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The effects of warming rate on the thermal tolerance of a southern population of striped bass (Morone saxatilis)

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The effects of warming rate on the thermal tolerance of a southern population of striped bass (*Morone saxatilis*)

An Honors Thesis submitted in partial fulfillment of the requirements for Honors in the Department of Biology

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Under the mentorship of Dr. Johanne Lewis

ABSTRACT

Climate change and global warming is an ever-growing concern for our environment and the survivability of the animals which inhabit it. With water temperatures expected to rise 2-3℃ in the next century, many aquatic organisms may be limited in their habitats based on their thermal tolerance. Southern populations of striped bass (*Morone saxatilis*) in the Southeastern United States could be some of the hardest hit by the effects of climate change due to their unusual life history as compared to the more northern populations of striped bass. These southern striped bass do not engage in coastal migrations in the summer, but rather choose to stay in the freshwater river environments, limiting their ability to find favorable water temperatures. This study aimed to find the upper threshold of thermal tolerance of these southern striped bass while also examining the differences between traditional short-term temperature ramps (Critical thermal maximum, CT_{max}) and newer, more environmentally relevant incremental temperature exposure (IT_{max}). CT_{max} and IT_{max} were both used to gauge the overall thermal tolerance of the species. Tests began at 20℃ and increased from there to give the closest thermal tolerance measures to wild fish as possible. Additionally, ventricle mass and respiration rate in respirations per minute were recorded to gain a better understanding of the overall ability of this population to handle changes in temperature.

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Background

Climate change is an increasingly concerning reality that is facing environments all across the planet. This is especially true for aquatic species due to the numerous related effects that rising temperatures also have on their environment. Higher water temperatures can lead to reduced oxygen solubility while at the same time increasing organisms' need for oxygen. When an increased need for oxygen is coupled with a decreased supply of oxygen, it becomes extremely difficult for aquatic organisms to survive in that environment. This forces them to either move to more suitable habitats or adapt by making some form of morphological or physiological changes to increase oxygen uptake and delivery to the rest of the body. Given the current projections for global warming, aquatic organisms could experience major complications sooner than expected. One study investigating a small North American stream fish found that the upper critical temperature (CT_{max}) of the fish in the study was on average only 10-11℃ above the maximum temperature for the stream at their field site. However, they also observed changes in fish behavior at temperatures beginning 5-6℃ below the CT_{max} (Turko, et al. 2020). If these findings are similar across other species of fish, the results could be catastrophic. For example, if the thermal maximum of a particular species of fish is only a few degrees above the maximum temperature of the rivers in which they inhabit, they may be regularly subjected to temperatures that cause increased metabolic and respiratory stresses due to their status as poikilotherms. Likewise, if fish do not show avoidance behaviors until they are within a few degrees of their thermal maximum, they may not be able to get to cooler waters in time to survive during the peak warming days of the summer. This would have major implications on the ability of the population to survive unexpected warming events during the summer season or could impact survivability of the population on a whole as waters warm due to global climate change.

A species of freshwater fish that may already be experiencing negative effects of global climate change is the striped bass (*Morone saxatilis*). Striped bass are a very common fish that inhabits both fresh and saltwater environments along the coasts of North America. The majority of striped bass populations, particularly those found north of the Carolinas, engage in seasonal, coastal, migrations following cooler ocean waters in order to stay in their ideal temperature range. However, the southern populations of striped bass (south of the Carolinas into the Gulf of Mexico) tend to stay within their home river systems year-round, limiting their access to cooler waters during the summer months and making them more susceptible to the impacts of human induced global warming. This problem is compounded even more by the addition of physical barriers such as dams that make it impossible for striped bass to travel upstream. One specific southern population of striped bass, within the Savannah River, is no longer self-sustaining and has to be stocked yearly with juvenile striped bass raised in aquaculture facilities by the Department of Natural Resources. One hypothesis as to why the southern populations are struggling as they are right now is climate change and the rising water temperatures present in the freshwater environments these fish call home. A 2019 study found these southern striped bass showed reduced performance and oxygen tolerance when acclimated to 30℃, the current mean temperature of the Savannah River in the summer, and 33℃, the projected temperatures of the late summer months with the current rate of global warming (Lleras 2019). This is significant because with the current temperatures of their environments and the expected rise of water temperatures by 2-3℃

