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AN ASSESSMENT OF THE LETHAL THERMAL MAXIMA FOR MOUNTAIN SUCKER

Luke D. Schultz^{1,2} and Katie N. Bertrand¹

ABSTRACT.—Temperature is a critical factor in the distribution of stream fishes. From laboratory studies of thermal tolerance, fish ecologists can assess whether species distributions are constrained by tolerable thermal habitat availability. The objective of this study was to use lethal thermal maxima (LTM) methodology to assess the upper thermal tolerance for mountain sucker *Catostomus platyrhynchus*, a species of greatest conservation need in the state of South Dakota. Adult fish were captured from wild populations in the Black Hills of South Dakota and acclimated to 20, 22.5, and 25 °C. Four endpoints (3 sublethal, 1 lethal) were recorded, with death being the most precise (lowest SE, easily discernible). The LTM for mountain sucker was 34.0 °C at 25 °C acclimation, 33.2 °C at 22.5 °C acclimation, and 32.9 °C at 20 °C acclimation. Compared to co-occurring species in the Black Hills, the LTM of mountain sucker is higher than that of salmonids but lower than that of 3 cypriniforms. Mountain sucker LTM is intermediate compared to other species in the family Catostomidae. These results suggest that the mountain sucker is not currently limited by water temperatures in the Black Hills but may be affected by stream warming as a result of climate change.

RESUMEN.—La temperatura es un factor crítico en la distribución de peces de río. Mediante estudios de laboratorio sobre la tolerancia termal, los ecólogos de peces pueden evaluar si las distribuciones de especies están limitadas por la disponibilidad de un hábitat termalmente tolerable. El propósito de este estudio fue evaluar la tolerancia termal superior del lechón de montaña *Catostomus platyrhynchus*, una especie con la máxima necesidad de conservación en el estado de Dakota del Sur, con metodología de la temperatura letal superior (TLS). Se capturaron peces adultos de poblaciones silvestres en las Colinas Negras de Dakota del Sur, y se aclimataron a los 20, 22.5 y 25 °C. Se registraron cuatro temperaturas límite (tres subletales y una letal), siendo la letal la más precisa (error estándar más bajo y fácilmente discernible). La TLS del lechón de montaña fue de 34.0 °C a una aclimatación de 25 °C, 33.2 °C a una aclimatación de 22.5 °C y 32.9 °C a una aclimatación de 20 °C. Cuando se comparó con especies que cohabitan las Colinas Negras, la TLS del lechón de montaña es mayor a la de los salmónidos, pero menor a la de tres cypriniformes. La TLS del lechón de montaña es intermedia cuando se compara con otras especies de la familia Catostomidae. Estos resultados sugieren que el lechón de montaña no está limitado por las temperaturas en las Colinas Negras, pero podría ser afectado por el calentamiento de la corriente como resultado del cambio climático.

Climatologists predict that global air temperatures will continue to increase into the future (Bates et al. 2008), and individual species, communities, and ecosystems will be forced to respond to these changes or face extirpation (Thomas et al. 2004, Parmesan 2006). In fisheries biology, recent work addressing the anticipated impacts of climate change has focused on the thermal criteria of fishes (e.g., Buisson et al. 2008). Water temperature regulates the distribution of stream fishes through direct and indirect effects (Ferguson 1958, Matthews 1998). Temperature directly affects fish metabolism, feeding, growth, and reproductive physiology (Hutchinson and Maness 1979, Matthews 1998, Clarke and Johnston 1999) and indirectly affects food availability (Brylinsky and Mann 1973, Hinz and Wiley 1998) and condi-

tion-specific competition (Baltz et al. 1982, De Staso and Rahel 1994, Tanguchi et al. 1998). For these reasons, temperature is one of the most commonly measured and manipulated variables in laboratory (e.g., Fry 1947, Brett 1952, Feminella and Matthews 1984, Smith and Fausch 1997) and field fisheries studies (e.g., Eaton et al. 1995, Welsh et al. 2001, Huff et al. 2005, Wehrly et al. 2007).

