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# LONG-TERM TRENDS OF STRIPED BASS HABITAT SUITABILITY UNDER A TEMPERATURE-OXYGEN SQUEEZE IN LAKE TEXOMA, OKLAHOMA AND TEXAS

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LONG-TERM TRENDS OF STRIPED BASS HABITAT SUITABILITY UNDER A TEMPERATURE-OXYGEN SQUEEZE IN LAKE TEXOMA, OKLAHOMA AND TEXAS

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BY THE COMMITTEE CONSISTING OF

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**Abstract**

Warmer epilimnetic water temperatures and reduced dissolved oxygen levels in deeper water are common stressors for fishes in freshwater reservoirs throughout the summer. We investigated the effects of a temperature–oxygen squeeze - a phenomenon that squeezes fish into a narrow, livable zone - on striped bass from 1995 to 2020 in Lake Texoma. This reservoir is located on the border of Texas and Oklahoma, possesses one of the largest self-sustaining populations of inland freshwater striped bass in the US, and is of high economic importance to the region. We used a trait-based approach to quantify 1) how the total volume of suitable habitat for striped bass has changed seasonally and across years, 2) the relative influence of temperature and oxygen on habitat suitability, and 3) whether a temperature-oxygen squeeze has affected the striped bass population and body condition. We found that the volume of suitable habitat for striped bass decreased over the course of each summer and was greatly influenced by day-to-day persistence and water level, but did not exhibit a significant linear decline over the years from 1995 to 2020. Additionally, the relative influence of temperature and oxygen on habitat suitability varied depending on the thresholds used to define the temperature-oxygen squeeze. We found no significant linear relationships between habitat volume, striped bass population, and body condition. One hypothesis that would explain this null result is that striped bass in Lake Texoma may be adapted to the seasonally stratified conditions, especially since habitat volume did not show a monotonic decline over time. We also detail other biophysical and statistical hypotheses that might explain why we did not detect an effect of a temperature-oxygen squeeze on striped bass. This study provides insights into future management of Lake Texoma and other reservoir fisheries as global change alters patterns in temperature, oxygen, and reservoir habitat.

# Chapter 1: Theoretical Framework

## 1. Overview

Globally, large watersheds and their freshwater biodiversity are at risk of climate change impacts and increased water demand. With increasingly variable temperatures and precipitation, there is expected to be a significant decrease in water resources by the end of the century (Bucak et al., 2017; United Nations, 2018). One such large watershed is the Red River Basin of the South (hereby referred to as the Red River Basin), an important water resource that flows through New Mexico, Texas, Oklahoma, Arkansas, and Louisiana. The basin serves as a major source of water for consumption and is also utilized for ecosystems, tourism, recreation, and cultural ceremonies (Xue et al., 2016). Thus, the basin provides societal, ecological, and economic benefits; however, climate change presents significant uncertainties.

While meeting human needs is imperative for water management, it is also essential to allocate water to in-stream flows and reservoirs to support ecosystem services and fisheries, which bring in millions of dollars annually to Oklahoma and Texas economies (Melstrom et al., 2017; NMFS, 2018). Most fish species in the south-central U.S. are drought tolerant; however, mass mortality can be caused by constant increases in human water use that act as mega-droughts (Fausch & Bramblett, 1991; Godfree et al. 2019). In combination with ecosystem modifications, water scarcity can result in declining freshwater biodiversity (Vörösmarty et al., 2010). Yet, there is limited knowledge of how changes in climate and hydrology will impact fish biodiversity both globally and specifically in the American Southwest as it has experienced decreasing streamflow events (McClure et al., 2013; Ruhí et al., 2016; Staudt et al., 2013). As a result, there is a need to develop a habitat suitability modeling framework that will describe

changes to freshwater fish habitat, allowing water managers to better plan for biodiversity conservation.

This thesis aims to understand how reservoir fish populations in the Red River Basin, specifically striped bass in Lake Texoma, are affected by changes in suitable habitat due to climate change and increased water use, helping determine which management strategies can best support freshwater sustainability. Land system science (LSS), biogeography, and water resources geography will support this project's theoretical framework. This chapter will begin by exploring how an LSS framework is important to understanding human influences on land use change and climate change, specifically using hydrologic change theories to delve into human-mediated effects on water systems. These changes to water systems impact the global water supply and ecosystem functions. The next section will use an ecological and conservation biogeography lens to explore the importance of biodiversity to maintaining ecosystem functions and how environmental and land use change impacts freshwater habitats and species distributions. The following section will delve into more specific effects of climate change on water systems and how integrative water resource management and ecological operations models can be used to determine water management strategies that balance human water needs with ecosystem needs. The final sections will connect LSS, biogeography, and water resources geography and locate the knowledge gaps for identifying future changes to biodiversity and potential solutions for water management planning in the Red River Basin, which will be expanded upon in Chapter Two.

## 2. Land System Science

### *2.1. Importance of land system science in understanding environmental changes*

Patterns of biodiversity and ecosystem processes have been altered by humans throughout time. Due to human development, such as urbanization or agriculture, more than 75% of Earth's land surface has been impacted, greatly reducing natural habitats (Ellis & Ramankutty, 2008). Some of these impacts include global extinctions and large changes in climate conditions compared to those previously seen in the natural record (Novacek & Cleland, 2001; Ruddiman, 2003). Because of this reconstruction of the terrestrial biosphere, human-dominated ecosystems make up more of the Earth's land surface than truly wild ecosystems (Ellis & Ramankutty, 2008). These ecosystem interactions are complex and dynamic, requiring a perspective that is not solely ecological, but social as well (DeFries et al., 2004; Ellis & Ramankutty, 2008).

LSS presents a framework to understand how the use of land by humans changes terrestrial processes, affecting local and global environments, as well as human well-being (Verburg et al., 2015). A land system includes all processes related to human land use, including socioeconomic, technological, and organizational uses, as well as its social and ecological consequences and systemic interdependencies (Verburg et al., 2013). As much as human action can alter the land, its effects on the land can consequently alter human actions where ecosystem services change. This means a feedback loop exists between land system changes and resulting ecosystem services, human well-being, and environmental decision-making (Crossman et al., 2013). These systems operate across various spatial and temporal scales. For example, land use changes over time have contributed to climate change, which is a global phenomenon, but how people deal with climate change can depend on its local impacts, as well as national and global land use planning efforts and policies (Verburg et al., 2015). Thus, place-based approaches are necessary to account for the complexity of LSS processes and consequences.

### *2.2. Water systems in LSS*

Complex dynamics can not only be seen in changes to terrestrial systems, but also in aquatic and atmospheric systems, such as through greenhouse gas emissions, increased water consumption, and habitat fragmentation (Verburg et al., 2015). Surface water and groundwater are vital to the land system and are necessary to consider when determining land use impacts on people and biodiversity, thus influencing management decisions. Hydrologic change/alteration theories are used to describe how humans have influenced major hydrological processes (i.e., changes to runoff, surface flows, evapotranspiration, etc.) by altering the water cycle for societal needs (Vörösmarty & Sahagian, 2000). Global water use has grown exponentially with human population growth and economic development, making it imperative to consider water supply in management decisions. Humans have altered the hydrologic cycle through land cover change, urbanization, industrialization, and infrastructure, such as dams, reservoirs, irrigation, and water basin transfers, that increase human water access (Ai et al., 2022; Bridgewater et al., 2017; Chakraborty, 2021; Deng et al., 2020).

Specifically, dams and reservoirs affect the water cycle by trapping freshwater runoff and rainfall in a large, concentrated area. Impoundments provide socio-economic benefits, such as support for tourism, flood control, energy creation, and drought mitigation (Połomski & Wiatkowski, 2023). However, dam and reservoir construction can also have negative environmental effects. In addition to affecting continental runoff, construction can result in a loss of surface runoff to groundwater, transform river flow to evaporation, change the timing of river discharge, and overall influence the water budget of river basins (Vörösmarty & Sahagian, 2000). In response to flow regulation by dams, the general trend has been significant reductions in flow magnitude and frequency, and changes to the timing and duration of flows (Magilligan et al., 2022). Dams have also impacted physicochemical properties of rivers, streams, and

reservoirs as there has been an increase in sediment trapping, thus decreasing water quality and changing channel structures, as well as changes in temperature and dissolved oxygen concentrations (Hannan, 1979; Magilligan et al., 2022; Ochs et al., 2023). While impoundments provide important water resources for people, they can profoundly influence ecological systems (Ai et al., 2022; Deng et al., 2020). Freshwater species reside in reservoirs, as well as the streams that they flow into, thus, water releases need to be planned to minimize negative effects on biodiversity.

Losses in ecosystem structure, function, and services have contributed to the global water crisis, especially in the face of climate change (Kaushal et al., 2017). Land use by human development has influenced the quantity and quality of water resources. Groundwater extraction and dam construction in semi-arid and arid landscapes, like the Red River Basin, have caused a significant decrease in the water supply (Field & Michalak, 2015; Taylor et al., 2013). Climate change has exacerbated this reduction in water supply by decreasing the amount of water stored on land as ice through warming and changes in precipitation (Field & Michalak, 2015; Kaushal et al., 2017). Because of these impacts, it is essential to understand the root causes and trends in water degradation, as well as trends in climate uncertainty to inform future water management strategies that protect freshwater environments and their ecosystem functions.

## 3. Biodiversity and Biogeography

### *3.1. Importance of biodiversity in ecosystem services and function*

Biodiversity loss has been a large consequence of land use and land cover changes in the Anthropocene. In addition to questions addressing the global water crisis, land system science can help explain the connection between biodiversity distribution and ecosystem service

production (Crossman et al., 2013; Nagendra et al., 2013; Zhang et al., 2022). Ecosystem services are provided by natural capital, such as soil, water, vegetation, and biota, thus land use change results in trade-offs between the production and value of different suites of ecosystem services (Foley et al., 2005). For example, grazing systems can enhance food production, but it comes at a cost to water purification, climate regulation, biodiversity, and habitat, among other ecosystem services (Smith et al., 2013). Changes to the land system can fragment or modify natural habitats, affecting terrestrial and aquatic biodiversity (Verburg et al., 2015). Because of habitat degradation, there has been a significant decline in species populations, and hundreds of species are being driven to extinction (Ceballos et al., 2017).

While the connection between biodiversity distribution and ecosystem service production and function has not been fully investigated, some important links have been established. Generally, more biodiverse ecosystems can maintain high productivity, modulate nutrient and energy fluxes, promote ecosystem stability, and support environmental health (Zhang et al., 2022). Biodiverse ecosystems can also help regulate the water cycle, increase water quality, and contribute to economic and recreational benefits. Yet, a high proportion of freshwater organisms are threatened or endangered, jeopardizing the vital ecosystem functions they provide (Revenga et al., 2005). By understanding changes to species habitat and ecosystem functions, management efforts can be made to conserve biodiversity and the socio-ecological values that species provide.

### *3.2. Biodiversity and biogeography theories*

Biodiversity change can be observed through multiple metrics, such as species extinctions, species abundance and community structure, habitat loss and degradation, and shifts in species distribution and biomes (Pereira et al., 2010). These metrics are responsive to global change. For example, aquatic species, like fish, may migrate within water systems as

temperatures fluctuate, though barriers or limited habitats can restrict their movement (Daufresne & Boet, 2007). This means that there may be a shift in the potential distribution of species as favorable conditions are vanishing in certain areas and appearing in others (Pereira et al., 2010). These metrics are informed by biogeography, which is a subfield of geography that determines the patterns and processes that drive species distributions and biodiversity (Sanmartín, 2012). Ecological biogeography is especially useful in predicting changes to species distributions caused by alterations in the land system and climate because it specifically looks at environmental factors at local spatial scales to explain distributions (Morrone & Crisci, 1995).

Within ecological biogeography are some key theories that are useful in understanding and modeling distributions of fish species in streams and reservoirs. The biogeography of freshwater fishes is related to their dispersal capability through factors like physical barriers (i.e., dams, weirs, culverts, etc.), physiological barriers (i.e., temperature, salinity, dissolved oxygen, etc.), or species interactions (Olden et al., 2010). Rivers are spatially and temporally variable environments that promote movement, but anthropogenic barriers can reduce connectivity, thus restricting dispersal (Daufresne & Boet, 2007; Olden et al., 2010; Rolls et al., 2014). Aside from physical barriers, organisms are theorized to be limited by their fundamental niche, which describes the place that species are adapted to based on the habitat, environmental space, and functional role of the species (Hutchinson, 1957). The theory of niche conservatism vs the theory of an evolving niche can be used to explore biodiversity patterns and mechanisms at varying temporal and spatial scales (Olden et al., 2010; Wiens & Graham, 2005). It is unclear whether fish species show evidence of a conserved or evolved niche, but these ideas are essential to testing hypotheses of species-environment relationships. In response to climate change, fish

species might move to a similar ecological niche if their ancestral traits are maintained, or they may stay if their niche has evolved (Olden et al., 2010; Wiens & Graham, 2005).