in the next 100 years, these southern striped bass populations could be in serious danger. If these southern populations experience habitats that place them outside of their optimal thermal niche for extended periods of time, they may not be able to sustain the metabolic rate necessary to survive (Portner and Peck 2010). It is also important to note that when organisms are outside of this optimal temperature range, they have to spend significantly more energy simply maintaining the physiological processes needed to survive. Due to the increased energy demand of survival in these conditions, organisms also have limited resources and energy available to perform other important activities such as feeding, reproducing and escaping predators. This study aims to find what the upper thermal tolerance limit is for these populations of striped bass, and if this limit coincides with the current summer highs of the Savannah River.

Thermal tolerance of aquatic organisms can be measured in a variety of ways. Many studies through the years have used critical thermal maximum, or CT_{max} to determine the thermal tolerance of these organisms. CT_{max} tests involve starting organisms at a common, set temperature before rapidly increasing the temperature of the water until the organisms reach loss of equilibrium and recording the temperature at which that state occurs. However, recently more studies have been leaning towards incremental thermal maximum, or IT_{max}, tests. This form of thermal tolerance testing involves slowly increasing the temperature of the water over a period of days rather than hours. It is thought that IT_{max} may be a better measure of the true upper thermal tolerance of organisms because it displays a temperature ramp rate that is closer to that experienced by the organisms in their natural environment. A recent study found that acute temperature increases like CT_{max} are not necessarily a good predictor of incremental temperature increases like IT_{max}. This 2022 study by Bartlett, et al., which performed both CT_{max} and IT_{max} on Atlantic salmon, found that there was no correlation between the two values and that one was in no way a predictor of the other. Based on the results of this study, CT_{max} could artificially overestimate the thermal tolerance of fish in the natural environment. The researchers noted that CT_{max} was a very useful tool in examining the physiological responses of fish to a warming environment, but that it was not necessarily the best measurement to determine the true thermal tolerance of a species. These results echoed those of a previous paper by Zanuzzo, et al. (2019), which found the same pattern in Atlantic cod. It was also worth noting that the Bartlett study found incremental thermal maximum was positively correlated with body size, while critical thermal maximum was negatively correlated with body size of the fish in the study. This study is significant because not only does it draw attention to the stark contrast between CT_{max} and IT_{max}, but it also uses a species that travels between fresh and saltwater much like the striped bass. To better understand the connection between these two methods, a secondary objective of this study is to determine if CT_{max} and IT_{max} will yield similar results in striped bass.

Based on previous research, it is predicted that the thermal tolerance of striped bass using both CT_{max} and IT_{max} will be near to or slightly above the 32℃ mark. This directly relates to the Lleras study which found a fifty percent mortality rate when acclimating striped bass to 32℃ for two weeks. Additionally, it is predicted that CT_{max} and IT_{max} will not display a correlation, and the IT_{max} value will be slightly below that of CT_{max} based on the results of both the Bartlett (2022) and the Zanuzzo (2019) studies.

Materials and Methodology:

Animal Collection and Care:

The striped bass for the study were collected from the Richmond Hill Hatchery and transferred to the Animal facility at Georgia Southern University. Fish were held in 200-gallon tanks with water temperature at 20°C and exposed to a 12:12 light/dark photoperiod cycle while being fed every other day to satiation with size appropriate fish pellets (Purina Aquamax Starter). Food was withheld for 24 hours before the experimental trial. Water chemistry was also monitored daily using the API Master Freshwater Test Kit to ensure the levels of ammonia, nitrate, and nitrite were all kept within an acceptable range. A 25-30% water change was performed if these levels exceeded the accepted range. Fish were held for at least two weeks before conducting any experimental trials. All experimental protocols received approval by the Georgia Southern University Animal Care and Use Committee under protocol #I21003.

