Journal of Applied Ichthyology DWK

J. Appl. Ichthyol. (2016), 1–5
Published 2016. This article is a U.S. Government work and is in the public domain in the USA
ISSN 0175–8659

Received: September 20, 2015
Accepted: November 26, 2015
doi: 10.1111/jai.12994

Short communication

Upper lethal temperature of larval pallid sturgeon *Scaphirhynchus albus* (Forbes and Richardson, 1905)

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Introduction

The pallid sturgeon *Scaphirhynchus albus* is an endangered species endemic to the Missouri-Mississippi River basin (Kallemeyn, 1983; Dryer and Sandvol, 1993; USFWS (U.S. Fish and Wildlife Service), 2014a). Dams and other diversions dating to the 1950s have resulted in blocked migration pathways, unnatural hydrographs, loss of riverine habitat, altered temperature regimes, and ecological traps; these alterations are suspected to inhibit pallid sturgeon spawning, recruitment, growth, and survival (Dryer and Sandvol, 1993; Ruelle and Keenlyne, 1993; Guy et al., 2015).

Extreme temperatures can lead to reduced metabolic function, delayed development, and direct mortality in fish (Harig and Fausch, 2002; Schultz and Bertrand, 2011). Alterations to thermal habitats have been identified as a mortality mechanism in *Scaphirhynchus* sturgeons (Kappenman et al., 2009, 2013; Phelps et al., 2010; Hupfeld et al., 2014). Anthropogenic alterations to rivers and tributaries in the Missouri-Mississippi River basin have created unnatural zones of cold and warm water that can act as ecological traps. These sinks include zones of reduced temperatures downstream of Missouri River dams, the result of hypolimnetic discharge from stratified reservoirs; seasonal zones of increased temperature caused by agricultural development that has reduced riparian zones and water volume; and zones of increased water temperature resulting from discharged effluent from electric generating power plants. Drift stage larval pallid sturgeon [e.g. a swim-up stage when larvae disperse hundreds of miles downstream (Braaten et al., 2012)] may be vulnerable to the effects of ecological sinks because they cannot avoid such areas (Guy et al., 2015), and may be more sensitive to extreme temperatures than juvenile or adult sturgeon (Blevins, 2011).

Examples of anthropogenic alterations leading to temperature extremes that negatively affect pallid sturgeon and sympatric shovelnose sturgeon *S. platorynchus* have been reported. In the Mississippi River, altered temperature conditions (greater than 28°C during the spawning season) have been identified as negatively affecting larval recruitment of *Scaphirhynchus* sturgeon (Phelps et al., 2010). In the Missouri River, stratified reservoirs and hypolimnetic dam releases [(e.g. 6–15°C decreases between compared river reaches (Braaten and Fuller, 2003)] from Fort Peck Dam (Montana) and Garrison Dam (North Dakota) have negatively affected growth and survival of *Scaphirhynchus* sturgeon at various life stages from embryo to adult (Everett et al., 2003; Kappenman et al., 2009, 2013). In the Des Moines River, increased water temperature (e.g. ranging 29–35°C in summer) resulting from riparian habitat reduction and agrarian use have been implicated as the mechanism for fish kills involving various age classes of shovelnose sturgeon (Hupfeld et al., 2014). In the Missouri River, concern over power plant effluent discharge led to a 2015 legal appeal (Sierra Club v Missouri Department of Natural Resources) which stated that a Missouri State operating permit does not consider the protection of pallid sturgeon in relation to discharge of effluent and that the current operation violates the Clean Water Act (e.g. allowing discharge greater than 32°C). Further, it has been widely recognized that discharged effluent may pose a threat to pallid sturgeon (Sackschewsky, 1997; USFWS (U.S. Fish and Wildlife Service) and NMFS (National Marine Fisheries Service), 2014b). While concerns exist, neither the effect of effluent flumes nor those of rapid increases in temperature on larval pallid sturgeon has been thoroughly examined.

A recent review (Blevins, 2011) noted that research was needed to determine the temperature requirements, tolerance, and preferences of pallid sturgeon, especially embryo and larval life stages. While there are now studies of the thermal tolerances of various life stages of shovelnose and pallid sturgeon (Kappenman et al., 2009, 2013; Hupfeld et al., 2014), little information is available specific to the pallid sturgeon larval stage. There are inter- and intra-species thermal niche differences between pallid and shovelnose sturgeon (Blevins, 2011), but with data gaps, managers often employ a surrogate species strategy to inform conservation planning and management and so we review the current knowledge for both species. Studies have shown that the thermal niche of newly fertilized pallid and shovelnose sturgeon embryos ranges from approximately 12 to 24°C (Kappenman et al., 2013) and that juvenile pallid and shovelnose sturgeon can tolerate temperatures exceeding 24°C for extended periods with juvenile sturgeon survival negatively affected at temperatures exceeding 26°C (Kappenman et al., 2009; Blevins, 2011). Additionally, Hupfeld et al. (2014) found that both juvenile and adult shovelnose sturgeon suffered loss of equilibrium and death at 30 and 33°C, respectively.