Ecological niche models (ENMs), species distribution models (SDMs), and habitat suitability models (HSMs) use niche conservatism to address biodiversity patterns at different scales by including environmental data and the ecological requirements of species (Wen et al., 2013). Generally, these models can forecast species distributions in space and time by determining species-environment relationships through occurrence/absence data and environmental variables (Olden et al., 2010; Wen et al., 2013). These terms are sometimes used interchangeably but have small differences in their purpose depending on the modelers intent to predict a species' fundamental niche, the current distribution of a species, or the potential distribution of a species based on suitable habitat characteristics (Brown & Griscom, 2022). Overall, these different species models are important for conservation decision-making as they can provide a tool for mapping distributions and suitable habitat in a credible and reproducible way; however, they are sensitive to data inputs which are often lacking (Sofaer et al., 2019).

While these models are useful for estimating the potential impacts of environmental change on fish species, they tend to be oversimplified or introduce errors as they can have small sample sizes, missing variables, and do not usually incorporate dispersal, demographic processes, and biotic interactions (Olden et al., 2010; Wen et al., 2013). Additionally, there are still many unexplored scenarios in fish conservation biogeography. SDMs have performed well when utilizing data from surveys and environmental predictors to characterize natural species distributions and predict the potential of invasive freshwater fish to expand their geographic range (Elith & Leathwick, 2009; Olden et al., 2010). But only recently are these models being used to predict future changes in fish distributions due to climate change. For example, a study in

France utilized national monitoring data to understand distributional changes in 32 stream fishes, determining that species are shifting towards higher elevations and upstream in response to climate change (Comte & Grenouillet, 2013). There is much difficulty in predicting species distributions, as well as a need for more studies that determine future impacts to fish habitat and populations. Thus, it is one of the core challenges of conservation biogeography to predict species' risks to a changing environment.

### *3.3. Conservation biogeography and trait-based approaches*

Species models are subject to some criticisms, but they are still valuable tools for forecasting losses to biodiversity at local spatial scales. Determining the biogeographic dynamics of imperiled species is a major goal of conservation biogeography, a type of biogeography that deals with maintaining biodiversity in anthropogenic ecosystems (Lomolino, 2004). Considering unique aquatic constraints can help researchers make conclusions about conserving fish biodiversity (Nagy et al., 2024; Olden et al., 2010). As mentioned, there are both physical and physiological constraints that can affect fish in streams and reservoirs.

Traditionally, biogeography has been studied through a taxonomic approach. However, looking at species-specific traits, rather than traditional taxonomic theories, can be utilized to understand how species will react to local and global changes and determine which species are more at risk of extinction (Nagy et al., 2024; Olden et al., 2010). There is a growing interest in investigating the functional traits of freshwater fishes, which are characteristics that improve an organism's performance or fitness (Winemiller, 2005). Like climate change as a mechanism for species distributions, trait-based approaches are a recent development in biogeography. Introducing this approach in species models can address some of the current critiques as they employ more complex theories that account for life history and macroecology, among other

aspects, to predict community responses to environmental change (Nagy et al., 2024; Olden et al., 2010). Under an uncertain climate, increasing knowledge of functional and physiological characteristics will allow for the identification of fish species that are vulnerable to changes in hydrologic regimes, as well as possible sites of refugia for those species.

## 4. Water Resources Geography

### *4.1. Climate change and water resources*

As human activities continue to contribute to climate change, it is imperative to understand how water systems are altered, thus affecting freshwater fish biodiversity. Globally, climate change drives shifts in water availability and changes water properties, such as the temperature profiles of streams, lakes, and reservoirs (Elliott et al., 2014; Miranda et al., 2020). As discussed, threats to the global water supply are a contemporary challenge, and climate change will exacerbate these water sustainability challenges in many regions. Recent assessments have shown that current and future climatic changes are making communities and ecosystems, such as rural communities in the Great Plains, more vulnerable due to increased warming, droughts, and more variable precipitation (Ojima et al., 2021; Ruhí et al., 2016). However, there is much uncertainty and stochasticity in future climate models that must be accounted for in water sustainability strategies.

General circulation models or global climate models (GCMs) use mathematical equations and large-scale oceanic and atmospheric processes to simulate the response of the global climate system to increases in greenhouse gas emissions (IPCC, 2013). GCMs determine how climatic variables, like temperature and precipitation, might change in the future under different representative concentration pathways (RCPs). RCPs offer scenarios of radiative forcing

trajectories resulting from different combinations of anthropogenic greenhouse gas emissions and land cover changes, where RCP 2.6 corresponds to low greenhouse gas emissions scenarios, and RCP 8.5 corresponds to high greenhouse gas emissions scenarios (IPCC, 2019; Moss et al., 2010). GCMs can be useful for analyzing hydrologic extremes, such as more variable precipitation and extreme drought, that put stress on water resources. However, they are typically in a coarse resolution format that is not ideal for understanding local-scale climatic changes (Bertrand & McPherson, 2018). Water managers must understand the local impacts of future intensification of climate change to make decisions that benefit their communities and sustain freshwater resources and ecosystems.

To address this limitation of GCMs, climate projections are often downscaled to higher resolutions. Using a suite of downscaled datasets allows for a more thorough risk assessment of future climate uncertainty (Bertrand & McPherson, 2019). Suites of downscaled datasets were used to determine that under RCP 8.5, severe drought is expected to increase in the western Red River Basin while heavy precipitation events will increase in the east (Bertrand & McPherson, 2018). RCP 2.6 even indicates this trend in the future to a lesser extent. These hydrologic extremes can result in negative economic impacts, damage to infrastructure, and changes in water quality and quantity, thus it is essential to communicate these results to water managers in the Red River Basin so they can plan for their respective changes based on location (Bertrand & McPherson, 2018; Bertrand & McPherson, 2019). Given the uncertainty and stochasticity of the future climate, water management strategies must be flexible to changing ecological conditions (Gain et al., 2021). Additionally, downscaled datasets and management strategies are more valuable when co-produced with modelers, climate experts, water resource managers, and decision-makers as they can result in more holistic and informational climate change assessments

that better prepare for changes in water resources (Bertrand & McPherson, 2018; Bertrand & McPherson, 2019; Pokhrel et al., 2016).

### *4.2. Water resource management planning and strategies*

In addition to utilizing downscaled climate models to inform water management decisions, the field of water resources geography offers other valuable theories and approaches, like integrated water resources management (IWRM). An IWRM approach can help find a balance between allocating water for societal needs as well as ecosystem needs by emphasizing interdisciplinary knowledge from different stakeholders (Cook & Spray, 2012; Grizzetti et al., 2016; Rahaman & Varis, 2005). IWRM theories are based on the principles of social equity, economic efficiency, and environmental sustainability to ensure water security (Rahaman & Varis, 2005). River Basin Management Plans under the EU Water Framework Directive are informed by these principles. The EU utilizes the concept of ecosystem services to safeguard its water resources, justifying the costs of water system protection and restoration (Grizzetti et al., 2016). Like the ecosystem service-based governance and social-ecological systems approaches of LSS, IWRM aims to optimize social, economic, and ecological benefits by assessing the trade-offs of human needs and ecosystem services while also understanding which stakeholders benefit from those trade-offs (Cook & Spray, 2012; van Rees, 2024). Thus, societal water needs cannot be managed without considering ecosystem needs, and vice versa.

Similarly, ecological operations models are designed to maintain the health of rivers and reservoirs while balancing human water needs by looking at reservoir operations, hydrologic models, and watershed management (Ai et al., 2022; Deng et al., 2020). Ecosystem-based modeling, specifically from the aquatic perspective, can help address gaps in the IWRM approach that do not fully explore the interrelations between human-environment nexus

assessments and ecosystem management (Hülsmann et al., 2019). Furthermore, sustainable water management systems support infrastructure that meets the needs of society while supporting ecological functions, like biodiversity (Poff et al., 2016). Using these approaches in the Red River Basin can determine locations and times where it would be best to adopt water conservation actions or specific water management strategies to benefit freshwater biodiversity under future water uncertainty.

## 5. Connecting LSS, Biogeography, and Water Resources Geography

Human development and consequent land use change have greatly altered natural systems, largely resulting in changes to climate, such as increased temperatures, more variable weather events, and droughts. In conjunction with climate change, increased human water use has exacerbated challenges to the global water supply, putting stress on many communities and ecosystems. Thus, greater inclusion of water systems in LSS research is imperative to account for the increased effects of water scarcity on social-ecological systems (Vadjunec et al., 2024). Specifically, it is essential to allocate water for consumptive uses, as well as ecosystem processes, as it can support the health of watersheds and local biodiversity.

Rivers and reservoirs support dynamic, biodiverse communities of fish that are shifting due to natural environmental variation and human activity that has resulted in land use change (Nagy et al., 2024). These changes can influence fish community abundance and composition in the long term. In fact, the interactive effects of habitat fragmentation and water scarcity are leading drivers of globally declining freshwater biodiversity (Vörösmarty et al., 2010). Biogeography methodologies like ENMs, SDMs, and HSMs that utilize species-specific trait

approaches and life history can be valuable tools for ensuring the conservation of freshwater fish biodiversity.

Models of fish distribution under climate change can help determine which fish species are at risk and the areas that are most in need of updates to water management strategies that ensure adequate habitat for those fish. However, water is typically managed as a physical resource for human use; thus, a more holistic approach is needed to protect freshwater habitats (van Rees, 2024). IWRM approaches and ecological operations models emphasize the need for interdisciplinary solutions that understand the trade-offs between societal and ecological demands. A combination of LSS, biogeography, and water resources knowledge, along with input from policy and management specialists is vital for creating local water management decisions that both provide water for human systems and conserve freshwater biodiversity.

## 6. Conclusion: Addressing Knowledge Gaps

The Red River Basin is a water-limited region predicted to be greatly affected by climate change. Downscaled climate models have shown increasing drought in some areas and heavy precipitation events in others, suggesting that water-resource and fisheries managers must prepare for hydrologic extremes depending on their location within the basin (Bertrand & McPherson, 2018; Bertrand & McPherson, 2019). Due to this stochastic climate and increase in water resource use, it is necessary to map hotspots of future water stress that allow for a better understanding of the impacts on freshwater fish distributions. The geographic subfields of LSS, biogeography, and water resources geography offer a foundation to explain how human alteration of the environment has led to climatic changes that are affecting water resources and the biodiversity that resides in freshwater habitats. The creation of a habitat suitability model for

fish in reservoirs will address several research gaps in these fields, including greater integration of water in LSS by analyzing social-ecological systems like reservoirs that are of importance to both people and organisms, understanding how environmental change has influenced patterns of freshwater fish biodiversity, and determining how water management strategies can mitigate these impacts.

Many social-ecological studies focus on land use land cover change as a mechanism for understanding land system sustainability but often leave out feedbacks between land use, water systems, and human well-being as they can be very complex, operating at both spatial and temporal scales (Crossman et al., 2013; Meyfroidt et al., 2018; Vadjunec et al., 2024). Moreover, this integration requires a holistic and interdisciplinary approach that includes a diverse group of stakeholders to make localized water management and policy decisions (Pokhrel et al., 2016; Verburg et al., 2015). My research will contribute to the LSS field by analyzing impacts to reservoir fisheries from habitat alteration caused by climatic changes to the land system. Thus, the goal is to promote the long-term sustainability of the human-freshwater system. Water will be further integrated into LSS research through ideas of water management, as well as climate change effects caused by human development and land use change.

Human actions have mediated the extirpation of native fish populations in river basins. In addition to land use change and climate change, the construction of water infrastructure has altered the dispersal of freshwater fish. The impact of these changes on fish biogeography and conservation is unclear and requires further research. My project will utilize species-specific physiological data, environmental variables, and hydrologic models to estimate impacts to reservoir fish habitat and understand the implications for future species populations. I will address several challenges in contemporary biogeography that could lead to a better

understanding of the effects of environmental change on patterns of freshwater fish biodiversity, including testing current and new biogeography theories, advancing trait-based biogeography, determining extinction risk in a changing environment, and understanding the effects of multiple stressors on freshwater fish biodiversity (Olden et al., 2010; Wen et al., 2013). Specifically, I will address these challenges by basing a habitat suitability model on the long-term impacts of a temperature-oxygen squeeze on striped bass. This integration of ecology and biogeography into water resource issues can provide pressing answers regarding the potential future of watershed health and subsequent conservation concerns.

While many studies have described changes to water systems from land use and climate change, there is a lack of understanding of how potential water management decisions might lessen future consequences of the water crisis in the Red River Basin (Al Radif, 1999; Gleick, 1993; Poff et al., 2016). Additionally, the social-ecological dynamics of a system must be recognized to design appropriate and adaptive water management tools (Cook & Spray, 2012; Ostrom, 2009). A solution to identifying strategies that are robust to climate uncertainty lies in the integration of science and policy. A habitat suitability model will allow decision-makers to explore how proposed water management decisions affect fish populations, possibly altering patterns of human water use. The creation of this tool will make use of many stakeholders, including climate and hydrology modelers, fisheries management agencies (Oklahoma Department of Wildlife Conservation and Texas Parks and Wildlife Department) and federal organizations (USGS South-Central Climate Adaptation Science Center). The interdisciplinary nature of this work is essential to informing water management solutions that benefit both people and the environment.