Critical Thermal Maximum (CT_{max}):

Experimental setup consisted of two separate water reservoirs including a larger experimental tank and a 35-gallon water tub used as an external heating tank. The experimental tank contained two respirometry chambers with netting on each side. One fish was placed in each chamber to allow for two fish to be examined at the same time while also keeping them separated for observational reasons. Pumps were employed to create a cycle of water between the experimental tank and the heating tank. The heating tank contained one 1000W heater and two 1500W heaters. Each tank was equipped with air stones to keep the water oxygenated. Fish were netted from the holding tank, placed in the chambers and allowed 2-3 hours to acclimate to the experimental tank (held constant at 20°C) before beginning the CT_{max} trial. The heating tanks were then gradually heated at a rate of approximately 0.4°C per minute, and fish were monitored throughout the entire experimental process to monitor changes in behavior. Two key behaviors that were noted were agitation temperature (T_{agt}) and CT_{max}. Agitation temperature was defined as a clear and forceful attempt to escape, often indicated by individuals repeatedly and rapidly swimming into the walls of the chamber in which they were enclosed. This behavior reflects physiological changes in the fish as a response to rising temperatures (Enders & Durhack 2022). CT_{max} was recorded as the temperature when the fish reached "loss of equilibrium" (LOE) - the inability to maintain an upright position in the water column for > 1 second (Lutterschmidt and Hutchison 1997). A one-minute video was taken of each fish every 2°C, and ventilation rate was recorded by counting the respirations in three 15 second intervals, averaging the three values, and multiplying this average by four to get the average number of respirations per minute.

Once fish reached LOE (the end-point of the trial) they were quickly removed from the tank, weighed (to nearest 0.1 g), and measurements of total and fork length (mm) were recorded. Fish were then euthanized with a blow to the head followed by cervical displacement. After euthanization, fish were dissected to remove the heart and hearts were carefully blotted to remove any fluid or blood. The ventricle was separated from the remainder of the heart tissue and its mass recorded (VM; to nearest 0.001 g). The ventricle mass (VM) was later used along with body mass (BM) to calculate relative ventricle mass (RVM %) using the following formula:

$$RVM = (VM * BM^{-1})*100$$

The CT_{max} trials in this study followed a similar protocol as previously published studies (0.3 - 0.5 C/min) and were also completed within ~ 1.5 hours. an average time of approximately 1.5 hours (Bartlett et al. 2022).

Incremental Thermal Maximum (IT_{max}):

The striped bass (n=15) assigned to the incremental thermal maximum trial were acclimated at 20℃ and held within the same 200-gallon tank. The trial began on October 2, 2023 and was still underway at the time of thesis submission (December 4, 2023). Temperature in the tank was increased by 0.25℃ per day with a 1000W in-tank heater (Hygger) that was adjusted every other day to keep a rate similar to the 0.3℃ per day accomplished by the Bartlett, et al. study (2022). Temperature was continuously recorded using an in-tank Hobo temperature logger and fish were monitored daily for activity and state of health. Initially, fish were fed to satiation every other day until water temperature reached 32℃. At this point fish were fed daily to satiation due to increase in food seeking behaviors by the fish during health status checks. Fish were to be removed from the tank as they met one of the two end-point markers: mortality or moribund (near death). After removal from the tank fish were euthanized to ensure mortality and measurements of body mass (g), total and fork lengths (mm) and ventricle mass (VM) were obtained as previously described for the CT_{max} trial.

Analysis:

All statistical analyses were performed using JMP statistical software. A correlation analysis was used to quantify the relationship between CT_{max} and body size, VM, and RVM as well as the relationship between Agitation window and body size, VM, and RVM. A Pearson's correlation coefficient and a p-value were generated and p-values

$\leq$0.05 were considered significant. Effect of temperature on ventilation rate was analyzed with a one-way ANOVA with differences between treatments analyzed with Tukey's post hoc test ($p \leq 0.05$ cutoff for significance).

