Nursery Habitat and Hatch Dates of Large River Fishes of the Lower Red River Catchment

by

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Abstract

Many freshwater fishes in North America are of conservation concern. Both fine-and coarse-scale physicochemical conditions affect the quantity and quality of nursery habitat and can influence the hatches and growth of juvenile fishes thereby affecting successful recruitment. My research objectives were to describe nursery habitats for an assemblage of large river fishes, and determine factors related to hatch dates and growth of age-0 fishes of the lower Red River catchment. I used an occupancy model framework to determine how hierarchical factors related to occupancy of juveniles in 38 different species. I found large river nursery habitats were generally defined by reaches with off-channel slackwater habitat, having deep pools but shallow thalweg depths, located further away from dams, and with low percentages of limestone lithology. Species within the same genera often exhibited variable relationships with river slope, amount of large woody debris, channel shape, discharge, and position of reaches within the stream network. I also used a hurdle model framework and linear regression to analyze the hatch success and growth of three Centrarchidae species: Spotted Bass *Micropterus punctulatus*, Orangespotted Sunfish *Lepomis humilis*, and Longear Sunfish *Lepomis megalotis*. Successful hatch probability of all three species was positively related to increasing discharge conditions, whereas hatch frequency was influenced by a variety of species-specific conditions. Successful reproduction in Orangespotted Sunfish and Longear Sunfish was observed much earlier (February) and at lower temperatures than previously documented for the species. I also documented spatial differences in Spotted Bass hatch success during wet versus dry years. Additionally, hatches of all three species varied by stream, with the most consistent and protracted hatches occurring in the unregulated Muddy Boggy Creek. Growth of the three species was positively associated with warmer water temperatures. My results indicate important species-specific relationships that shape nursery habitats use and successful hatching. If the goal is to improve recruitment by fishes, consideration of the important species-specific differences would be beneficial if improvements are made to nursery habitats in the catchment. Moreover, careful consideration of dam operations will help maintain proper phenology and juvenile growth in certain parts of the river network.

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Table of Contents

List of Tables

Table Page

List of Figures

Chapter I: Introduction

Freshwater ecosystems are among the most diverse ecosystems on Earth; however, they may also be the most endangered (Reid et al. 2019). Despite covering only 2.3% of the Earth’s surface, freshwater ecosystems account for 9.5% (126,000 species) of the world’s described animal species (Balian et al. 2008). Dudgeon et al. (2006) lists over-exploitation, flow modification, water pollution, habitat-degradation, and invasive species as the five major threats to biodiversity. Many of these threats work interactively and can include cumulative effects on ecosystems (Richter et al. 1997). Additional human activities further intensify the threats to freshwater biodiversity by affecting many of the natural biological and ecological processes associated with lotic organisms (Allan and Flecker 1993; Richter et al. 1997; Palmer and Ruhi 2019). Impoundments, in particular, have been related to declines of native fish populations, particularly as related to reproductive success (Bergstedt and Bergersen 1997; Larinier 2001; Agostinho et al. 2008; Fenkes et al. 2016).

Dams are now integrated into many fragmented riverscapes and can affect many natural processes of riverine ecosystems. Dams are a significant threat to riverine fishes as approximately 65% of the world’s large rivers are impounded (Grill et al. 2019). Dam construction alters flow and temperature regimes, and have reduced both habitat heterogeneity and riverscape connectivity (Magilligan and Nislow 2005; Olden and Naiman 2010; Brewer et al. 2016). Dams disrupt natural flow patterns including the magnitude, duration, frequency, timing, and rate of change (Poff et al. 1997; Poff and Zimmerman 2010), and similar changes are associated with altered thermal regimes

(Caissie 2006). The remaining fragmented landscape may be problematic for migrating fishes that are downstream but require habitat that is upstream of the dam (e.g., migrating salmon, Hilborn 2013; and Paddlefish, Zigler et al. 2004) or fishes that rely on downstream drift dynamics to position their offspring in suitable nursery habitats (Worthington et al. 2014). Impoundments also alter the sediment regime and downstream power which affects the creation and maintenance of nursery habitats (Grant et al. 2003). For example, the suspended sediment load in the lower Missouri River has been reduced by 83 % since closure of the most downstream dam (Jacobson et al. 2009) and fish nursery habitat has largely been diminished due to the associated flow regulation and channelization (Tracy-Smith et al. 2012). The quality and quantity of both spawning and nursery habitats are key for maintaining successful reproduction and recruitment by fishes (Rochette et al. 2010).

Successful reproduction is influenced by a variety of abiotic and biotic factors. Abiotic factors including temperature, discharge patterns, and photoperiod are the primary environmental factors related to successful spawning. Warmwater fishes often initiate spawning after optimal temperatures are reached in the spring (Holland 1986). Fish species have variable relationships with flow patterns (Kennard et al. 2007); however, flow is an important determinant in reproductive success of many lotic fishes (Brown and Ford 2002). Photoperiod is an additional spawning cue for some species (de Vlaming 1972; Haworth and Bestgen 2017). Some biotic factors that affect reproduction include competition, predation, disease, and behavior. Competition for resources including shelter and mate selection can have a significant effect on reproductive success (Grimardias et al. 2010; Thériault et al. 2011; Evans et al. 2013). In some species, individuals compete for mates, and the presence of the opposite sex influences spawning behavior (Bisazza and Marconato 1988; Balshine-Earn et al. 1998). Predation can also have a significant effect on reproductive success, especially in areas that have been altered to favor predator habitat (Rieger et al. 2004). Moreover, fungus and disease can also play a role in reducing reproductive success (Pickering 1989; Khoo 2000). For example, a precipitous decline in Smallmouth Bass *Micropterus dolomieu* young during the first two weeks post hatch was found to be related to fungus, predation, and disease (Olah and Farkas 1978; Hanson et al. 2009; Walsh et al. 2018). Combined, the biotic and abiotic factors that affect successful reproduction are complex and varied, and they can have a significant effect on the survival of juveniles and the abundance of adults where stock-recruitment relationships have been demonstrated.

The precise mechanisms that warmwater fish use to initiate spawning are not fully understood, though the general approach has been described for some fishes. In many species, hormonal changes triggered by environmental cues can stimulate the release of eggs and sperm. For example, in Honmoroko *Gnathopogon caerulescens*, increases in water temperature and day length stimulate the release of gonadotropin, which triggers the development of oocytes and sperm (Okuzawa et al. 1989). A similar hormonal response occurs in many warmwater fishes (Peter and Crim 1979; Stagey et al. 1979). In some species, spawn timing is influenced by social cues, such as the presence of a mate or the availability of suitable spawning habitat (Marsden et al. 1995; Pender and Kwak 2002). Ultimately, the decision to spawn can be convoluted and is influenced by both internal and external cues. To complicate matters, many large river fishes do not reproduce each year (i.e., skip spawning, Lackmann et al. 2023) and may also reproduce at unusual times of the year (Hamel et al. 2020). For example, Prairie Chub *Macrhybopsis australis* larvae were sampled inadvertently during November, well outside of the assumed spawning window (Wedgeworth 2021). Complex life cycles in riverine fishes may be more common than previously believed and environmental disturbances may disrupt natural spawning phenologies. Thus, we need more information on the timing of spawning and the factors that relate to successful reproduction.

Temperature and flow are two important environmental factors that can affect the mechanisms associated with fish recruitment (i.e., movement of juveniles into the adult population). Water temperature can have a significant effect on the timing and success of spawning and hatching of propagules. For example, warmer water temperatures can cause eggs to develop more quickly (Firkus et al. 2018), but can also increase mortality (e.g., increase the opportunity for fungus, Yanong 2003). Alternatively, cooler water temperatures slow egg and larvae ontogeny (Hardy and Litvak 2004; Eenennaam et al. 2005). Slower development may either reduce mortality risk by providing a more stable environment for embryonic development (Johnston 2006) or increase mortality because the propagules are unable to escape unsuitable habitat (e.g., pelagic spawning fishes, Worthington et al. 2014). Flow is also key to successful fish recruitment because it affects the distribution of eggs and larvae. For example, high flows can transport eggs and larvae downstream, which can increase survival by reducing the risk of predation and increasing the availability of food (McDowall 2009; Cañas and Pine III 2011; Fuentes et al. 2016). Alternatively, for other groups of fishes, high flows can cause eggs and larvae to become entrapped in unsuitable habitat. For example, flood releases in some of the fragmented Great Plains rivers are hypothesized to push drifting eggs and larvae of pelagophil fishes (i.e., broadcaster spawners) into reservoirs where they are less likely to survive (Brewer et al. 2016). Overall, the relationship between temperature and flow is complex and can vary depending on the species and ecosystem. Understanding these relationships, especially for closely related taxa that may respond similarly, is important for managing fish populations and understanding responses of different taxa to perturbations.

Following successful reproduction, lotic age-0 fish experience high mortality rates, though proper nursery habitats can be key to first-year survival. Nursery habitats are used by larval and juvenile fish to increase survival during nascent stages by providing shelter from high water velocity (Keckeis et al. 1997), predators (Baker and Sheaves 2005), and containing higher concentrations of food (King 2004). For example, Aburto-Oropeze et al. (2007) found that reef fish in the Gulf of California experienced increased survival when ample nursery habitats were available. Nursery habitats within large rivers typically are shallow, slow-moving sections of river (Love et al. 2017); however, these habitats can often be limited (Naus and Adams 2018), and juvenile fishes in nursery grounds may compete for resources (Nunn et al. 2012). Although we understand the importance of nursery habitats for riverine fishes, there is a paucity of knowledge describing quality nursery habitats in large river ecosystems. Thus, management of these important nursery habitats within large river systems is often lacking.

Understanding both nursery habitats for juvenile fish and the factors related to successful reproduction are useful for developing conservation and restoration targets. By delineating nursery habitats that are important for large river fishes, managers can work to improve recruitment of rare or valued species by protecting or restoring important habitats. For example, Kaemingk et al. (2007) suggested that newly formed habitats in the Niobrara and Missouri rivers of South Dakota may improve and restore fish diversity. Additionally, the identification of flow regimes beneficial to native fishes can be used by managers to implement environmental flows in regulated rivers. For example, King et al. (2014) documented that environmental flows mimicking more natural flow regimes (i.e., magnitude, duration, frequency, timing, and rate of change; Poff et al. 1997) benefited native fish spawning and recruitment in the Murray River, Australia. Overall, discerning nursery habitats and conditions that lead to successful hatch and growth by juvenile fishes allows managers to better predict variability in year classes.

Basic ecological information on the early life stages of native fishes of the lower Red River catchment is needed for managers to develop proactive conservation and management strategies. Therefore, the goal of my thesis is to develop baseline data that provides agencies with a better understanding of the factors influencing the success of fishes during their early life stages. Specifically, my study aimed to first quantify nursery habitat for the lower Red River fish assemblage, including consideration of reach-scale factors that are often overlooked. Quantifying large river nursery habitat for fishes can provide managers with tools to facilitate habitat protection for young fishes to successfully recruit. However, an understanding of nursery habitat is incomplete without a basic understanding of the environmental conditions that lead to successful hatching. Therefore, my second objective was to determine those factors that are related to successful hatching and growth of age-0 Spotted Bass *Micropterus punctulatus*, Longear Sunfish *Lepomis megalotis*, and Orangespotted Sunfish *Lepomis humilis*. I chose these three fishes because they are economically (i.e., the fishery) and ecologically important and we know surprisingly little about their early life history in general. Collectively, my study results will provide the required information for agencies to develop proactive management strategies relative to recruitment and important nursery habitats of these species, which are becoming increasingly threatened in large rivers (e.g., Missouri River, Goto et al. 2015; Kim 2020).

Study Area

The Red River catchment drains more than 241,00 km^2 from east-central New Mexico to Louisiana and is affected by flow regulation. The upstream portion of the catchment is located in the semi-arid regions west of the Cross Timbers (26 to 29 cm of annual rainfall, Woods et al. 2005) and becomes more humid in the eastern and southern portion of the catchment (127 to 152 cm of annual rainfall, McCorkle et al. 2016). The Red River terminates near the "three rivers confluence" where the Red River, Old River and the Atchafalaya River combine with the distributary outflow of the Mississippi River into the Atchafalaya basin (Figure 1). A mix of savanna, woodland, and grasslands comprise the Cross Timbers region where flow variability and stream drying are common (Mollenhauer et al. 2022). The mainstem Red River is a relatively wide, sand bed river that forms the Oklahoma-Texas border. The upper and lower portions of the Red River catchment are divided by Lake Texoma (impounded by Denison Dam in 1944, Riggs and Bonn 1959). Lake Texoma was impounded for recreation and hydropower and there are currently no minimum flow releases or ramping rates. Discharge releases represent either flood flows or flows associated with power generation, resulting in discharge fluctuations during spring and summer of most years (Figure 2).

My study area was located in the lower portion of the catchment where the Red River is influenced by several major tributaries: the Kiamichi River, Muddy Boggy Creek, Bois D'Arc Creek, Choctaw Creek, and the Blue River. Below Denison Dam, the mainstem Red River is unimpounded until it reaches a sequence of locks and dams in Louisiana. The mainstem river of the lower catchment shifts to an alluvial valley and sand-bed river except for areas immediately downstream of Lake Texoma where downcutting has led to exposed bedrock (Woods et al. 2005). The river is braided in many sections and large woody debris is common in the channel. The major tributaries traverse several upland ecoregions, but the lower portion of the tributaries are separated by impoundments in most cases. The Muddy Boggy River is an exception and is free flowing except for its smaller tributary (Clear Biggy Creek) which is impounded by Pine Creek Reservoir. The upland tributaries typically comprise cobble and gravel streambeds that transition to silt and sand in their lower extents. Unlike the Red River in Oklahoma, the mainstem river in Arkansas has been heavily dredged and contains several wing dike structures that direct flow to create deeper water. As the river progresses downstream, it transitions to a deeper alluvial channel until it reaches the first lock and dam in Louisiana.

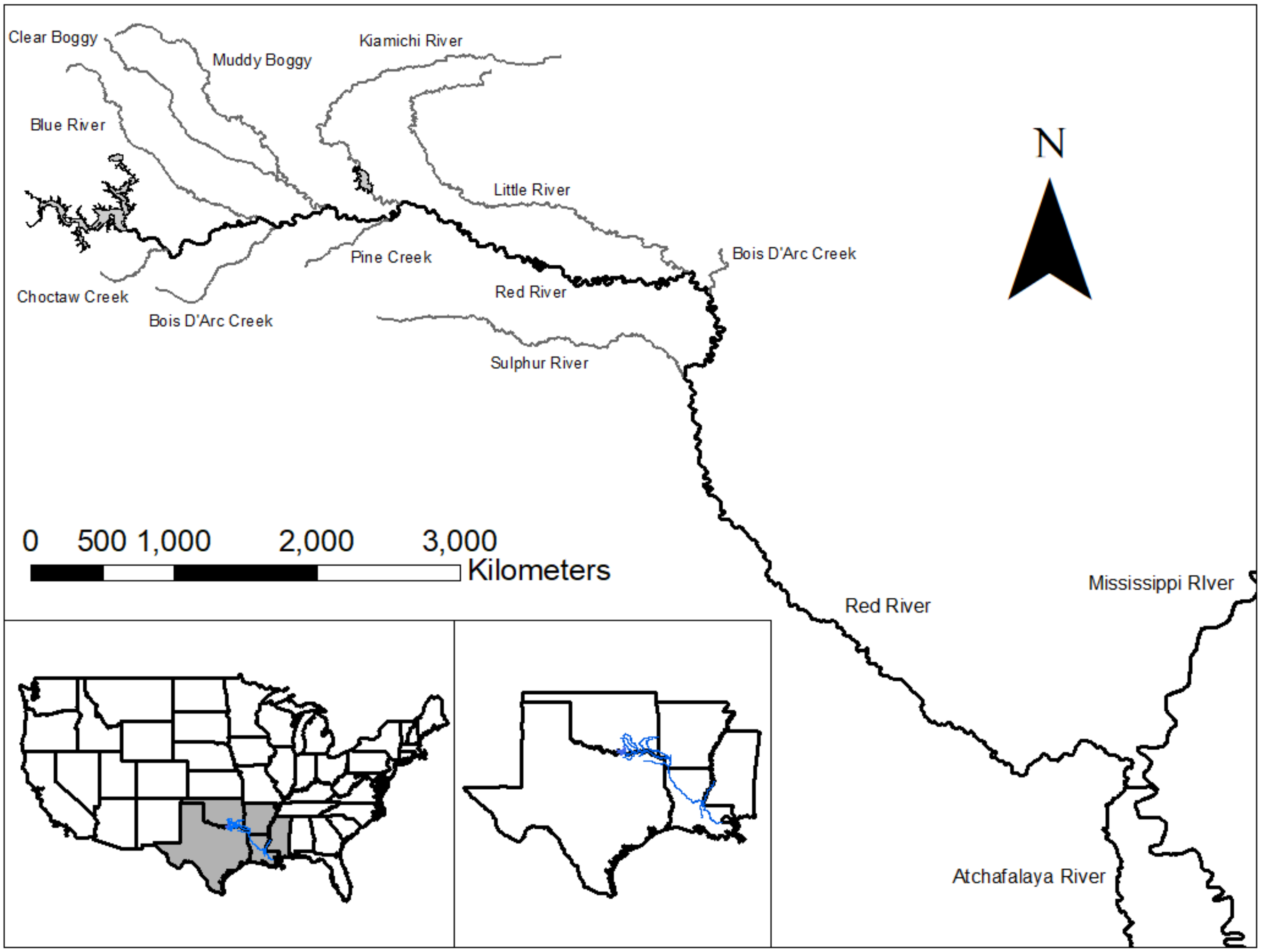


Figure 1. The lower Red River catchment from Lake Texoma to the "three rivers confluence" where the Red River, Old River and the Atchafalaya River meet and combine the distributary outflow of the Mississippi River with the Atchafalaya catchment. Many of the major tributaries are impounded including Bois D'Arc Creek which began holding water in 2021 but is closed to recreation.

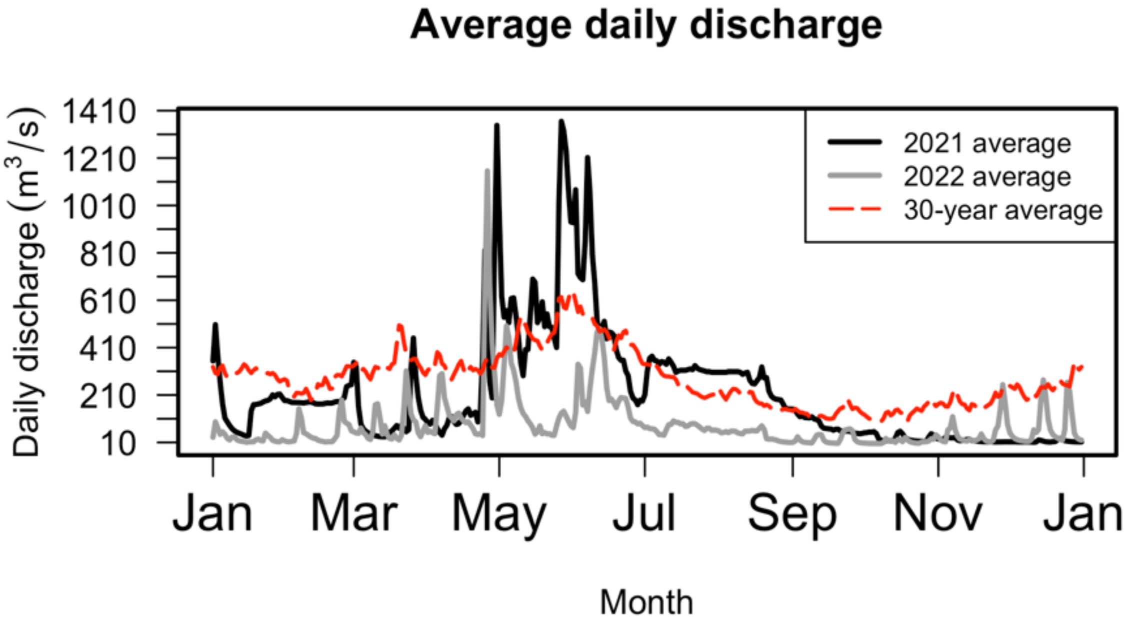


Figure 2. Average daily discharge during 2021 (black line) and 2022 (gray line). The red dashed line indicates the 30-year average discharge. Data were obtained from U.S. Geological Survey, Red River stream gage 07335500 at Arthur City, TX.