Fish abundance in a stream reach is a response to abiotic and biotic variables, including temperature. An individual fish can survive anywhere that conditions are within its range of tolerance, but the abundance of a species depends on the ability of individuals to grow and reproduce, and is generally greatest when conditions are closest to optimum (Huey and Stevenson 1979). Laboratory assessments of

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thermal tolerance can be used to draw inferences about the distribution of a species along a temperature gradient. Great Plains stream fishes evolved in habitats often characterized by high temperatures, high salinity, and low dissolved oxygen (Dodds et al. 2004), and the distribution of fishes reflects interspecific differences in physicochemical tolerance (Matthews 1987). In the Brazos and South Canadian rivers, species distributions and abundances in warm and drying pools matched the temperature and salinity tolerances estimated from laboratory studies (Matthews and Maness 1979, Ostrand and Wilde 2001). Thus, thermal tolerance measured in the laboratory may be a predictor of fish presence and abundance in the field and an important variable to consider in the conservation of imperiled fishes (e.g., Smith and Fausch 1997, Torgersen et al. 1999, Selong et al. 2001, Harig and Fausch 2002).

Low and high water temperatures limit fish distributions. Low temperatures have sublethal effects, including delayed egg and larval development (Harig and Fausch 2002), whereas high temperatures may increase susceptibility to predation or direct mortality. The effects of climate change are likely to increase the occurrence of high air and stream temperatures (IPCC 2007). Based on an evaluation of stream water temperatures and fish distributions in the United States, a global mean surface air-temperature increase of 4.4 °C would reduce available habitat for cold- and cool-water fish by 50% rangewide (Eaton and Scheller 1996). Laboratory studies can estimate thermal tolerance of fishes, assess the relative vulnerability of different fishes to increasing water temperatures (e.g., Smith and Fausch 1997), and predict habitat overlap between native and nonnative species (Carveth et al. 2006), all of which aid in selecting suitable conservation areas.

This study empirically derived the lethal thermal maxima for mountain sucker *Catostomus platyrhynchus*. Although the mountain sucker is secure across its range (NatureServe 2011), regional trends suggest declines at finer scales. A series of long-term studies on Sagehen and Martis creeks and Stampede Reservoir in eastern California indicated declines in mountain sucker total abundance, relative abundance, and spatial distribution between the 1950s and 1980s (Erman 1973, 1986, Gard

and Flittner 1974, Moyle and Vondracek 1985, Decker 1989). In the Missouri River drainage of Wyoming, Patton et al. (1998) found that mountain sucker distribution had declined on at least 3 spatial scales (i.e., site, stream, and subdrainage) since the 1960s. In South Dakota, mountain sucker is listed as a species of greatest conservation need (SDGFP 2006), and a long-term analysis indicated that the species had significantly declined in density and spatial distribution since routine sampling began in the 1960s (Schultz and Bertrand in press).

Since the mountain sucker inhabits mostly coolwater streams (Hauser 1969, Scott and Crossman 1973, Baxter and Stone 1995, Sigler and Sigler 1996, Belica and Nibbelink 2006) and other catostomids show temperature-regulated distribution (e.g., Li et al. 1987, Eaton et al. 1995, Huff et al. 2005), high water temperatures likely constrain mountain sucker distribution. As the climate warms (Bates et al. 2008), mountain sucker distribution may be further limited by warming stream temperatures. The objective of this study was to assess the upper thermal tolerance of mountain sucker in the laboratory. These results will improve understanding of mountain sucker biology and factors that threaten peripheral populations. They will also inform management decisions and predictions of the consequences of elevated stream temperatures resulting from climate change in the Black Hills of South Dakota and across the range of mountain sucker.

METHODS

Field Collection and Laboratory Acclimation

Mountain suckers (TL 78–179 mm) were captured in August 2010 by electrofishing from Whitewood Creek near Whitewood, South Dakota (44.4722°N, 103.6242°W), and Elk Creek near Lead, South Dakota (44.2769°N, 103.6956°W), in the Black Hills. Mean August water temperature in Whitewood Creek was 18.1 °C (± 0.2 °C) for the period 2007–2010. Fish were transported in an aerated transport truck and placed into holding tanks at South Dakota State University (Brookings, SD). Prior to beginning preexperiment manipulations, we allowed fish to adjust to our laboratory conditions (temperature, feeding, dissolved oxygen) for 6 days. Pilot studies identified proper feeding and handling protocols. Fish were