Results*:*

Morphological Measurements

The fish used in this study were all juvenile striped bass (< 1 year old). The average mass of the fish used in the CT_{max} trial was 35.0 ± 15.8g (ranging from 14.2 to 61.37g). The average total length of the fish was 142.2 ± 22.2 mm with a minimum length of 105 mm and a maximum of 173 mm. Fork length yielded an average of 122.8 ± 20.3 mm with values from 89 to 150 mm. Mean ventricle mass was found to be 0.025 ± 0.010 g, and RVM was 0.074 ± 0.017 g. The body mass and length data for the fish used in the IT_{max} trial was not available as the IT_{max} trial had not concluded by the submission date of the thesis.

Markers of Upper Thermal Tolerance

The average point of agitation was found to be 30.7±1.0°C. Mean CT_{max} of the striped bass in the study was 32.7±1.3°C. Based on these two values, the agitation window was found to be 1.9±1.2°C. CT_{max} was not significantly correlated with body mass when all nine fish were included in the analysis ($r= 0.372$; $p=0.325$). However, when the one outlier was removed from the analysis, CT_{max} was positively correlated with body size ($r = 0.849$; $p = 0.007$). There was no significant correlation found between CT_{max} and ventricle mass (VM) or relative ventricle mass (RVM). Additionally, there was no significant correlation found between the agitation window and body size, VM, or RVM.

Ventilation Rate

The average ventilation rate (respirations per minute) of striped bass in CT_{max} trials was: 95±14 at the start, 97±18 at 20°C, 104±20 at 22°C, 107±21 at 24°C, 110±22 at 26°C, 112±21 at 28°C, 116±19 at 30°C, and 148±10 at 32°C. All 9 fish are represented in averages from the start until 28°C. The value for 30°C represents measurements from 8 fish that survived to this point, and the value for 32°C represents 6 surviving fish. No fish survived long enough past 34°C for a ventilation rate to be recorded. The one-way anova analysis showed that temperature had a significant effect on ventilation rate (p=0.00013). The Tukey's post hoc analysis indicated that there was no significant difference in ventilation rate between 18 - 30 degrees. However, there was a significant increase in ventilation rate in fish at 32°C compared to fish at 18 - 28 degrees, but there was not a significant difference between ventilation rate in fish exposed to 30 and 32°C.

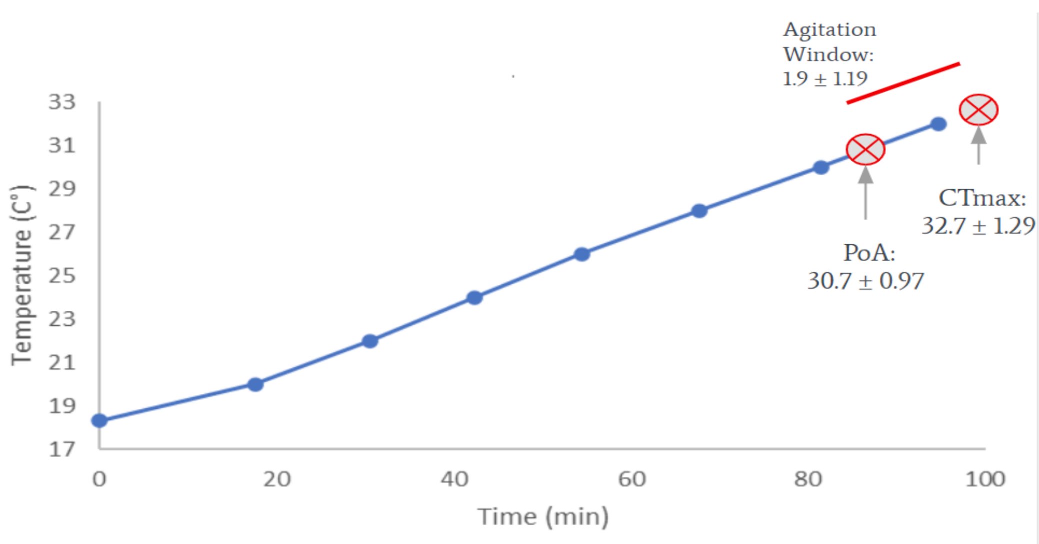

Figure 1. CT max ramp rate showing the increase in temperature by time in minutes. Mean point of agitation (PoA), critical thermal maximum (CT_{max}), and agitation window are shown with standard deviations.