Chapter II: Nursery habitat associations of juvenile native fishes in the lower Red River catchment

Introduction

Determining the factors that influence fish distributions is valuable for both ecological understanding and management planning (Schade and Bonar 2005; Esselman and Allan 2011; Devarajan et al. 2020). Distributions, particularly those of riverine species, can be used to discern species assemblages, metapopulations, movement of species, and critical habitat (Dorazio et al. 2006; Falke et al. 2010; Chandler et al. 2015). Rosenfeld and Hatfield (2006) describe how designation of critical habitat continues to be one of the most convoluted problems of species management because of the multifaceted aspects of biology, ecology, locality, and landscape constraints. However, the designation of critical habitats is essential for management planning. For example, Esselman and Allan (2011) developed a reserve stream network for native fishes in the several rivers draining to the coast of Belize in an effort to conserve critical management zones. Nonetheless, many distributional studies do not account for both the fine and coarse-scale habitat constraints placed on species' distributions.

Advances in geospatial analysis have improved our understanding of habitats, including those influencing riverine fish by allowing inclusion of coarse-scale landscape factors. Coarse-scale landscape constraints, such as climate and geology, are considered higher level determinants of fish distributions (Hynes 1975). Thus, as geospatial data and analyses improves, so does the accuracy of distributions via the inclusion of these coarse-scale habitat parameters (Mollenhauer et al. 2022). For example, Torgersen et al. (2006) used existing geospatial layers to analyze the distribution and abundance of riverine fishes in the Blue Mountains of northeastern Oregon. Although advancements have been made in our understanding of riverine fish distributions, few studies have used the inclusion of coarse-scale landscape constraints to delineate the nursery habitats of juvenile fishes, particularly complete assemblages (Devarajan et al. 2020).

Riverine nursery habitats are important for the success of age-0 fishes and are often threatened habitats due to human landscape modifications. Riverine nursery habitats typically provide warmer water temperatures (King 2004), shelter from high water velocity and predators (Reeves 2006), and also tend to have higher concentrations of food (Fuiman and Werner 2002). Refugia from high water velocity is particularly important in large river systems (Rempel et al. 1999; Freeman et al. 2001) as it can better allow young fish to acquire the resources necessary for survival without being displaced (Hart and Finelli 1999). Nursery habitats facilitate higher growth rates in young fishes so they are better prepared to move to alternative habitats and survive their first winter (Humphries et al. 1999). For example, Hoxmeier and Devries (1997) found that American Paddlefish *Polyodon spathula* in the lower Alabama River, Alabama, used oxbow lakes as nursery areas, suggesting a growth benefit prior to reaching reproductive size. Flow modification due to damming, climate change, habitat loss, and invasive species have the potential to decrease both the quality and quantity of nursery habitats (Rochette et al. 2010). The loss of nursery habitat can result in recruitment bottleneck because fishes are the most environmentally sensitive during early ontogeny (Fuiman and Werner 2002).

Nursery habitats used by a myriad of native species occupying large river systems are not well understood, despite the importance of the information for conservation and management. Riverine nursery habitat has traditionally been defined by both relatively shallow water and low-velocity habitats (Love et al. 2017). Additionally, tributaries (Pracheil et al. 2009), pools (de Ávila-Simas et al. 2014), sandbars (Tracy-Smith et al. 2012), side channels (Pease et al. 2006), and floodplains (King 2004) are considered important nursery habitats in mainstem rivers. However, in large, braided rivers some of these channel features can be relatively rare, particularly due to human modifications (Blodgett and Stanley 1980; Mollenhauer et al. 2022). Moreover, there is no spatial context for defining nursery habitat for different assemblage members. For example, Naus and Reid Adams (2018) found differences in juvenile fish assemblages of tributary versus oxbow nursery habitats in the Fourche LaFave River, Arkansas. Therefore, the traditional definition of nursery habitat is too general to effectively aid in developing meaningful conservation and management actions.

Determining occupancy by large river fishes, including the larval and juvenile life stage, can be extremely difficult (Falke et al. 2010; Archdeacon et al. 2018). Rivers with variable flows and wide channels can exacerbate sampling challenges by reducing gear effectiveness (Casselman et al. 1990), leading to a variable and often imperfect species' detection. For example, the sandbed streams of the Central Great Plains, including the Red River, have wide, braided river channels with dynamic flow regimes and nursery habitats that continuously shift through time (e.g., a backwater may be present during wet months and absent during dry months; Matthews and Hill 1980). Because of imperfect detection, the resulting occupancy relationships may be biased (Dorazio 2007) including spurious relationships (e.g., negative association with water depth when detection is affected by discharge, Baker et al. 2017). Therefore, it is important to account for detection when surveying larval and juvenile fishes in large river systems.

My first thesis objective was to determine the factors related to nursery habitats used by juvenile fishes of the lower Red River catchment using an occupancy model framework. By using an occupancy model framework, I assessed the probability of species' occupancy after accounting for gear detection. The identification of nursery habitats is important for understanding native fish ecology, and may benefit agency policy makers interested in protecting critical rearing habitats with limited available resources (Wilson et al. 2005; Seddon et al. 2007; Rahel and Olden 2008; Riaz et al. 2020). It is also beneficial to understand coarse-scale covariates and species-specific differences in defining nursery habitats because similar species may be affected by different constraints, and assuming that they have the same relationships may result in unintentional management consequences.

Methods

Site Selection

I sampled 67 reaches (hereafter sites, ≈ 275-m long) in the lower Red River catchment between Denison Dam, Oklahoma, and the Arkansas-Louisiana state line during the warm-weather season of 2021 and 2022 (Figure 1). Each site consisted of several channel unit complexes including pools, sandbars, back dunes, backwaters, side channels, and runs. My sites were haphazardly chosen in areas across the catchment in relatively close proximity to river access and with permissions from private landowners if applicable. Sites were a minimum of 250-m apart to prevent disturbing fish from adjacent reaches while sampling. Each site was surveyed multiple times over one season.

My sampling season was May through October because this is when age-0 fish tend to occupy nursery habitat before encountering their first winter (Scheidegger and Bain 1995), and it was reasonable to consider sites closed at the species level (i.e., most adults have initiated spawning by May). I sampled each site (i.e., hereafter survey) approximately three times during my sampling season to account for incomplete sampling detection (see statistical analyses section).

Fish Sampling

I sampled age-0 fishes using three different gear types during daylight hours. Using a combination of gears diminishes some of the sampling bias associated with a single gear approach (Clark et al. 2007). For example, passive gears tend to target more active individuals (Fago 1998). Each site was sampled with mini-fyke nets, beach seines, and larval tows. First, I set 3 mini-fyke nets (0.6 m X 4.5 m lead, 0.6 X 1.2 m trap, 3-mm mesh) in < 2 m of water at locations adjacent to the shoreline to target small-bodied fishes (Eggleton et al. 2010). Mini-fyke nets are commonly used to sample age-0 fishes (Eggleton et al. 2010) and sometimes capture higher numbers of fishes when compared to other gears (Fago 1998; Pope et al. 2009; Snow et al. 2017). Next, I used a beach seine (1.8 m X 4.6 m, 3-mm mesh and 1.8 m X 9.2 m, 3-mm mesh) to sample wadeable habitat across the reach using a modified (i.e., smaller) version of the encirclement technique (Bayley and Herendeen 2000). Transects were established throughout wadeable habitat at each site and seine hauls were completed across each transect. Individual seine hauls were limited to 25 m to maintain gear efficiency (Bayley and Herendeen 2000; Lombardi et al. 2014). I quantified total seine distance, seine width, and maximum water depth for each haul and calculated the water volume sampled during each survey. Last, I completed a sub-surface larval tow (0.5-m mouth diameter, 1.65-m length, 500-µm mesh) at a representative location of deeper water (i.e., where I could not seine or set fyke nets). Each tow was completed for approximately 10 minutes and volume of water filtered was quantified using a flow meter (General Oceanics Mechanical Flowmeter Model 2030R) attached to the mouth of the net. All larval fishes were preserved in 70% ethanol and brought back to the lab and identified using Auer's (1982) larval fish key .

Environmental Conditions

I quantified physicochemical factors across multiple spatial scales (i.e., reach, segment, and catchment) to account for the hierarchical arrangement of river ecosystems. My reaches (i.e., sites) consisted of a 200-to 300-m section of the river containing a variety of channel unit features (e.g., sandbars, backwaters, and pools) and the reach reflected the finest scale of my observations. Segments represent the physicochemical conditions between two 5th order tributary confluences, where multiple reaches may occur. Catchments were the total upstream area draining to the downstream end of each sample reach or site. Coarser-scale (e.g., segment and catchment) habitat factors apply to multiple reaches that occur within the same stream segment or catchment (i.e., nested). Stream habitat is inherently hierarchical where finer levels of organization are nested within coarser landscape constraints (Hynes 1975; Frissell et al. 1986; Imhof et al. 1996). For example, finer-scale channel unit conditions (i.e., substrate) used by fish are often influenced by coarse factors (i.e., drainage area and geology) of the surrounding catchment (Wiens 2002; Olson 2012; Mollenhauer et al. 2019).

I quantified six covariates that I hypothesized would relate to detection of juvenile fishes via my sampling gears (Table 1). I measured sampling effort (i.e., area sampled) because greater effort may result in higher species' detection (Simonson and Lyons 1995). I quantified calendar day and water temperature (1.0 °C) simply because as fish grow, they become more active and more susceptible to my sample gears (Goffaux et al. 2005; Guy et al. 2009). Abundance also changes during the first summer of life via spawning events and high early life mortality and can affect detection (Wedgeworth 2021). Water clarity was quantified because clearer water allows fishes to evade gears more easily (Mollenhauer et al. 2018). I also measured dissolved oxygen (1.00 mg/L) because decreased oxygen can inhibit fish detection (Coutant 1985; Tyler and Targett 2007). Lastly, high discharge is a primary factor that affects fish detection because it influences our ability to adequately or effectively sample different habitats (Lyon et al. 2014).

My six detection covariates were quantified at three locations during each survey. The calendar day and sampling effort were recorded for each survey. I measured water temperature (1.0 °C) and dissolved oxygen (DO, 1.00 mg/L) at 0.5 m below the water's surface using a handheld, multi-parameter, water-quality meter (YSI ProDSS). I measured water clarity (1.0 cm) using a secchi disk (Preisendorfer 1986). These measurements were quantified at three locations within each survey and an average was applied to that survey. Daily discharge was obtained from the nearest U.S. Geological Survey stream gage and applied to each survey (Table 3). For the exception of discharge, the other detection covariates were quantified at three locations and the average applied to each survey.

I quantified six occupancy covariates during each survey that I hypothesized would relate to nursery habitat of river fishes (Table 2). Bioenergetics are an important consideration for growth of age-0 fishes (Johnson et al. 2006; Korman and Campana 2009; Nislow et al. 2015); thus, I quantified the percentage of slackwater habitat (forewater, backwater, and side-channels, Galat et al. 2004) using a tape measurer (1.0 m) and range finder (Simmons Volt 600 Laser Rangefinder, 1.0 m) to calculate the percent of the total site area. The area of deeper pool areas at each site was quantified using sidescan sonar Humminbird Helix 12) where I measured the distance in the reach containing large (> 2 m) decline in thalweg depth. Large woody debris (hereafter LWD) and other complex habitat features are used by juvenile fishes to avoid predation (Everett and Ruiz 1993; Roni and Quinn 2001; Thompson et al. 2018). Thus, I quantified the percent of LWD (diameter > 10 cm and length > 1.5 m, Kaeser and Litts 2008) at each site and width-to-thalweg depth ratios (W:D) that describe channel shape (i.e., wide and shallow or narrow and deep). Although cross sectional depths are typically used to describe W:D, I validated use of thalweg depth by comparing a subsample (n =12) of cross-sectional ratios to my thalweg ratios and they yielded similar results (i.e., on average +/- 3.6 m). I also quantified salinity (1.0 ppt) at each survey because conditions can be quite variable in this catchment (Hargrave and Taylor 2010), and salinity can influence the osmoregulatory ability of fishes with a wide range of tolerances in freshwater fishes (Matthews et al. 1977).

I quantified zooplankton density and species composition because of its role as an important food source to juvenile fishes (Bottom and Jones 1990; Fernando 1994). I quantified zooplankton at each site using a vertical planktonic tow net (12.7 cm diameter, 40 cm length, 80-µm mesh). The net was lowered 1.2 m into the water column and pulled back to the surface. Three subsamples were taken across each site. I rinsed the samples and preserved them in 70% ethanol for later processing in the laboratory. Samples were filtered through 300-µm, 200-µm, 100-µm, and 80-µm sieves, respectively, to remove sediment and concentrate samples. Samples were then stored in 70% ethanol. A 1-mL subsample was pipetted (VWR Ergonomic High Performance Single-Channel 100 – 1000 µL pipettor) from each sample, and all organisms in the subsample were enumerated on a 1-mm^2 gridded Segewick-Rafter cell (Wildlife Supply Company, Model# 1801-G20). Organisms were grouped into superior taxa clades (e.g., Cladocera, Copepoda, and Rotifers) and enumerated.

I used U.S. Geological Survey (USGS) stream gage data to quantify aspects of flow patterns to relate to occupancy of nursery habitat at the segment scale. Similar to detection, I obtained the gage data from the nearest USGS gages (Table 3) and applied those data to reaches nested within the same stream segments. However, for occupancy, discharge metrics were calculated over the entire season (May-Oct). I chose the median discharge value for the season to represent the general discharge conditions within the segment.

I used existing geospatial data and GIS tools (ESRI 2022) to calculate my remaining occupancy covariates: distance to nearest upstream dam, river sinuosity, slope, drainage area, limestone lithology, and a landscape disturbance index (Table 2). At each site (reach scale), I quantified the distance of my downstream sample reach to the nearest upstream dam (1.0 km) using the National Hydrology Dataset (NHDplus; U.S. Geological Survey 2017) flowlines and ArcGIS Pro spatial analyst. The Great Plains are home to many pelagic broadcast spawning fishes that require discharge events to successfully reproduce and develop in the downstream drift (Perkin et al. 2015b;

Worthington et al. 2018). Many of these pelagophils are thought to spawn downriver of dams (Mollenhauer et al. 2021), thus, only certain portions of the river may have nursery habitats available depending on the drift requirements (i.e., may be hundreds of kilometers downriver depending on flow, Worthington et al. 2014).

At the segment scale, I measured the sinuosity and slope using the NHDplus flowlines and GIS spatial analysis. The sinuosity (0.1 index) of a stream describes channel meander and was calculated by dividing the thalweg length by the straight-line distance of the segment. Choice of spawning location is associated with channel sinuosity (Fukushima 2001; Lazarus and Constantine 2013); therefore, nursery habitats may also be influenced by sinuosity. Higher stream gradients (i.e., slopes) can increase water velocity (Camana et al. 2016), which can negatively affect nursery habitat occupancy. Therefore, I calculated segment slope (1.0 %) as the change in elevation between the upstream and downstream extent of each stream segment and divided by the thalweg length (i.e., channel distance measured down the middle of the channel; Bain and Stevenson 1999).

I used the NHDplus flow lines, the National Land Cover Dataset, and National Geologic Map Database to calculate the remaining catchment-scale occupancy covariates (i.e., drainage area, landscape disturbance, and limestone lithology). First, I measured the area draining to the downstream extent of each reach (hereafter drainage area, 1.0 km^2), using the watershed tool in ArcGIS Pro. A drainage area describes the size and relative position of a reach within a stream network, and can affect juvenile fish assemblage composition (Schlosser 1995). I also quantified landscape disturbance (hereafter LDI) following Brown and Vivas (2005) using the 2021 National Land Cover Dataset (further

NLCD; Dewitz 2021) and a modification of Mouser et al. (2019) (see below). Human land-use modifications can disproportionately affect the quality and quantity of riverine nursery habitat (Schlosser 1995; Rochette et al. 2010; Britton and Pegg 2011). However, land-cover types tend to be multicollinear because they sum to 100% (Ainiyah et al. 2016); thus, combining land cover into a single index is helpful when analyzing data using multiple regression scenarios (Genovese et al. 2001).

I characterized the level of LDI following a modification of Brown and Vivas (2005) provided by Mouser et al. (2019). First, I assigned each land-use category a coefficient value based on the level of disturbance following Mouser et al. (2019), where higher coefficients are given to features considered to have greater disturbance. For example, urban land use disproportionately affects fish populations compared to pasture land (Cooper et al. 2013) and is, therefore, assigned a higher coefficient (Mouser et al. 2019). Because Brown and Vivas (2005) used more detailed classification than the categories available through the NLCD, I reclassified multiple fine-resolution categories to fit categories available through the NLCD. For example, I combined multiple livestock and pasture categories into a single NLCD category to describe pasturelands. The final coefficient values were: open-space development (1.83), low-intensity development (7.31), medium-intensity development (7.31), high-intensity development (8.67), pasture and hay (2.99), cultivated crops (4.54), and undisturbed (1.00). The remaining undisturbed categories included natural land covers (i.e., open water, barren land, deciduous forest, evergreen forest, mixed forest, shrub and scrub, herbaceous grassland, woody wetland, and emergent herbaceous wetlands). I multiplied the disturbance coefficient by the proportion of the corresponding land class in each drainage area. The sum of these values was used to characterize the catchment disturbance.

Because catchment limestone compositions control local pH and water hardness conditions (Frissell et al. 1986; Stevenson 1997; Lehane et al. 2004) that can affect egg survival (Mount 1973; Parker and McKeown 1987; Swain et al. 2020), I quantified the percentage contained within the catchment draining to each site. I gathered State Geologic Map Compilation (SGMC) geology data from the USGS National Geologic Map Database (Horton et al. 2017), and applied it to the previously calculated drainage areas. I then calculated the percentage each geologic category within the drainage areas.

Statistical Analyses

I built a multispecies single-season occupancy model (MSOM) for juvenile native fishes to quantify nursery habitat use (MacKenzie et al. 2002). An occupancy model allows for the estimation of a probability of occurrence while accounting for incomplete detection by the sampling gears. Variation in both detection and occupancy is explained by collected environmental covariates (Mackenzie 2006). I chose an occupancy model framework because imperfect detection of species by sampling gears is typical within aquatic ecosystems (Britton et al. 2011; Benoit et al. 2018; Wedderburn 2018). Accounting for false absences (i.e., the failure to detect a species when it is present) is important for developing meaningful occupancy relationships (i.e., not just modeling gear inefficiencies).

I built an occupancy model (OM) using temporally replicated surveys at sites to create a detection history (1 if the species is detected, and 0 if it is not). Repeated surveys allows for the model to create estimates of both a detection probability (p_i) and an occupancy probability (ψ_i) (Kéry and Royle 2016). The four assumptions of an OM are: 1) the occupancy state must be "closed" (i.e., to the species and not individuals), 2) there is no unexplained heterogeneity in detection, 3) there is no unexplained heterogeneity in occupancy, and 4) the sites are independent of each other (Bailey and Adams 2005). I met the assumption of species' closure by establishing a season (i.e., May – October) during the spawning season of many native fishes of the catchment (e.g., after the water has reached >18°C). My season ended while juvenile fishes were still using nursery habitat but before water temperatures declined appreciably during late autumn. The second and third OM assumptions were met with the inclusion of both detection (Table 1) and occupancy (Table 2) covariates to explain variation in detection or occupancy probabilities (MacKenzie et al. 2002). I met the final assumption by spacing my sites at least 250 m apart so surveying one site did not influence detection at an adjacent site. Lastly, I included grouping factors to account for the nested nature of river systems to account for pseudoreplication in these data.