Through this exploration of research methodologies and theories, we have seen that LSS, biogeography, and water resources geography form a framework that supports the creation of a habitat suitability model for reservoir fish in the Red River Basin. There is much to explore regarding the connections between the land system and water, the effects of climate change on future freshwater biodiversity, and potential water management strategies. As climate change and human consumptive water use increases, affecting large watersheds like the Red River Basin, the development of a habitat suitability model will be imperative to ensuring long-term human-freshwater sustainability and biodiversity conservation. Chapter Two discusses the creation of a habitat suitability model that aims to understand how reservoir volume suitable for freshwater fish is impacted by changes in water properties from climate change and increased human water use. Specifically, I investigate these ideas through a study that models the impact of a temperature-oxygen squeeze on striped bass habitat, populations, and body condition in Lake Texoma, a major reservoir in the Red River Basin.

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## Chapter 2: Reservoir Habitat Suitability Model for Striped Bass in Lake Texoma

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### 1. Introduction

Warming water temperatures and hypoxia are common stressors in lakes and reservoirs around the world (Woodward et al., 2010; Woolway et al., 2022). One mechanism by which these stressors impact reservoir fisheries is through a temperature-oxygen squeeze (Coutant, 2013). During summer stratification in eutrophic lakes and reservoirs, surface waters are often too hot for freshwater species, but deeper, cooler waters are hypoxic, resulting in a narrow volume of water that meets species' biological requirements. Thus, the fish are squeezed into a narrow layer between intolerably warm surface waters and intolerably hypoxic deeper waters. Globally, the impacts of this phenomenon have been investigated for many species, including trout, zebra mussels, salmon, sturgeon, and striped bass, among others, with reported changes in water depth distribution, growth and survival, and community dynamics (Berge, 2009; Gantz et al., 2022; Kerker, 2020; Rowe & Chisnall, 1995; Secor & Niklitschek, 2001; Young, 2016). Specifically, in the southeast and south-central United States, lab and field studies on striped bass

(*Morone saxatilis*) have generally supported the hypothesis that large adults will occupy cooler waters below 25°C, if available, and avoid dissolved oxygen (DO) levels of 2-3 mg/L or less (Coutant, 1985; Coutant, 2013). However, this thermal threshold of 25°C has been recognized in some systems as an upper preference limit instead of a tolerance limit, as adult striped bass can withstand higher temperatures (Coutant, 2013; Matthews et al., 1985; Matthews et al., 1989; Zale et al., 1990).

Coutant led early laboratory and telemetry studies that demonstrated size-specific thermal preferences of striped bass, with larger adults selecting 16–22°C waters and smaller individuals tolerating 20–27°C, while avoiding hypoxic conditions (Coutant, 1978; Coutant, 1980; Schaich & Coutant, 1980; Waddle, 1980). In Tennessee reservoirs, severe squeeze conditions have resulted in crowding into limited cool-water areas, malnutrition, disease, and die-offs, but responses differ among study systems (Coutant, 1978; Coutant, 1985; Coutant, 2013). In reservoirs with access to cooler tributaries, tailwaters, springs, or river channels, striped bass occupy true thermal refuges (Coutant, 2013). When true thermal refuges are unavailable, striped bass can inhabit mid-depth areas in reservoirs, often without observed mortalities (Coutant, 2013). Nonetheless, feeding reductions and potential condition impacts occur when oxygenated temperatures exceed about 27°C, and prolonged exposure to warm, low-oxygen conditions can be lethal when food is limited (Coutant, 2013; Zale et al., 1990). Thus, site-specific thermal limits and impacts of a habitat squeeze are determined by the size of adult striped bass, availability of true refuge areas, duration of exposure to warm temperatures, and bioenergetic balance.

Changes in temperature and oxygen in lakes and reservoirs have the potential to reduce the suitable habitat volume for striped bass, especially within the humid and subtropical areas of

the US. One such reservoir is Lake Texoma, located on the border of Oklahoma and Texas. Recreational fishing supports Oklahoma and Texas economies by generating approximately $3.04 billion and $7.7 billion annually, respectively (American Sportfishing Association & Southwick Associates, 2023; York, 2024). Lake Texoma, known as the "Striper Capital of the World," is one of the few reservoirs in the United States with a naturally producing striped bass fishery, attracting millions of people to the lake every year (Mauck, 1986; Sager et al., 2024). Over one million striped bass were introduced to Lake Texoma from South Carolina, Virginia, and New York populations between 1965 and 1974, and natural reproduction was verified in 1975 (Hysmith et al., 2008; Sager et al., 2024). Striped bass also play an essential role as a top predator, controlling prey populations, and are an indicator of ecosystem health (Fay et al., 1983). Specifically, gizzard and threadfin shad represent most of the striped bass' diet, and winter kills of these forage species have negatively impacted year-class strength (Sanger et al., 2024). Thus, Lake Texoma's striped bass fishery is economically, recreationally, and ecologically important to the region and beyond. Lake Texoma also serves as a source of water for municipal, industrial, and environmental services by generating hydropower, increasing economic growth, supporting freshwater ecosystems, and encouraging recreational opportunities.

Fisheries managers suggest that striped bass are at risk of overfishing, habitat loss, changes in prey abundance, disease, and the negative consequences of global warming (Sager et al., 2024). While most fish species in the south-central U.S. are drought-tolerant and have broad thermal tolerances, the combination of climatic droughts and accelerating human water use can create conditions for a mega-drought (Fausch & Bramblett, 1991; Godfree et al., 2019; Miranda et al., 2020). For example, low inflows into Lake Texoma caused a severe drought from 2011 to 2014, resulting in a decline in fish catch from 2014 to 2016 (Sager et al., 2024). Additionally,

Lake Texoma is situated in the Red River Basin, where severe drought is expected to worsen in the west, and heavy rainfall events are predicted to increase in the east under both high and low emissions scenarios (Bertrand & McPherson, 2018). These future changes in climate and hydrology will result in a patchy spatial distribution of water stress across the basin (Sabzi et al., 2019). In combination with ecosystem modifications, water scarcity can result in declining freshwater biodiversity and changes to fish assemblages (Miranda et al., 2020; Vörösmarty et al., 2010). This could greatly impact Lake Texoma and the broader Red River Basin region, as it relies on the many benefits that fish species like striped bass provide.

To cope with these climatic changes, striped bass may migrate within reservoirs, though limited suitable habitats due to a temperature-oxygen squeeze can restrict their movement (Coutant, 2013; Daufresne & Boet, 2007). Striped bass migrate upstream in the Washita and Red River arms during the spring to spawn (Summers, 1982). While some medium and many small striped bass remain in warmer up-lake areas, large adults move down lake by late May, where they reside deep in the main basin throughout the summer (Matthews et al., 1989; Sager et al., 2024). Large adult striped bass located by transmitters, echolocation, and gillnets occupied mid-depths near the dam, and their movements within the water column became more constricted with higher surface temperatures and more hypoxic conditions in late summer and early fall (Matthews et al., 1985; Matthews et al., 1989; Summers, 1982). As surface temperatures ranged from 28-30°C, they occupied the coolest areas directly above the chemocline where temperatures were close to 28°C. Despite exposure to high temperatures, no apparent mortalities were observed for adult striped bass in Lake Texoma during these studies (Matthews et al., 1985).

Large striped bass in Lake Texoma reside in the main basin during the summer due to the lack of available refuge sites, which are discrete, cool locations with ample oxygen (Coutant,

2013; Matthews et al., 1989; Summers, 1982). While striped bass in systems with true refuges will migrate to tributaries in the summer, those in Texoma remain in the lower lake as it stratifies at around 11-14 m compared to around 9-12 m in the Washita River Arm (Coutant, 2013; Sager et al., 2024). This allows for a greater percentage of cool, oxygenated waters. Furthermore, intentional releases from a floodgate adjacent to the location of hydropower generation along the dam in Texoma facilitates oxygen uptake, influencing tailrace water quality and providing a localized refuge for striped bass during lake stratification, thus reducing stress and subsequent mortalities (Ashby et al., 1999; Sager et al., 2024). However, once in the tailrace, there is no fish lift for striped bass to return to the reservoir. These studies of fish habitat usage, along with other fish biotelemetry studies of reservoirs in the south-central US, have been conducted to better understand the spatial distribution of striped bass under a temperature-oxygen squeeze (Coutant, 2013). Despite the depth of research, there has been a lack of habitat modeling utilizing this hypothesis, which is a necessary step to assess the vulnerability of reservoir fish habitats under climate uncertainty (Coutant, 2013; Miranda et al., 2020; Olden et al., 2010). Reservoir water quality models and habitat suitability models can be used to identify future limiting habitats, allowing for fisheries and reservoir managers to determine mitigation strategies that conserve striped bass populations and fish biodiversity.

This research aims to develop a habitat suitability model for managing reservoirs and shaping water conservation strategies that protect reservoir fisheries in the face of climate change. This challenge is explored through a study of striped bass in Lake Texoma. Specifically, a trait-based approach is utilized to model the amount of water volume associated with suitable habitat conditions for striped bass from 1995 to 2020 through the concept of a temperature-oxygen squeeze. Three main research questions (RQs) will be addressed. First, how is striped

bass habitat suitability in Lake Texoma changing seasonally and interannually with a temperature-oxygen squeeze from 1995 to 2020 (RQ1)? Second, what are the combined and individual influences of temperature and DO on suitable habitat volume (RQ2)? Third, what is the impact of a temperature-oxygen squeeze in Lake Texoma on striped bass populations and body condition (RQ3)? Ultimately, this study of striped bass in Lake Texoma intends to provide a framework to explore reservoir fish species dynamics and determine best management practices of reservoir waters under a changing climate.

## 2. Study Area

The Red River Basin is located in the south-central United States and flows through New Mexico, Texas, Oklahoma, Arkansas, and Louisiana. It is the second largest river basin by area in the southern Great Plains, draining 169,890 $km^2$ (Matthews et al., 2005). The average yearly rainfall ranges from 500 to 1,300 mm, with a west-to-east gradient, representing multiple ecoregions (EPA, 2013). Its land cover is dominated by grasslands used for farming, with areas of mixed woodlands and shrublands. The basin has a population of over 4 million people. Situated within the Red River Basin is Lake Texoma, a 36,000 ha impoundment, which lies on the border of Oklahoma and Texas (Fig. 1). It was created through the construction of the Denison Dam by the US Army Corps of Engineers (USACE) in 1944 and is the 12$^{th}$ largest reservoir in the United States (Sager et al., 2024). The average water elevation is 188 m above mean sea level (AMSL) with the flood control pool reaching 195 m AMSL. The main basin experiences stratification in the summer from July to mid-September, as there is oxygen depletion in the hypolimnion (Hubbs, 1976). Southwest winds enable dissolved solids in the

reservoir waters to be well-mixed; however, when these winds decrease in the summer, separation and subsequent stratification occur.

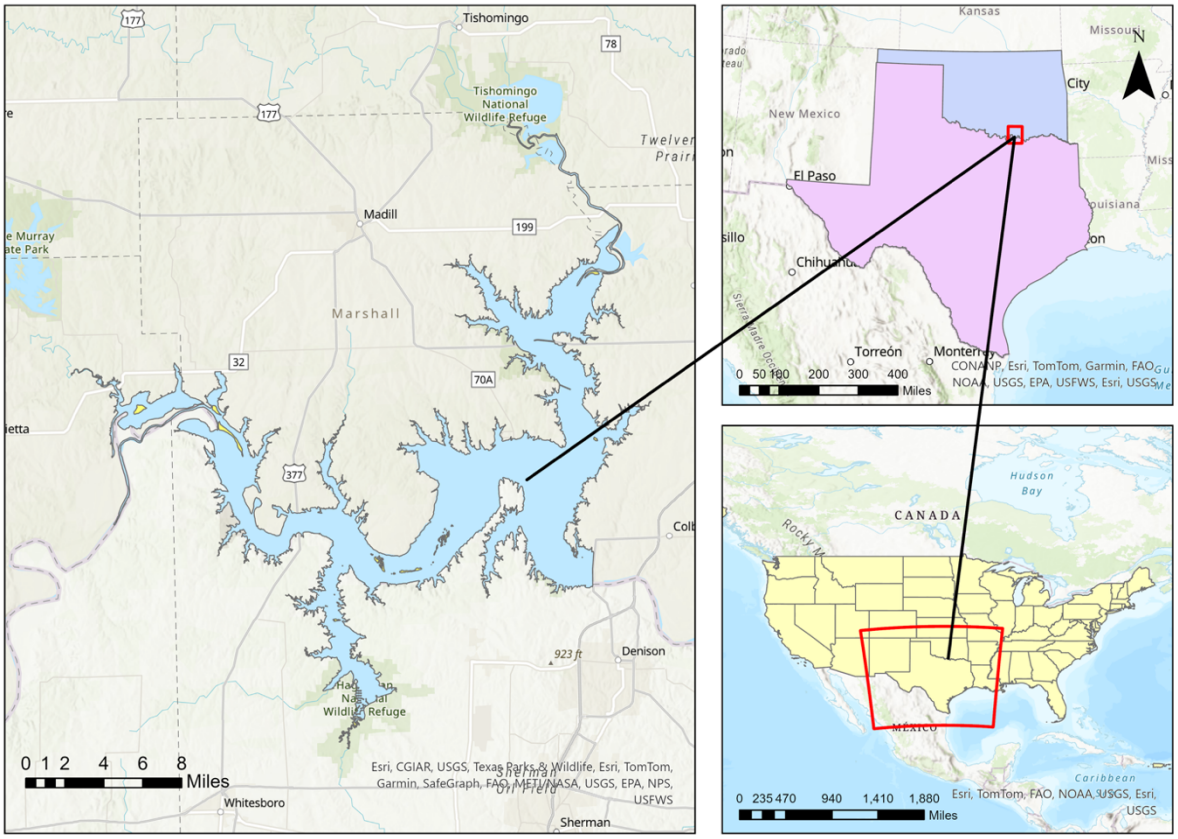


**Figure 1.** Study area location. Lake Texoma is located on the border of Oklahoma and Texas in the United States and is a major reservoir in the Red River Basin.