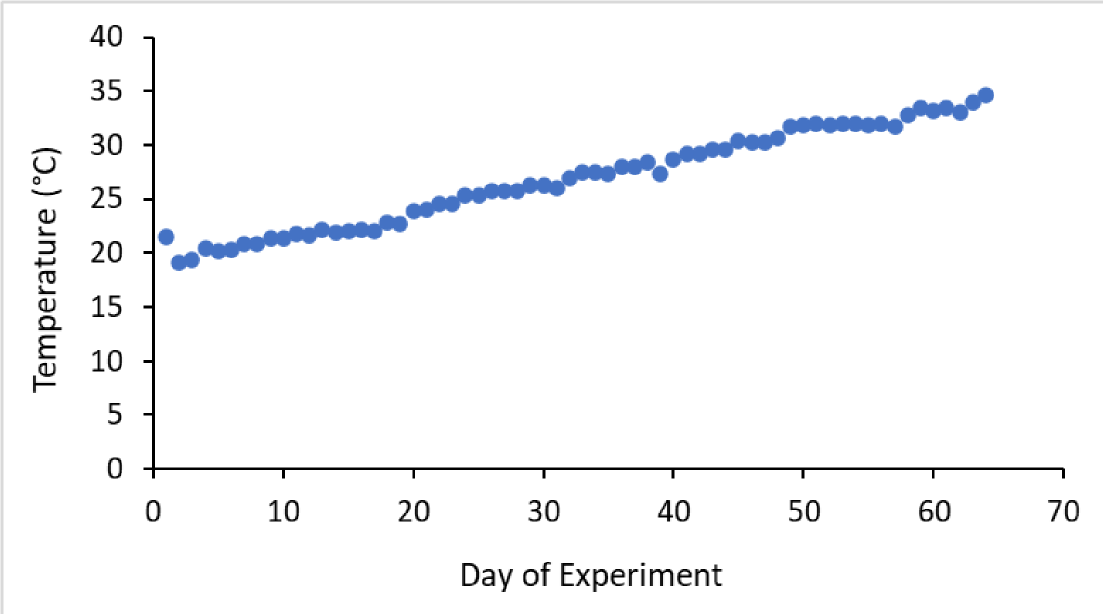

Figure 2. IT_{max} ramp rate showing the change in temperature by time in days as recorded by the in-tank Hobo temperature logger.