In this experiment, an upper lethal temperature (ULT) for pallid sturgeon larvae was measured to better understand which temperatures limit larval survival. To determine a ULT, we used a direct transfer method, also known as the plunge method or ILT (incipient lethal temperature; Fry et al., 1946; Brett, 1952; Kilgour and McCauley, 1986; Beitinger et al., 2000). The ILT method incorporates exposure time; fish are transferred from an acclimation temperature directly into a constant-temperature test tank and time to death is measured. The ULT was defined as the temperature at which the fish showed signs leading to mortality in the form of a loss of equilibrium and slowing operculum movement (Cox, 1974). The ULT was quantified using measures of changing swimming behavior, loss of equilibrium, and larval mortality for both 50 and 100% death rates. Note in this study that we used a single acclimation temperature of 22°C, a temperature ~4°C above optimum for embryo development (Kappenman et al., 2013) and representative of what pallid sturgeon larvae might experience in the wild during swim-up and out-migration. The plunge method (e.g. ILT) appealed to us as it presented an ecologically relevant 'worst case scenario'; such a scenario would allow no acclimation period for newly hatched drifting larvae (e.g. free-swimming embryo) that rapidly entered into a discharge flume or a similar thermal sink.

Materials and methods

Larval source

Pallid sturgeon larvae age 0–4 days post-hatch, ranging from approx. 6.1–9.7 mm TL (based on a sub-sample), were used for this experiment. Embryos were incubated, hatched, and all larvae held at 22°C in a single tank monitored daily and adjusted when ±0.5°C different than the targeted 22°C temperature. Larvae were progeny from broodstock collected from the Yellowstone and Missouri rivers in Montana, USA and spawned at the Miles City Fish Hatchery, Montana according to standard procedures (USFWS (U.S. Fish and Wildlife Service), 2005). While held, broodstock were exposed to increasing temperatures from ~10 to ~18°C to simulate natural vernalization. After spawning and fertilization at ~18°C, embryos were gradually exposed to an increase in temperature (+1°C h^{-1}) until 22°C, and then transported to the Bozeman Fish Technology Center (BFTC).

Seven-day exposure at target temperatures from 20 to 28°C. We attempted to determine the temperatures that were lethal to 50 (LT50) and 100% (LT100) of pallid sturgeon larvae using a direct transfer (e.g. ILT plunge method) and a 7-days constant temperature exposure. The water source and experimental thermal system apparatus used are described in Kindschi et al. (2008). Larvae acclimated at 22°C were exposed to target temperatures of 20, 22, 24, 26, and 28°C. The actual mean test temperatures (±SD) during the 7-days exposure varied from the target temperatures and were 20.18 (0.12), 21.75 (1.23), 24.30 (0.25), 26.22 (0.20), and 28.02 (0.31). Means and SD were generated from temperature data loggers set to 24-min intervals and placed in each of the five head tanks. Each temperature treatment was conducted in triplicate (e.g. three tanks per temperature, fed from a head tank) and 20 larvae were placed in each replicate tank. Larvae were moved directly from the 22°C holding tank water to the test temperature water. Fish that were transferred into the 20 and 22°C treatments (e.g. means of 20.18 and 21.75°C) acted as the comparative controls. The test endpoint was mortality, and loss of equilibrium was also noted. Observations of mortality were made continuously for the first 60 min post-transfer, once every 60 min between 60 and 180 min post-transfer, and in 24 h increments thereafter for a total of 7 days. Larvae were not fed throughout the trial. The percent survival data was arcsine transformed and analyses of variance with Bonferroni means comparison tests were used to compare survival among treatments. The accepted significance level was 0.05 and all values are reported to mean ± SE.