I transformed and standardized my data prior to model development. I first began with my detection covariates. Dissolved oxygen, visibility, seining effort, and discharge were log-transformed due to their right-skewedness. Next, I checked my detection covariates to ensure they were not multicollinear ($|r| > 0.50$; Roever et al. 2014) using Pearson's correlation coefficient (Table 4). All detection variables had $|r| \leq 0.35$ and were therefore, retained for the model building process. I completed the same process for my occupancy covariates (Table 5). The percent of limestone lithology, slope, LWD, thalweg depth, W:D, and zooplankton counts were all log transformed due to skewed distributions. Additionally, drainage area, percent of deep pools, and percent of slackwater were transformed into categorical variables based on natural breaks in these data (i.e., bimodal). Categorical transformation of drainage area represented either high (>50,000 km^2) or low (<50,000 km^2) drainage areas, whereas deep pools and slackwater represented either presence or absence. Categorical covariates were tested for independence by evaluating frequency at which they occurred together at each site. The W:D was multicollinear with drainage area ($| r | = 0.69$), salinity ($| r | = 0.53$) and LDI ($| r | = 0.52$). Median discharge was also multicollinear with zooplankton ($| r | = -0.63$). Lastly, slope was highly negatively correlated with sinuosity ($| r | = -0.53$). I retained W:D, median discharge, and slope for model development. Lastly, all continuous covariates were standardized to a mean of zero and a standard deviation of one to improve model convergence and interpretation (Mackenzie and Royle 2005; MacKenzie et al. 2017).

I built my occupancy model using covariates to inform the variation in both detection and occupancy. I built the detection component of the model by choosing two covariates that were hypothesized to share relationships among juvenile fishes and gear detection (i.e., not species specific) so more emphasis could be placed on the occupancy portion of the model. To determine which detection covariates should be retained, I fit a global detection model and assessed the effect sizes of the covariates. Discharge and water temperature had the greatest effects sizes and are commonly used to explain detection (Maire et al. 2019; Carpenter-Bundhoo et al. 2023); therefore, I fit the detection model with these two parameters to avoid overfitting the model. Moreover, I tested for trap effects (i.e., increase or decrease in detection probability after first detection) within the model (Mollenhauer et al. 2018) by assigning a 1 after each detection to see changes in detection probability. The detection component of the model is expressed as:

$$logit(p_{ij}) = \Sigma_{k=1}^{38} a_{0k} + \Sigma_{m=1}^{2} \Sigma_{n=1}^{2} \beta_m X_{n[ij]},$$

$$for\ i = 1, 2 \ldots. N\ for\ j = 1, 2 \ldots. J,$$

$$a_{0k} \sim t(\mu, \sigma^2, \upsilon),$$

$$\beta_m \sim t(\mu, \sigma^2, \upsilon),$$

Where:
p_{ij} = detection probability during survey *j* at site *i*
a_{0k} = mean species deflection *k* from the assemblage mean intercept
β_m = mean assemblage slope
X_n = detection covariates

The occupancy portion of the model was built similarly to the detection portion, except I fit species-specific relationships using the covariates. The detection component was held constant as the occupancy component was fit. I fit the occupancy component with the presence of slackwater, the presence of deeper-water pools, high or low drainage area, and the continuous covariates of thalweg depth, W:D, LWD, distance to the nearest upstream dam, median discharge, slope, and percent limestone lithology. Each species was modeled around the group mean, hyperparameter μ. The interpretation is similar to a random-slopes model where individual species are treated as random intercepts rather than focusing on interspecies differences. The resulting occupancy probabilities are interpreted similar to individual models but with the power of a single model (Kéry and Royle 2016). I also included grouping factors for both segment and sample year to account for any unexplained variability within the model. The inclusion of grouping factors within the model also accounts for pseudoreplication and spatial correlation created by the nested site study design (Wagner et al. 2006).

The occupancy component of the model is expressed as:

$$logit\ (\psi_i) = \Sigma_{k=1}^{38} a_{0k} + \Sigma_{k=1}^{38} a_{POOLk[i]} + \Sigma_{k=1}^{38} a_{SLACKk[i]} + \Sigma_{k=1}^{38} a_{DRAINk[i]}$$

$$+\Sigma_{m=1}^{7} \Sigma_{k=1}^{38} \Sigma_{n=1}^{7} \beta_m X_{n[i]},$$

$$\Sigma_{k=1}^{38} \gamma_{Rk[i]} + \Sigma_{k=1}^{38} \gamma_{Yk[i]}, \text{ for i = 1, 2….N,}$$

$$a_{0k}, a_{POOLk}, a_{SLACKk}, a_{DRAINk} \sim t(\mu, \sigma^2, \upsilon),$$

$$\beta_{mk} \sim t(\mu, \sigma^2, \upsilon),$$

$$\gamma_{Rk} \sim t(\mu, \sigma^2, \upsilon), \text{ for R = 1, 2….3,}$$

$$\gamma_{Yk} \sim t(\mu, \sigma^2, \upsilon), \text{ for Y = 1….2}$$

Where:
ψ_i = species probability of occurrence at site *i*
a_{0k} = species *k* deflection from the assemblage mean intercept
a_{POOLk} = categorical variable deep pools where no deep pools was the reference
a_{Slackk} = categorical variable slackwater where no slackwater was the reference
a_{DRAINk} = categorical variable drainage area where high drainage area was the reference
β_{mk} = species *k* deflection from assemblage mean slope *m*
X_n = continuous occupancy covariates
γ_{Sk} = segment grouping factor for species *k*
γ_{Yk}= year grouping factor for species *k*

I used vague, uninformative priors to calculate the posterior distributions. When informative prior information is not available, vague uninformative priors are used to give the model a starting point for estimating parameters with minimal effect on the model results (Kruschke 2014; Kéry and Royle 2016). Vague truncated normally distributed priors (i.e., t-distribution) were given to main effects, and vague gamma priors were applied to their standard deviations. The t-distribution adds a normality parameter υ (see equation above) which accounts for heavy tails and can improve model fit (Kruschke 2014). Lastly, uniform priors were given to the detection and occurrence intercepts to aid in model convergence.

I assessed the posterior distribution of the model and covariates using Markov Chain Monte Carlo (MCMC) simulations (Marjoram et al. 2003). Due to the large number of covariates included in the model, 150,000 iterations were run on 3 chains with a burn-in of 10,000 and thinning of 5. The model was fit using the package jagsUI (Kellner 2015) and the program JAGS (Plummer 2003) within the statistical computing software R (Version 4.2.2, R Core Team 2022). The back transformed logit parameter was used to calculate the detection and occurrence probabilities. Model convergence was evaluated using the Brooks-Gelman-Rubin statistic $\hat{R}$ (Gelman et al. 1992, 2000), where parameter estimations, $\hat{R} < 1.1$, indicate appropriate mixing of chains. Lastly, I used an omnibus goodness-of-fit test (i.e., evaluating chi-squared discrepancies; MacKenzie and Bailey 2004), where $\hat{c}$ values within 1.00 to 1.02 are considered to have adequate dispersion (Kéry and Royle 2016). Additionally, the Bayesian p-value also provides a posterior predictive check, where values near 0.5 (i.e., values that are not close to 0 or 1) are considered to fit the observed data (Kruschke 2014; Kéry and Royle 2016; Conn et al. 2018).

Results

Fish Sampling

I completed 242 surveys across 104 (37 repeated across both years) sites in the lower Red River catchment during 2021 and 2022 (Table 6). During 2021 and 2022, 54 sites and 97 surveys, and 50 sites and 145 surveys were completed respectively. Of the 67 sites, 39% (n = 26) were in the Oklahoma portion of the Red River (hereafter OK Red), 36% (n = 24) in the Arkansas portion of the Red River (hereafter AR Red), and 25% (n=17) were located in the major tributaries of Texas, Oklahoma, and Arkansas (hereafter tributaries).

I sampled 246,172 fishes during both sample seasons, including 70 species and 37 genera (Table 7). The most abundant species was Red Shiner *Cyprinella lutrensis* (n = 117,736), followed by Bullhead Minnow *Pimephales vigilax* (n = 47,060), and Mosquitofish *Gambusia affinis* (n = 15,057). Conversely, the rarest species with only one individual sampled were Blackspotted Topminnow *Fundulus olivaceus*, Flier *Centrarchus macropterus*, Highland Stoneroller *Campostoma spadiceum*, Ribbon Shiner *Lythrurus fumeus*, and Yellow Bullhead *Ameiurus natalis*. I sampled juveniles of 42 different fishes in the families Atherinopsidae, Catostomidae, Centrarchidae, Cyprinidae, Clupeidae, Fundulidae, Ictaluridae, Lepisosteidae, Moronidae, Percidae, and Sciaenidae (Table 7). Although the abundant species were the same between juvenile and adult life stages, the rarest species with juveniles collected was the Skipjack Herring *Alosa chrysochloris* (n = 2). Juvenile fishes had higher counts in the mainstem river compared to the tributaries (i.e., 26,482 in the Red River and 7,761 in combined tributaries); however, mainstem sites accounted for 75% of the total sites, whereas the tributaries accounted for only 25%.

Environmental Conditions

Physicochemical conditions varied among sites and by stream location (i.e., OK Red, AR Red, and tributaries) particularly among the tributaries and the mainstem Red

River (both AR and OK sections) (Table 8). As expected, drainage areas increased with sites downriver from the tributaries (3,280 km^2) through the OK Red (115,170 km^2) to the AR Red (128,723 km^2). The OK Red had a shallower thalweg depth, on average (2.07 m), when compared to both the AR Red (2.69 m), and tributaries (2.39 m). Tributaries had generally deeper and narrower river channels, whereas the mainstem Red River had wider and shallower channels. However, the AR Red had a deeper and narrower channel compared to the OK Red. As expected, given the ecoregion differences, the tributary sites had higher limestone composition (9.46 %) compared to both portions of the mainstem Red River. The major tributaries also had lower average salinity levels (0.27 ppt) when compared to the Red River (OK Red – 0.51 ppt and AR Red – 0.40 ppt). Lastly, sinuosity and LDI were, on average, more similar across stream locations than other conditions (Table 8).

Average detection covariates varied across surveys; however, covariates were more similar between stream locations, on average, than occupancy covariates. Surveys completed earlier in the season had lower average water temperatures (27.4 °C), and higher scaled discharges (0.003), on average, than later surveys (temperature – 28.3 °C, and discharge – 0.0008). Tributary reaches were surveyed, on average, earlier (calendar date - 73) than those in the mainstem Red River (OK Red - 84 and AR Red - 87) due to river access (i.e., some ramps are only useable during higher discharge conditions). Water clarity was higher during surveys of the OK Red (43.2 cm) than both the AR Red (28.6 cm) and tributaries (36.8 cm). Lastly, dissolved oxygen and seining effort was similar among surveys and stream locations.

Occupancy Modeling

Prior to model building, I omitted data from a few sites and species. I retained data from 99 of the 104 sites for analyses. I omitted 5 sites because some had single surveys and others were missing physicochemical covariate information. Additionally, I retained data on 38 species for modeling. I omitted 4 species from model development because they were either ubiquitous, extremely rare, or non-native. Species with extremely high (e.g., Red Shiner and Mosquitofish), or low naïve occupancy (e.g., Striped Bass) were removed from the dataset to aid in model convergence. I also omitted Common Carp because the focus of my study was native fishes.

My final model converged and had adequate fit (Table 9). All model parameters displayed appropriate chain mixing with $\hat{R}$ <1.1 (Kéry and Royle 2016). The MSOM displayed adequate dispersion of posterior values ($\hat{c}$ of 1.003), and adequate goodness-of-fit with a Bayesian p-value of 0.505.

The probability of detection and occupancy varied by species; however, some relationships with covariates were shared though there were differences in effect sizes. The group mean detection probability was 0.19, with the individual species ranged from 0.04 to 0.70 (Figure 2). Species detection increased with increasing water temperatures, and discharge conditions (Table 10; Figure 3). Further, the group mean occupancy probability was 0.57 with the individual species ranging from 0.15 to 0.96 (Figure 2). All 38 juvenile species had positive occupancy relationships with reaches having deep pools and slackwater habitats present, and the distance from the nearest upstream dam (Figures 4-7). Lastly, all species had a negative occupancy relationship with deeper thalwegs and the percentage of limestone within the catchment (Figures 4-7). Although species had the same relationship with thalweg depth, the effect size of these relationships differed (Figure 11). Some species (e.g., Longear Sunfish and Bantam Sunfish *Lepomis symmetricus*) had relatively weak negative relationships, whereas Warmouth *Lepomis gulosus* and Redear Sunfish *Lepomis microlophus* had stronger relationships.

Several nursery habitat relationships were species specific (Table 11). The occupancy relationships with drainage area, segment slope (Figure 8), amount of LWD, W:D ratio (Figure 9), and seasonal median discharge (Figure 10) were variable among species and taxonomic groups. Five species (Chub Shiner *Notropis potteri*, Gizzard Shad *Dormosa cepedianum*, Mississippi Silverside *Menidia audens*, Threadfin Shad *Dormosa petenense*, and White Bass *Morone chrysops*) were positively associated with larger drainage areas, whereas all other species were negatively related. The majority of juvenile species were negatively associated with LWD except for Channel Catfish *Ictalurus punctatus*, Longnose Gar *Lepisosteus osseus*, and Slough Darter *Etheostoma gracile*. Seasonal median discharge had a generally positive relationship with most juvenile fishes; however, Longear Sunfish *Lepomis megalotis*, Orangespotted Sunfish *Lepomis humilis*, Logperch *Percina caprodes*, and Silver Chub *Macrhybopsis storeriana* had negative relationships with median discharge. The segment slope and W:D ratio were split between positive and negative relationships among all species. For example, Dusky Darter *Percina sciera* exhibited a strong negative relationship with slope, whereas Freshwater Drum *Aplodinotus gruuniens* had a strong positive relationship (Figure 8). Moreover, Blacktail Shiner *Cyprinella venusta* had a strong negative relationship with W:D ratio, whereas Shoal Chub *Macrhybopsis hyostoma* exhibited a strong negative relationship (Figure 9). Lastly, the grouping factors of segment and year accounted for variance of 1.425 and 1.194 respectively.

Discussion

My results indicate that nursery habitats in large rivers are largely context dependent, even for closely related species. Nursery habitats in the lower Red River can generally be described as reaches containing off-channel slackwater habitat, having deep pools, with shallow average thalweg depths, further away from dams with lower percentages of limestone geology. Although taxonomically similar species are often thought to use similar habitats that is not always the case (Lowe-McConnell 1987). For example, I found that Green Sunfish *Lepomis cyanellus* and Redear Sunfish *Lepomis microlophus* were positively associated with wider, shallower channels, whereas Bantam Sunfish, Bluegill *Lepomis macrochirus*, Longear Sunfish, and Orangespotted Sunfish tended to occur in reaches with narrower and deeper channels. Although these species are not of conservation concern, it demonstrates the perils of assuming closely related species share habitat choices because they have other shared traits (e.g., body morphology, feeding strategies). Changes in channel slope also appeared to provide context dependency to nursery habitats where fishes in the genera *Ictalurus*, *Ictiobus*, *Pomoxis*, *Lepomis*, and *Dorosoma* all had species with opposing relationships with segment slope. Increased slope can lead to stronger water velocities (Gordon et al. 1992), create more heterogenous water depths (Troutman et al. 2007), and diversify the channel units within the river segment (Harvey and Bencala 1993). It appears that more common species may be more tolerant of homogenous water depths with low water velocities (e.g., Spotted Bass and Bluegill); however, rarer species (e.g., Skipjack Herring and Bigmouth Buffalo) may benefit from the higher water velocity that creates more diverse habitats (Marchetti and Moyle 2001; Walters et al. 2003). Although the mechanisms for these associations are unknown, these varying relationships within closely related species indicate that river slope and W:D lead to different nursery habitat for assemblage members.

The nursery habitat in the mainstem Red River tended to be associated with species with certain traits, whereas the limited nursery habitat available in the tributaries were important to a variety of species. Fish species such as the Mississippi Silverside, Gizzard Shad, Threadfin Shad, White Bass, and Chub Shiner were more strongly associated with the mainstem Red River, whereas all remaining species (87%) of the species I collected were more strongly associated with the major tributaries. The five species primarily associated with the mainstem are all open substrate spawners (Balon 1975) that scatter their eggs, although specific requirements (i.e., substrate type used, parental care) differ among the species (Frimpong and Angermeier 2010). Chub Shiner, for example, is likely a broadcast spawner that relies on moving water to maintain eggs and larvae in suspension during development (Worthington et al. 2018) and typically spawning over sand substrate (Lee et al. 1980). The tributaries in the lower catchment also contain some sandy substrate; however, there are more areas consisting of mud, fine gravel, silt, and rocky shoals when compared to the mainstem (Pigg and Hill 1974; Pigg 1977) and their fragment length has been sufficiently shortened in many cases due to impoundments. Tributaries were positively associated with fish recruitment in the Missouri River of South Dakota (Pracheil et al. 2009). Tributaries tend to provide lower discharge conditions than mainstem rivers (Beckmann et al. 2005; Pracheil et al. 2009), and may function as important source populations for many assemblage members

(D’Amelio and Wilson 2008; Laub et al. 2018). Unfortunately, the impoundments in the catchment may limit available nursery habitat in the tributaries, emphasizing the need to prevent further degradation of the remaining free-flowing tributaries.

Although some species shared relationships with physicochemical factors, the strength of the relationships varied among species, indicating vulnerabilities for some species. Longear Sunfish, Bluegill, Orangespotted Sunfish, and Bantam Sunfish all had weak negative relationships with thalweg depth, whereas the effect size of this parameter was much stronger for Warmouth, Redear Sunfish, and Green Sunfish probability of occupancy. Juvenile fishes, in general, tend to be associated with shallower channels (Lobb and Orth 1991); however, some species may be more vulnerable to channelization that would result in wider and narrower channels (Langler and Smith 2001). Stronger competitors (e.g., Spotted Bass, Longear Sunfish, and White Bass) may have weaker relationships with thalweg depth because of their ability to thrive in variable habitats or serve as more of a generalist related to habitat (Travnichek et al. 1995; Guenther and Spacie 2006; Edge et al. 2020). As another example, occupancy of most juvenile fishes was negatively related to the percentage of LWD in the reach. Although some juvenile fishes use large woody debris for shelter of mainstem rivers (Cederholm et al. 1997; Roni and Quinn 2001; Clark et al. 2007), LWD may also increase predation risk due to the association with piscivores (e.g., Catfishes and black basses; Daugherty and Sutton 2005; Goclowski et al. 2013). In large rivers, juvenile fish likely benefit from complex habitat with lower velocity that offers both habitat for spawning fishes but also juvenile development but with reduced predation risk.

Contradictory to my hypothesis, seasonal discharge was generally positively related to juvenile fish occupancy and may be related to food availability or proximity to spawning areas. During low discharge seasons, many backwaters, forewaters, and side channels were somewhat disconnected from the river or in some cases, completely dry. Higher discharge conditions facilitate enhanced connectivity between the main river channel and important slackwater habitats (Górski et al. 2013; Spurgeon et al. 2019) to provide access to important nursery grounds (Junk et al. 1989; Poff et al. 1997; Zeug and Winemiller 2008). Higher discharges conditions can lead to lower zooplankton concentrations within river channels (Spaink et al. 1998; Thorp and Mantovani 2005). However, zooplankton may be residing in off-channel slackwaters in higher concentrations (Vietz et al. 2013) than in the main channel. The positive associations between juvenile fishes and both slackwater and higher discharge conditions emphasizes the importance of the connectivity between the off-channel habitats and the main river channel. In dynamic river systems such as the Red River, nursery habitats may function temporally where slackwater nurseries shift in location and quantity though the course of a year. The ephemeral nature of off-channel nursery habitats can cause juvenile fishes to be cut off from the main river channel for a period of time (Lyon et al. 2010), presenting a unique transient definition of large river nursery habitats, one that temporally oscillates with discharge conditions. The importance of connection between mainstem and off-channel habitats may also be due to the proximity of spawning habitat and rearing habitat (Richards et al. 1992). For example, Smallmouth Bass has been shown to segregate spawning and rearing habitat where rearing habitat provides areas of lower predation risk and bioenergetic benefits (Miller and Brewer 2020). A similar situation could be anticipated for large rivers where suitable nursery habitats are chosen due to proximity to suitable spawning areas. Lack of suitable spawning habitat may also be why distance to the nearest upstream dam is important in defining nursery habitats.