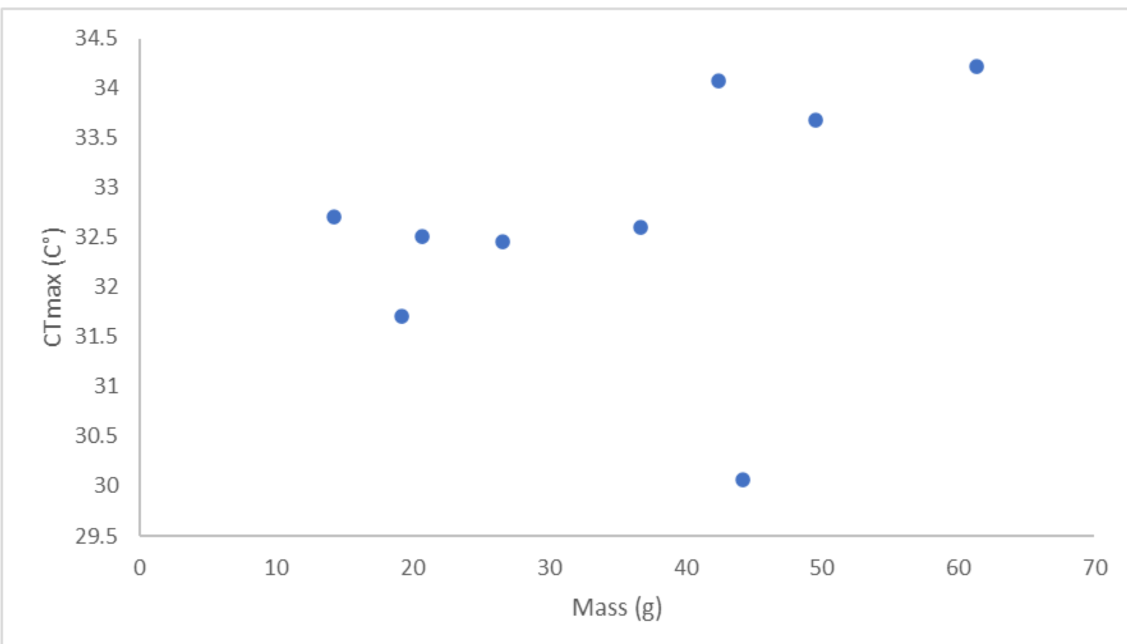

Figure 3. CT_{max} values versus body mass (g). Data points represent individual fish (n=9).

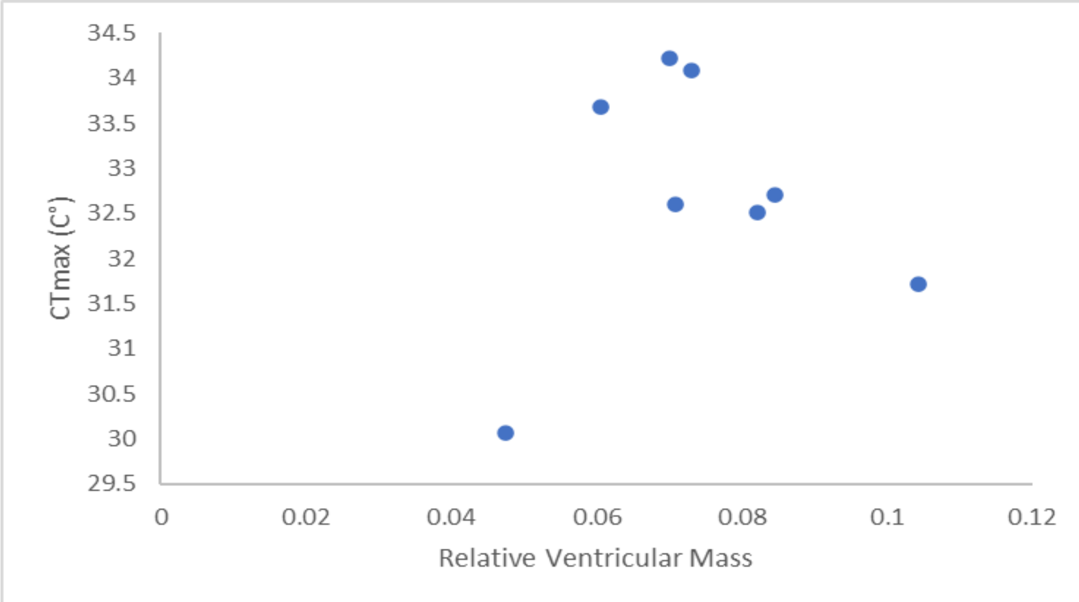

Figure 4. CT $_{max}$ values versus the relative ventricular mass. Data points represent individual fish (n=9).

