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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 ± 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 ± 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 ± 0.44 BL s^{-1} at 15 °C; narrowly variable: 4.52 ± 0.23 BL s^{-1} at 21 °C; widely variable: 3.90 ± 0.24 BL s^{-1} at 11 °C, mean ± 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).

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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 vitreus*; 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