As expected, accounting for detection was important in modeling occupancy of juvenile big river fishes. Accounting for incomplete detection for riverine fishes has been indicated as important in a variety of studies (McManamay et al. 2014; Reid and Haxton 2017; Staton et al. 2022) including other large rivers (Scheidegger and Bain 1995; Pritt et al. 2014; Pracheil et al. 2019). Warmwater fishes generally spawn during the spring and early summer in the Great Plains ecoregion (Fausch and Bestgen 1997). As water temperatures warm, juvenile fishes grow faster (Coutant 1976; McDowall 1994; Robinson and Childs 2001), become more active (Lyon et al. 2008), and achieve larger sizes (Keast 1980; Schlosser 1987) thereby increasing detection. In addition to temperature, I also found detection increased with increasing discharge. Although increased discharge conditions may negatively influence sampling gear efficacy (Casselman et al. 1990; Rabeni et al. 2009; Gwinn et al. 2016), these conditions also increase connectivity with important off-channel slackwater habitats (Junk et al. 1989; Nakamoto et al. 2020) and increase the availability of shallow water habitats until some threshold is reached (Tracy-Smith et al. 2012). My work emphasizes the need to account for incomplete detection in variable, large river environments.

Accounting for incomplete detection is particularly important to assess changes in distributions or occupancy over time, both of which are important when invasive species that may compete for food sources have been introduced. Accounting for detection is also important when surveying for smaller-bodied, rarer, and cryptic species within aquatic ecosystems (Albanese et al. 2011; Schloesser et al. 2012; Wedderburn 2018), but may also help understand fish-habitat relationships of more common species (Sliwinski et al. 2016; Guillera-Arroita 2017). In fact, some species are quite difficult to detect, but are quite common across a catchment (Mollenhauer et al. 2022). The importance of accounting for detection when sampling for small, juvenile fishes in the lower Red River basin is evident from the low detection rates of some species with relatively high occupancy. (e.g., Silver Chub *Macrhybopsis storeriana*, Logperch *Percina carbonaria*, and Redear Sunfish *Lepomis microlophus*). Without accounting for detection probability, occupancy estimates would have been much lower than the modeled outcome (Mackenzie et al. 2009) and relationships with the nursery habitat parameters would be altered (see also Gerber et al. 2020). By accounting for detection, I was able to produce a presumably less biased estimate of true occupancy within the lower Red River catchment. With the introduction of invasive Bighead Carp and Silver Carp in the catchment (Birdsall 2023), concerns over changes in occupancy or condition of juvenile fishes may be warranted (Schrank et al. 2003). In other catchments, there is evidence that changes to the juvenile assemblage occur as densities of carp increase (DeBoer et al. 2018). Having baseline data on the assemblage of juvenile fishes will be important for monitoring changes in these populations over time and evaluating future management actions.

Increasing either the quality or quantity of nursery habitat is becoming a common management goal in larger rivers; thus, understanding species-specific needs and providing information on surrogate species options may be useful. Low-velocity habitats are used by a variety of riverine fishes (Scheidegger and Bain 1995; Johnson and Jennings 1998). Flows that are associated with the formation of complex littoral zones, connections with backwater habitat, and the formation of sandbars are considered as restoration options in large rivers. For example, building sandbars, reconnecting floodplains, and providing low-water nursery habitat were goals of considerations for flow alternatives on the lower Missouri River (USFWS (U.S. Fish and Wildlife Service) 2000). If the goal of species management is to maintain or increase recruitment of the species associated with my study, then understanding the differences between coarse-scale and species-specific nursery habitats would be beneficial. Agencies sometimes select surrogate species for management objectives when little is known about a species of interest (Caro and O'Doherty 1999). However, species-specific relationships with environmental conditions and coarse-scale landscape constraints indicate that selection of surrogate species will, in some cases, be misguided. There is a trade-off between management of individual species of concern and indistinct practices that may apply to broader fish assemblages (Wiens et al. 2008). Traditionally defined nursery habitats can be used for assessing finer scale habitat (Fremling et al. 1989; Humphries et al. 2006); however, proper evaluations for habitat placement require an understanding of the coarse-scale habitat conditions that shape the context dependency among species (Allan 2004; Elith and Leathwick 2009). Moreover, important landscape constraints (e.g., position within the stream network and gradients) may act as filters (Poff 1997) for the nursery habitats available to a species and would be beneficial to consideration when defining nursery habitats. Agencies with limited funding would benefit from an understanding of shared nursery habitats where some species act as legitimate surrogates for others. It is essential to develop a broader view of conditions that define a quality nursery habitat for species of interest when devising conservation and restoration practices and when selecting surrogate species for other management objectives.

Table 1. Detection covariates with their associated spatial scale, resolution, and a description of the ecological importance (Justification). Bold covariates were retained for model building after consideration of correlations and effect sizes.

Scale	Covariate	Justification
Reach	Calendar day (24 h)	As fish grow larger and increase in abundance during the season, they are easier to detect[1]
	Temperature (1.0 °C)	Fish move more and grow larger in warmer conditions making them easier to detect.[1,2]
	Clarity (1.0 cm)	Higher clarity water may allow fish to more easily evade gears.[3]
	Dissolved oxygen (1.00 mg/L)	Decreased dissolved oxygen levels can make fish harder to detect .[4]
	Seine effort (1.0 m^2)	Higher sampling effort can increase species detection.[5]
Segment	**Discharge** (m^3/s)	High flows can reduce gear efficiency, making fish more difficult to detect.[6,7]

1. (Brewer and Ellersieck 2011) 2. (Coutant 1976) 3. (Zamor and Grossman 2007) 4. (Tyler and Targett 2007) 5. (Pritt et al. 2014) 6. (Nunn et al. 2012) 7. (Love et al. 2017)

Table 2. Occupancy covariates with their associated spatial scale, resolution, and a description of the ecological importance (Justification). Bold covariates were retained for model building after consideration of correlations | r |<0.50. Parameters with * indicate they were transformed to categorical covariates due to the distribution of these data. LDI indicates landscape disturbance index, LWD indicates large woody debris, and Dam indicates the distance from the nearest upstream dam.

Scale	Covariate	Justification
Reach	Salinity (1.0 ppt)	Salinity levels in the Red River basin are highly variable and may influence occupancy.[1]
	Zooplankton (1.0 #)	Increased zooplankton densities may increase juvenile fish occupancy because they are the primary food source.[2]
	Thalweg depth (1.0 m)	Juvenile fishes may be negatively associated with deeper channel depths.[3]
	Width-to-depth (1.0 m)	Wider, shallower channels may be more positively associated with nursery habitat.[4]
	LWD (1.00 %)	Juvenile fish may be positively associated with LWD because they use it as shelter.[4,5]
	***Slackwater** (1.00 %)	Juvenile fish likely occupy reaches containing slackwaters because they are important nursery habitats for large river fishes.[6]
	***Deep pools** (1.00 %)	Pools offer low-velocity areas within the main channel and can positively influence occupancy.[7]
	Dam (1.0 km)	Dams are potential spawning locations of migratory species and affect flow regimes.[7,8]
Segment	**Discharge** (m^3/s)	Reaches experiencing lower discharges may be beneficial for juvenile species.[9,10]
	Sinuosity (1.0 index)	More sinuous stretches of river may contain more habitat complexity that can be used by juvenile fishes.[11]

	Slope (1.00%)	Higher stream gradients have higher water velocities which may negatively influence juvenile species occupancy.[12]
Catchment	***Drainage area** (1.0 km^2)	Juvenile fish may occupy nursery habitats within tributaries more strongly than the mainstem river.[13]
	LDI (1.0 index)	Human disturbance can degrade nursery habitat negatively influencing occupancy.[14]
	Limestone (1.00%)	Limestone composition controls local pH levels which can affect egg survival.[15,16]

1. (Hargrave and Taylor 2010) 2. (Fernando 1994) 3. (Lamouroux et al. 1998) 4. (Thomson et al. 2001) 5. (Everett and Ruiz 1993) 6. (Galat et al. 2004) 7. (Schwartz and Herricks 2005) 7. (Poff et al. 1997) 8. (Soares et al. 2022) 9. (Nunn et al. 2012) 10. (Love et al. 2017) 11. (Warfe and Barmuta 2006) 12. (Camana et al. 2016) 13. (Pracheil et al. 2009) 14. (Schlosser 1995) 15. (Frissell et al. 1986) 16. (Swain et al. 2020)

Table 3. Location, gage number, and latitude and longitude coordinates for USGS stream gages used for occupancy analysis. Data were collected from May through October to create season averages during 2021 and 2022.

Location	USGS Stream gage	Lat	Long
Denison, TX	07331600	33.81899124	-96.5633264
Arthur City, TX	07335500	33.8751049	-95.5019023
De Kalb, TX	07336820	33.68400005	-94.6943774
Honey Grove, TX	07332622	33.74416667	-95.9611111
Texarkana, TX	07344210	33.30416667	-94.1513889
Index, AR	07337000	33.55194444	-94.0411111
Fulton, AR	07341500	33.60734285	-93.8137942
Spring Bank, AR	07344370	33.08944444	-93.8594444
Blue, OK	07332500	33.99704088	-96.2410985
Unger, OK	07335300	34.02676714	-95.7502479
Hugo, OK	HGL02 (Army Corps)	34.011667	-95.380278

Table 4. Pearson's Correlation matrix for my detection covariates. Temperature (Temp), dissolved oxygen (DO), visibility, seining effort (Seine), and discharge (Q) were all measured during each survey. Calendar day (Day) is the associated calendar date within the season for the survey.

Covariate	Temp	DO	Visibility	Day	Seine	Q
Temp	1.00					
DO	0.09	1.00				
Visibility	0.11	0.17	1.00			
Day	-0.11	-0.09	0.26	1.00		
Seine	0.03	-0.26	0.20	0.18	1.00	
Q	-0.03	0.35	-0.03	-0.29	-0.10	1.00

Table 5. Pearson's Correlation matrix for occupancy covariates. All field collected covariates represent conditions for the season. Reach-scale variables are: salinity (Salt), zooplankton count (Zoops), average thalweg depth (Thalweg), width to depth ratio (WD), large woody debris (LWD), and distance from nearest upstream dam (Dam). Segment-scale variable are: median discharge (Q_50), slope, and sinuosity (Sin). Catchment-scale variables are: landscape disturbance index (LDI), and limestone lithology (Lime).

Covariate	Salt	Zoops	Thalweg	WD	LWD	Dam	Q_50	Sin	Slope	LDI	Lime
Salt	1.00										
Zoops	-0.19	1.00									
Thalweg	-0.18	-0.20	1.00								
WD	0.53	0.00	-0.47	1.00							
LWD	-0.20	-0.17	-0.13	-0.22	1.00						
Dam	0.30	0.09	-0.09	0.19	0.07	1.00					
Q_50	0.13	-0.63	0.28	0.13	-0.04	0.12	1.00				
Sin	-0.25	0.18	0.10	-0.30	0.10	0.42	-0.16	1.00			
Slope	-0.14	-0.06	-0.10	-0.25	0.23	0.33	-0.22	-0.53	1.00		
LDI	0.71	0.05	-0.11	0.52	-0.33	0.32	0.08	-0.30	-0.24	1.00	
Lime	-0.01	-0.22	-0.02	0.27	-0.20	0.06	0.26	0.02	-0.37	-0.21	1.00

Table 6. Number of sites and surveys completed in 2021 and 2022. Sites and surveys were divided into sample locations of the Oklahoma portion of the Red River (OK Red), Arkansas portion of the Red River (AR Red), and tributaries of the Red River (e.g., Blue River, Kiamichi River, Muddy Boggy Creek, Bois D'Arc Creek, Garland Creek, and Choctaw Creek).

	2021	2021	2022	2022		
Location	*Sites*	*Surveys*	*Sites*	*Surveys*	*Total Sites*	*Total Surveys*
OK Red	22	39	18	51	40	90
AR Red	21	41	18	54	39	95
Tributaries	11	17	14	40	25	57
Total	54	97	50	145	104	242

Table 7. Number of fish species sampled during 2021 and 2022. Common name, scientific name, and whether a juvenile was detected during any of the surveys or years is indicated with X.

Common Name	**Scientific Name**	**Juvenile**	**2021 #**	**2022 #**	**Total**
Alligator Gar	*Atractosteus spatula*		-	2	2
Bantam Sunfish	*Lepomis symmetricus*	X	-	16	16
Bigeye Shiner	*Notropis boops*		1	35	36
Bigmouth Buffalo	*Ictiobus cyprinellus*	X	1	4	5
Black Buffalo	*Ictiobus niger*		-	2	2
Black Crappie	*Pomoxis nigromaculatus*	X	113	178	291
Blackspotted Topminnow	*Fundulus olivaceus*		1	-	1
Blackstripe Topminnow	*Fundulus notatus*	X	42	36	78
Blacktail Shiner	*Cyprinella venusta*	X	725	1032	1757
Blue Catfish	*Ictalurus furcatus*	X	1	6	7
Bluegill	*Lepomis macrochirus*	X	1085	903	1988
Bluntnose Darter	*Etheostoma chlorosomum*		6	3	9
Brook Silverside	*Labidesthes sicculus*	X	110	113	223
Bullhead Minnow	*Pimephales vigilax*	X	6332	40728	47060
Carpiodes spp.	*Carpiodes spp.*		2	-	2
Catostomidae spp.	*Catostomidae spp.*		5	-	5
Channel Catfish	*Ictalurus punctatus*	X	42	29	71
Chub Shiner	*Notropis potteri*	X	1945	8102	10047
Common Carp	*Cyprinus carpio*	X	-	17	17

Dormosa spp.	*Dormosa spp.*		4	334	338
Dusky Darter	*Percina sciera*	X	12	83	95
Emerald Shiner	*Notropis atherinoides*	X	1518	5901	7419
Flathead Catfish	*Pylodictis olivaris*		3	1	4
Flier	*Centrarchus macropterus*		1	-	1
Freshwater Drum	*Aplodinotus grunniens*	X	59	359	418
Ghost Shiner	*Notropis buchanani*		-	947	947
Gizzard Shad	*Dorosoma cepedianum*	X	664	4131	4795
Golden Shiner	*Notemigonus crysoleucas*		5	83	88
Golden Topminnow	*Fundulus chrysotus*		21	13	34
Green Sunfish	*Lepomis cyanellus*	X	24	130	154
Highland Stoneroller	*Campostoma spadiceum*		-	1	1
Hybrid Sunfish	*Lepomis spp.*		297	914	2
Ictiobus spp.	*Ictiobus spp.*		3	-	3
Largemouth Bass	*Micropterus salmoides*		1	3	4
Logperch	*Percina caprodes*	X	8	84	92
Longear Sunfish	*Lepomis megalotis*	X	142	1910	2052
Longnose Gar	*Lepisosteus osseus*	X	19	69	88
Mississippi Silverside	*Menidia beryllina*	X	2714	8713	11427
Mississippi Silvery Minnow	*Hybognathus nuchalis*		1	1	2
Mosquitofish	*Gambusia affinis*	X	3844	11213	15057
Orangespotted Sunfish	*Lepomis humilis*	X	1665	2186	3851
Pallid Shiner	*Hybopsis amnis*		8	25	33

Pirate Perch	*Aphredoderus sayanus*		1	23	24
Plains Killifish	*Fundulus zebrinus*		-	4	4
Pomoxis spp.	*Pomoxis spp.*		25	1	26
Pugnose Minnow	*Opsopoeodus emiliae*		-	21	21
Red Shiner	*Cyprinella lutrensis*	X	32786	84950	117736
Redear Sunfish	*Lepomis microlophus*	X	1	49	50
Redspot Darter	*Etheostoma artesiae*		-	2	2
Ribbon Shiner	*Lythrurus fumeus*		1	-	1
River Carpsucker	*Carpiodes carpio*	X	314	802	1116
River Darter	*Percina shumardi*		8	8	16
Sand Shiner	*Notropis stramineus*	X	26	421	447
Scaly Sand Darter	*Ammocrypta vivax*		-	4	4
Shoal Chub	*Macrhybopsis hyostoma*	X	446	595	1041
Shortnose Gar	*Lepisosteus platostomus*	X	41	132	173
Silver Chub	*Macrhybopsis storeriana*	X	32	789	821
Silverband Shiner	*Notropis shumardi*		16	21	37
Skipjack Herring	*Alosa chrysochloris*	X	1	1	2
Slenderhead Darter	*Percina phoxocephala*		-	39	39
Slough Darter	*Etheostoma gracile*	X	7	58	65
Smallmouth Buffalo	*Ictiobus Bubalus*	X	42	7	49
Spotted Bass	*Micropterus punctulatus*	X	312	1655	1967
Spotted Gar	*Lepisosteus oculatus*	X	3	18	21
Spotted Sucker	*Minytrema melanops*	X	-	9	9

Striped Bass	*Morone saxatilis*	X	1	5	6
Suckermouth Minnow	*Phenacobius mirabilis*	X	12	24	36
Tadpole Madtom	*Noturus gyrinus*		4	3	7
Threadfin Shad	*Dorosoma petenense*	X	1486	8287	9773
Warmouth	*Lepomis gulosus*	X	47	229	276
Weed Shiner	*Notropis texanus*		-	29	29
Western Sand Darter	*Ammocrypta clara*		43	19	62
Western Starhead Topminnow	*Fundulus blairae*		-	2	2
White Bass	*Morone chrysops*	X	138	635	773
White Crappie	*Pomoxis annularis*	X	812	990	1802
Yellow Bullhead	*Ameiurus natalis*		1	-	1
Total			58033	188139	246172

Table 8. Detection and occupancy covariate sample sizes (N), mean, standard deviation (SD), and ranges (minimum and maximum values). The covariates were grouped together by stream location: Oklahoma portion of the Red River (OK Red), Arkansas portion of the Red River (AR Red), or tributary (e.g., Blue River, Kiamichi River, Muddy Boggy Creek, Bois D'Arc Creek, Garland Creek, and Choctaw Creek). All detection covariates were measured at each survey. Occupancy covariates were averaged across surveys to reflect a single, seasonal value. Scaled discharge is the segment-level flow measurements scaled by drainage area to allow for comparison across stream network (i.e., high flow in smaller rivers is not comparable with high flow in a larger river). LWD indicates large woody debris, LDI indicates landscape disturbance index, and Dam indicates the distance from the nearest upstream dam.