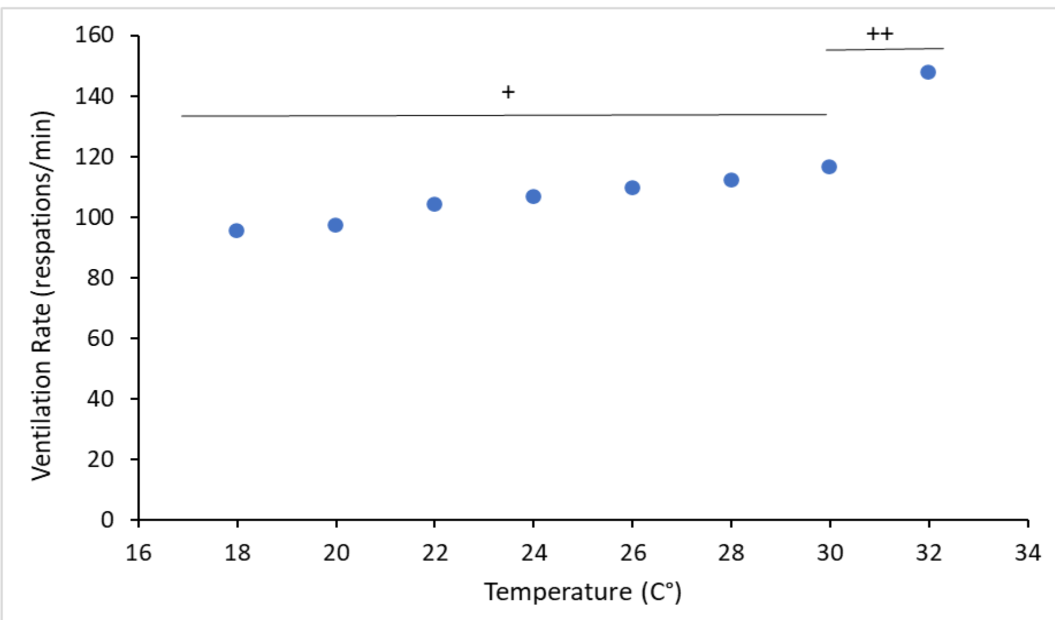

Figure 5. Ventilation rate in respirations per minute by temperature. Data presented as mean values (n=9 for 18 - 28°C, n = 8 for 30°C, n=6 for 32°C. No significant difference is indicated by data beneath horizontal line “+”. A significant difference is indicated by data beneath horizontal line “++”.

Discussion:

The results of the CT_{max} trials raised some significant concerns for the southern populations of striped bass such as those in the Savannah River. With the Savannah River reaching temperatures upwards of 31℃ during the summer months each year (USGS), striped bass could regularly be experiencing river temperatures near the experimentally determined point of agitation, 30.7℃, during the late summer months. This could lead striped bass to seek out cooler waters upstream, highlighting the point of agitation as an avoidance behavior that could lead to negative impacts on other physiological processes (McDonnell 2015). If these fish are having to expend energy seeking out cooler waters, they have less energy available to direct to other physiological processes which could lead to problems such as decreased immune responses and reduced reproductive output. These problems could decrease the survivability of both individuals and populations as a whole. Even though this avoidance behavior is there as an evolutionary behavior designed so that fish will seek more habitable environments before it is too late, this is often made more difficult by humans through development and damming of rivers. These human behaviors can create uncrossable barriers that prevent striped bass from traveling upstream to cooler waters making the rising water temperatures even more devastating. It is also notable that a significant increase was observed in the respiration rate of striped bass as they reached their point of agitation (Figure 5), meaning striped bass experiencing these temperatures in the environment are also susceptible to extreme metabolic stress. This also raises the concern that if water temperatures rise at the current projected rate of 2-3℃ over the next 100 years, our experimental CT_{max} results suggest large sections of the Savannah River could very well be uninhabitable for striped bass within our lifetime because of its summer highs. With the average CT_{max} value of the fish in the study being 32.7℃, water temperatures in the Savannah River could reach this point in the summer before water temperatures even increase by 2℃. It is also notable that the agitation window, which is the temperature gap between the point of agitation and the loss of equilibrium, was on average 1.9℃ for the individuals in this study. This study suggests that striped bass typically begin to seek cooler waters around 1.9℃ before they reach their thermal maximum.

Based on our data, there appears to be a slight positive correlation between the mass of the individual fish in the CT_{max} trials and their loss of equilibrium point. This is different from the findings of other studies (Turko, et al. 2020) which found a correlation between body condition of adult fish but not juvenile fish like those in this study. Larger fish tended to have a slightly higher CT_{max} (Figure 3). Future research could be conducted to determine if there is a true relationship between body size and CT_{max} in striped bass.

RVM was measured to see the relationship between cardiovascular properties and thermal tolerance. RVM has previously been shown to be one possible factor supporting increased thermal tolerance in long term exposure to higher temperatures such as those seen in IT_{max} studies (Bartlett, et al. 2022). In this study, RVM did not appear to yield any real correlation with CT_{max} at all (Figure 4). This is similar to the results of the study by Bartlett, et al. (2022) for CT_{max}, in which no correlation was found. However, other studies have found positive correlations between CT_{max} and RVM in other species of fish (Anttila et al., 2013). Future research should be done to determine if there is a correlation between these variables in striped bass.