## 3. Methods

Our analysis involved three main steps. First, we used modeled profiles of temperature and DO to estimate the daily volume of suitable habitat for striped bass in Lake Texoma for the period of 1995 to 2020. Second, we quantified seasonal and interannual variability in the volume of suitable habitat using a generalized additive model. Third, we fit linear regression models to

quantify the relationship between three representations of suitable habitat volume under a summer temperature-oxygen squeeze and striped bass population size and condition during the following winter. These steps were conducted under three potential striped bass thermal limits (25°C, 28°C, and 30°C) and DO conditions of at least 3 mg/L.

### *3.1. Data collection and preparation*

#### *3.1.1. Deep learning model for temperature and dissolved oxygen*

We used a deep learning (DL) model developed by Suaza-Sierra (2024) that predicted vertical temperature and DO profiles by depth using observed data for training and testing. To develop this model, lake storage data and surface water levels were gathered from the Texas Water Development Board's Water Data for Texas portal and used to validate model outputs (Fig. 2). The Texas Water Development Board obtains lake levels from partner organizations that maintain gauges at the reservoirs, taking real-time water elevation measurements and transmitting them back to those organizations. The USACE site DSNT2 and the United States Geological Survey (USGS) site 07331500 collect measurements for the lake. These calibrated and validated models generated a daily time series of mean water depths and the corresponding temperature and DO concentrations from 0-10 m depths in Lake Texoma.

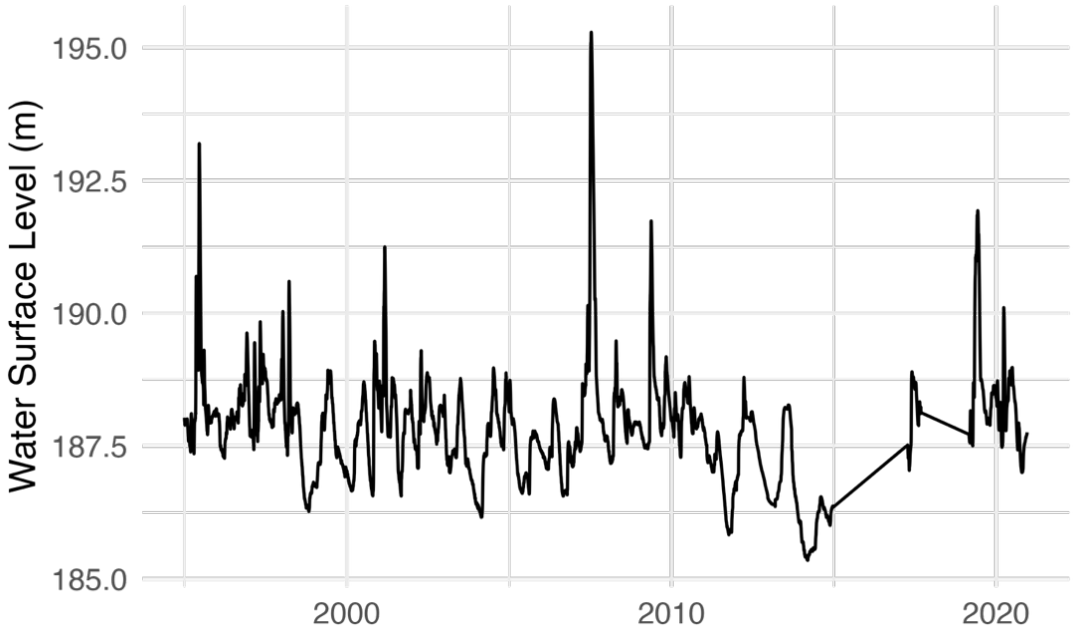


**Figure 2.** Daily water surface levels for Lake Texoma from 1995 to 2020, collected from Water Data for Texas. Water levels vary by season and by year. Straight lines indicate missing data.

The Lake Texoma DL model performed well under both stratified and unstratified seasonal conditions (Average Validation Loss = 0.50°C, Root Mean Squared Error = 0.74°C, Mean Absolute Error = 0.50°C, and $R^2 = 0.99$). The dates spanned January 1, 1995 to December 14, 2020, with missing values from December 31, 2014 to April 10, 2017 and September 9, 2017 to February 28, 2019. Upon completion of the DL model, Suaza-Sierra's final dataset included the date, depth (meters), predicted water temperature (°C), predicted DO (mg/L), and surface water level (meters). Every date had temperature and DO values for 0-10 m depths at 1 m intervals from the surface of the lake.

*3.1.2. Lake Texoma bathymetry*

To calculate the total volume of suitable striped bass habitat from vertical profiles of temperature and DO, we first created a complete bathymetric raster of Lake Texoma by merging four spatial data sets. A partial bathymetric raster is available from the Texas Water Development Board (2003), but only includes bathymetry to the top of the conservation pool of the reservoir (i.e., up to 188.062 m AMSL). However, water surface elevations during our study period frequently rose above the conservation pool into the flood pool, with a maximum daily surface water level of 195.29 m AMSL. We downloaded three digital elevation model (DEM) tiles from the USGS, National Geospatial Program, and mosaicked them to cover the entire area of Lake Texoma. The bathymetry raster was subtracted from this DEM raster to create a raster that included all possible water elevation levels. The map projection of this raster was UTM Zone 14N.

*3.2. Striped bass habitat estimates in Lake Texoma*

We calculated the volume of daily suitable habitat available to striped bass using a trait-based approach, considering specific water temperature and DO requirements. Previous research on the temperature-oxygen squeeze hypothesis suggests that striped bass have a preferred thermal limit of 25°C but can tolerate temperatures as high as 28-30°C when avoiding low oxygen conditions of 2-3 mg/L (Coutant, 2013). Based on these conclusions, three different thermal limits were considered and DO was consistent across scenarios at a minimum of 3 mg/L to estimate the daily water volume of suitable habitat for striped bass in Lake Texoma: (1) an upper thermal preference range of 25°C and minimum 3 mg/L DO, (2) an upper thermal tolerance range of 28°C and minimum 3 mg/L DO, and (3) an acute upper thermal tolerance range of 30°C and minimum 3 mg/L DO.

Using the modeled vertical profiles of temperature and DO values, and the bathymetric raster, we calculated the surface area at each unique water depth (i.e., a horizontal disc with a height of 1 m that spanned the reservoir) and the suitable water volume within the environmental bounds of striped bass for every day and at each depth interval. Since each cell represents one specific elevation value relative to the water bottom, all areas of the lake in the bathymetry raster at or below each water level were identified. The number of associated raster cells was counted and multiplied by the raster cell area (486.06 x 486.06 m) to determine the water level's surface area. For example, if the water surface level for a given day was 193 m, the model would count all cells in the raster with a value of 193 and below, and multiply the cell count by the cell area to calculate the surface area at a 0 m depth. This process would then be repeated at 1 m intervals from 193 m to 183 m, as the hydrologic model had temperature and DO data for the top 10 m of water volume every day. While there is likely more suitable habitat volume beyond 10 m at different times of the year, our models focused on the impact of a summertime temperature-oxygen squeeze. Thus, it was assumed that DO was too low beyond 10 m during the late summer and early fall. At every date and depth, we determined if the given temperature and DO values fell within the defined ranges for each of the three combinations of thermal and oxygen limits. If both values were suitable, the habitat volume at that depth equaled the surface area because depths were at 1 m intervals. If either the temperature or the DO values were outside the defined ranges, the volume was 0. The volumes at 0-10 m depths were then summed to determine the daily habitat volume within the acceptable environmental bounds of striped bass from 1995 to 2020.

### *3.3. Understanding habitat changes, their drivers, and impacts on striped bass*

### *3.3.1. Temporal variation in modeled suitable habitat volume*

To address our first research question (RQ1), we analyzed seasonal and interannual changes in the total volume of suitable habitat for striped bass for the years 1995 to 2020. For seasonal changes in habitat suitability, we grouped the data by day of year and calculated the mean and standard deviations of the daily suitable habitat volume for striped bass under the different temperature and DO assumptions.

For long-term temporal changes in habitat suitability, we used generalized additive models (GAMs) to capture nonlinear seasonal dynamics, long-term trends, and temporal dependence. First, we checked for autocorrelation and found that the daily habitat volume time series exhibited strong temporal autocorrelation (lag-1 autocorrelation $\rho_1 = 0.97$, 0.95, and 0.92 for the upper thermal preference, upper thermal tolerance, and acute upper thermal tolerance ranges, respectively), violating the independence assumption of linear regression models and motivating the use of models that explicitly account for temporal dependence. Thus, we utilized GAMs fitted with the *bam* function in the *mgcv* package in R, which is designed for large time-series datasets (version 2024.04.2+764; R Core Team, 2024; Wood, 2017). Models assumed a Gaussian error distribution and identity link function and were estimated using fast restricted maximum likelihood (fREML) with discretization enabled for computational efficiency.

For each squeeze range, we fit the following model structure:

$$\text{Habitat}_t = \beta_0 + f(\text{Habitat}_t - 1) + f\left(\text{DayOfYear}_t\right) + f(\text{Date}_t) + f(\text{WaterLevel}_t) + \varepsilon_t$$

where: $f(\text{Habitat}_t - 1)$ is a smooth term of the lagged response variable (one-day lag) to account for temporal autocorrelation in daily habitat volume, $f(\text{DayOfYear})$ is a cyclic cubic

regression spline capturing within-year seasonal structure, $f$(Date) is a smooth term capturing long-term trends in habitat availability through time (with time expressed as fractional years, i.e., 1995.003 is January 1, 1995, and so on), $f$(WaterLevel) represents the effect of daily water surface elevation (m AMSL) on habitat volume, and $\varepsilon_t$ is the residual error term. Smooth terms were fit using thin-plate regression splines, except for day of year, which was modeled using a cyclic cubic spline to enforce continuity between the end and beginning of the calendar year. Basis dimensions (k) were set conservatively, and effective degrees of freedom (edf) were used to assess the complexity of fitted relationships. Partial effect plots were examined to interpret the independent contribution of each predictor after accounting for other model components.

### *3.3.2. Influence of environmental variables on habitat suitability*

To address our second research question (RQ2), we manipulated the habitat model to determine which environmental stressor (temperature or $DO_{3mg/L}$) was a greater driver of striped bass habitat suitability under three thermal limits for the temperature-oxygen squeeze ranges. Similar to the daily suitable habitat volume calculation under each temperature-oxygen squeeze range, we quantified daily habitat volume when neither stressor was considered, only DO was considered, only temperature was considered, and both stressors were considered. The mean daily suitable habitat volume was calculated for each of these scenarios and plotted. This allowed for the visual comparison of suitable water volume under each stressor scenario and squeeze range to better understand how the environmental stressors influenced habitat suitability for striped bass in Lake Texoma. The environmental stressor with the greatest difference between total available habitat volume in the first 10 m and suitable habitat volume was considered to have more influence on habitat suitability within that squeeze range.

### *3.3.3. Impacts of a temperature-oxygen squeeze on striped bass*

To address our third research question (RQ3), we fit linear regression models to determine if there was a relationship between the modeled volume of suitable habitat under a temperature-oxygen squeeze and striped bass population sizes and body condition in the following winter. The daily suitable habitat volume estimates were further used to calculate three habitat indicators for each year that were representative of the modeled temperature-oxygen squeeze. The first value was the yearly minimum habitat volume. This represents an abrupt temperature-oxygen squeeze or "pulse" disturbance for the striped bass (Bender et al., 1984). The second value was the minimum average volume across a 14-day rolling period. Starting at the beginning of the year, the volumes associated with the first 14 days were averaged. Moving to the second day of the year, the volumes of the following 14 days were averaged, and so on throughout the year. Of those 14-day averages, the minimum value was selected for each year. Similarly, the third value was the minimum average volume across a 30-day rolling period. These two values represent variations of a long-term temperature-oxygen squeeze or "press" disturbance for striped bass (Bender et al., 1984). The maximum press disturbance was set to 30 days because some studies have shown that striped bass can tolerate water temperatures above their thermal preference, from 25-29°C, for periods of up to one month (Coutant, 2013; Zale et al., 1990). We calculated these three indicators of habitat volume for each of the striped bass temperature and DO squeeze ranges, resulting in nine independent variables for the linear regression models.