OK Red					
Detection	*N*	*Mean*	*SD*	*Min*	*Max*
Calendar Day (24 hr.)	114	84.13	38.32	21.00	173.00
Temperature (°C)	114	27.15	2.90	19.03	31.67
Clarity (cm)	114	43.16	30.33	8.67	167.00
Dissolved Oxygen (mg/L)	114	8.03	3.78	2.69	17.61
Seine Effort (m^2)	114	683.38	311.65	182.92	2487.68
Scaled Discharge (daily)	114	0.0017	0.0016	0.00001	0.0069
Occupancy					
Salinity (ppt)	39	0.51	0.11	0.15	0.66
Zooplankton (#)	39	33.35	42.76	0.00	158.33
Thalweg Depth (m)	39	2.07	1.08	0.42	4.53
Width to Depth (m)	39	115.02	54.96	37.87	256.17
LWD (%)	39	2.20	1.79	0.00	6.00
Slackwater (%)	39	9.31	18.39	0.00	100.00
Deep Pools (%)	39	5.45	10.53	0.00	36.00
Dam (m)	39	105.74	50.51	20.36	197.92

Scaled Discharge (median)	39	0.0018	0.0011	0.0006	0.0028
Sinuosity (index ratio)	39	1.56	0.34	1.03	1.99
Slope (%)	39	0.04	0.01	0.02	0.06
Drainage Area (km^2)	39	115170.10	6395.87	100597.90	120548.90
LDI (index ratio)	39	1.97	0.02	1.95	2.00
Lithology (%)	39	2.46	0.24	1.76	2.58

AR Red

Detection	*N*	*Mean*	*SD*	*Min*	*Max*
Calendar Day (24 hr.)	114	86.51	39.46	23.00	174.00
Temperature (°C)	114	28.18	3.26	18.57	32.83
Clarity (cm)	114	28.61	8.53	6.67	47.00
Dissolved Oxygen (mg/L)	114	7.03	2.75	1.92	15.07
Seine Effort (m^2)	114	660.37	246.77	126.96	1396.56
Scaled Discharge (daily)	114	0.0019	0.0015	0.0003	0.0060
Occupancy					
Salinity (ppt)	39	0.40	0.12	0.16	0.59
Zooplankton (#)	39	73.62	77.38	0.50	274.33
Thalweg Depth (m)	39	2.69	1.23	0.40	5.47
Width to Depth (m)	39	81.68	50.19	20.04	245.05
LWD (%)	39	2.11	2.94	0.00	13.50
Slackwater (%)	39	27.87	38.10	0.00	100.00
Deep Pools (%)	39	27.73	41.40	0.00	100.00
Dam (m)	39	142.65	74.14	28.82	280.47
Scaled Discharge (median)	39	0.0020	0.0012	0.0007	0.0038
Sinuosity (index ratio)	39	1.81	0.28	1.12	2.05
Slope (%)	39	0.03	0.01	0.02	0.07
Drainage Area (km^2)	39	128723.10	8044.70	120597.80	144676.70
LDI (index ratio)	39	1.94	0.02	1.91	1.96
Lithology (%)	39	2.48	0.07	2.36	2.56

Tributaries

Detection	*N*	*Mean*	*SD*	*Min*	*Max*
Calendar Day (24 hr.)	72	72.83	30.87	20.00	172.00
Temperature (°C)	72	28.63	2.99	20.43	32.07

Clarity (cm)	72	36.83	19.48	0.10	76.67
Dissolved Oxygen (mg/L)	72	7.12	3.34	2.72	16.90
Seine Effort (m^2)	72	602.63	200.65	253.92	1373.56
Scaled Discharge (daily)	72	0.0020	0.0074	0.000005	0.0547
Occupancy					
Salinity (ppt)	25	0.27	0.20	0.00	0.65
Zooplankton (#)	25	45.01	42.53	0.00	153.00
Thalweg Depth (m)	25	2.39	1.21	0.70	5.46
Width to Depth (m)	25	28.84	19.43	11.02	92.29
LWD (%)	25	7.92	5.99	0.50	20.00
Slackwater (%)	25	3.15	7.09	0.00	32.72
Deep Pools (%)	25	18.89	20.76	0.00	100.00
Dam (m)	25	82.80	56.56	1.83	180.02
Scaled Discharge (median)	25	0.0011	0.0007	0.00005	0.0018
Sinuosity (index ratio)	25	1.82	0.19	1.34	2.00
Slope (%)	25	0.07	0.05	0.04	0.30
Drainage Area (km^2)	25	3289.45	2277.39	27.13	6273.99
LDI (index ratio)	25	1.70	0.29	1.40	2.38
Lithology (%)	25	9.46	14.04	0.00	50.00

Table 9. Model estimates from the final occupancy model. ψ (Psi) and p are the group mean occupancy and detection estimates within the study area respectively. $\hat{R}$ (R-hat) is the measure of model convergence. $\hat{c}$ (c-hat) is a measure of posterior dispersion. The Bayesian p-value represents the goodness-of-fit test for the model. Segment and year sigma are a measure of the variance captured by the grouping factors.

Coefficient	**Mean**	**LHDI**	**UHDI**
ψ (group)	0.571	0.184	0.929
p (group)	0.187	0.118	0.258
$\hat{R}$	1.00	0.995	1.003
$\hat{c}$	1.003	0.892	1.116
Bayesian p-value	0.505	0.00	1.00
Segment - Sigma	1.429	0.699	2.289
Year - Sigma	1.176	0.00	2.627

Table 10. Detection model coefficients for species (probability scale) and covariates (logit scale) included in the in the final model, and their lower (LHDI) and upper (UHDI) 95% high density intervals. Daily average water temperature was collected during each survey and discharge measurements were obtained from the nearest USGS stream gage.

Coefficient	**Median**	**LHDI**	**UHDI**
Discharge	0.265	0.180	0.349
Temperature	0.263	0.179	0.342
Bantam Sunfish	0.064	0.023	0.165
Bigmouth Buffalo	0.058	0.020	0.155
Black Crappie	0.336	0.249	0.436
Blackstriped Topminnow	0.044	0.011	0.151
Blacktail Shiner	0.075	0.022	0.225
Blue Catfish	0.043	0.013	0.134
Bluegill	0.587	0.501	0.668
Brook Silverside	0.084	0.029	0.215
Bullhead Minnow	0.390	0.315	0.476
Channel Catfish	0.237	0.144	0.359
Chub Shiner	0.439	0.348	0.534
Dusky Darter	0.041	0.010	0.145
Emerald Shiner	0.122	0.067	0.214
Freshwater Drum	0.285	0.211	0.374
Gizzard Shad	0.351	0.282	0.436
Green Sunfish	0.276	0.190	0.394
Logperch	0.142	0.071	0.263
Longear Sunfish	0.703	0.620	0.777
Longnose Gar	0.154	0.090	0.268
Mississippi Silverside	0.254	0.189	0.337
Orangespotted Sunfish	0.553	0.462	0.638
Redear Sunfish	0.091	0.040	0.193

River Carpsucker	0.511	0.426	0.601
Sand Shiner	0.052	0.018	0.136
Shoal Chub	0.153	0.088	0.259
Shortnose Gar	0.075	0.031	0.172
Silver Chub	0.085	0.041	0.164
Skipjack Herring	0.061	0.022	0.165
Slough Darter	0.149	0.064	0.306
Smallmouth Buffalo	0.089	0.040	0.196
Spotted Bass	0.697	0.629	0.758
Spotted Gar	0.055	0.014	0.159
Spotted Sucker	0.092	0.030	0.261
Suckermouth Minnow	0.068	0.024	0.167
Threadfin Shad	0.418	0.349	0.490
Warmouth	0.251	0.157	0.372
White Bass	0.331	0.253	0.424
White Crappie	0.580	0.498	0.663

Table 11. Occupancy model coefficients for species (probability scale) and their covariates (logit scale) for the final model, and their lower (LHDI) and upper (UHDI) 95% high density intervals. The occupancy coefficient represents the probability of species occupancy within the study area. Continuous variables included were distance from the nearest upstream dam (Dam Distance), median discharge for the season (Discharge), percentage of limestone lithology within the catchment (Limestone), percentage of large woody debris within the reach (LWD), the percentage slope of the segment (Slope), average thalweg depth of the reach (Thalweg), and the width-to-depth ratio of the reach (W:D). Categorical variables were 1) pools: where the absence of deep pools was the reference, 2) slackwater: where the absence of slackwater was the reference, and 3) drainage area: where high drainage area was the reference.

Coefficient	Median	LHDI	UHDI
Bantam Sunfish - Dam Distance	0.159	-0.518	0.878
Bantam Sunfish - Discharge	0.366	-1.612	2.328
Bantam Sunfish - Drainage Area	-2.018	-5.781	1.508
Bantam Sunfish - Limestone	-0.747	-2.736	0.719
Bantam Sunfish - LWD	-1.240	-3.042	0.153
Bantam Sunfish - Occupancy	0.197	0.013	0.799
Bantam Sunfish - Pools	0.189	-0.902	1.320
Bantam Sunfish - Slackwater	1.056	-1.369	3.066
Bantam Sunfish - Slope	0.684	-1.478	3.303
Bantam Sunfish - Thalweg	-0.228	-1.305	1.262
Bantam Sunfish - W:D	-0.049	-1.369	1.233
Bigmouth Buffalo - Dam Distance	0.187	-0.500	0.891

Bigmouth Buffalo - Discharge	0.609	-0.941	2.255
Bigmouth Buffalo - Drainage Area	-1.569	-5.265	2.083
Bigmouth Buffalo - Limestone	-0.879	-2.828	0.349
Bigmouth Buffalo - LWD	-0.892	-2.608	0.576
Bigmouth Buffalo - Occupancy	0.224	0.018	0.823
Bigmouth Buffalo - Pools	0.188	-0.935	1.308
Bigmouth Buffalo - Slackwater	1.303	-0.761	3.509
Bigmouth Buffalo - Slope	0.328	-2.127	3.288
Bigmouth Buffalo - Thalweg	-0.361	-1.437	0.962
Bigmouth Buffalo - W:D	0.088	-0.996	1.435
Black Crappie - Dam Distance	0.197	-0.435	0.865
Black Crappie - Discharge	1.299	0.129	2.623
Black Crappie - Drainage Area	-1.486	-4.145	1.242
Black Crappie - Limestone	-0.824	-2.841	0.615
Black Crappie - LWD	-1.242	-2.510	-0.185
Black Crappie - Occupancy	0.776	0.250	0.974
Black Crappie - Pools	0.381	-0.544	1.563
Black Crappie - Slackwater	1.205	-0.350	2.768
Black Crappie - Slope	1.315	-0.292	3.252
Black Crappie - Thalweg	-0.534	-1.542	0.286
Black Crappie - W:D	0.004	-0.892	0.893
Blackstriped Topminnow - Dam Distance	0.181	-0.490	0.904
Blackstriped Topminnow - Discharge	0.585	-1.212	2.412
Blackstriped Topminnow - Drainage Area	-2.026	-6.235	2.005
Blackstriped Topminnow - Limestone	-0.738	-2.767	0.655
Blackstriped Topminnow - LWD	-0.939	-2.799	0.560

Blackstriped Topminnow - Occupancy	0.149	0.008	0.770
Blackstriped Topminnow - Pools	0.190	-0.908	1.322
Blackstriped Topminnow - Slackwater	1.091	-1.346	3.288
Blackstriped Topminnow - Slope	-0.524	-3.265	2.289
Blackstriped Topminnow - Thalweg	-0.592	-1.984	0.497
Blackstriped Topminnow - W:D	0.160	-1.036	1.763
Blacktail Shiner - Dam Distance	0.161	-0.513	0.866
Blacktail Shiner - Discharge	1.227	-0.524	3.165
Blacktail Shiner - Drainage Area	-3.266	-7.902	0.537
Blacktail Shiner - Limestone	-0.626	-2.503	0.885
Blacktail Shiner - LWD	-0.070	-1.402	1.350
Blacktail Shiner - Occupancy	0.301	0.025	0.848
Blacktail Shiner - Pools	0.283	-0.750	1.474
Blacktail Shiner - Slackwater	1.018	-1.280	3.062
Blacktail Shiner - Slope	0.399	-2.292	3.784
Blacktail Shiner - Thalweg	-0.756	-2.234	0.223
Blacktail Shiner - W:D	-0.150	-1.513	0.971
Blue Catfish - Dam Distance	0.221	-0.443	0.960
Blue Catfish - Discharge	0.298	-1.668	2.103
Blue Catfish - Drainage Area	-1.400	-5.420	2.961
Blue Catfish - Limestone	-0.689	-2.601	0.778
Blue Catfish - LWD	-0.190	-1.983	1.737
Blue Catfish - Occupancy	0.210	0.015	0.815
Blue Catfish - Pools	0.252	-0.806	1.374
Blue Catfish - Slackwater	1.506	-0.373	4.121
Blue Catfish - Slope	-0.727	-3.214	1.782

Blue Catfish - Thalweg	-0.349	-1.630	1.062
Blue Catfish - W:D	0.202	-0.999	1.926
Bluegill - Dam Distance	0.120	-0.550	0.810
Bluegill - Discharge	0.731	-0.486	2.056
Bluegill - Drainage Area	-2.011	-5.000	0.992
Bluegill - Limestone	-0.693	-2.294	0.554
Bluegill - LWD	-0.487	-1.579	0.537
Bluegill - Occupancy	0.950	0.606	0.996
Bluegill - Pools	0.264	-0.761	1.361
Bluegill - Slackwater	1.612	0.189	3.530
Bluegill - Slope	0.639	-0.933	2.568
Bluegill - Thalweg	-0.510	-1.509	0.357
Bluegill - W:D	-0.181	-1.315	0.796
Brook Silverside - Dam Distance	0.186	-0.498	0.880
Brook Silverside - Discharge	0.929	-0.664	2.494
Brook Silverside - Drainage Area	-2.216	-5.858	1.328
Brook Silverside - Limestone	-0.900	-2.840	0.312
Brook Silverside - LWD	-0.439	-1.946	1.051
Brook Silverside - Occupancy	0.256	0.021	0.832
Brook Silverside - Pools	0.266	-0.741	1.404
Brook Silverside - Slackwater	1.023	-1.346	3.075
Brook Silverside - Slope	0.542	-1.415	2.834
Brook Silverside - Thalweg	-0.706	-2.173	0.264
Brook Silverside - W:D	0.141	-0.928	1.541
Bullhead Minnow - Dam Distance	0.181	-0.465	0.869
Bullhead Minnow - Discharge	0.558	-0.906	2.009

Bullhead Minnow - Drainage Area	-1.010	-4.060	2.455
Bullhead Minnow - Limestone	-0.782	-2.320	0.331
Bullhead Minnow - LWD	-1.200	-2.683	0.025
Bullhead Minnow - Occupancy	0.863	0.349	0.987
Bullhead Minnow - Pools	0.310	-0.616	1.478
Bullhead Minnow - Slackwater	1.897	0.291	4.294
Bullhead Minnow - Slope	0.005	-1.514	1.839
Bullhead Minnow - Thalweg	-0.663	-2.013	0.283
Bullhead Minnow - W:D	0.022	-1.075	1.287
Channel Catfish - Dam Distance	0.215	-0.413	0.903
Channel Catfish - Discharge	0.947	-0.249	2.211
Channel Catfish - Drainage Area	-1.904	-4.956	1.257
Channel Catfish - Limestone	-0.750	-2.501	0.544
Channel Catfish - LWD	0.877	-0.663	2.373
Channel Catfish - Occupancy	0.725	0.186	0.970
Channel Catfish - Pools	0.275	-0.624	1.365
Channel Catfish - Slackwater	0.989	-0.849	2.671
Channel Catfish - Slope	0.527	-1.331	3.011
Channel Catfish - Thalweg	-0.367	-1.348	0.671
Channel Catfish - W:D	0.120	-0.848	1.278
Chub Shiner - Dam Distance	0.242	-0.408	0.954
Chub Shiner - Discharge	0.725	-0.542	2.066
Chub Shiner - Drainage Area	0.065	-3.102	3.367
Chub Shiner - Limestone	-0.854	-2.546	0.256
Chub Shiner - LWD	-1.264	-2.825	0.031
Chub Shiner - Occupancy	0.746	0.147	0.973

Chub Shiner - Pools	0.113	-1.061	1.082
Chub Shiner - Slackwater	1.012	-0.778	2.701
Chub Shiner - Slope	-2.035	-3.858	-0.446
Chub Shiner - Thalweg	-0.048	-1.047	1.450
Chub Shiner - W:D	0.506	-0.654	2.411
Dusky Darter - Dam Distance	0.187	-0.480	0.904
Dusky Darter - Discharge	0.251	-1.821	2.190
Dusky Darter - Drainage Area	-2.775	-7.360	1.220
Dusky Darter - Limestone	-0.708	-2.688	0.763
Dusky Darter - LWD	-0.560	-2.400	1.178
Dusky Darter - Occupancy	0.156	0.009	0.766
Dusky Darter - Pools	0.185	-0.951	1.313
Dusky Darter - Slackwater	0.893	-2.071	2.928
Dusky Darter - Slope	0.719	-1.873	3.994
Dusky Darter - Thalweg	-0.292	-1.370	1.186
Dusky Darter - W:D	-0.138	-1.532	1.054
Emerald Shiner - Dam Distance	0.171	-0.498	0.859
Emerald Shiner - Discharge	1.628	-0.415	3.783
Emerald Shiner - Drainage Area	-0.393	-3.885	3.772
Emerald Shiner - Limestone	-0.534	-2.205	1.106
Emerald Shiner - LWD	-0.709	-2.477	0.760
Emerald Shiner - Occupancy	0.528	0.077	0.938
Emerald Shiner - Pools	0.281	-0.708	1.453
Emerald Shiner - Slackwater	1.195	-0.812	3.416
Emerald Shiner - Slope	-1.147	-3.887	1.433
Emerald Shiner - Thalweg	-0.167	-1.203	1.266

Emerald Shiner - W:D	-0.071	-1.357	1.165
Freshwater Drum - Dam Distance	0.149	-0.524	0.839
Freshwater Drum - Discharge	1.381	-0.143	3.163
Freshwater Drum - Drainage Area	-0.848	-3.900	2.488
Freshwater Drum - Limestone	-0.522	-2.575	1.020
Freshwater Drum - LWD	-1.186	-2.689	0.114
Freshwater Drum - Occupancy	0.727	0.174	0.967
Freshwater Drum - Pools	0.213	-0.794	1.243
Freshwater Drum - Slackwater	1.964	0.322	4.422
Freshwater Drum - Slope	-0.482	-1.918	1.194
Freshwater Drum - Thalweg	-0.468	-1.514	0.508
Freshwater Drum - W:D	0.274	-0.822	1.957
Gizzard Shad - Dam Distance	0.183	-0.469	0.874
Gizzard Shad - Discharge	0.958	-0.667	2.867
Gizzard Shad - Drainage Area	0.348	-3.114	4.132
Gizzard Shad - Limestone	-0.859	-2.700	0.410
Gizzard Shad - LWD	-0.247	-1.423	0.964
Gizzard Shad - Occupancy	0.837	0.289	0.985
Gizzard Shad - Pools	0.184	-0.938	1.206
Gizzard Shad - Slackwater	1.715	0.095	4.184
Gizzard Shad - Slope	0.276	-1.312	2.180
Gizzard Shad - Thalweg	-0.094	-1.096	1.311
Gizzard Shad - W:D	0.035	-1.025	1.343
Green Sunfish - Dam Distance	0.169	-0.494	0.844
Green Sunfish - Discharge	0.514	-0.795	1.893
Green Sunfish - Drainage Area	-1.212	-4.262	2.106

Green Sunfish - Limestone	-0.747	-2.402	0.419
Green Sunfish - LWD	-0.731	-2.261	0.533
Green Sunfish - Occupancy	0.714	0.172	0.966
Green Sunfish - Pools	0.138	-0.999	1.139
Green Sunfish - Slackwater	1.437	-0.280	3.607
Green Sunfish - Slope	1.438	-0.557	3.911
Green Sunfish - Thalweg	-0.056	-1.087	1.330
Green Sunfish - W:D	0.033	-1.042	1.176
Logperch - Dam Distance	0.145	-0.537	0.833
Logperch - Discharge	-0.549	-2.375	1.007
Logperch - Drainage Area	-2.415	-5.824	0.894
Logperch - Limestone	-0.894	-2.820	0.289
Logperch - LWD	-0.454	-1.784	0.758
Logperch - Occupancy	0.512	0.083	0.929
Logperch - Pools	0.250	-0.711	1.319
Logperch - Slackwater	0.896	-1.298	2.728
Logperch - Slope	-0.463	-2.338	1.594
Logperch - Thalweg	-0.386	-1.294	0.616
Logperch - W:D	-0.134	-1.254	0.888
Longear Sunfish - Dam Distance	0.201	-0.415	0.869
Longear Sunfish - Discharge	-1.076	-2.995	0.293
Longear Sunfish - Drainage Area	-2.014	-4.817	1.075
Longear Sunfish - Limestone	-0.688	-2.298	0.608
Longear Sunfish - LWD	-0.270	-1.107	0.534
Longear Sunfish - Occupancy	0.964	0.668	0.997
Longear Sunfish - Pools	0.125	-0.895	1.019