At the time of thesis submission IT_{max} trials are still underway but the temperature in the experimental tank has already progressed to 34.75°C with all 15 fish still alive, active and feeding regularly (Figure 2). Therefore, the results of our research will show IT_{max} to be higher than CT_{max} by upwards of 2°C. These results are contrary to the predictions made prior to testing that were based on studies such as those conducted by Bartlett, et al. (2022) and Zanuzzo, et al. 2019. Our study, on the other hand, points to the incremental warming protocol allowing the fish with more time to make physiological adjustments, enabling them to survive longer in warming environments. These adjustments, for the most part, are directly related to oxygen consumption because of the decreased oxygen present at increased temperatures. This could include increasing heart rate, reallocation of blood flow, or an increased respiration rate (Claireaux and Chabot 2016). There are a few possible reasons for these differences including variation in thermal tolerance and physiology across species or the conditions in which the fish are kept. The IT_{max} values in this trial may still not represent the "true" thermal maximum of striped bass in the wild even with a more gradual, natural temperature ramp. The laboratory setting in which this experiment was conducted could allow the striped bass IT_{max} values to artificially overshoot their thermal tolerance in a natural setting. Previous literature shows that striped bass exist in an energetically compromised state when acclimated to 33°C (Lleras 2019). This means that fish in the wild experiencing these temperatures may not be able to survive when they also have to search for food or handle environmental stressors. The fish in this study spent the entire time in a controlled setting while being fed to satiation daily, meaning they could direct the majority of their resources to the physiological processes needed to survive.

The data collected in this study is important in highlighting one of the key possible reasons as to why the Savannah River population of striped bass is no longer self-sustaining. The similarities between the upper thermal limit of striped bass and the summer high temperatures for the Savannah River indicate that there could be a large amount of heat related stress on striped bass populations in the river throughout the summer months. The data collected in this study is also beneficial to the Richmond Hill Hatchery to allow them to determine if they are able to sample specimens on particular days of the year depending on the temperature and stress level of the fish. Rising temperatures could even force hatchery staff to stop raising striped bass for stocking purposes altogether in favor of more thermally tolerant striped bass x white bass hybrids.

This study was limited to examining the thermal tolerance of one particular developmental stage of striped bass. Future research should be conducted to determine if the thermal tolerance varies among different developmental stages to see if one particular life stage is playing a major role in the unsustainability of the Savannah River population in particular. It could also be useful to examine how the thermal tolerance of adult stages of striped bass compare to those of the juveniles in this study. Recent studies have found thermal tolerances to be much more variable in juveniles than adults in fish such as redside dace (Turko, et al. 2020). It remains to be seen if these differential thermal tolerances based on age are seen in striped bass. It is also worth noting that the reproductive success of female striped bass in general may be suffering in the Savannah River as has been seen in other locations where cool water summer habitats have been reduced similarly (Coutant 1987 and Harrell, et al. 1990). Lastly, research could also be done on the long-term effects global warming has on striped bass as they develop. A

2021 study by Del Rio found the paired effects of hypoxia and warmer temperatures on developing fish to have lasting effects that impact individual fish survival in rivers. In that study, researchers focused on how those stressors impacted groups of developing fish over time individually. If the results of this study on salmon are also shown in striped bass, summer high water temperatures could have crippling effects on populations throughout the year.

Conclusion:

Overall, this study highlights the problems that global warming could spell for the nonmigratory southern populations of striped bass. If there is not a change in the current projection of global warming, many of these populations could cease to exist entirely. This study highlights where the thermal limit of these striped bass might be while providing a point of reference as to when the southern populations such as those in the Savannah River may no longer be able to survive. The results of this study also provided another clue as to why the Savannah River population itself is no longer self-sustaining. It remains to be seen whether or not the thermal tolerance of developmental stages of striped bass is more limiting to the population's overall sustainability.

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