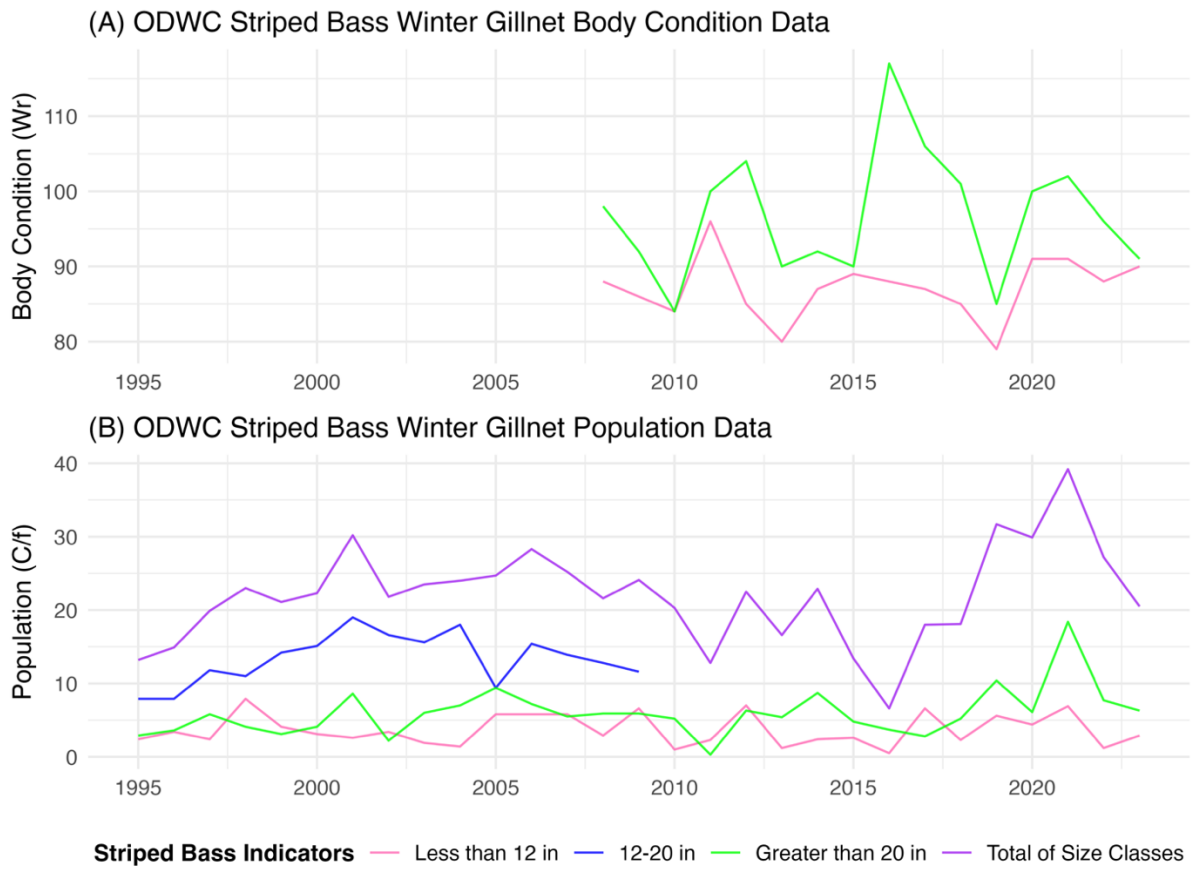


**Figure 3.** Yearly striped bass winter gillnet data collected by the ODWC. The ODWC recorded (a) relative weights (Wr) and (b) fish catch per net night (C/f) for three size classes of < 12 in, 12-20 in, and > 20 in. Wr represents striped bass body condition and C/f represents striped bass population.

The dependent variables of population and body condition were gathered from the Oklahoma Department of Wildlife Conservation (ODWC) Lake Texoma Fisheries Management Plan (Sager et al., 2024; Fig. 3). The plan contains data for the total number, fish catch per net night (C/f), and relative weights (Wr) of < 12 in, 12-20 in, and > 20 in size groups for striped bass from 1982 to 2023. Size classes (< 12 in, 12–20 in, > 20 in) and fisheries metrics (C/f and Wr) follow ODWC and Texas Parks and Wildlife Department (TPWD) monitoring and

management practices and were used here to maintain consistency with the original dataset. Differences in data collection and reporting between years likely reflect staffing changes and updates to data management tools (M. Mauck, ODWC, Personal Communication, 2026). Relative weights are a measure of fish wellbeing and were quantified by the ODWC according to methods outlined by Brown and Murphy (1991) for striped bass (Smith, 2012). For the fish catch per net night, data were available for all years and all size groups, except for 12-20 in groups after 2009. Additionally, data were only available for relative weights from 2008 to 2023 for < 12 in and > 20 in size groups. Since 1993, this data has been jointly collected by the ODWC and TPWD through winter gillnetting samples for a couple weeks in February. This resulted in six dependent variables used in the models: (1) the yearly total catch per net night, (2) the catch per net night of fish < 12 in, (3) the catch per net night of fish 12-20 in, (4) the catch per net night of fish > 20 in, (5) the relative weights of fish < 12 in, and (6) the relative weights of fish > 20 in. Thus, with the 9 independent variables and 6 dependent variables, we ran 54 total linear regression models to evaluate the impacts of a temperature-oxygen squeeze on striped bass population and body condition, with the yearly striped bass descriptor as a function of the temperature-oxygen squeeze habitat volume from the previous summer (Table 1). Statistical significance of models was evaluated at an alpha of 0.05, and significant results were interpreted cautiously as 54 linear regression models inflated type-1 error.

**Table 1.** Different combinations of temperature-oxygen squeeze ranges, indicators of summer habitat volume resulting from a temperature-oxygen squeeze, and striped bass descriptors of population and body condition used to conduct 54 linear regression models. All regressions were run at an annual scale.

| Temperature-Oxygen Squeeze Range | Habitat Indicators | Striped Bass Descriptors |
|---|---|---|
| Upper Thermal Preference (25°C and 3 mg/L) | Minimum Habitat Volume ($m^3$) | Total Fish per Net Night (C/f) |
| | | Fish per Net Night (C/f) of < 12-inch Striped Bass |
| Upper Thermal Tolerance (28°C and 3 mg/L) | Minimum Average Habitat Volume of a 14-day Period ($m^3$) | Fish per Net Night (C/f) of 12–20-inch Striped Bass |
| | | Fish per Net Night (C/f) of > 20-inch Striped Bass |
| Acute Upper Thermal Tolerance (30°C and 3 mg/L) | Minimum Average Habitat Volume of a 30-day Period ($m^3$) | Relative Weights (Wr) of < 12-inch Striped Bass |
| | | Relative Weights (Wr) of > 20-inch Striped Bass |

## 4. Results

### *4.1 Seasonal habitat suitability*

We found consistent seasonal trends in the volume of preferred habitat for striped bass in Lake Texoma (Fig. 4; RQ1). Based on the three defined temperature and DO ranges, the modeled mean suitable habitat volume remained relatively stable in the winter and spring months, declined in early summer, reached lows in late summer and early fall, and rose again in late fall (Fig. 4). On average, the model showed that Lake Texoma had a maximum volume of over 2 billion $m^3$ in the first 10 meters of water depth from the surface. Under the acute upper thermal tolerance range, the average water volume suitable for striped bass decreased by about one quarter to less than 1.5 billion $m^3$ in the summer (Fig. 4C). For the upper thermal tolerance range, average suitable summer habitat volume decreased by about three quarters to 500 million

$m^3$ (Fig. 4B). For the upper thermal preference range, average suitable summer habitat volume decreased to nearly 0 $m^3$, meaning that there was little to no suitable habitat in the reservoir (Fig. 4A). Overall, the results of our model demonstrated that a temperature-oxygen squeeze occurs in Lake Texoma each summer, and more strict biological requirements leave striped bass with less suitable water volume.

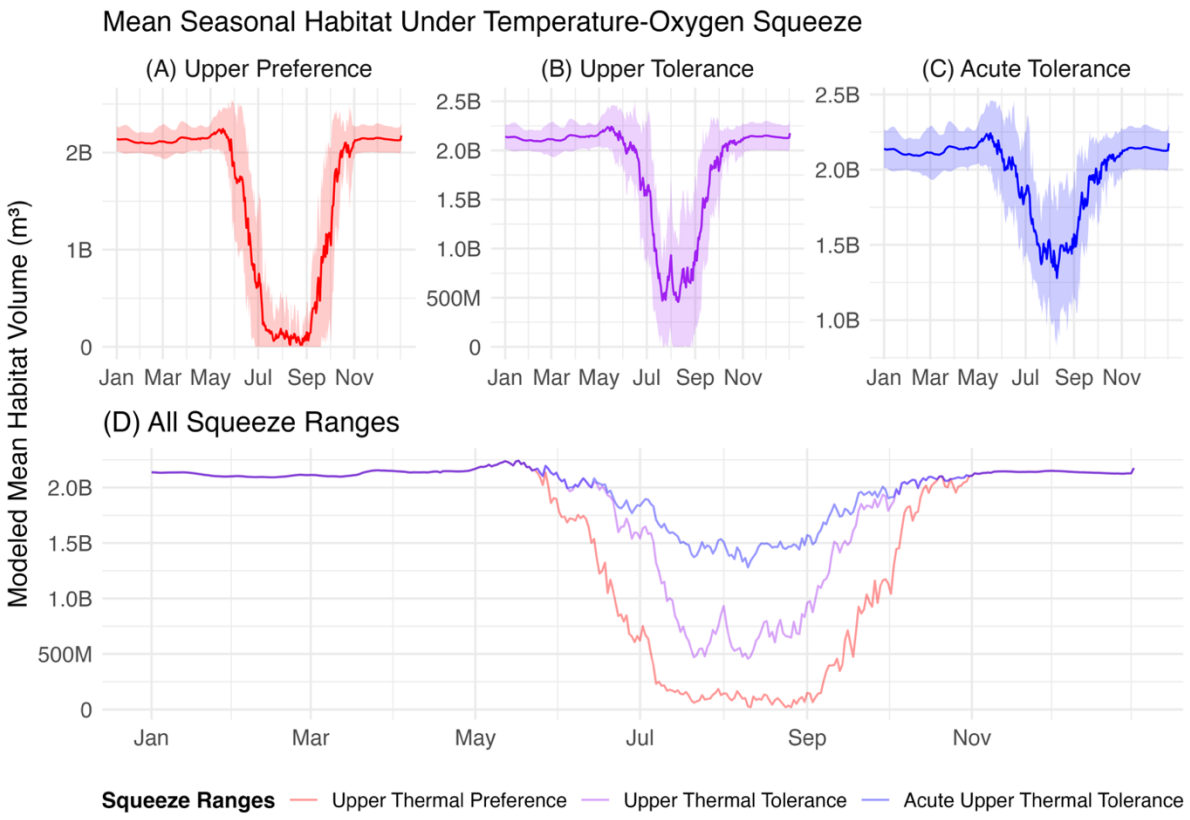


**Figure 4.** Mean seasonal habitat volume suitable for striped bass in Lake Texoma based on three temperature-oxygen squeeze ranges: (a) upper thermal preference (25°C and 3 mg/L), (b) upper thermal tolerance (28°C and 3 mg/L), and (c) acute upper thermal tolerance (30°C and 3 mg/L). (d) Each squeeze range resulted in different volumes of suitable habitat in the summer. In all

panels, solid lines display the mean value calculated across years 1995 to 2020. In panels a-c, the shaded envelopes display standard deviation across those years.

*4.2 Temporal dynamics of habitat suitability*

GAMs explained a substantial proportion of the variability in daily suitable habitat volumes for the upper thermal preference, upper thermal tolerance, and acute upper thermal tolerance ranges ($R^2$ = 0.94, 0.91, and 0.86, respectively; Fig. 5A; RQ1). The one-day lagged habitat volume was a highly significant predictor of habitat volume in each model, indicating strong temporal persistence ($p < 0.001$; F = 3136.54, 4159.53, and 3203.80). While the relationship between habitat volume and lagged habitat was nonlinear (edf = 3.88, 3.85, and 3.57), the plotted smooth trend showed close to proportional relationships between one day's suitable habitat volume and the previous day's suitable habitat volume (Fig. 5B). Nonlinear trends can be explained by the influence of seasonal stratification dynamics on habitat suitability.

Seasonality was also a significant predictor of habitat volume across all thermal thresholds ($p < 0.001$). Cyclic smooths showed a prominent nonlinear mid-summer contraction in suitable habitat volume (edf = 14.74, 14.06, and 11.74; F = 47.60, 34.08, and 33.79; Fig. 5C). Furthermore, the magnitude of the squeeze differed between each range, with the upper thermal preference experiencing many 0 volume days, the upper thermal tolerance experiencing fewer 0 volume days, and the acute upper thermal tolerance experiencing no 0 volume days.

Long-term interannual smooths differed between squeeze ranges. The upper thermal preference range showed an insignificant negative linear trend, the upper thermal tolerance range showed an insignificant near flat linear trend, and the acute upper thermal tolerance range showed a significant nonlinear trend ($p = 0.30$, 0.86, and 0.005; edf = 1.00, 1.00, and 6.56; Fig.