held in 5000-L rectangular tanks that were supplied with rock and wood cover, exposed to a 12-hour light:12-hour dark photoperiod, and supplied with a diet of attached periphyton collected from local waterbodies, supplemented with live and frozen chironomid larvae. Water was circulated using small submersible pumps to ensure homogeneous water temperatures throughout the holding tank. Mortality associated with transport and adjustment to laboratory conditions was <3%. Following the initial adjustment period, 18 fish (mean TL = 124 mm, SD = 25.42 mm) were placed into each of 3 separate tanks and acclimated (i.e., temperature change <1 °C per hour) to different temperatures: 20, 22.5, and 25 °C ($n = 18$ for each acclimation temperature). These acclimation temperatures were based on field data from streams across the Black Hills, and should represent the highest prolonged (12+ hour) temperatures that mountain sucker experiences in natural conditions (Simpson 2007). To mimic the natural diel conditions to which fish would normally be exposed, daily temperature fluctuations (± 1.5 °C) occurred during the acclimation period; the mean daily temperature in each tank remained constant. Water was continuously aerated and replaced every 3 days to reduce nontemperature-related stress. Following the onset of acclimation conditions, fish were held for at least 10 days before further testing.

Lethal Thermal Maxima Procedure

We used the lethal thermal maxima (LTM) procedure to assess the upper thermal tolerance of mountain sucker. With the LTM method, fish are subjected to progressively higher water temperatures until they reach the death endpoint (Becker and Genoway 1979); we recorded 1 lethal and 3 sublethal estimates of thermal tolerance (Carveth et al. 2006) for mountain sucker. The temperature was recorded at (1) initial loss of equilibrium (the ability to maintain an upright position); (2) final loss of equilibrium (no longer able to self-right; Becker and Genoway 1979, Lutterschmidt and Hutchinson 1997); (3) flaring opercula (fish movement except for opercula flaring ceased; Beitinger et al. 2000); and (4) death (no heartbeat or other motion visible). Our observation of initial loss of equilibrium is ecologically important because, in this condition, a fish demonstrates

that physiological damage has occurred, and that it may be unable to escape predation or other threats.

Assessment of LTM involved randomly selecting and removing one fish at a time from acclimation tanks and transferring it to a 3.8-L glass container on an electric hot plate filled with water from the acclimation tank. The container was continuously monitored (digital thermometer) and aerated to ensure consistent and homogeneous temperature and oxygen levels. Water temperature in the container was raised at a constant rate of 0.3 °C per minute, as Beitinger et al. (2000) recommended for small-bodied fishes. Hot-plate settings were adjusted to maintain a constant rate of increase. The 4 endpoints (Carveth et al. 2006) were recorded to the nearest 0.1 °C, and each individual was measured (total length, mm) following death.

Statistical Analyses

We assessed the influence of total length on thermal tolerance using linear regression. We used a one-way ANOVA to compare temperature endpoints between acclimation temperatures. To infer the relative thermal tolerance of mountain sucker, we compared the LTM of mountain sucker to that of co-occurring species in the Black Hills and across mountain sucker range, and to that of other catostomids.

RESULTS

The LTM was 34.0 °C for mountain sucker acclimated to 25 °C, 33.2 °C for those acclimated to 22.5 °C, and 32.9 °C for those acclimated to 20 °C (Table 1). LTM did not vary significantly with total length ($r^2 = 0.03$, $P = 0.25$), so all fish tested were pooled in subsequent analyses. Ending temperatures increased significantly with acclimation temperature for all endpoints (initial equilibrium loss: $F_{2,43} = 46.95$, $P < 0.01$; final loss of equilibrium: $F_{2,43} = 40.23$, $P < 0.01$; flaring opercula: $F_{2,43} = 33.38$, $P < 0.01$; death: $F_{2,43} = 42.09$, $P < 0.01$). All fish reacted similarly during the LTM procedure: swimming activity increased as temperature approached the endpoints. The most statistically precise endpoint was death (SE = 0.094), followed closely by final loss of equilibrium (SE = 0.106) and flaring opercula (SE = 0.107). Initial loss of equilibrium, a commonly used endpoint in other studies, was difficult to

TABLE 1. Measured lethal thermal maximum temperatures at 4 measured endpoints for mountain sucker *Catostomus platyrhynchus* acclimated to 20.0, 22.5, and 25.0 °C. Confidence intervals (95%) are reported in parentheses.

