Effects of Starvation on Thermal Tolerances of Juvenile Tiger Muskellunge

Richard A. Snow, *Oklahoma Department of Wildlife Conservation, Oklahoma Fishery Research Laboratory, 500 E. Constellation, Norman, OK 73072*

Daniel E. Shoup, *Department of Natural Resource Ecology and Management, Oklahoma State University, 008C Agriculture Hall, Stillwater, OK 74078*

Michael J. Porta, *Oklahoma Department of Wildlife Conservation, Oklahoma Fishery Research Laboratory, 500 E. Constellation, Norman, OK*

Abstract: Geographical range of a species can be limited by environmental conditions such as temperature. This is important to understand when trying to establish a new fish population on the fringe of their range. The Oklahoma Department of Wildlife Conservation (ODWC) has been stocking tiger muskellunge (*Esox masquinongy* × *E. lucius)* in Lake Carl Etling in northwestern Oklahoma since 2014 with little success. This reservoir experiences a broad range of temperatures that could affect recruitment of tiger muskellunge, especially during times of the year when prey are not abundant. To explore the possible effects of temperature and prey availability on post-stocking survival, temperature tolerances of juvenile tiger muskellunge were determined in laboratory trials using starved and fed fish ($n = 9$ each) acclimated to temperatures of 20, 24, and 28°C. We used the lethal thermal maxima (LTM) procedure to determine the upper thermal tolerances of starved and fed tiger muskellunge subjected to a 1°C h^{-1} increase. Response variables consisted of three sub-lethal responses (initial loss of equilibrium, final loss of equilibrium, loss of motion) and the temperature at which death occurred. The temperature at which final loss of equilibrium, loss of motion, and death occurred generally increased with acclimation temperature for fed fish but decreased with acclimation temperature for starved fish. At 20°C acclimation, no difference was observed between fed and starved fish, but the feeding treatments were always significantly different at the 28°C acclimation temperature. Starvation lowered the thermal tolerance of juvenile tiger muskellunge, which could negatively affect stocking success if stocked fish do not have access to ample vulnerable forage as reservoir water temperatures increase seasonally.

Key words: thermal maxima, environmental conditions, *Esox masquinongy* × *E. lucius*, hybrid

Tiger muskellunge are hybrids created by spawning female muskellunge (*Esox masquinongy*) with male northern pike (*Esox lucius*). Tiger muskellunge have been stocked in reservoirs and lakes to provide a sport fishery and/or for biological control of some fish species (e.g., white sucker [*Catostomus commersonii*] and black crappie [*Pomoxis nigromaculatus*], Siler and Beyerle 1986; brook trout [*Salvelinus fontinalis*], Koenig et al. 2015; northern pike minnow [*Ptychocheilus oregonensis*], Sorel et al. 2016). The increasing popularity of tiger muskellunge for biological control has even led to stockings by the Oklahoma Department of Wildlife Conservation (ODWC) in Oklahoma, a location that pushes the southern environmental boundary for this species. Assuming that their native range would mirror that of the parent species, suitable environmental conditions would primarily consist of a mesothermal, relatively shallow (<12 m), productive, and mesotrophic-eutrophic environment (Casselman and Lewis 1996).

In fall 2014, the ODWC began stocking tiger muskellunge at Lake Carl Etling (64.3 ha), Oklahoma. Tiger muskellunge were stocked to serve as a biological control of common carp (*Cyprinus carpio*), gizzard shad (*Dorosoma cepedianum*), and green sunfish (*Lepomis cyanellus*) and to create a unique sport fishery. These stockings were expected to be successful, because Lake Carl Etling sustained a population of northern pike from 1966 to 1992 (ODWC unpublished data). A natural spring provided a thermal refuge for these fish until mid 1980s, when it ceased flowing due to changing land use and increased water use in the watershed (Lucky and Becker 1999). Stocking of northern pike was discontinued in 1976; thereafter, natural reproduction sustained the population until the reservoir nearly drained during a drought in 1992, extirpating the northern pike population. The reservoir remained low until 2013, when heavy rains returned the lake to full pool conditions, and the tiger muskellunge stocking program began. However, monthly sampling from 2014–2016 has collected only one recruited tiger muskellunge. Lake Carl Etling experiences high temperatures during the summer ranging from 27–33°C, which could affect the survival and recruitment of stocked tiger muskellunge.