Longear Sunfish - Slackwater	0.428	-1.404	1.907
Longear Sunfish - Slope	0.064	-1.400	1.486
Longear Sunfish - Thalweg	-0.682	-1.702	0.106
Longear Sunfish - W:D	-0.047	-0.907	0.806
Longnose Gar - Dam Distance	0.207	-0.458	0.909
Longnose Gar - Discharge	0.010	-1.777	1.486
Longnose Gar - Drainage Area	-1.223	-4.672	2.934
Longnose Gar - Limestone	-0.713	-2.312	0.546
Longnose Gar - LWD	0.016	-1.492	1.591
Longnose Gar - Occupancy	0.661	0.123	0.966
Longnose Gar - Pools	0.149	-1.107	1.181
Longnose Gar - Slackwater	1.596	-0.122	4.162
Longnose Gar - Slope	-0.300	-2.197	1.944
Longnose Gar - Thalweg	-0.189	-1.148	1.024
Longnose Gar - W:D	-0.042	-1.225	1.181
Mississippi Silverside - Dam Distance	0.138	-0.544	0.828
Mississippi Silverside - Discharge	1.563	-0.165	3.403
Mississippi Silverside - Drainage Area	0.781	-2.555	4.408
Mississippi Silverside - Limestone	-0.867	-2.833	0.387
Mississippi Silverside - LWD	-0.860	-2.571	0.615
Mississippi Silverside - Occupancy	0.671	0.140	0.963
Mississippi Silverside - Pools	0.281	-0.669	1.400
Mississippi Silverside - Slackwater	1.580	-0.137	3.820
Mississippi Silverside - Slope	1.410	-0.570	3.702
Mississippi Silverside - Thalweg	-0.235	-1.263	1.042
Mississippi Silverside - W:D	0.330	-0.783	2.047

Orangespotted Sunfish - Dam Distance	0.218	-0.415	0.897
Orangespotted Sunfish - Discharge	-0.398	-1.588	0.738
Orangespotted Sunfish - Drainage Area	-1.338	-4.062	1.372
Orangespotted Sunfish - Limestone	-0.885	-2.795	0.281
Orangespotted Sunfish - LWD	-0.275	-1.378	0.758
Orangespotted Sunfish - Occupancy	0.883	0.378	0.988
Orangespotted Sunfish - Pools	0.176	-0.812	1.121
Orangespotted Sunfish - Slackwater	0.965	-0.614	2.368
Orangespotted Sunfish - Slope	-0.353	-1.461	0.873
Orangespotted Sunfish - Thalweg	-0.388	-1.232	0.408
Orangespotted Sunfish - W:D	-0.136	-1.081	0.736
Redear Sunfish - Dam Distance	0.145	-0.543	0.845
Redear Sunfish - Discharge	0.114	-1.472	1.745
Redear Sunfish - Drainage Area	-1.831	-5.358	1.635
Redear Sunfish - Limestone	-0.686	-2.612	0.953
Redear Sunfish - LWD	-0.972	-2.989	0.588
Redear Sunfish - Occupancy	0.346	0.038	0.880
Redear Sunfish - Pools	0.204	-0.850	1.320
Redear Sunfish - Slackwater	1.244	-0.824	3.326
Redear Sunfish - Slope	1.068	-0.893	4.094
Redear Sunfish - Thalweg	-0.317	-1.369	0.922
Redear Sunfish - W:D	0.132	-0.947	1.544
River Carpsucker - Dam Distance	0.188	-0.481	0.869
River Carpsucker - Discharge	0.585	-0.914	2.037
River Carpsucker - Drainage Area	-0.515	-3.653	3.308
River Carpsucker - Limestone	-0.804	-2.539	0.299

River Carpsucker - LWD	-0.881	-2.248	0.286
River Carpsucker - Occupancy	0.903	0.418	0.991
River Carpsucker - Pools	0.201	-0.844	1.266
River Carpsucker - Slackwater	1.446	-0.338	3.811
River Carpsucker - Slope	-1.071	-3.014	0.855
River Carpsucker - Thalweg	-0.192	-1.140	1.062
River Carpsucker - W:D	0.395	-0.754	2.194
Sand Shiner - Dam Distance	0.164	-0.501	0.866
Sand Shiner - Discharge	1.112	-0.646	3.089
Sand Shiner - Drainage Area	-1.095	-4.626	2.771
Sand Shiner - Limestone	-0.776	-2.787	0.663
Sand Shiner - LWD	-0.067	-1.623	1.585
Sand Shiner - Occupancy	0.254	0.020	0.849
Sand Shiner - Pools	0.245	-0.834	1.363
Sand Shiner - Slackwater	1.590	-0.198	4.259
Sand Shiner - Slope	1.439	-1.386	5.076
Sand Shiner - Thalweg	-0.586	-2.051	0.511
Sand Shiner - W:D	0.138	-1.011	1.746
Shoal Chub - Dam Distance	0.183	-0.465	0.879
Shoal Chub - Discharge	0.978	-0.649	2.761
Shoal Chub - Drainage Area	-0.970	-4.363	2.794
Shoal Chub - Limestone	-0.688	-2.543	0.723
Shoal Chub - LWD	-0.471	-1.941	0.871
Shoal Chub - Occupancy	0.526	0.084	0.925
Shoal Chub - Pools	0.326	-0.619	1.585
Shoal Chub - Slackwater	1.105	-0.968	3.121

Shoal Chub - Slope	-2.021	-4.795	0.231
Shoal Chub - Thalweg	-0.524	-1.805	0.579
Shoal Chub - W:D	0.345	-0.831	2.036
Shortnose Gar - Dam Distance	0.167	-0.518	0.863
Shortnose Gar - Discharge	0.952	-0.543	2.528
Shortnose Gar - Drainage Area	-1.002	-4.429	2.758
Shortnose Gar - Limestone	-0.806	-2.691	0.541
Shortnose Gar - LWD	-0.533	-2.357	1.182
Shortnose Gar - Occupancy	0.278	0.025	0.852
Shortnose Gar - Pools	0.230	-0.823	1.327
Shortnose Gar - Slackwater	1.370	-0.551	3.757
Shortnose Gar - Slope	1.480	-0.913	4.535
Shortnose Gar - Thalweg	-0.453	-1.781	0.753
Shortnose Gar - W:D	0.287	-0.858	1.981
Silver Chub - Dam Distance	0.194	-0.478	0.894
Silver Chub - Discharge	-0.717	-2.909	1.238
Silver Chub - Drainage Area	-0.893	-4.208	2.886
Silver Chub - Limestone	-0.705	-2.666	0.807
Silver Chub - LWD	-1.115	-3.027	0.402
Silver Chub - Occupancy	0.335	0.032	0.867
Silver Chub - Pools	0.206	-0.856	1.314
Silver Chub - Slackwater	1.150	-0.929	3.153
Silver Chub - Slope	-0.601	-2.643	1.442
Silver Chub - Thalweg	-0.250	-1.254	1.013
Silver Chub - W:D	0.017	-1.208	1.469
Skipjack Herring - Dam Distance	0.190	-0.481	0.900

Skipjack Herring - Discharge	0.903	-0.693	2.585
Skipjack Herring - Drainage Area	-1.382	-5.073	2.479
Skipjack Herring - Limestone	-0.910	-2.839	0.291
Skipjack Herring - LWD	-0.355	-2.053	1.316
Skipjack Herring - Occupancy	0.251	0.021	0.842
Skipjack Herring - Pools	0.266	-0.772	1.377
Skipjack Herring - Slackwater	1.398	-0.529	3.742
Skipjack Herring - Slope	-0.495	-2.790	1.908
Skipjack Herring - Thalweg	-0.369	-1.509	0.806
Skipjack Herring - W:D	0.001	-1.211	1.363
Slough Darter - Dam Distance	0.175	-0.503	0.867
Slough Darter - Discharge	0.182	-1.610	1.912
Slough Darter - Drainage Area	-4.270	-8.988	-0.206
Slough Darter - Limestone	-0.742	-2.523	0.583
Slough Darter - LWD	0.172	-1.169	1.782
Slough Darter - Occupancy	0.424	0.051	0.908
Slough Darter - Pools	0.210	-0.830	1.322
Slough Darter - Slackwater	0.677	-2.108	2.458
Slough Darter - Slope	0.702	-1.648	3.581
Slough Darter - Thalweg	-0.422	-1.558	0.698
Slough Darter - W:D	-0.276	-1.710	0.752
Smallmouth Buffalo - Dam Distance	0.190	-0.489	0.882
Smallmouth Buffalo - Discharge	0.603	-1.023	2.307
Smallmouth Buffalo - Drainage Area	-2.000	-5.910	1.712
Smallmouth Buffalo - Limestone	-0.652	-2.554	0.844
Smallmouth Buffalo - LWD	-0.686	-2.325	0.757

Smallmouth Buffalo - Occupancy	0.350	0.035	0.875
Smallmouth Buffalo - Pools	0.271	-0.739	1.391
Smallmouth Buffalo - Slackwater	1.536	-0.257	3.924
Smallmouth Buffalo - Slope	-1.310	-3.533	0.880
Smallmouth Buffalo - Thalweg	-0.457	-1.451	0.530
Smallmouth Buffalo - W:D	0.082	-1.062	1.464
Spotted Bass - Dam Distance	0.125	-0.537	0.800
Spotted Bass - Discharge	0.660	-0.582	1.960
Spotted Bass - Drainage Area	-1.227	-4.217	1.827
Spotted Bass - Limestone	-0.701	-2.359	0.664
Spotted Bass - LWD	-1.305	-2.659	-0.112
Spotted Bass - Occupancy	0.962	0.645	0.997
Spotted Bass - Pools	0.320	-0.573	1.451
Spotted Bass - Slackwater	1.863	0.409	3.940
Spotted Bass - Slope	1.365	-0.650	3.642
Spotted Bass - Thalweg	-0.683	-1.936	0.224
Spotted Bass - W:D	-0.081	-1.156	0.913
Spotted Gar - Dam Distance	0.193	-0.474	0.928
Spotted Gar - Discharge	0.156	-1.868	2.010
Spotted Gar - Drainage Area	-3.108	-7.890	0.871
Spotted Gar - Limestone	-0.696	-2.614	0.869
Spotted Gar - LWD	-0.500	-2.236	1.218
Spotted Gar - Occupancy	0.201	0.013	0.801
Spotted Gar - Pools	0.197	-0.865	1.353
Spotted Gar - Slackwater	0.974	-1.499	2.994
Spotted Gar - Slope	0.925	-1.684	4.054

Spotted Gar - Thalweg	-0.284	-1.391	1.148
Spotted Gar - W:D	-0.113	-1.461	1.084
Spotted Sucker - Dam Distance	0.151	-0.541	0.847
Spotted Sucker - Discharge	0.088	-1.742	1.759
Spotted Sucker - Drainage Area	-2.532	-6.297	1.010
Spotted Sucker - LWD	-0.237	-1.719	1.349
Spotted Sucker - Occupancy	0.254	0.020	0.830
Spotted Sucker - Pools	0.198	-0.894	1.258
Spotted Sucker - Slackwater	0.948	-1.529	2.805
Spotted Sucker - Slope	-0.449	-2.818	1.861
Spotted Sucker - Thalweg	-0.525	-1.617	0.435
Spotted Sucker - W:D	0.066	-1.091	1.382
Spotted Sucker -Limestone	-0.900	-2.889	0.305
Suckermouth Minnow - Dam Distance	0.159	-0.550	0.853
Suckermouth Minnow - Discharge	-0.174	-2.345	1.675
Suckermouth Minnow - Drainage Area	-2.357	-6.323	1.302
Suckermouth Minnow - Limestone	-0.688	-2.490	0.719
Suckermouth Minnow - LWD	-0.275	-1.806	1.329
Suckermouth Minnow - Occupancy	0.282	0.024	0.849
Suckermouth Minnow - Pools	0.267	-0.769	1.422
Suckermouth Minnow - Slackwater	0.973	-1.665	2.972
Suckermouth Minnow - Slope	1.954	-0.720	5.533
Suckermouth Minnow - Thalweg	-0.536	-1.863	0.560
Suckermouth Minnow - W:D	-0.125	-1.432	0.971
Threadfin Shad - Dam Distance	0.187	-0.478	0.882
Threadfin Shad - Discharge	0.325	-1.421	2.126

Threadfin Shad - Drainage Area	0.764	-2.697	5.005
Threadfin Shad - Limestone	-0.936	-2.679	0.186
Threadfin Shad - LWD	-0.651	-2.174	0.791
Threadfin Shad - Occupancy	0.886	0.389	0.992
Threadfin Shad - Pools	0.256	-0.728	1.346
Threadfin Shad - Slackwater	1.687	0.084	3.928
Threadfin Shad - Slope	-0.793	-2.788	1.607
Threadfin Shad - Thalweg	-0.409	-1.499	0.702
Threadfin Shad - W:D	0.183	-0.839	1.604
Warmouth - Dam Distance	0.232	-0.413	0.927
Warmouth - Discharge	0.064	-1.186	1.246
Warmouth - Drainage Area	-1.966	-4.805	0.905
Warmouth - Limestone	-0.703	-2.623	0.865
Warmouth - LWD	-0.408	-1.540	0.649
Warmouth - Occupancy	0.658	0.143	0.951
Warmouth - Pools	0.255	-0.660	1.340
Warmouth - Slackwater	0.986	-0.932	2.601
Warmouth - Slope	0.873	-0.514	2.391
Warmouth - Thalweg	-0.767	-1.813	0.020
Warmouth - W:D	-0.383	-1.662	0.537
White Bass - Dam Distance	0.125	-0.580	0.815
White Bass - Discharge	0.854	-0.637	2.499
White Bass - Drainage Area	0.223	-3.091	3.812
White Bass - Limestone	-0.856	-2.925	0.414
White Bass - LWD	-0.858	-2.189	0.223
White Bass - Occupancy	0.779	0.235	0.977

White Bass - Pools	0.167	-0.970	1.172
White Bass - Slackwater	1.322	-0.478	3.484
White Bass - Slope	-0.073	-1.613	1.764
White Bass - Thalweg	-0.362	-1.479	0.869
White Bass - W:D	0.061	-1.109	1.507
White Crappie - Dam Distance	0.204	-0.445	0.894
White Crappie - Discharge	1.549	0.076	3.247
White Crappie - Drainage Area	-0.447	-3.418	2.812
White Crappie - Limestone	-0.498	-1.970	0.882
White Crappie - LWD	-0.990	-2.249	0.100
White Crappie - Occupancy	0.938	0.545	0.995
White Crappie - Pools	0.296	-0.627	1.397
White Crappie - Slackwater	0.906	-0.899	2.540
White Crappie - Slope	-0.066	-1.415	1.598
White Crappie - Thalweg	-0.302	-1.192	0.662
White Crappie - W:D	-0.183	-1.310	0.763

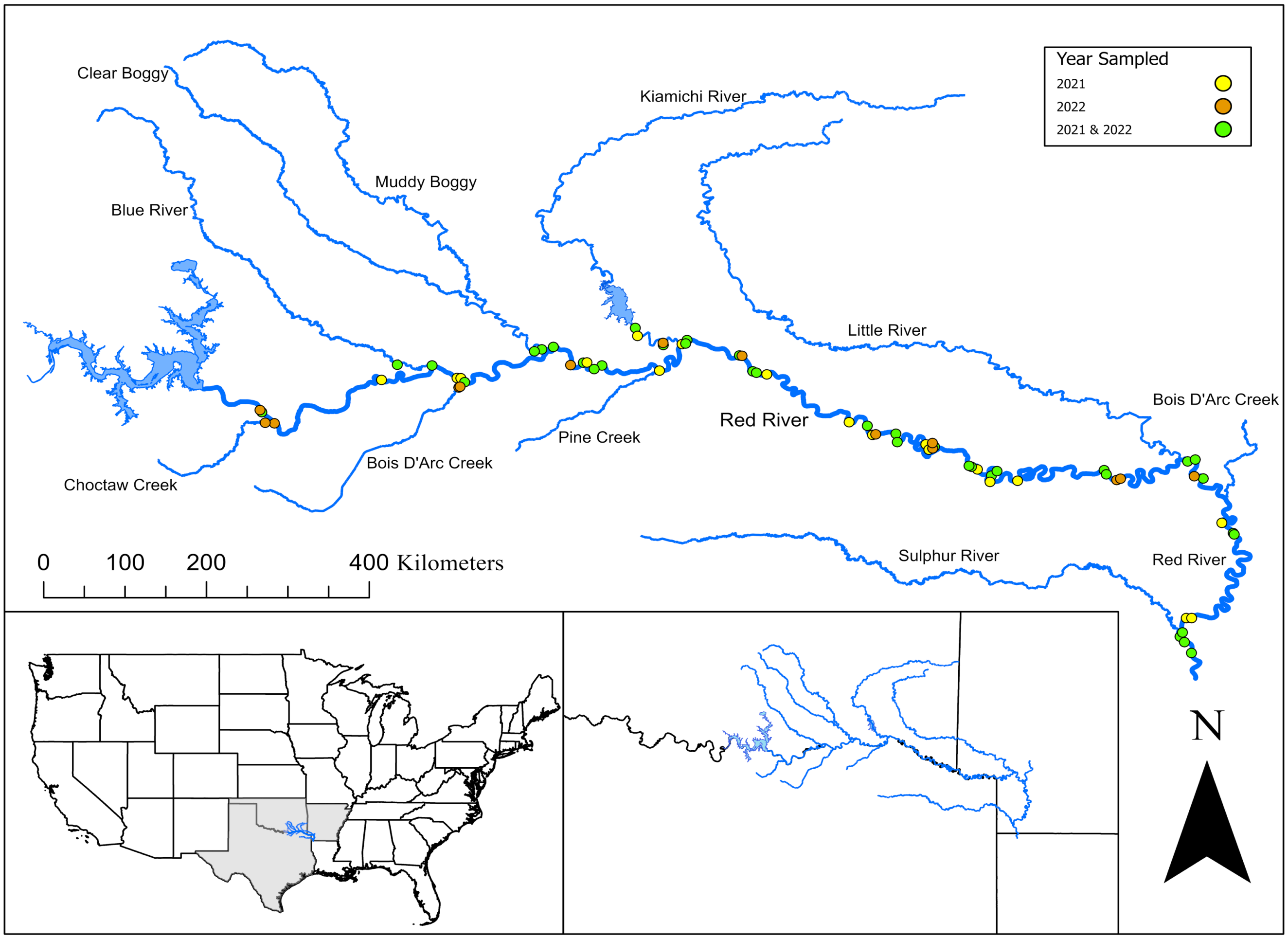


Figure 1. Map of the lower Red River catchment showing sites surveyed during the 2021 and 2022 sampling season. Sites were distributed across the mainstem Red River and tributaries of the lower Red River catchment. Yellow circles indicate sites that were only surveyed during 2021. Orange circles indicate sites that were only surveyed during 2022. The green circles indicate sites that were surveyed during both 2021 and 2022.

