). Swimming performance was ~29–33% greater at low temperatures (11 °C and 13 °C) in fish maintained in the widely variable treatment compared to fish maintained in the stable treatment. This plasticity in temperature sensitivity would likely allow juvenile *A. medirostris* to fulfil a myriad of critical tasks, such as, feeding, habitat selection and inter-biome migrations under highly variable thermal regimes (Nelson, 1989; Plaut, 2001). The narrowly variable thermoperiod induced an intermediate phenotype where the thermal sensitivity of swimming performance was slightly reduced at low temperatures, but these differences were not significant. Similar findings have been observed in alpine newt larvae (*T. alpestris*), where exposure to a fluctuating thermal regime (amplitude ± 9 °C) induced a 10% increase in maximal swimming performance at low test temperatures, due to reduced thermal sensitivity (Měráková and Gvoždík, 2009). Plastic responses in *T. alpestris* were also dependent on the magnitude of temperature fluctuations experienced, and no acclimation response was induced in response to a narrowly fluctuating regime (amplitude ± 5 °C) (Měráková and Gvoždík, 2009). The effect of daily temperature fluctuations on critical swimming speeds have also been assessed in Chinese bream (*Parabramis pekinensis*) (Peng et al., 2014). Swimming performance was similar between fish maintained at 20 ± 5 °C compared to fish maintained at constant temperatures (15 °C and 25 °C) but the thermal sensitivity of performance was not adequately assessed as only one test temperature was used. To our knowledge, this is the first study to assess how the temperature sensitivity of fish swimming performance responds to daily thermal fluctuations.

Adopting a widened thermal performance breadth was associated with a trade-off in lowered swimming performance at the mean temperature (i.e. 15 °C). Swimming performance was ~33% lower at 15 °C in fish maintained under the widely variable thermoperiod compared to fish maintained in the stable treatment. In many ectotherms maximum performance is traded-off against performance breadth and this is termed the generalist-specialist trade-off (Angilletta, 2006; Izem and Kingsolver, 2005). For example, cold-acclimated mosquito fish (*Gambusia holbrooki*) widened their thermal performance breadth so that performance was maintained at low temperatures, but this came at the expense of reduced performance at warm temperatures (Seebacher et al., 2015a). The mechanisms underlying this trade-off remain unresolved but are postulated to be linked to physiological alterations which facilitate cold acclimation (e.g. membrane fluidity and increases in thyroid hormones) but reduce performance at high temperatures (Seebacher et al., 2015a). Our findings differ to this typical generalist-specialist trade-off relationship. Maximum swimming performance was similar among treatment groups but occurred at different test temperatures. Swimming performance was highest at 15 °C, 21 °C and 11 °C in the stable, narrow and wide thermoperiod treatments, respectively. Underlying plasticity in cardio-respiratory functions (e.g. increased cardiac output, gill surface area or blood oxygen-carrying capacity) in fish exposed to variable thermoperiods may have enabled oxygen delivery capacity, and hence performance, to reach maximal levels in all treatment groups without trade-offs at lower/higher temperatures (Franklin et al., 2007; Pörtner, 2001). However, further experimental work is required to confirm this. The equivalent performance maxima observed among thermoperiod treatments suggests that minimal costs were associated with adopting a thermal generalist strategy in response to daily thermal fluctuations.

4.2. Effect of thermoperiods on growth

Although thermal variation is theorised to raise metabolic demands at the cost of growth gains (Ruel and Ayres, 1999), growth rates were accelerated under widely variable conditions, and remained unchanged under narrowly variable conditions (rejecting P_2). Similar responses have been observed in yellow perch (*Perca flavescens*), where exposure to a high magnitude of daily thermal variation (23 ± 4 °C) significantly increased growth rates compared to a static temperature (23 °C) but growth rates remained unchanged in fish exposed to a small magnitude of thermal variation (23 ± 2 °C) (Coulter et al., 2016). Growth gains observed in *P. flavescens* were linked to increased feeding rates and food conversion efficiency (Coulter et al., 2016). It is likely that *A. medirostris* maintained in the widely variable thermoperiod increased food consumption and feeding efficiency, but the small size of feed used made this difficult to quantify. The timing of feeding can also be a critical factor in determining growth gains under variable thermoperiods (Brett, 1971; Diana, 1984). For example, it has been postulated that fish can maximise metabolic efficiency by allowing feeding activity to coincide with warm temperatures where feeding efficiency is highest, and by resting at cool temperatures where maintenance costs are minimised (Brett, 1971). Since a constant and abundant food supply was available in the present study, *A. medirostris* may have timed feeding efforts to correspond with temperatures in the cycle where feeding rate and digestion efficiency were optimised, but further experiments are needed to confirm this.

Previous work has shown optimal growth performance and feeding efficiency of *A. medirostris* to occur between 15 and 19 °C and decline at temperatures outside this range (Mayfield and Cech, 2004). Fish maintained in the narrowly variable treatment were exposed to temperatures below this range, whilst fish maintained in the widely variable treatment were exposed to fluctuations above and below this range. Uncharacterised plasticity in the thermal sensitivity of metabolism may also be partly responsible for our observed results. For example, butterfly larvae (*Erynnis propertius*) exposed to variable temperatures lowered their basal energetic requirements by reducing the thermal sensitivity of metabolism, compared to larvae exposed to stable temperatures (Williams et al., 2012). Similarly, successive exposure to heat cycles induced altered metabolic phenotypes in rainbow trout (*Oncorhynchus mykiss*; Callaghan et al., 2016). In the present study, fish may have lowered the thermal sensitivity of metabolism at temperatures above and below the optimal range for growth (15–19 °C; Mayfield and Cech, 2004), so that maintenance costs were minimised, and feeding activity and digestive efficiency were maintained across a widened thermal breadth.