Critical thermal maximum is a measurement of thermal tolerance associated with ectothermic vertebrates and invertebrates

(Becker and Genoway 1979) which can geographically limit an organism's abundance and range (Hubenova and Zaikov 2013). Body temperature of most fishes is a direct function of water temperature and can have effects on growth, reproduction, physiological behavior, immune system function, mortality, and early life history (Beitinger et al. 2000, Stewart and Allen 2014). In most environments, gradual changes in water temperature within a species' known thermal tolerance range are usually survivable, but when an unexpected or rapid increase in water temperature occurs, thermal stress may lead to death. However, hybrid fitness may equal or exceed that of parental species over a wide range of environments (Rosenfield et al. 2004). For example, thermal tolerance of Florida largemouth bass (*Micropterus salmoides floridanus*; 41.9°C) and F$_1$ hybrid largemouth bass (*Micropterus salmoides* × *M. s. floridanus*; 41.6°C) were similar, but thermal tolerance of both Florida largemouth bass and F$_1$ hybrids were higher than the thermal tolerance of northern largemouth bass (*Micropterus salmoides*; 38.5°C, Beitinger et al. 2000).

Quantification of temperature tolerance has been studied for many species (see review by Beitinger et al. 2000). Most studies dealing with thermal tolerance of muskellunge, northern pike, and/or tiger muskellunge focused on early life stages, and few studies have evaluated thermal tolerances of juveniles or adults. Cole and Bettoli (2014) found that small muskellunge selected water temperatures (23.5°C) that were significantly higher than those selected by intermediate (22.0°C) and large muskellunge (21.5°C), which suggested an ontogenetic shift in thermal tolerance. Scott (1964) found that young muskellunge, northern pike, and tiger muskellunge can tolerate temperatures of 34.5–35.5°C when acclimated to temperatures of 25, 27.5, or 30°C. Similarly, Bonin and Spotila (1978) reported high thermal maxima of fry muskellunge (29.9–35.6°C) and tiger muskellunge (30.9–36°C), but found that thermal tolerance increased with age for both species. However, they speculated that the greater thermal tolerance of juvenile fish at increasing sizes was the result of very slow acclimation to warmer temperatures (Bonin and Spotila 1978). After their first year of life, fish usually begin exhibiting less thermal tolerance with age. For instance, sub-adult northern pike have a substantially lower lethal temperature limit (29.4°C; Casselman 1978) than what Scott (1964) found for juvenile pike. Wagner and Wahl (2007) found that age 2 muskellunge in Illinois selected a mean water temperature of 24.1°C and avoided temperatures >32°C, which is considerably higher than maximum temperatures selected by larger muskellunge in Melton Hill Lake, Tennessee (25°C; Cole and Bettoli 2014). Understanding the thermal tolerance of juvenile tiger muskellunge is important because thermal limits (and associated dissolved oxygen levels) have been identified as a possible factor defining the distribution of the larger esocid species (Wagner and Wahl 2007, Cole and Bettoli 2014).

High water temperatures could limit the success of tiger muskellunge stocked into systems such as Lake Carl Etling that are outside the native range of either parental species, but additional research is needed to determine the maximum temperature in which stocked juveniles can survive. Lake Carl Etling experiences frequent high turbidity (e.g., mean secchi measurement was 23.4 cm from October 2015 through May 2017) and laboratory experiments indicate that secchi depths ≤26 cm reduces foraging success of juvenile tiger muskellunge (ODWC unpublished data). Therefore, a starvation component was also added to the study design to see if starvation interacts with thermal stress. Thus the objectives of this study were to assess the upper thermal tolerance of juvenile tiger muskellunge and evaluate the effect of starvation on thermal tolerance. Results from this study will be useful to managers considering tiger muskellunge stocking outside of the native range of the parental species.