5D). Insignificant linear trends were likely driven by the more restrictive thermal thresholds, which often caused the complete depletion of daily suitable habitat volume. The significant nonlinear pattern indicated dips and recoveries over time, with a large decline in suitable habitat volume around 2010 and increased volume leading up to 2020.

Finally, the partial effect of water level also differed between squeeze ranges. The upper thermal preference range showed a significant nonlinear trend, the upper thermal tolerance range showed a significant linear trend, and the acute upper thermal tolerance range showed a significant nonlinear trend ($p < 0.001$; edf = 4.33, 1.00, and 5.43; Fig. 5E). The upper thermal preference and upper thermal tolerance both showed that as water level increased, so did suitable habitat volume, with the preference range having more of an exponential trend, and the tolerance range having a more proportional relationship between water level and habitat volume. The acute upper thermal tolerance range indicated a different relationship where, as water level increased, so did suitable habitat volume, until water level reached approximately 191 m and suitable habitat volume began to decrease as water level increased. These differences suggest that hydrologic expansion of the upper 10 m disproportionately affects suitable habitat volume defined by the most and least restrictive thermal limits, while the intermediate threshold responds more uniformly.

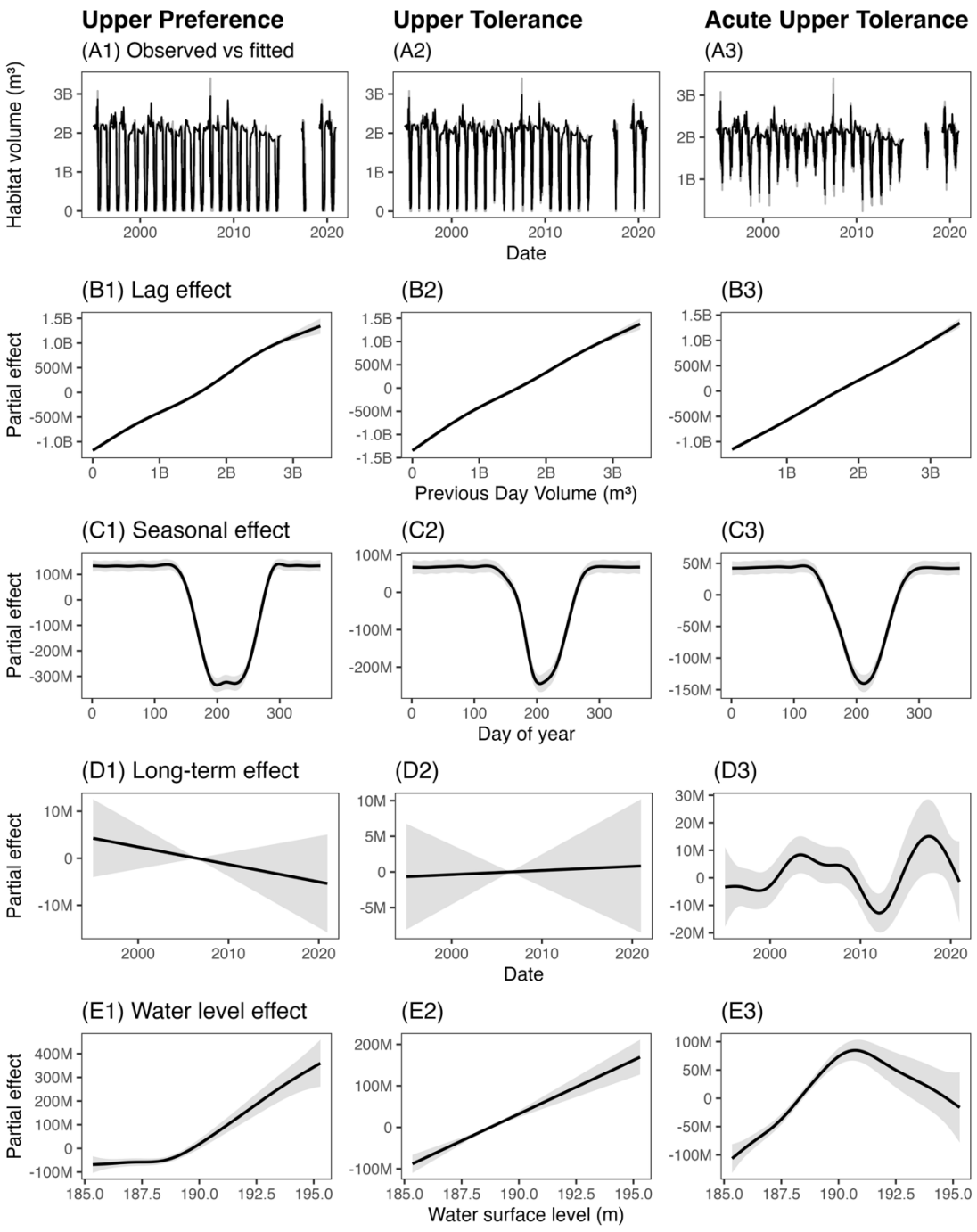


**Figure 5.** Generalized additive models (GAMs) depicting overall model fit (A1-3) and smooth functions of the partial effect of covariates on daily suitable habitat volume. Covariates include day-to-day dependence (B1-3), seasonality (C1-3), long-term trends (D1-3), and water level (E1-3) for each temperature-oxygen squeeze range of upper thermal preference (column 1), upper

thermal tolerance (column 2), and acute upper thermal tolerance (column 3). In the full GAM, grey lines represent observed data and black lines represent the fitted model. The plots for each covariate show 95% confidence intervals in grey and the estimated smooth effect in black.

*4.3 Influence of temperature and DO on habitat*

Fluctuations in available habitat were driven more often by meeting the DO threshold than by the thermal thresholds (Fig. 6; RQ2). Under the acute upper thermal tolerance range, DO was the dominant driver of suitable habitat volume, with temperature exhibiting little influence as the amount of habitat volume available when constrained by DO alone was almost the same as the amount of habitat volume available when constrained by both DO and temperature combined (Fig. 6C). For the upper thermal tolerance range, temperature and DO had a similar influence on suitable habitat volume as they both resulted in around one quarter to two fifths less suitable volume in the summer compared to the control (Fig. 6B). In early summer, DO was a slightly greater driver, and in late summer and early fall, temperature was a slightly greater driver. However, for the upper thermal preference range, temperature was a greater driver than DO as it resulted in about three quarters less water volume of suitable habitat in the summer compared to the control, whereas the DO level threshold only reduced suitable habitat volume by about one quarter (Fig. 6A). In this range, the differences in suitable habitat between temperature-only and DO-only scenarios were not as severe as the differences in the acute upper thermal tolerance range, which showed the thermal threshold exhibiting very little to no influence on habitat. Generally, temperature and DO influenced suitable habitat volume differently depending on the temperature-oxygen squeeze and thermal limits of striped bass.

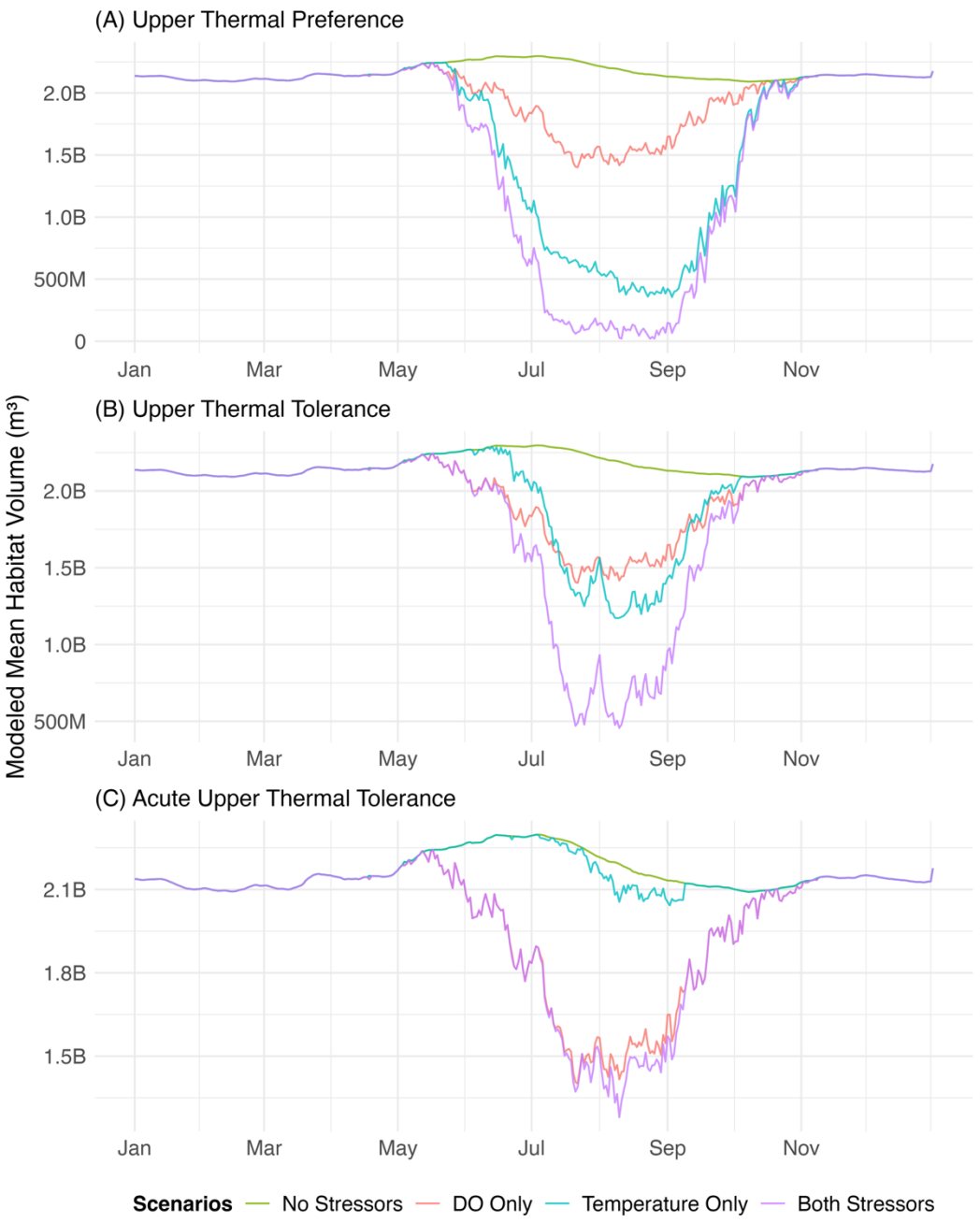


**Figure 6.** Influence of environmental drivers (temperature and DO) on mean seasonal habitat volume suitable for striped bass in Lake Texoma based on the (a) upper thermal preference range, (b) upper thermal tolerance range, and (c) acute upper thermal tolerance range. Each panel shows the total volume of water in the top 10 m of the reservoir (the "No Stressors" scenario in green) and the suitable habitat volumes calculated by considering only DO limits ("DO Only" in

orange), only temperature limits ("Temperature Only" in blue), and both DO and temperature ("Both Stressors" in purple).

*4.4 Impacts of a temperature-oxygen squeeze on striped bass*

Despite dramatic reductions in the water volume of habitat suitable for striped bass each summer (Figs. 4 and 5), we found little evidence for a relationship between the yearly ODWC striped bass winter gillnet data (i.e., fish catch per net night and relative weights of different size classes) and yearly indicators of modeled suitable habitat volume under a temperature-oxygen squeeze (RQ3). The 54 linear regression models showed p-values ranging from 0.047 to 0.978 (Fig. 7). Of these 54 models, only relative weights for the largest size class of striped bass (> 20 in.) showed a significant negative relationship to the annual minimum daily habitat volume calculated from the upper thermal tolerance squeeze range ($p < 0.05$, $R^2 = 0.30$). However, given that all but one of the 11 observations had an annual minimum daily habitat volume of 0 $m^2$, the statistical power of this relationship is heavily influenced by a single data point. We also found one marginally significant positive trend (p-value = 0.06, $R^2 = 0.16$) for the relationship between C/f of > 20 in striped bass and the annual minimum daily habitat volume for the acute upper thermal tolerance range. Figure 7 shows examples of these trends for C/f of > 20 in striped bass and each of the three representations of a temperature-oxygen squeeze under the acute upper thermal tolerance range.