Relative growth rates observed in the widely variable thermoperiod were lower than values reported for similarly aged (65 dph) juvenile *A. medirostris* exposed to temperatures cycling between 19 and 24 °C each day (specific growth rate: ~9.29%; Allen et al., 2006b). This difference is to be expected because temperatures (minimum, mean and maximum) in the Allen et al. (2006b) study were higher, but this comparison suggests *A. medirostris* can grow more efficiently under thermoperiods with a higher mean temperature than used here. Indeed, responses to thermal variation can differ depending on the mean temperature (Oligny-Hebert et al., 2015). Diel thermal fluctuations near the thermal optima (15 ± 2.5 °C) for juvenile *S. salar* had no effect on standard metabolic rate (SMR) compared to stable temperatures (15 °C), but daily thermal fluctuations around a higher mean temperature (20 ± 2.5 °C) increased SMR by ~34% compared to fish held at a stable 20 °C (Oligny-Hebert et al., 2015). The directionality of the effect of daily thermal variation on SMR and RGR likely depends on whether daily temperatures deviate from the optimal thermal performance range (Hokanson et al., 1977), coupled with the organism's capacity to acclimate to such deviations. Future efforts should aim to disentangle these factors to deepen our understanding of organismal responses to thermal variation beyond the dichotomy of stable versus

variable conditions.

4.3. Effect of thermoperiods on CTMax

Upper thermal tolerance (CTMax) is positively correlated with acclimation temperature and can respond seasonally, where heat tolerance increases during summer (Beitinger and Bennett, 2000; Fangue and Bennett, 2003; Schaefer et al., 1999). Comparatively few studies have examined the effect of daily thermal variation on CTMax. For the most part, studies have reported higher CTMax values in ectotherms acclimated to cyclical thermal regimes compared to stable regimes (Kern et al., 2015; Otto, 1974; Schaefer and Ryan, 2006), and heat hardening responses to daily maximums are thought to be responsible (Maness and Hutchison, 1979). In contrast to our prediction (P$_3$), CTMax of juvenile *A. medirostris* were independent of thermoperiod treatment. This finding suggests that CTMax acclimates to mean rather than maximum temperatures in the environment. Nevertheless, CTMax values were well above peaks in both variable thermoperiod treatments (+ 10–14 °C in the widely and narrowly variable thermoperiod treatments, respectively) suggesting a wide safety margin. Acclimation responses may have been elicited if fish experienced daily thermal fluctuations approaching upper and lower limits (i.e. CTMax and CTMin). Future endeavours could test if the proximity of thermal variation to thermal tolerance limits influences acclimation responses of CTMax. Comparable findings have been observed in juvenile Channel catfish (*Ictalurus punctatus*) and Chinese bream (*Parabramis pekinensis*), where no differences were observed in CTMax between fish exposed to constant and fluctuating temperatures (Díaz and Bückle, 1999; Peng et al., 2014). Together these findings suggest that the effect of daily thermal fluctuations on CTMax may be species specific or linked to the proximity of temperature fluctuations to thermal tolerance limits.

4.4. Ecological implications

Disparities observed in RGR between the stable and widely variable thermoperiod treatments highlight the need to include the effects of thermal fluctuations into bioenergetics models. Indeed, bioenergetics models which integrate the effects of thermal variation on ectotherm energetic demands have been proposed (Holsman and Danner, 2016). The bulk of studies examining growth and metabolism in *A. medirostris* have been conducted on individuals chronically exposed to a constant water temperature prior to measurements (Allen et al., 2006a; Linares-Casenave et al., 2013; Mayfield and Cech, 2004); however, exposing fish to fluctuating thermal regimes better mimic habitats, which often experience diel temperature changes (Enders et al., 2006). Moreover, responses to altered waterway operations and climate change can be assessed by experimentally manipulating the magnitude of thermal variability (Enders and Boisclair, 2016). Our findings suggest that the energy budget of juvenile *A. medirostris* modelled at a mean temperature of 15 °C may be underestimated depending on the variability around the mean.

Further investigation is required for a holistic understanding of the effects of thermal variation on *A. medirostris*. Responses likely differ among embryonic, larval, juvenile and adult life-stages. For example, the thermal window for successful development in embryonic and larval *A. medirostris* is narrow and marked increases in mortality and deformity rates occur at temperatures ≥ 17.5 °C (Van Eenennaam et al., 2005); therefore, exposing early life-stages to daily maximums of 21 °C, in the widely variable thermoperiod, would likely be deleterious. Responses to daily thermal variation may also differ between northern and southern distinct population segments of *A. medirostris*. For example, opposite responses in SMR (increases versus decreases) have been observed between two populations of juvenile *S. salar* exposed to the same daily thermal fluctuations (Oligny-Hebert et al., 2015). Adding further complexity, human-induced thermal variation may be stochastic but only responses to predictable thermal variation were characterised

here. Plastic responses to stochastic thermal variation may be dampened (Manenti et al., 2014), and comparisons between responses to predictable (e.g. daily and seasonal) and unpredictable (e.g. thermal pulses) thermal variation may provide valuable insight. Nonetheless, our findings show that the widely variable thermoperiod accelerated fish growth rates and elicited a plastic response, where the thermal sensitivity of swimming performance was blunted. These findings suggest anthropogenic thermal variability, within the range tested here, to be benign or beneficial to juvenile *A. medirostris* but further assessments examining other life-stages are recommended before prescribing management actions.

Declarations of interest

None.

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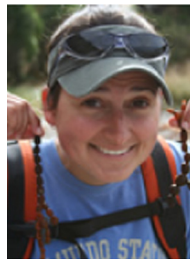
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