Five-minute exposure at target temperatures from 28 to 34°C. Results from the tank-to-tank transfer did not show any differences in larval survival among the temperature treatments during the initial 6 h of the experiment. Given those results, we used a direct transfer method in which larvae from the 22°C holding tank were transferred into 375 ml of hatchery water held in a 500 ml Erlenmeyer flask. The flask was then placed in a 2000 ml beaker filled with 1250 ml of water and placed on an electric hot plate (catalog No. 11-100-100H, Fisher Scientific Isotemp Basic Hotplate; www.fishersci.com). The beaker-flask water bath apparatus was designed to prevent direct contact of larvae with a hot surface. We attempted to target exposure temperatures of 28, 30, 32, and 34°C to determine a ULT for pallid sturgeon larvae. The low temperature (28°C) was chosen to overlap the highest temperature used in the 7 days tank trial temperature exposure. The authors performed a series of simulated trials with the experimental apparatus prior to the actual experiment; using the control knob and graduated scale settings of the hot plate we determined the settings and timing needed to achieve and maintain a 5 min exposure within ±0.4°C of target temperatures of 28, 30, 32, and 34°C; we provide the actual minimum and maximum temperature and the final DO (mg L^{-1}) at 5 min for each treatment in Table 1. The trial was performed on day 1 (6+ h) of the tank-to-tank transfer to ensure that the larval development stage was identical. Five larvae were placed into the flask of water, and each temperature trial was run in duplicate. Loss of equilibrium and mortality of larvae was assessed continuously for 5 min. Loss of equilibrium was categorized as (i) initial, when the fish was still capable of righting itself (Rajaguru, 2002), or (ii) final, the point at which the fish could no longer right itself (Becker and Genoway, 1979; Rutledge and Beitinger, 1989; Smale and Rabeni, 1995). Mortality was defined as the cessation of opercular movement (Becker and Genoway, 1979). Dissolved oxygen (DO) and temperature

Table 1
Five minute exposure at target temperatures from 28 to 34°C. Dissolved oxygen (DO) and minimum and maximum temperatures for trials 1 and 2 for each treatment

	Trial 1		Trial 2	
Treatment	DO (mg L^{-1})	Temp. (°C)	DO (mg L^{-1})	Temp. (°C)
28	5.56	27.9–28.4	5.76	27.8–28.4
30	5.49	29.7–30.2	6.01	29.6–30.2
32	5.83	31.8–32.3	5.72	31.5–32.4
34	5.65	33.6–34.2	5.59	33.7–34.3

were continually monitored using a YSI model 55 m (YSI Incorporated, Yellow Springs, OH) and an Ertco High Precision Thermometer (Barnstead International, Dubuque, IA). Observation was continuous; it was noted that larvae stayed in the water column and did not come in contact with the side or bottom of the flask while alive.

Results

Seven-day exposure at target temperatures from 20 to 28°C

The trial showed that the ULT of pallid sturgeon larvae acclimated to 22°C exceeded 28.02°C, the greatest mean temperature tested with this apparatus. Percent survival of larvae at 7 days after transfer from the acclimation tank (22°C) to treatment tanks with mean temperatures ranging from 20.18 to 28.02°C varied from 88 to 100%, and was not significantly different among treatments (no different than control groups with means of 20.18 and 21.75°C, or groups of any greater test temperature; Fig. 1). No larvae exhibited a loss of equilibrium, and swimming behavior was not observed to differ among larvae at various treatments

Five-minute exposure at target temperatures from 28 to 34°C

The ULT of larvae acclimated to 22°C was 32°C. Mortality did not occur at 28°C or 30°C; at 28°C larvae did not lose equilibrium; at 30°C the first loss of equilibrium was observed at 30 s post-transfer, but all larvae recovered and continued to burst swim and maintain position in the water column throughout the 5 min exposure. At 32°C larvae exhibited initial loss of equilibrium at 20 s post-transfer, final loss of equilibrium at 1 min 20 s post-transfer, first mortality at 2 min 37 s post-transfer, and 50% mortality at 5 min post-transfer. At 34°C larvae exhibited initial loss of equilibrium at 10 s post-transfer, final loss of equilibrium at 18 s post-transfer, first mortality at 50 s post-transfer, and 100% mortality at 1 min 20 s post-transfer.

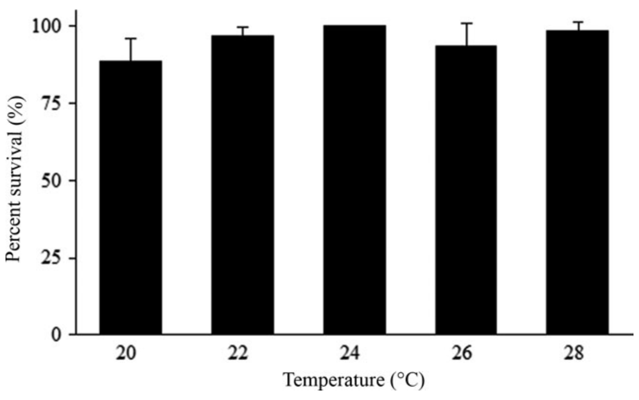

Fig. 1. Mean (+SD) survival (%) of pallid sturgeon *Scaphirhynchus albus* larvae acclimated to 22°C, directly transferred to temperatures ranging from 20 to 28°C, and held for 7 days to determine upper lethal temp. No statistically significant differences among treatments