Endpoint	Acclimation temperature (°C)		
	20.0	22.5	25.0
Initial equilibrium loss	31.5 (30.8–32.2)	32.4 (32.2–32.6)	33.4 (33.2–33.6)
Final equilibrium loss	32.3 (32.0–32.6)	32.6 (32.4–32.8)	33.6 (33.3–33.9)
Flaring opercula	32.5 (32.1–32.9)	32.7 (32.4–33.0)	33.7 (33.5–33.9)
Death	32.9 (32.6–33.2)	33.2 (33.0–33.4)	34.0 (33.8–34.2)

TABLE 2. Comparison of the laboratory thermal tolerance for catostomids and other fishes that may occur with mountain sucker *Catostomus platyrhynchus*. Endpoints include EQ loss (final loss of equilibrium) and FO (flaring opercula).

Co-occurring species (Black Hills region)	CTMaxima (°C)	Acclimation temp. (°C)	Endpoint	Reference
Fathead minnow <i>Pimephales promelas</i> ^a	36.1	25	EQ loss	Carveth et al. (2006)
Creek chub <i>Semotilus atromaculatus</i> ^a	35.7	26	EQ loss	Smale and Rabeni (1995)
Desert sucker <i>Catostomus clarkii</i>	35.1	25	EQ loss	Carveth et al. (2006)
White sucker <i>Catostomus commersoni</i> ^a	34.9	26	EQ loss	Smale and Rabeni (1995)
Leatherside chub <i>Lepidomeda copei</i> (juvenile)	34.6	23	EQ loss	Billman et al. (2008)
Mountain sucker <i>Catostomus platyrhynchus</i>	33.6	25	EQ loss	This study
Shortnose sucker <i>Catostomus brevirostris</i>	32.7	20	EQ loss	Castleberry and Cech (1992)
Klamath largescale sucker <i>Catostomus snyderi</i>	32.6	20	EQ loss	Castleberry and Cech (1992)
Speckled dace <i>Rhinichthys osculus</i>	32.4	20	EQ loss	Castleberry and Cech (1992)
Longnose dace <i>Rhinichthys cataractae</i> ^a	31.4	15	FO	Kowalski et al. (1978)
Mottled sculpin <i>Cottus bairdi</i>	30.9	15	FO	Kowalski et al. (1978)
Northern hogsucker <i>Hypentelium nigricans</i>	30.8	15	FO	Kowalski et al. (1978)
Brown trout <i>Salmo trutta</i> ^a	29.8	20	EQ loss	Lee and Rinne (1980)
Brook trout <i>Salvelinus fontinalis</i> ^a	29.8	20	EQ loss	Lee and Rinne (1980)
Rainbow trout <i>Oncorhynchus mykiss</i> ^a	29.4	20	EQ loss	Lee and Rinne (1980)
Arctic grayling <i>Thymallus arcticus</i>	29.3	20	EQ loss	Lohr et al. (1996)
Cutthroat trout <i>Oncorhynchus clarkii clarkii</i>	27.6	10	EQ loss	Heath (1963)

^aOccurs with mountain sucker in the Black Hills.

discern and provided the least statistically precise endpoint (SE = 0.156).

DISCUSSION

The LTM provided more statistically precise estimates of upper thermal tolerance than 3 sublethal endpoints we examined for mountain sucker. Death was also the most easily distinguishable endpoint in our tests, because we were able to observe the loss of heartbeat. In other fishes, this criterion may be more difficult to discern. Although the rapid rate of temperature change we employed does not mimic the rates predicted to occur under climate change, it provides an empirical measure of thermal tolerance that is easily comparable with other studies. For mountain sucker, the LTM was 34.0 °C when the fish were acclimated to 25 °C. The mountain sucker appears to have an intermediate thermal tolerance among fishes in the Black Hills but is considerably more tolerant to high temperatures than the 3 co-occurring spe-

cies of salmonids (i.e., brook trout *Salvelinus fontinalis*, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss*) in the Black Hills and elsewhere, indicating that mountain sucker is less susceptible to elevated water temperatures and climate change than these salmonids (Table 2). Our laboratory results are consistent with field studies of mountain sucker-dominated assemblages, which occupied warmer habitats in Utah than assemblages characterized by introduced brown trout (Giddings et al. 2006).