Methods

Tiger muskellunge (*n* = 1100) averaging 238 mm TL were transported from Speas Fish Hatchery in Casper, Wyoming, to the Bryon State Fish Hatchery in Burlington, Oklahoma, in October 2016. Fish were stocked into a 0.6-ha pond and fed fathead minnows (*Pimephales promelas)* and bluegill (*Lepomis macrochirus*) for 10 days to increase mean TL to >250 mm, whereupon 72 tiger muskellunge averaging 260 mm TL (range 219–292) were seined from the pond and transported to the Oklahoma Fishery Research Lab in Norman, Oklahoma, where they were placed in a 3032-L raceway with slow water exchange and aeration at approximately 18.7 °C. Tiger muskellunge were fed a diet of fathead minnows for seven days before being used in the experiment. Trials were conducted in 45.5-L aquaria that were covered with 19-mm R4 Styrofoam sheathing insulation (The Dow Chemical Company, Midland, Michigan). Tanks were aerated throughout the trials and temperatures were maintained with 300-W submersible heaters (Aquatop, Brea, California). Temperature and dissolved oxygen were monitored using an YSI pro series 2030 (Xylem Inc., Yellow Springs, Ohio). Temperature fluctuated ±0.32°C around the desired temperature and dissolved oxygen was ≥6 ppm throughout all trials.

Three acclimation temperatures (20, 24, and 28°C) were chosen based on the range of surface temperatures (24–28°C) recorded from Lake Carl Etling. A fourth treatment, a control group, was also used where fish were acclimated to 20°C and experienced no increase in temperature during the trials. Tiger muskellunge were randomly assigned to treatments and transferred to aquaria (one fish per aquarium) to acclimate for three days at the holding temperature (20°C). During the entire acclimation period of the

experiment, fish were fed *ad libitum* (at least six fathead minnows were kept in each tank at all times) and 33% of the total volume of water changed on every third day to maintain water quality. For the starvation trials, the same procedure was used, except no fathead minnows were present during acclimation. After three days of initial acclimation to the tanks, temperatures were increased to the assigned acclimation temperature over the next three days (i.e., no temperature change for the 20°C; 1.3°C d⁻¹ increase for 24°C; 2.6°C d⁻¹ increase for 28°C). Once each tank was at its designated acclimation temperature, fish were held for an additional seven days before testing thermal tolerances. A total of nine replicates were conducted at each acclimation temperature with both starved and fed fish. Three replicates of all treatments (including one control treatment) were run at the same time to account for any temporal effects in the study.

We used the lethal thermal maxima (LTM) procedure (Becker and Genoway 1979, Schultz and Bertrand 2011) to assess the upper thermal tolerances of tiger muskellunge. Water temperatures were increased 1°C h⁻¹ until the fish died. Four response variables were measured. Temperatures were recorded (nearest 0.1°C) at four standard response variables: 1) initial loss of equilibrium (the ability to maintain an upright position), 2) complete loss of equilibrium (no longer able to self-right), 3) loss of motion (fish movement ceased except for opercular flaring), and 4) death (no motion at all; Becker and Genoway 1979, Lutterschmidt and Hutchinson 1997, Currie et al. 1998, Beitinger et al. 2000, Rajaguru 2002, Schultz and Bertrand 2011, Deslauriers et al. 2016).

A MANOVA was conducted to test for the effect of acclimation temperature and feeding regime on all four response variables using MANOVA in SAS (PROC GLM, SAS Institute 2013). Separate two-way ANOVAs (testing acclimation temperatures, feeding regime (fed or starved), and their interaction as fixed effects) were used to determine which response variables (initial loss of equilibrium, final loss of equilibrium, loss of motion, and death) had significant effects when the MANOVA was significant. Controls were not used in any statistical test because metrics of thermal stress were never observed for these fish. Tukey HDS post-hoc tests were used to test for pair-wise differences when ANOVAs indicated significant differences existed. All statistical analyses were conducted at a significance level of $P \leq 0.05$.