Discussion

Experiments showed that larval pallid sturgeon have a greater tolerance for high water temperatures than newly fertilized pallid sturgeon embryos (Kappenman et al., 2013) and a similar upper thermal tolerance as juvenile *Scaphirhynchus* sturgeon (Kappenman et al., 2009; Hupfeld et al., 2014). Results from this experiment provide evidence that pallid sturgeon larvae acclimated to 22°C can withstand exposure to 28°C water for 7 days without a loss of equilibrium or mortality. While short-term exposure to temperatures less than or equal to 28°C was not immediately lethal to larval pallid sturgeon, if larval pallid sturgeon possess a similar thermal tolerance as the juvenile *Scaphirhynchus* sturgeon, temperatures near 28°C might likely induce stress and lead to increased mortality (Kappenman et al., 2009; Phelps et al., 2010). Further, the loss of equilibrium and mortality thresholds we observed in larval pallid sturgeon were similar to the temperatures determined to cause a loss of equilibrium and mortality in shovelnose sturgeon (above ~30°C; Hupfeld et al., 2014).

Much of the pallid sturgeon range temperatures rarely exceed the lethal temperature defined by this study. However, anthropogenic changes to habitat and climate change are deteriorating freshwater habitats at a rate that continues to threaten *Scaphirhynchus* sturgeon (Ficke et al., 2007; Hupfeld et al., 2014). The threat of mortality to pallid sturgeon larvae due to temperatures exceeding the ULT determined in these experiments is most likely to exist in rivers with extreme temperature alterations due to flow reductions and summer temperature extremes, or in areas immediately affected by power plant thermal effluent. The larval drift ecology of pallid sturgeon may increase the likelihood of exposure to a thermally altered habitat; dependent on fluvial patterns, larval pallid sturgeon post-hatch can be transported hundreds of miles downstream from spawning areas (Braaten et al., 2012). It is important to consider that, over time, increased mortality can have a population level effect on abundance (Hupfeld et al., 2014).

This study utilized an ILT method with a single acclimation temperature. The information we provide can begin to inform management efforts to combat the detrimental effects of habitat alterations and climate change, but also highlights the need for additional studies. Scientifically accepted laboratory techniques have been developed to determine the temperature tolerances of fishes and to establish thermal criteria (Fry et al., 1946; Brett, 1956; Fry, 1971; Zale, 1984; Kilgour and McCauley, 1986; Armour, 1991; McCullough, 1999). The methods can be divided into three general categories: (i) the critical thermal maximum or minimum (CTM) method; (ii) the upper or lower incipient lethal temperature (ILT) method; and (iii) the acclimated chronic exposure method (ACE), which is a hybrid of the ILT method and a modified CTM method (Zale, 1984; Selong et al., 2001). Each laboratory method has comparable pros and cons, and we provide no new insight into this widely discussed field of study (but see reviews by Beitinger et al., 2000; Mora and Maya, 2006). It is important to consider that in fishes, the low and high tolerance limits are affected by acclimation (initial) temperature (Fry, 1971; Elliott, 1981); in general, a higher acclimation temperature will result in a higher ULT (Fry, 1971; Carveth et al., 2006). Additionally, gradual increases in temperature, such as those employed in CTM studies, can also lead to an increase in thermal tolerance. An IULT study (determined when an increase in acclimation temperature no longer increased ULT) requires the use of additional acclimation temperatures but would provide value; the ULT associated with environmentally relevant acclimation to 24, 26, 28, and 30°C might inform specific case studies. Laboratory studies utilizing the ACE and CTM method, especially the effects of chronic exposure, as well as field studies investigating flume discharge, dispersal, and habitat impacts would also be useful in determining the effect of altered thermal conditions on pallid sturgeon.

Acknowledgements

This study was supported by the USFWS Bozeman Fish Technology Center. We thank Matt Toner, Jason Ilgen, and Cal Fraser for their help in fish culture operations at BFTC. We thank Mike Rhodes and staff at the Miles City State Fish Hatchery for spawning broodstock. We thank participating members of the upper basin pallid sturgeon workgroup for broodstock collection and agency staff of MTFWP, USGS, USACOE, WAPA, and USFWS for additional support.

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