On the basis of recent available field temperature data from 11 streams (Simpson 2007, Schultz unpublished data), mountain sucker does not appear to be thermally limited in the Black Hills of South Dakota. During the drought summer of 2005, Simpson (2007) sampled streams across the Black Hills and observed a maximum stream temperature of 27.4 °C in Whitewood Creek (44.4172°N, 103.6933°W), which is only 5.0 °C less than the mean temperature at which we observed initial loss of equilibrium. Because LTM methods do not

assess fish responses over extended periods of exposure, our results provide a very conservative baseline at which mountain sucker might experience negative effects of increased temperature resulting from climate change. It is likely that negative effects will be observed in situ at temperatures <32.4 °C, if exposure to those temperatures is extended over multiple days. Of the 8 streams in the Black Hills in which the mountain sucker still occurs, White-wood Creek contains the greatest densities (Schultz and Bertrand in press). From 2008 to 2010, we collected mountain sucker from the warmest streams in the Black Hills (i.e., highest mean weekly stream temperatures were 20.5 °C; Schultz unpublished data).

In warmer areas of its range, mountain sucker has the potential to be thermally limited, but habitat overlap with other native and nonnative species is more important in explaining its distribution and abundance. Mountain sucker is thought to be replaced by bridgelip sucker *Catostomus columbianus* (both belong to subgenus *Pantosteus*) along thermal and channel slope gradients in Pacific Northwest streams (Li et al. 1987). In Oregon, bridgelip sucker was not found in streams exceeding 25.7 °C (Huff et al. 2005), and white sucker *Catostomus commersonii* occurs in habitats with weekly mean temperatures up to 27.3 °C (Eaton et al. 1995). These findings suggest that white sucker could outcompete both bridgelip and mountain sucker in warmer stream segments and represents a threat to these fishes outside its native range.

LTM methodology is commonly used for assessing thermal tolerance in fishes. Critical thermal maximum (CTM) and upper incipient lethal temperature (UILT) methods are 2 common alternatives to LTM. Both LTM and CTM provide a standard measure of thermal tolerance for an organism with a limited number of individuals, and are often used to make comparisons among species and infer ecological patterns (e.g., Matthews and Maness 1979, Carveth et al. 2006). In both procedures, test fish are subjected to linearly increasing or decreasing temperature until a predefined endpoint is reached (Beitinger et al. 2000). In the CTM method, the predefined endpoint is generally sublethal (e.g., loss or failure of equilibrium, flaring opercula), and fish typically survive following the test. The UILT procedure involves acclimatizing fish at different temperatures prior to exposure to a

series of constant test temperatures and tracking fish survival over time (Fry 1947). Although numerous researchers have tried to predict UILT using CTM or LTM data (e.g., Kilgour et al. 1985, Kilgour and McCauley 1986, Lohr et al. 1996), the 2 procedures provide different measurements. Abrupt transfer procedures (UILT) measure only death, while CTM and LTM procedures measure both mortality and partial acclimation (Kilgour and McCauley 1986, Beitinger et al. 2000). Disadvantages of LTM and CTM procedures include their inability to account for exposure time and potentially unrealistic rates of temperature increase; however, the advantage of these procedures is that they generate standardized measurements of thermal tolerance that are easily comparable across species. Additionally, because these procedures require smaller numbers of animals to complete the test, they are especially valuable for species of concern (Beitinger et al. 2000).

An understanding of mountain sucker thermal criteria will aid in the conservation of this native stream fish and help explain observed distribution patterns in the Black Hills and across its range. An assessment of the realized thermal niche (e.g., Bettoli 2005, Huff et al. 2005) for mountain sucker would further aid in understanding the ecological mechanisms underlying observed fish assemblages in the Black Hills. Of particular interest would be the overlap of preferred temperature ranges between mountain sucker and introduced salmonids to evaluate negative interactions between these species. Finally, these results distinguish between suitable and unsuitable habitat for mountain sucker across its range and contribute to predictions of the potential consequences of elevated stream temperatures resulting from climate change (Mohseni et al. 1999). In the Black Hills, the distribution of mountain sucker currently does not appear to be constrained by temperature; however, climate change scenarios (IPCC 2007) predict mean annual global air-temperature increases of 1.8–4.0 °C (range 1.1–6.4 °C). If the upper range of these projections is realized, water temperature will surpass the temperature at which we estimated initial loss of equilibrium for mountain sucker. Thermally suitable habitat for mountain sucker in streams of the Black Hills would diminish considerably under these conditions, including substantial loss in areas with the highest recorded mountain sucker

densities (i.e., Whitewood Creek). However, this outlook is highly conservative because it accounts for only climatic thermal effects. The potential consequences of altered flood and drought intensity and duration, industrial thermal pollution, and interactions with introduced species will likely increase the sensitivity of native fishes to increasing stream temperatures.

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