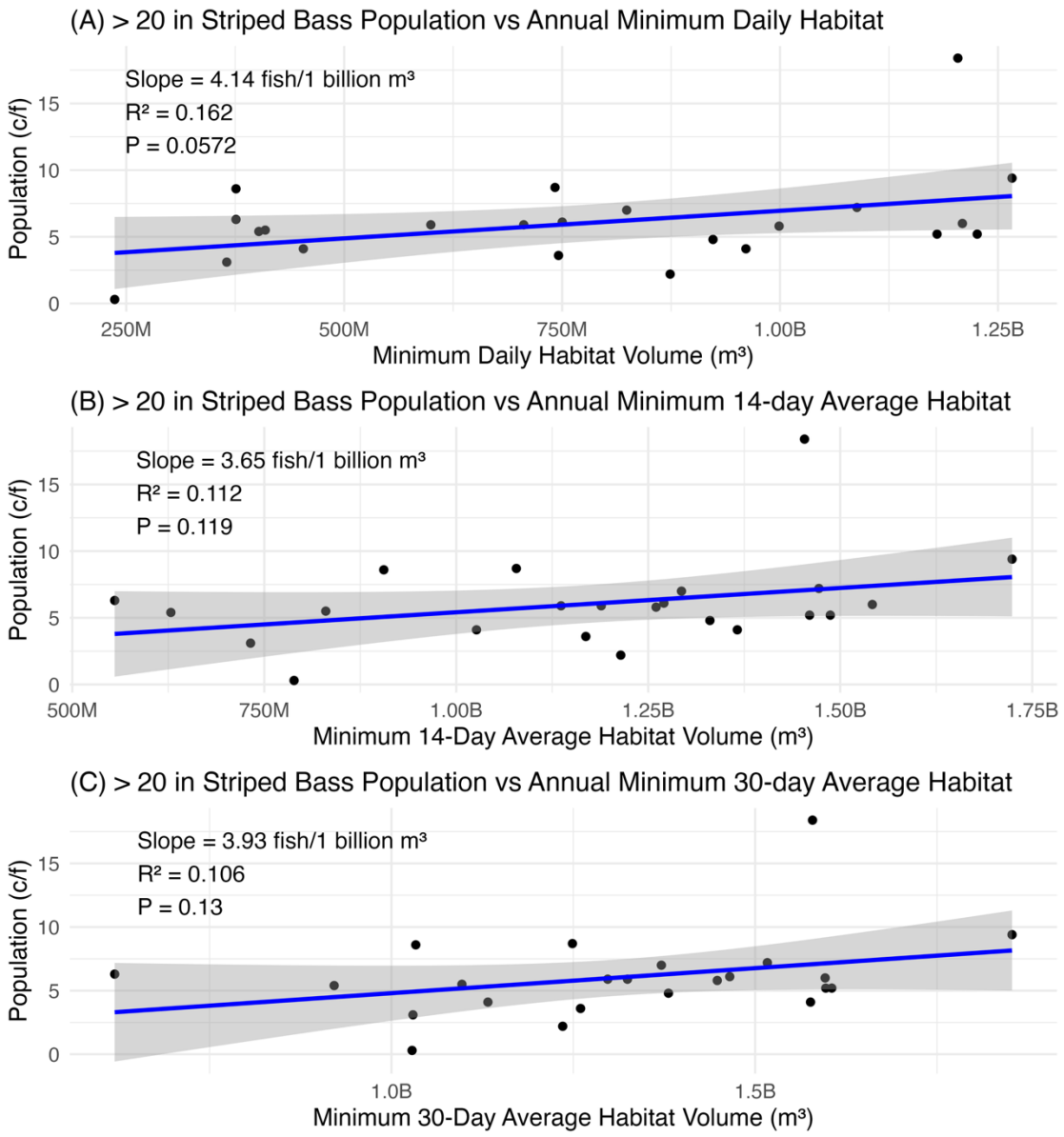


**Figure 7.** Three examples of linear regression models investigating the relationships between the yearly catch (C/f) of greater than 20 in striped bass and (a) the yearly minimum daily habitat volume, (b) the yearly minimum average volume of a 14-day rolling period, and (c) the yearly minimum average volume of a 30-day rolling period under the acute upper thermal tolerance range.

## 5. Discussion

This study provides valuable insights into modeling freshwater habitat suitability for striped bass in Lake Texoma under a temperature-oxygen squeeze, while also exploring whether such a squeeze affected striped bass populations and body condition in Lake Texoma from 1995 to 2020. The modeled habitat available to striped bass in Lake Texoma changed seasonally, with less suitable habitat volume available in the summer within striped bass' environmental bounds. Partial effects of seasonality, day-to-day persistence, and reservoir water level significantly influenced model results. However, insignificant interannual linear trends and a significant nonlinear trend were found for the effect of time, indicating that suitable summer habitat volume due to stratification has not experienced a significant proportional change across years. This model also revealed differences in the strength of environmental drivers, with temperature being a stronger driver of habitat suitability than DO in the upper thermal preference range, temperature and DO being of similar influence in the upper thermal tolerance range, and DO being a stronger driver than temperature in the acute upper thermal tolerance range. Finally, despite annual seasonal changes in the modeled volume of suitable habitat, annual striped bass populations were not significantly impacted by the summer temperature-oxygen squeeze, suggesting that a complex set of processes may be influencing striped bass dynamics in Lake Texoma.

Overall, our models demonstrated that over more than two decades, modeled habitat volume, based on DO and temperature conditions suitable for striped bass, experienced regular seasonal changes. Specifically, the model showed that more restrictive thermal thresholds caused a floor effect where summertime suitable habitat was frequently limited or nonexistent, so changes in water level that increase basin area and volume can have a big effect on suitable

habitat volume when thermal and DO criteria are met (Quillfeldt, 2022). However, at a higher thermal threshold, habitat suitability dynamics are structure-dominated. At higher water levels, stratification intensifies, sharpening thermal gradients, reducing mixing of layers, and accelerating oxygen depletion, which results in less suitable water volume (Birt et al., 2025; Jane et al., 2023; Kraemer et al., 2015). These dynamics may be exacerbated by climate change in the future, as warmer surface water temperatures hold less DO than cooler temperatures (Jane et al., 2021). A study of 57 Texas reservoirs, including Lake Texoma, determined that temperature and DO were correlated to atmospheric predictors, and global climate change is expected to increase water temperatures and decrease levels of DO (Gelca et al., 2016). Thus, climate related changes in water level, air temperature, thermocline, and chemocline in reservoirs have the potential to alter water quality and habitat structure for striped bass and other freshwater fishes. Such alterations can reduce survival of certain fish species and facilitate changes in fish assemblages, geographic distributions, and invasions by non-native fishes (Budnik et al., 2021; Lynch et al., 2016; Miranda et al., 2020). An uncertain climate and its potential to change ecological systems is especially important to consider in water management decisions of already water-limited regions like the Red River Basin.

While the hydrologic and habitat suitability models demonstrate that a temperature-oxygen squeeze is annually occurring in Lake Texoma during the summer, our study showed no indication that a temperature-oxygen squeeze has significantly influenced long-term striped bass population and body condition patterns. In accordance with this finding, Matthews and others (1985) observed that striped bass exposed to high water temperatures did not have any apparent mortalities and were robust with well-developed reproductive organs around the time of their study from 1982 to 1984. Other studies in Oklahoma and Texas reservoirs demonstrated that

striped bass could survive high temperatures for about one month with a sufficient bioenergetic balance (Farquhar & Gutreuter, 1989; Zale et al., 1990). Like Texoma, systems without true refuges have generally shown stable striped bass populations during the summer temperature-oxygen squeeze (Coutant, 2013). Furthermore, the ODWC and TPWD have continuously made changes to length and bag limit restrictions on striped bass in Lake Texoma to meet the needs of both the fishery and angling public, resulting in a relatively stable striped bass population since the establishment of current regulations in 1996 (Sager et al., 2024). Conversely, many studies of different reservoirs in the southern United States have shown evidence of summer mortality, disease, and malnutrition of large adult striped bass due to the squeeze (Coutant, 1978; Coutant, 2013; Lewis, 1985; Lewis et al., 1979; Matthews, 1985; Young & Isley, 2004). Therefore, studies in southern United States reservoirs have differing conclusions regarding the impacts of a temperature-oxygen squeeze on striped bass, possibly due to differences in fisheries management efforts and striped bass adaptability.

One hypothesis for why we did not find evidence of temperature-oxygen squeeze impacts is that, without a significant long-term linear decline in habitat suitability, striped bass might have become adapted to the annual stratified summer conditions in Lake Texoma, enabling them to tolerate warm water temperatures and low DO concentrations. The adaptability of striped bass in Lake Texoma specifically could be driven by the lake morphology, which lacks refuge sites with cool, oxygenated waters (Coutant, 2013; Matthews et al., 1989; Summers, 1982). In these systems without true refuges, striped bass have successfully inhabited mid-depths at temperatures above their preference with no apparent mortalities but sometimes resulted in poor body condition (Farquhar & Gutreuter, 1989; Grimes, 1987; Grimes, 1993; Jackson & Hightower, 2001; Matthews et al., 1985; Matthews et al., 1989). Additionally, conversations

with the ODWC region fisheries supervisor, Matt Mauck, revealed that the lake destratifies in late September or early October, around the time that striped bass become overly stressed, allowing them to narrowly avoid detrimental impacts and further implying that they can tolerate high temperatures for a limited period in the summer (M. Mauck, ODWC, Personal Communication, 2025). Another possible explanation is the timing of striped bass monitoring. While the ODWC and TPWD conduct yearly gillnet sampling, it is done in the winter instead of the summer or fall when lake stratification occurs, causing the temperature-oxygen squeeze (Hubbs, 1976; Sager et al., 2024). Sampling of adult striped bass in Lake Buchanan, Texas, found that relative weights increased significantly per day from summer to early spring (Smith, 2012). Consequently, the effects of a temperature-oxygen squeeze on striped bass may not have been fully captured in the models as body conditions could have improved by the time late winter sampling was conducted.

Another hypothesis is that factors other than a temperature-oxygen squeeze could be influencing striped bass populations and body conditions to such an extent that they mask the effect of the squeeze. The ODWC has identified a combination of potential drivers of striped bass populations, such as the discharge of flood waters, winter kills of threadfin shad (a primary forage species), algal blooms, overcrowding, drought, limited spawning opportunities, angler harvest, and catch and release mortality (Sager et al., 2024). Winter kills of threadfin shad can cause abrupt, system-wide collapses of the forage base before the growing season, strongly limiting striped bass growth and year-class strength in the following year (M. Mauck, ODWC, Personal Communication, 2025), whereas summer mortality is more episodic and confounded with direct thermal and oxygen stress on striped bass (Adams et al., 1982; Sager et al., 2024). Studies by the ODWC reported significant striped bass die-offs and a decrease in fish catch in

Lake Texoma both in 2011 after a harsh winter killed threadfin shad and from 2014 to 2016 following a severe multi-year drought (Fig. 3; Sager et al., 2024). Some of these issues will be further exacerbated by climate change, underscoring a need to recognize the most influential combination of factors on striped bass dynamics.

These factors can also be related to the effects of a temperature-oxygen squeeze, demonstrating the complexity of processes shaping reservoir fish populations. Previous studies of the effects of a temperature-oxygen squeeze on striped bass have revealed that survival is related to the duration of exposure and bioenergetic balance, meaning that greater food availability can help mitigate the impacts of long-term exposure to a squeeze (Coutant, 2013; Thompson & Rice, 2013; Zale et al., 1990). This provides another possible explanation for why we did not find a significant relationship between the temperature-oxygen squeeze and striped bass population in Lake Texoma. However, increased drought and heat waves in the future under climate change can intensify annual water level fluctuations and expose fish to higher water temperatures, which could exacerbate the squeeze and greatly influence striped bass survival (Barrett et al., 2024; Miranda et al., 2020). Air temperatures have become warmer across the Red River Basin and are projected to increase up to 6-7°C by the end of the century in multiple global climate models and high emissions scenarios, increasing water surface temperatures (Bertrand & McPherson, 2019). Future models of habitat suitability should account for the interaction of multiple factors on striped bass population dynamics, informing best management practices for fisheries and water resources in reservoirs under climate uncertainty.

Limitations of this study include potentially insufficient data and model assumptions like linearity and outliers. The hydrological model was missing some temperature and DO data in the years of 2015 to 2019. Additionally, sampling of striped bass size groups and analysis by the

ODWC and TPWD has changed interannually, resulting in only 11 to 23 observations per indicator of striped bass population and body condition (Sager et al., 2024). The missing data could have influenced the results of this study by altering the estimates of suitable habitat volume under each temperature-oxygen squeeze range and impacting model results and insights. Furthermore, the striped bass models assume that the relationships are linear and do not consider outliers in winter gillnet samples or in changes to habitat volume associated with extremes in water level from flood or drought events (Figs. 2 and 3). Despite these limitations and insignificant relationships, it is understood that the temperature-oxygen squeeze hypothesis has mixed support (Coutant, 2013). Conclusions from previous studies conducted in Lake Texoma and insights from Lake Texoma fisheries managers support the idea that a temperature-oxygen squeeze is occurring in the lake but might not be significantly influencing striped bass populations and body condition.

Understanding how future climate change will impact striped bass habitat in reservoirs is imperative for managers of reservoir fisheries. Based on striped bass tolerances to extreme water quality conditions, water management strategies can be developed to control DO and temperature in Lake Texoma to some extent. Reducing nutrient runoff into the reservoir and maintaining water levels can help prevent an increase in algal blooms, which further decrease DO concentrations (Yasarer & Sturm, 2016). Optimization models can be created to manage water withdrawals in the reservoir that control the thermal and chemical regimes for fisheries needs while balancing human water needs (He et al., 2022; Weber et al., 2017). Additionally, managers like Mauck believe that temperature is limiting their ability to grow large fish in Lake Texoma. While conditions that allow striped bass to reach their historic trophy sizes have been lacking, recreational fishing regulations and improved harvest of small adult fish have been

implemented to maintain stable populations of the species and can be further improved in the future (Coutant, 2013, Sager et al., 2024). These monitoring and managing tools can reduce anthropogenic stressors, restore key reservoir features, and provide more refugia habitat for striped bass (Miranda et al., 2020).