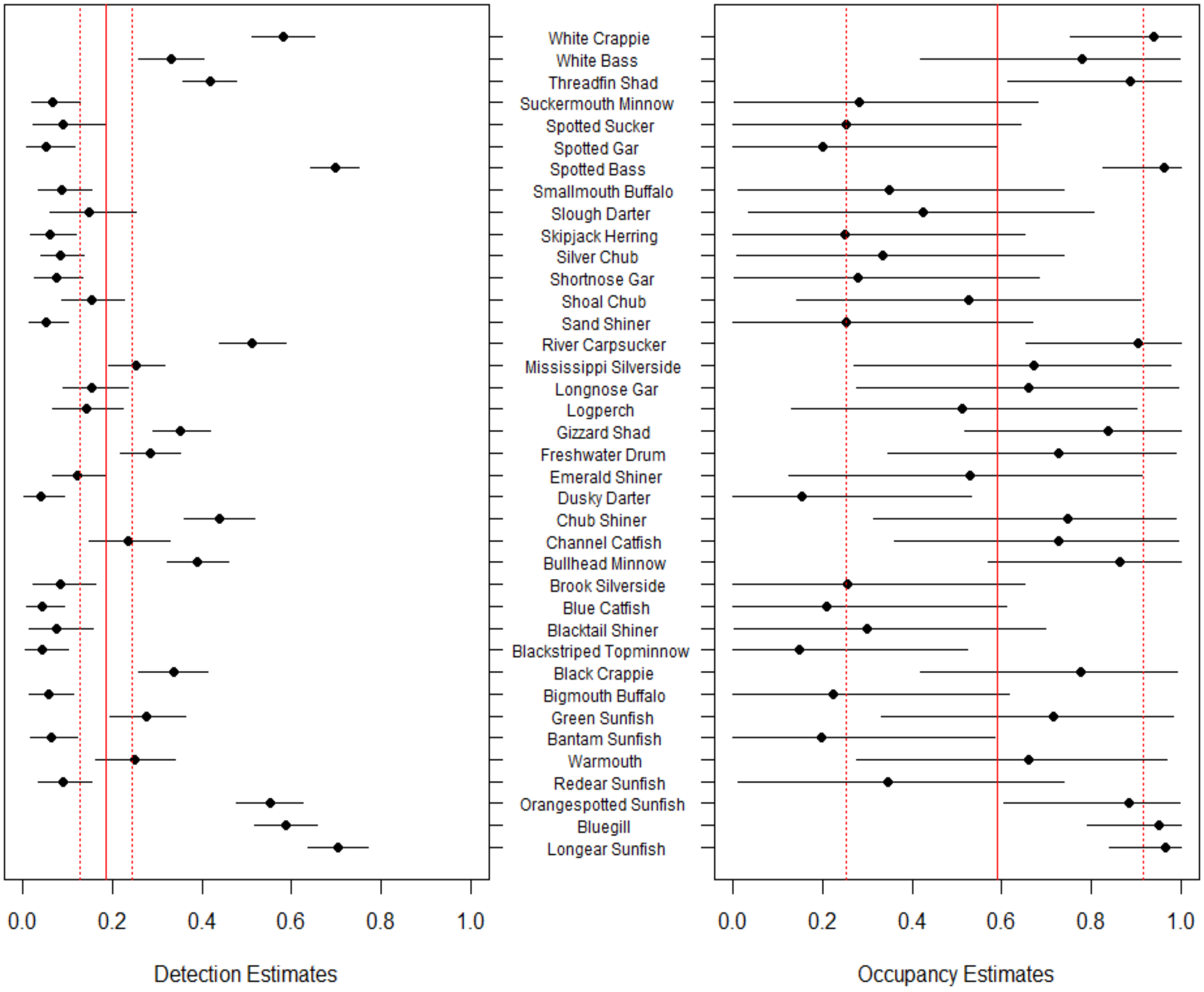


Figure 2. Species detection and occupancy estimates from the final occupancy model. The black points represent the median (most likely) values from the posterior distribution for each species. The black bars represent the 90% credible intervals for those species. The solid red line shows the group mean (all species) for both the detection and occupancy estimates and the dotted red lines show the 90% credible intervals for those estimates.

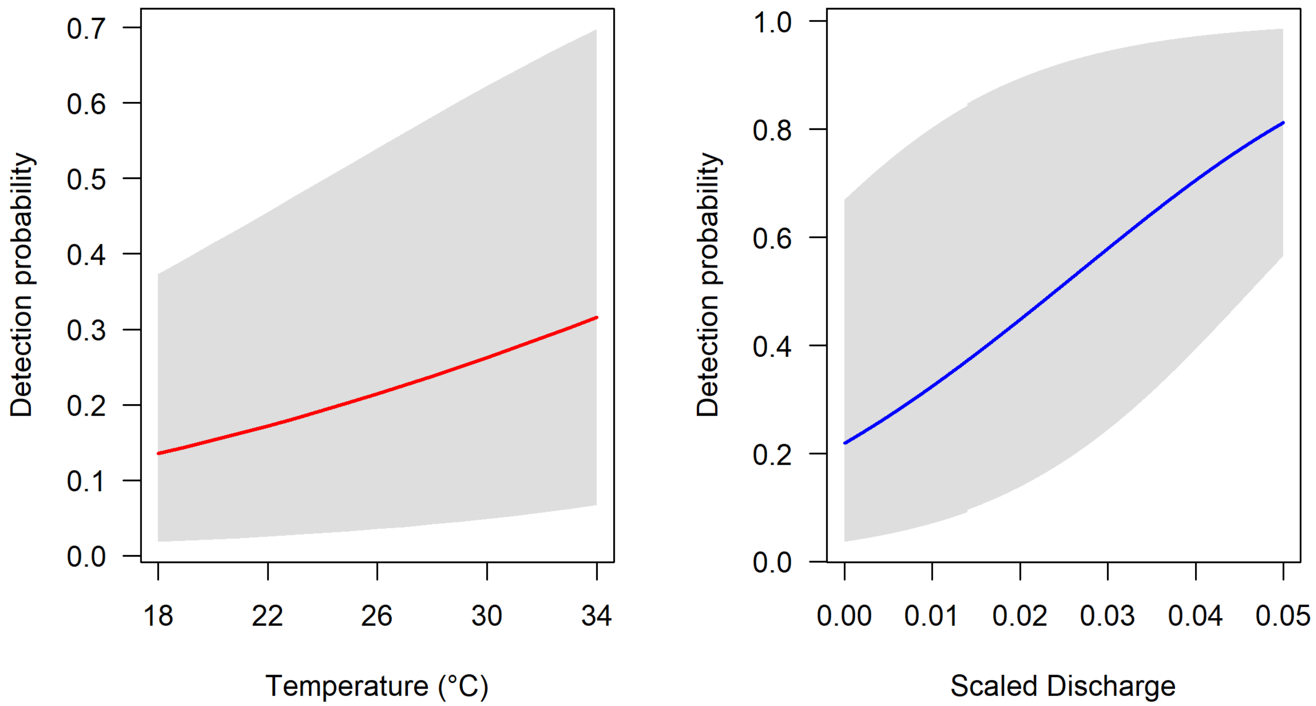
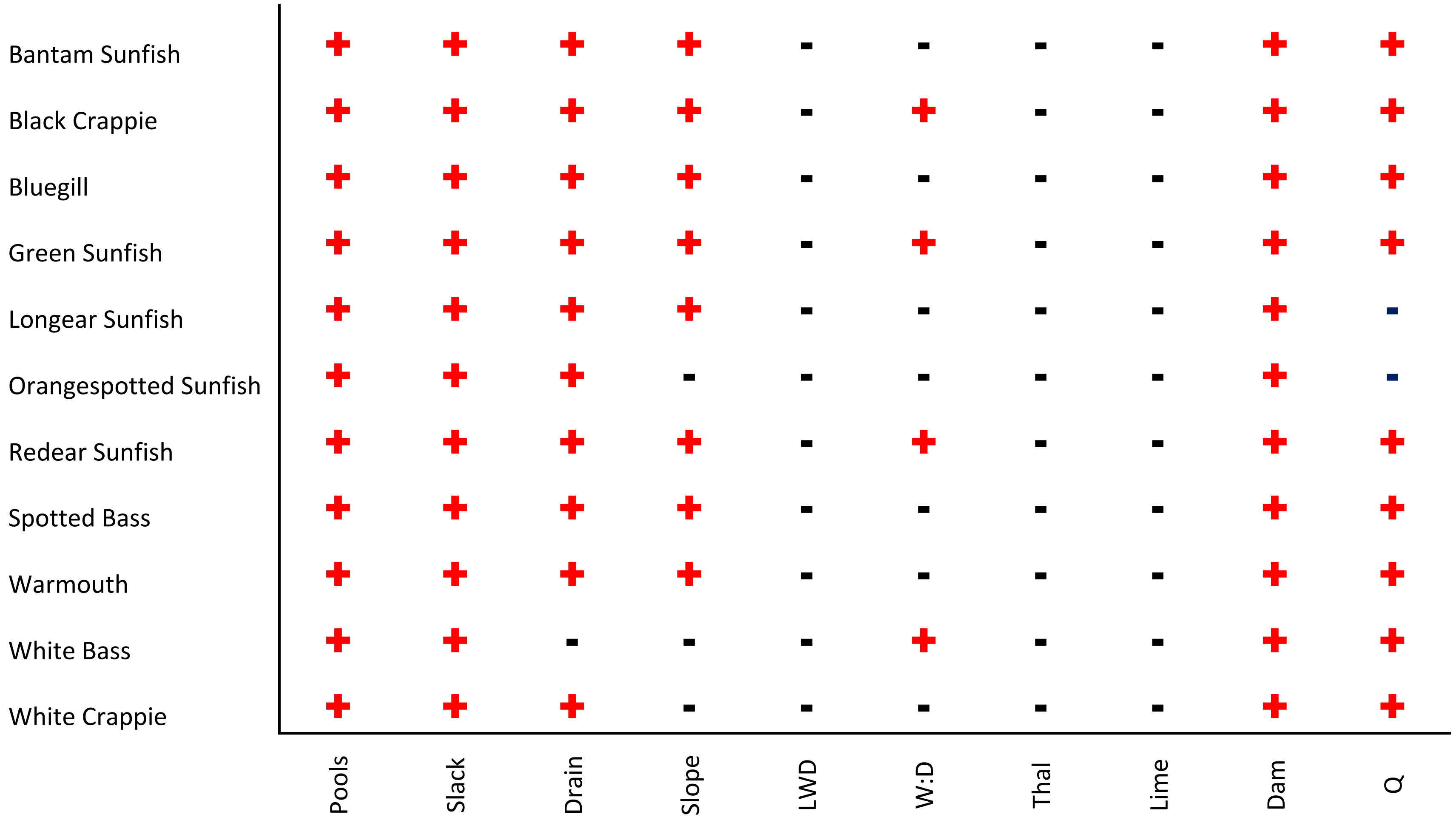
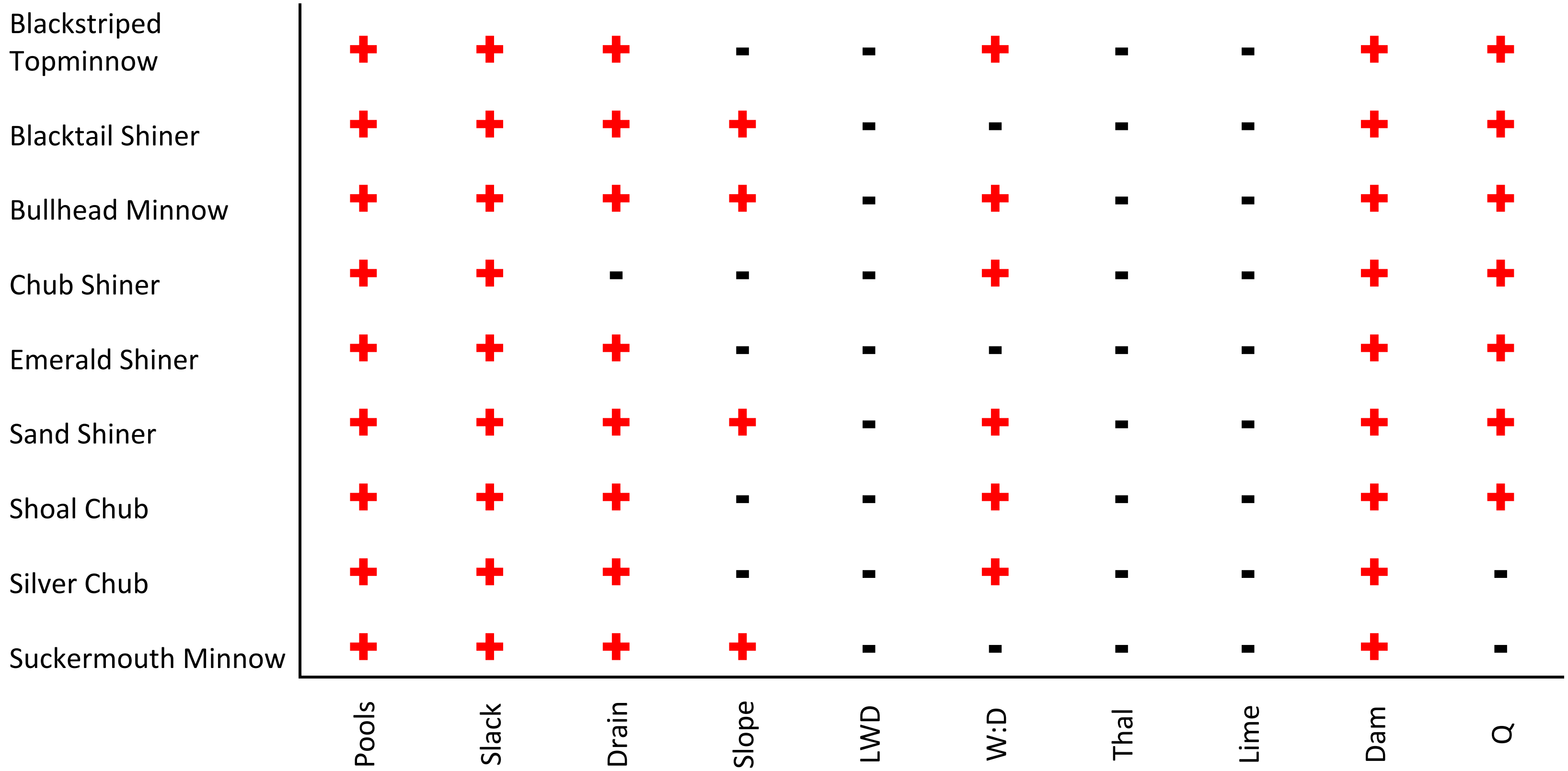


Figure 3. Relationships between water temperature, scaled discharge and the probability of detecting all species within the assemblage. The shaded gray areas represent the 90% credible intervals, and the solid line indicates the mode. The mode was estimated with all other model covariates held at mean values.



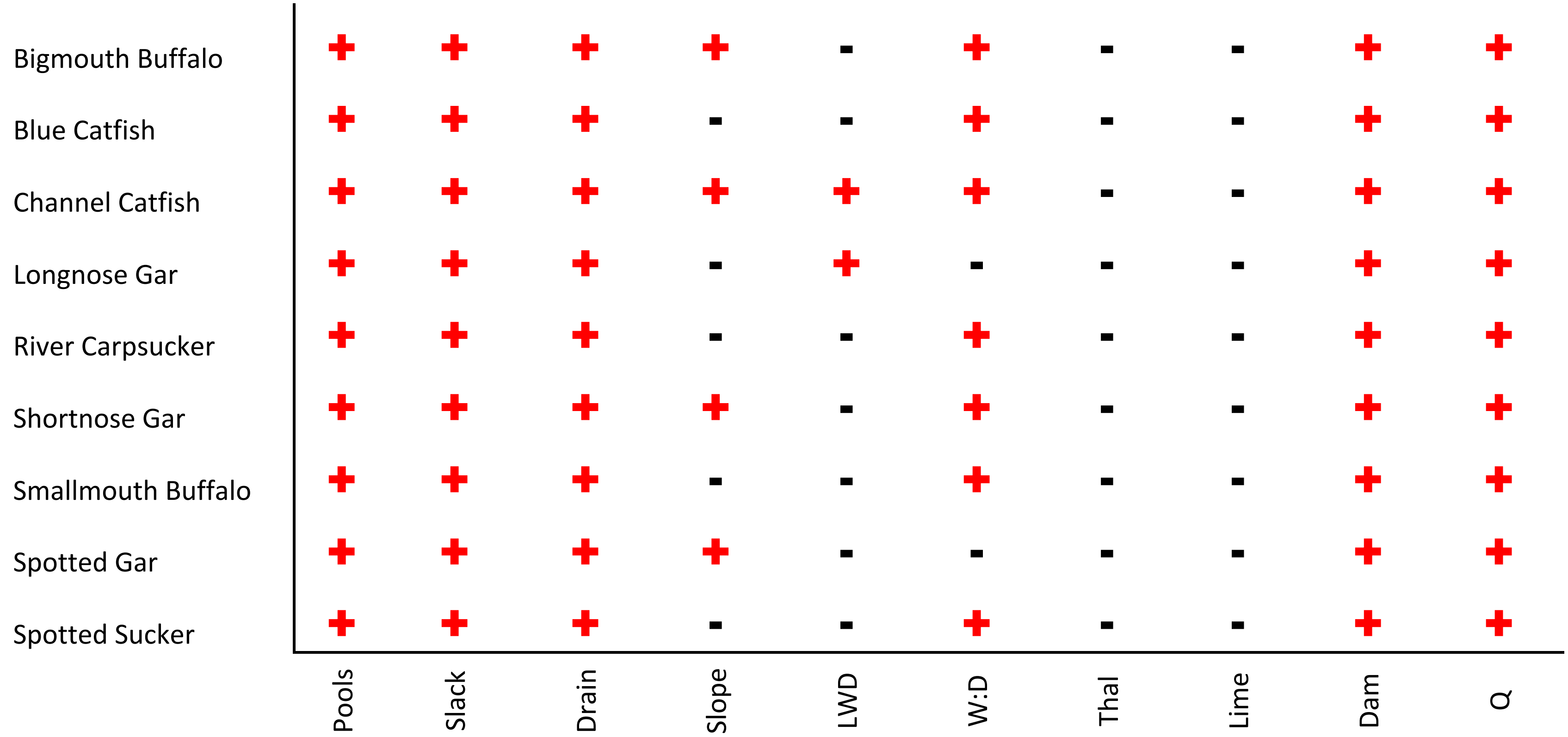
	Pools	Slack	Drain	Slope	LWD	W:D	Thal	Lime	Dam	Q
Bantam Sunfish	+	+	+	+	-	-	-	-	+	+
Black Crappie	+	+	+	+	-	+	-	-	+	+
Bluegill	+	+	+	+	-	-	-	-	+	+
Green Sunfish	+	+	+	+	-	+	-	-	+	+
Longear Sunfish	+	+	+	+	-	-	-	-	+	-
Orangespotted Sunfish	+	+	+	-	-	-	-	-	+	-
Redear Sunfish	+	+	+	+	-	+	-	-	+	+
Spotted Bass	+	+	+	+	-	-	-	-	+	+
Warmouth	+	+	+	+	-	-	-	-	+	+
White Bass	+	+	-	-	-	+	-	-	+	+
White Crappie	+	+	+	-	-	-	-	-	+	+

Figure 4. Occupancy relationships of Centrarchidae and Moronidae species. Positive relationships are indicated with a red plus sign (+). Negative relationships are indicated with a black negative sign (-). Slack is the presence of slackwater, Drain is the drainage area where low drainage area is the reference, LWD is large woody debris, W:D is width to depth ratio, Thal is average thalweg depth, Lime is percentage of limestone, Dam is the distance from nearest upstream dam, and Q is the median discharge value.