Results

Three tiger muskellunge in the fed treatment died during the acclimation period for 28°C and five additional fish in the starvation treatment died during acclimation period for 28°C. No other fish died during the trial. This resulted in nine replicates for all treatments except for the 28°C acclimation treatment, wherein six

replicates were completed for the fed treatment and four replicates were completed in the starved treatment.

Acclimation temperature and feeding level affected the four response variables (MANOVA Wilk's lambda = 0.40, $F = 11.73$, $P \leq 0.01$). The temperature at which fish exhibited all four measured thermal stress responses had a significant interaction between acclimation temperature and feeding treatment, indicating that the effect of these two variables were not independent and the pattern for one varies depending on the treatment level of the other factor (F range 4.07 to 22.03, df = 2, 40, $P \leq 0.02$; Figure 1).
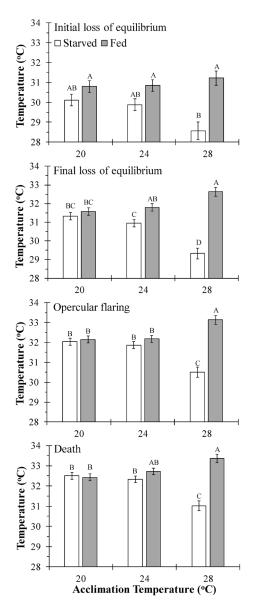

Figure 1. Comparison of the effects of acclimation temperature (20, 24, and 28°C) and feeding treatment (fed or starved) on the mean temperature (±SE) at which response variables (initial loss of equilibrium, final loss of equilibrium, loss of movement, and death) were observed for juvenile tiger muskellunge. Letters indicate significant differences.

Specifically, temperature tolerance was greatest at the highest ac-climation temperature for fed fish, but lowest at this temperature when fish were starved. There was less difference between fed and starved fish at the lowest and intermediate acclimation tempera-tures. At 20°C acclimation, no difference was observed between fed and starved fish, and at 24°C acclimation, fed and starved fish only differed with respect to the temperature at which final loss of equilibrium occurred (Figure 1). All four response variables differed between fed and starved fish with the 28°C acclimation treatment.

Discussion

This is the first study to investigate the effects of starvation on thermal tolerance of juvenile tiger muskellunge. We found that starvation affected the temperature at which final loss of equilib-rium occurred at acclimation temperatures ≥24°C. However, the biggest differences in response variables were detected in the 28°C acclimation trials. When fish were starved, the 28°C acclimation treatment resulted in 55.5% dying before the acclimation period ended; whereas when fish were fed, only 33% of died during accli-mation. Further, the temperature at which thermal stress responses were observed were 2–3°C lower for starved fish than for fed fish in the 28°C acclimation treatment. For fed fish, we found that higher acclimation temperatures resulted in tolerance of higher tempera-tures before thermal stress responses were detected, but the oppo-site was true for starved fish. Control-group fish experienced no signs of thermal stress, and none died during starved or fed treat-ments, suggesting that stress from increased temperature was the likely cause of death for fish that died. This conclusion is further supported by the fact that these fish showed signs of stress as they neared the acclimation temperature. This suggests that high food availability would be important to survival of tiger muskellunge stocked in environments with high summer temperatures.

Other studies that examined the effect of starvation on ther-mal tolerance have produced conflicting results. Some studies have found starvation makes fish less tolerant of thermal stress. For ex-ample, starvation of larval North Sea herring (*Clupea harengus*), cod (*Gadus morhua*) and flounder (*Platichthys flesus*) intensified the harmful effects of high temperature and low salinity (Yin and Blaxter 1987). However, other studies have found little to no ef-fect of starvation or reduced ration on thermal tolerance of fishes (Woiwode and Adelman 1992, Verhille et al. 2015).

Fed juvenile tiger muskellunge responded similarly to many other species of fish when acclimated to different temperatures. As acclimation temperature increased, mean LTM temperatures also typically increased (Otto 1973, Woiwode and Adelman 1992, Schulz and Bertrand 2011, Deslauriers et al 2016, Fernando et al.