Our habitat suitability model represents a novel approach that uses species-specific traits and daily models of reservoir conditions to identify limiting habitats for freshwater fishes and allows us to better understand how they might be impacted by climate change and intensifying stratification. By recognizing that less suitable water conditions are expected in the future in large reservoirs located in the humid subtropical region of the United States, reservoir fisheries managers can better prepare for the management and conservation of economically and ecologically important fish species (Gelca et al., 2016; Miranda et al., 2020). Water is typically managed as a physical resource for human use, overlooking its vital interconnections across ecosystems and importance to other living organisms. Hence, a more holistic water management strategy is needed to protect freshwater habitats (van Rees, 2024). Lessons learned from local and regional scale studies can provide useful insights into designing such management strategies. Our study of Lake Texoma's fishery serves as an important study site as it has a rare, self-sustaining striped bass population that attracts millions of visitors annually and contributes substantially to local economies. However, increasing regional water demand has raised concerns about maintaining adequate water quality and the potential negative impacts on aquatic organisms and recreational activities (Sager et al., 2024). To address these challenges, reservoir and fisheries managers must work together to assess the trade-offs in allocating water for human uses and fisheries needs, particularly in water-limited regions. Thus, the long-term sustainable management of freshwater resources and biodiversity is essential both locally and globally.

## 6. Conclusion

Reservoir fisheries provide irreplaceable benefits to communities and the environment, posing a need to understand how they may be affected by changes in water quality. In Lake Texoma, striped bass, a species of economical, recreational, and ecological importance, is exposed to a temperature-oxygen squeeze, which is expected to exacerbate with rising water temperatures and decreased DO concentrations in the future. The use of a reservoir water quality model and habitat suitability model allowed for the identification of potentially limiting habitats under various temperature-oxygen squeeze scenarios. While the modeled suitable habitat volumes did not have a significant relationship to striped bass populations and body condition in Lake Texoma, mortalities have been observed and striped bass are no longer reaching historical trophy sizes in the reservoir. Thus, further work should be conducted to determine primary factors influencing striped bass populations and sizes in Lake Texoma and aid the ODWC and TPWD in their efforts to maintain a successful striped bass fishery under an uncertain climate. Future work could include targeted summer sampling of striped bass in Lake Texoma, expanding the model to account for other environmental factors and their combined effect on striped bass, and using this study as a framework to investigate the impacts of a temperature-oxygen squeeze on other reservoirs and fish species. Continued research can provide a better understanding of environmental stressors and guide sustainable fisheries management and conservation in major southern and south-central United States reservoirs.

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## Chapter 3: Geographic Implications of the Lake Texoma Study

Freshwater environments are under increasing pressure from climate change, human water use, water scarcity, and land use changes, threatening both ecological and social systems (Kaushal et al., 2017; Matta et al., 2026; Woodward et al., 2010; Vörösmarty et al., 2010). Specifically, reservoirs were designed to manage human needs for water supply, flood control, and hydropower generation, but they are also complex biological systems that must be sustainably managed (Tundisi, 2018). Alterations in reservoir habitat can endanger communities of freshwater species, putting the ecosystem services that they provide at risk (Yasarer & Sturm, 2016). Thus, it is essential to understand how species respond to changes in water quality and structure, both for biodiversity conservation and advancing human-freshwater sustainability. Chapter One discussed the theoretical framework behind these environmental challenges through the lenses of Land System Science (LSS), biogeography, and water resources geography. Chapter Two applied this framework by exploring the mechanisms and impacts of a temperature-oxygen squeeze on striped bass in Lake Texoma, an ecologically, culturally, and economically important reservoir fishery. Findings suggest that striped bass in Lake Texoma show resilience to a seasonal temperature-oxygen squeeze, challenging assumptions about habitat limitations and informing integrated water management. This final chapter will briefly synthesize the insights gained from the empirical research, connecting them to foundational theories, and advancing our geographic understanding of fish conservation and broader freshwater sustainability.

This study of Lake Texoma adds to over four decades of research conducted in the United States on the temperature-oxygen squeeze hypothesis for striped bass, originally proposed by Coutant (1978; 2013). The depth of literature on this topic is quite impressive, but gaps

remain as conclusions are inconsistent across study systems (Coutant, 2013). The results of my research align with a subset of studies showing that striped bass lacking true refuges are often more resilient to the impacts of a seasonal temperature-oxygen squeeze compared to systems where cooler waters with sufficient oxygen were easily accessible in the summertime (Farquhar and Gutreuter, 1989; Grimes, 1987; Grimes, 1993; Jackson & Hightower, 2001; Matthews et al., 1985; Matthews et al., 1989). The results were also consistent with previous striped bass studies performed in Oklahoma and Texas, which generally found that striped bass could withstand temperatures above 25°C without any apparent mortalities (Farquhar & Gutreuter, 1989; Matthews et al., 1985; Zale et al., 1990). Our results imply that striped bass in Lake Texoma exhibit an adaptive capacity, allowing them to withstand annual environmental stressors. Moreover, these findings contribute to contemporary biogeography theories by demonstrating that certain species do not necessarily require optimal conditions to maintain stable populations.

Beyond species-specific responses, these findings also reflect broader social-ecological dynamics emphasized in LSS. My work on striped bass examined how variations in climate and hydrology have influenced long-term freshwater habitat suitability in a managed reservoir system. LSS perspectives emphasize that there are systemic interdependencies between social, ecological, and economic uses of land and water (Verburg et al., 2013). Additionally, feedback loops exist between changes to the land system and resulting ecosystem services, human well-being, and environmental decision-making (Crossman et al., 2013). Thus, environmental change is driven by interacting factors. This study supports LSS perspectives by demonstrating that water quality characteristics (i.e., temperature and dissolved oxygen), basin morphology, hydrology, and temporal dynamics collectively influence suitable habitat availability for striped bass in Lake Texoma. The intensity of seasonal stratification and water level fluctuations are

further affected by the interplay of land management practices, climate, and reservoir operations (Guo & Liu, 2024; Li et al., 2024; Wang et al., 2024). Therefore, feedbacks between land, water, and atmospheric processes have ecological impacts, and a greater integration of water into LSS is necessary to better understand how to maintain the resilience of social-ecological freshwater systems in the face of global and local change.

In addition to these system-level drivers, this study highlights the complexity of biological responses within freshwater ecosystems. Similar to the drivers of reservoir water quality, there are multiple interacting factors that shape fish species survival. Results of this study showed that while striped bass distribution in Lake Texoma is influenced by a seasonal temperature-oxygen squeeze, it does not significantly impact yearly catch and relative weights. Striped bass dynamics are, thus, likely determined by not only the quality of freshwater habitat, but also prey availability, bioenergetics, hydrology, fisheries regulations, and reservoir management decisions (Sager et al., 2024). This result reinforces social-ecological systems principles and provides insights for water resources geography, specifically integrated water resources management (IWRM) and translational water research (TWR). Water is typically managed as a physical resource for human use, while ecosystem health and habitat for freshwater species tend to not be considered in water management decisions or are considered as an afterthought (van Rees, 2024). Applications of IWRM and TWR concepts can successfully navigate the tradeoffs of competing water uses through interdisciplinary perspectives that view water as a resource, risk, and object, as well as habitat and an ecological driver (van Rees, 2024; van Rees & Reed, 2025). Consistent with TWR frameworks and necessary to investigating how water has shaped ecological dynamics in Lake Texoma, the striped bass model considered water as both habitat and an ecological driver.

Despite these theoretical and empirical contributions, it is important to acknowledge key limitations of this study. Coutant and other biogeographers have called for the increased use of modeling tools by fishery and water resource managers to identify limiting habitats as climate change progresses (Coutant, 2013; Elith & Leathwick, 2009; Olden et al., 2010; Wen et al., 2013). Still, it is acknowledged that niche models and habitat suitability models have sources of error and uncertainties that often stem from a lack of available data or do not account for complex ecological interactions (Olden et al., 2010; Wen et al., 2013). The habitat suitability model for striped bass in Lake Texoma encountered similar difficulties. While this work would not have been possible without Suaza-Sierra's hydrologic model of daily temperature and DO estimates, we were limited by data, as the model was missing some daily observations and striped bass sampling of Lake Texoma only occurred once every year in the winter (Sager et al., 2024; Suaza-Sierra, 2024). This caused the model to represent an ecological time lag, instead of directly modeling relationships between an annual temperature-oxygen squeeze and striped bass conditions during the same summer. Modeling efforts would benefit from even greater data availability that allows research concepts like environmental stress to be operationalized, resulting in more accurate conclusions that best support water sustainability and biodiversity conservation.

Even with these limitations, this work contributes to broader challenges in conservation biogeography for freshwater fishes. Challenges include testing current and creating new theories in biogeography, advancing a trait-based biogeography, understanding the interactive effects of multiple stressors, and improving conservation planning strategies for freshwater fishes (Olden et al., 2010). By using a trait-based approach to develop the habitat suitability model, we investigated how striped bass' life history traits influence their dependence on certain habitat

features to better understand how changes in climate and water management might put the Lake Texoma population at risk (Nagy et al., 2024; Olden et al., 2010). However, since striped bass in Lake Texoma were not significantly impacted by an annual temperature-oxygen squeeze over the past 25 years, this population appears to not be limited by their established habitat requirements, challenging the niche conservatism hypothesis. Niche conservatism has been historically debated, especially when comparing species-environment relationships across time and space (Olden et al., 2010; Wiens & Graham, 2005). While some striped bass populations in southeastern US reservoirs have had significant die-offs due to the squeeze, the Lake Texoma population shows adaptation to the stratified summer conditions, implying that striped bass ecology might be geographically and evolutionarily labile (Coutant, 2013). As the Lake Texoma striped bass fishery might be less vulnerable than other reservoirs to future environmental stress, place-based management is necessary to address species population differences and promote biodiversity conservation (Miranda et al., 2020; Verburg et al., 2015).

These theoretical insights have direct implications for how Lake Texoma is currently managed. Management of the Lake Texoma fishery is shared between the ODWC and TPWD, but joint management efforts were not an expectation until more recently. The ODWC and TPWD maintained separate regulations for fish species until 1997, and still conduct annual striped bass gillnet surveys separately, with ODWC and TPWD personnel teams each taking 15 sites (Cummings & Bennett, 2025; Sager et al., 2024). Despite data being shared, analyzed, and presented at yearly Lake Texoma meetings, each agency compiles their own fisheries management plan documents that present data differently (Cummings & Bennett, 2025; Sager et al., 2024). These efforts are also not specifically designed to monitor overall biodiversity and ecological integrity, as they focus on prey species and major sportfish like striped bass. It would

be useful to directly consider ecological integrity in assessments, as losses in ecosystem structure, function, and services have contributed to the global water crisis, leading to not just ecological impacts, but also social and economic (Kaushal et al., 2017). While the ODWC and TPWD have made significant strides toward multi-jurisdictional cooperative management of Lake Texoma, even greater collaboration between agencies and incorporation of interdisciplinary knowledge in reservoir assessments would benefit the multiple stakeholders of water resources in this region.

In addition to institutional coordination, stakeholder perspectives further shape management outcomes. Communications with Matt Mauck, the Regional Supervisor of the Fisheries Division at the ODWC, were essential throughout the process of constructing my thesis. These conversations revealed that the reservoir and fisheries managers of Lake Texoma consider input from scientists, policymakers, and the public when making management decisions that can impact the ecosystem services provided by the region's water resources. Reports state that the Lake Texoma fishery is valued at more than $40 million annually, with sportfishing trips to lakes in Oklahoma typically having an economic value of $60 per trip (Melstrom et al., 2017; Sager et al., 2024). Given the value that Lake Texoma provides, the angling public has shown similar interests to fishery managers, who want to protect natural resources. Anglers have been satisfied with the regulations put on fish catch that have stabilized the striped bass population in Lake Texoma in recent years (Sager et al., 2024). Thus, incorporating principles of LSS and IWRM through interdisciplinary communication and action will help agencies assess trade-offs between human and ecosystem needs to optimize social, economic, and ecological benefits (Cook & Spray, 2012; van Rees, 2024).

By modeling species-specific habitat responses within a managed water system, this research bridges disciplinary gaps and provides insights for balancing ecological conservation with human water needs. Utilization of the habitat suitability modeling tool will aid reservoir managers in Lake Texoma and beyond to put science into action to conserve biodiversity, following the ideals of IWRM and TWR (Islam et al., 2023; van Rees & Reed, 2025). The call for "science for solutions" among the hydrological science community has been especially inspiring in developing this work to result in tools and conclusions that can make a direct impact to reservoir management (Arheimer et al., 2024; van Rees & Reed, 2025). The continued integration of science into policy and management decisions of water resources and freshwater biodiversity will be imperative in addressing future global water sustainability challenges.

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