2016). We found that LTM for fed fish was ~32°C for fish accli-mated to 20°C or 24°C, and ~33°C for fed fish acclimated to 28°C. Both Scott (1964) and Bonin and Spotila (1978) conducted studies using fry and fingerling tiger muskellunge, and found higher lethal limits than we documented for larger fish, suggesting that thermal tolerance decreases with size for juvenile tiger muskellunge.

Mortality of tiger muskellunge observed during the 28°C ac-climation period (3 fed and 5 starved), could be the result of the 2.6°C d⁻¹ increase in water temperature. Previous studies have used varying temperature change rates. Schultz and Bertrand (2011) and Deslauriers et al. (2016) increased water temperature in their studies by 1°C h⁻¹; however, Xia et al. (2017) increased wa-ter temperature at a rate of 1°C d⁻¹. When evaluating decreasing temperature effects on lionfish (*Pterois volitans*), Kimball et al. (2004) decreased temperature at a rate of –1°C d⁻¹. None of these studies observed mortalities during the acclimation period. The rate of increase used in our study was conservative compared to warming rates of 1°C h⁻¹ used in several studies. It is possible that the acclimation temperature (28°C) and exposure duration, and not the rate of warming, are contributing to the mortality. Tiger muskellunge, northern pike, and muskellunge died of starvation after 2.75 days at temperatures ranging from 32–33°C (Scott 1964). Therefore, the inability of fed or starved juvenile tiger muskellunge to keep up with dietary needs throughout the duration of our ac-climation period may have been the largest factor affecting fish in the highest acclimation temperature treatment (28°C). Further research should evaluate the effects of reduced body mass and ex-posure duration on temperature tolerance on tiger muskellunge.

Fish occurring on the southern edge of their native range often have higher thermal tolerance than those from northern ranges, so producing tiger muskellunge for stocking in southern habitats may be more successful if brood stock from southern populations are used. For example, southern populations of common killifish (*Fudulus heterclitus;* Fangue et al. 2006), mosquitofish *Gambusia affinis* (Otto 1973), and muskellunge (Wolter 2012) are able to withstand higher temperatures than those from northern popula-tions. Knowledge of the critical thermal maximum and minimum for Florida largemouth bass (*Micropterus salmoides floridanus*) has been used to make stocking decisions for this species outside of its native range (Fields et al. 1987). It is possible that the northern pike and muskellunge from northern populations that were used to produce tiger muskellunge used in this experiment influenced our results. Additional research is needed to determine if using northern pike and muskellunge from more thermally-tolerant southern populations for tiger muskellunge production could en-hance the thermal tolerance of offspring.

Our results suggest temperature may negatively affect survival

of stocked tiger muskellunge in Lake Carl Etling (and potentially any southern habitats), especially if they have difficulty capturing food. Soon after stocking tiger muskellunge, we observed symptoms of thermal stress at temperatures as low as 28.5°C, and surface water temperatures routinely exceed this during the summer in Lake Carl Etling. Koch and Steffense (2013) found that northern pike in Kingsman Lake in southcentral Kansas become vulnerable to anglers when fish congregate near cold water springs seeking thermal refuge during the hottest months of the year. In the early 1980s, attempts to excavate the natural spring that provided thermal refuge in Lake Carl Etling were unsuccessful. With the loss of this refuge, water temperatures at Lake Carl Etling may impact tiger muskellunge stocking success, however it may not be the only environmental factor affecting survival.

Understanding juvenile tiger muskellunge thermal tolerance will aid in distinguishing between suitable and unsuitable environments when considering stocking locations. Acclimation to warmer water temperatures generally improved thermal tolerance, suggesting the ability to tolerate gradual temperature changes during the hottest part of the year. Furthermore, food availability could be an important factor in determining if tiger muskellunge can survive in thermally stressful environments. Other environmental stressors (predation risk, turbulent water from wind/wave action, etc.) should also be studied in the future as they may further refine our understanding of where tiger muskellunge are unlikely to survive when stocked at the southern extent of their range.

Acknowledgments

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