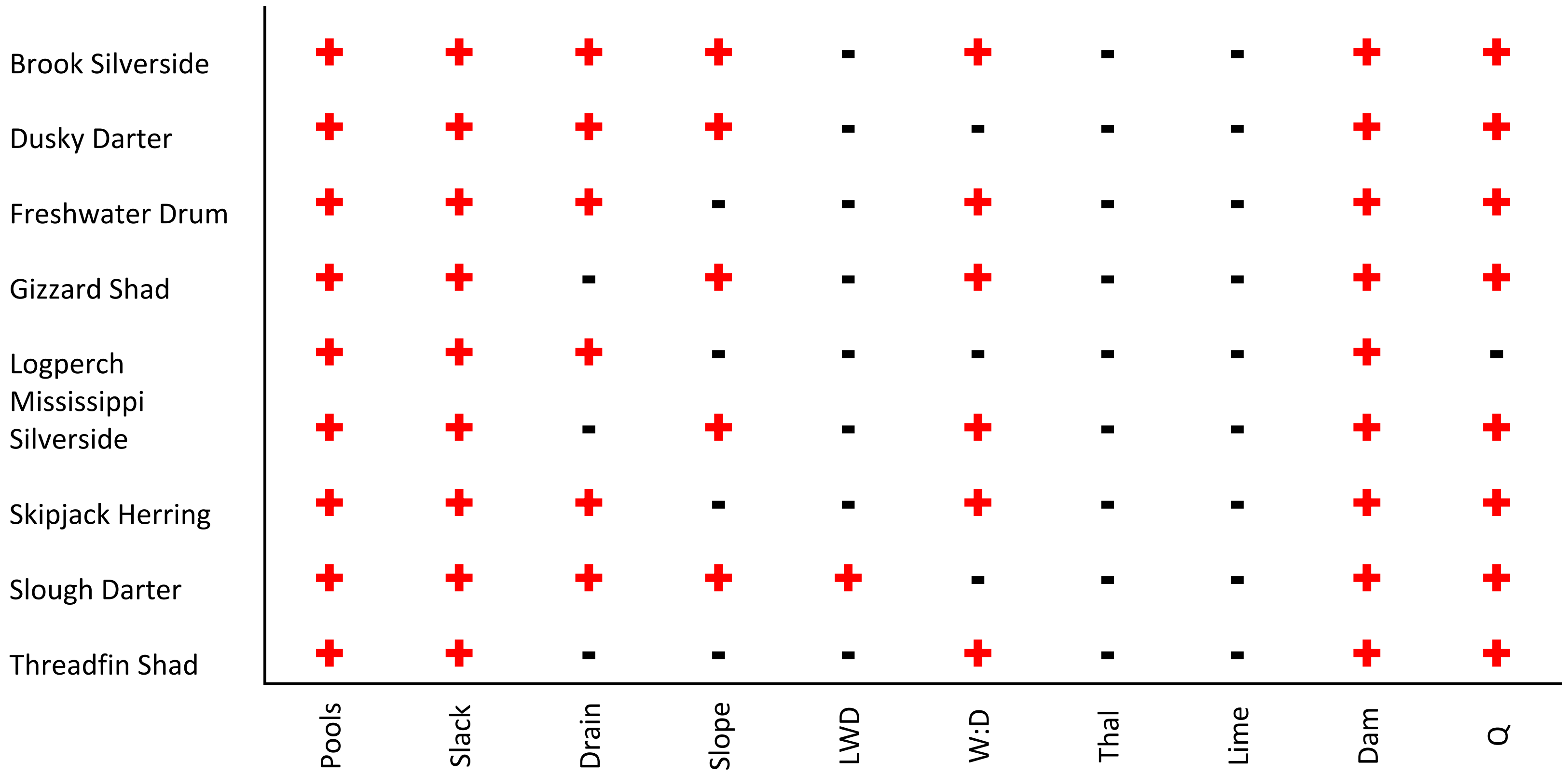
	Pools	Slack	Drain	Slope	LWD	W:D	Thal	Lime	Dam	Q
Blackstriped Topminnow	+	+	+	-	-	+	-	-	+	+
Blacktail Shiner	+	+	+	+	-	-	-	-	+	+
Bullhead Minnow	+	+	+	+	-	+	-	-	+	+
Chub Shiner	+	+	-	-	-	+	-	-	+	+
Emerald Shiner	+	+	+	-	-	-	-	-	+	+
Sand Shiner	+	+	+	+	-	+	-	-	+	+
Shoal Chub	+	+	+	-	-	+	-	-	+	+
Silver Chub	+	+	+	-	-	+	-	-	+	-
Suckermouth Minnow	+	+	+	+	-	-	-	-	+	-

Figure 5. Occupancy relationships of Cyprinidae species. Positive relationships are indicated with a red plus sign (+). Negative relationships are indicated with a black negative sign (-). Slack is the presence of slackwater, Drain is the drainage area, LWD is large woody debris, W:D is width to depth ratio, Thal is average thalweg depth, Lime is percentage of limestone, Dam is the distance from nearest upstream dam, and Q is the median discharge value.



	Pools	Slack	Drain	Slope	LWD	W:D	Thal	Lime	Dam	Q
Bigmouth Buffalo	+	+	+	+	-	+	-	-	+	+
Blue Catfish	+	+	+	-	-	+	-	-	+	+
Channel Catfish	+	+	+	+	+	+	-	-	+	+
Longnose Gar	+	+	+	-	+	-	-	-	+	+
River Carpsucker	+	+	+	-	-	+	-	-	+	+
Shortnose Gar	+	+	+	+	-	+	-	-	+	+
Smallmouth Buffalo	+	+	+	-	-	+	-	-	+	+
Spotted Gar	+	+	+	+	-	-	-	-	+	+
Spotted Sucker	+	+	+	-	-	+	-	-	+	+

Figure 6. Occupancy relationships of common large river fish families Catostomidae, Ictaluridae, and Lepisosteidae species. Positive relationships are indicated with a red plus sign (+). Negative relationships are indicated with a black negative sign (-). Slack is the presence of slackwater, Drain is the drainage area, LWD is large woody debris, W:D is width to depth ratio, Thal is average thalweg depth, Lime is percentage of limestone, Dam is the distance from nearest upstream dam, and Q is the median discharge value.



	Pools	Slack	Drain	Slope	LWD	W:D	Thal	Lime	Dam	Q
Brook Silverside	+	+	+	+	-	+	-	-	+	+
Dusky Darter	+	+	+	+	-	-	-	-	+	+
Freshwater Drum	+	+	+	-	-	+	-	-	+	+
Gizzard Shad	+	+	-	+	-	+	-	-	+	+
Logperch	+	+	+	-	-	-	-	-	+	-
Mississippi Silverside	+	+	-	+	-	+	-	-	+	+
Skipjack Herring	+	+	+	-	-	+	-	-	+	+
Slough Darter	+	+	+	+	+	-	-	-	+	+
Threadfin Shad	+	+	-	-	-	+	-	-	+	+

Figure 7. Occupancy relationships of remaining fish families Atherinidae, Clupidae, Percidae, and Sciaenidae. Positive relationships are indicated with a red plus sign (+). Negative relationships are indicated with a black negative sign (-). Slack is the presence of slackwater, Drain is the drainage area, LWD is large woody debris, W:D is width to depth ratio, Thal is average thalweg depth, Lime is percentage of limestone, Dam is the distance from nearest upstream dam, and Q is the median discharge value.

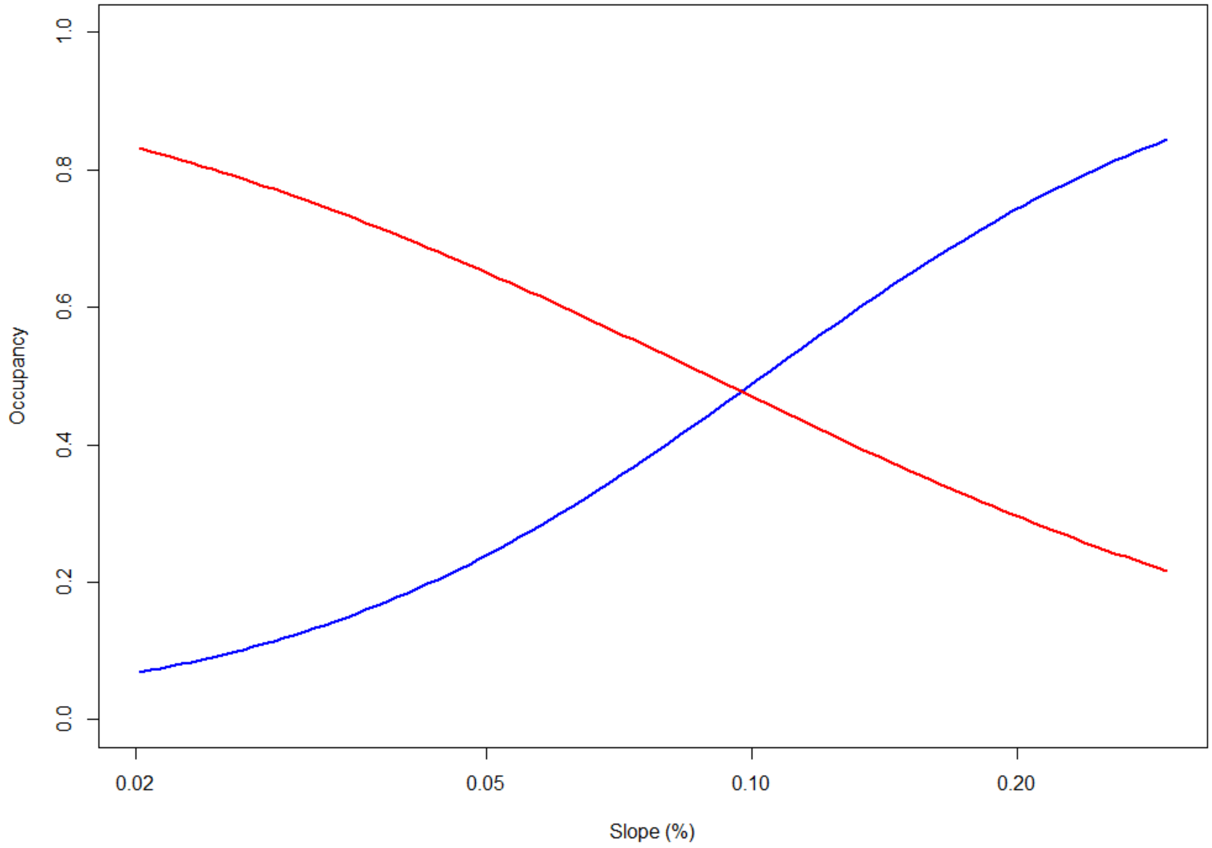


Figure 8. Relationships between the probability of occupancy of Dusky Darter *Percina sciera* (red line) and Freshwater Drum *Aplodinotus gruuniens* (blue line) and the percentage segment slope as a deflection from the group mean. See Table 10 for estimates of uncertainty (HDI's).

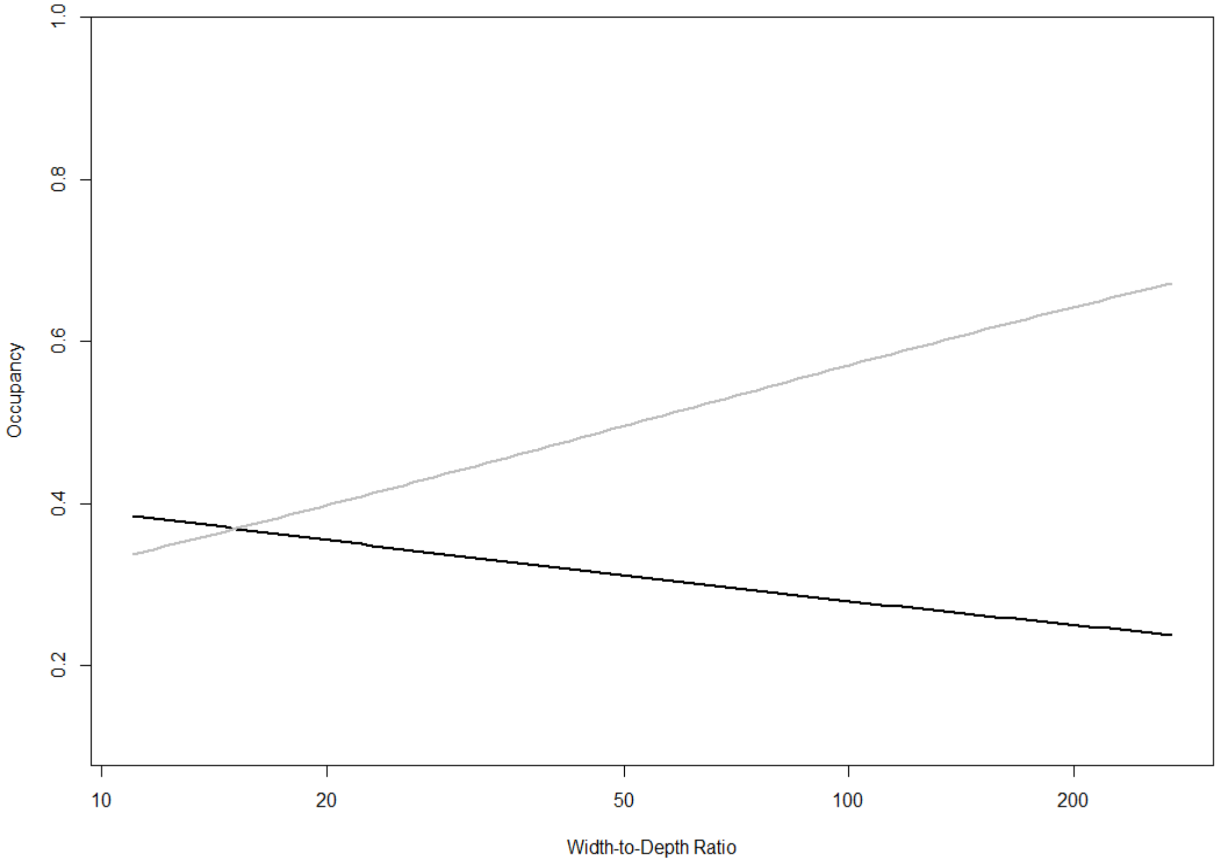


Figure 9. Relationships between the probability of occupancy of Blacktail Shiner (black line) and Shoal Chub *Macrhybopsis hyostoma* (gray line) and width-to-depth ratio as a deflection from the group mean. See Table 10 for estimates of uncertainty (HDI's).

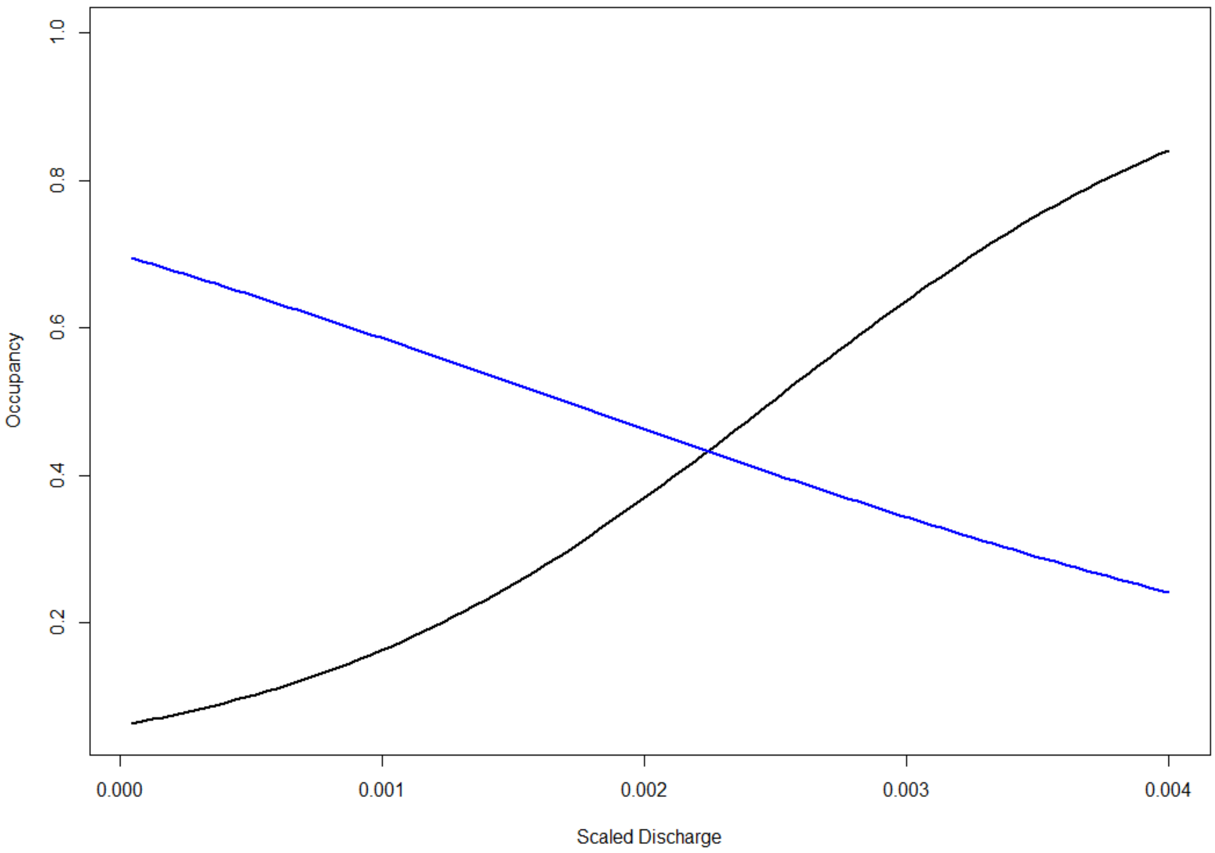


Figure 10. Relationships between the probability of occupancy of Blacktail Shiner *Cyprinella venusta* (black line) and Longnose Gar (blue line) and median scaled discharge as a deflection from the group mean. See Table 10 for estimates of uncertainty (HDI's).

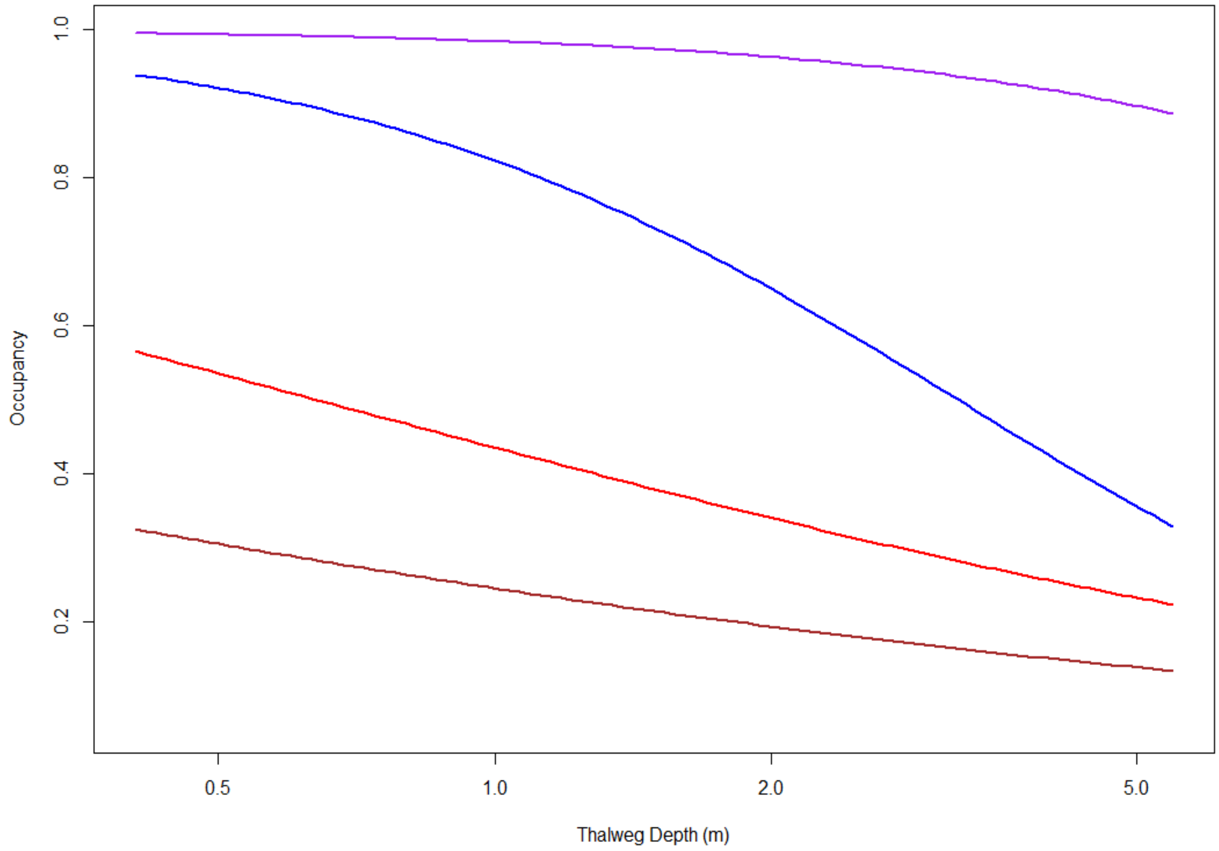


Figure 11. Relationships between the probability of occupancy of four *Lepomis* species: Longear Sunfish (purple), Warmouth (blue), Redear Sunfish (red), and Bantam Sunfish (brown) and the average thalweg depth as a deflection from the group mean. See Table 10 for estimates of uncertainty (HDI's).

Chapter III: Environmental factors associated with hatch date and growth of Spotted Bass, Longear Sunfish, and Orangespotted Sunfish in a large river catchment

Introduction

Survival during the first year of life is key to the success of fishes in lotic ecosystems (Gido and Jackson 2010). First-year survival affects cohort strength and reflects the reproductive success of a species (Campana 1996; Garvey et al. 2002; Humphries et al. 2020). In fisheries science, cohort strength and reproductive success of a species are typically evaluated by the survival of individuals from the early life stages into the adult population, referred to as recruitment (Ludsin et al. 2014; Humphries et al. 2020). Successful recruitment of age-0 fishes into the larger population of fish is essential for both maintaining and bolstering a population (Ricker 1954; Maceina and Pereira 2007; Humphries et al. 2013). However, recruitment can fluctuate among years resulting in periods of high or low recruitment (Houde 2016). Environmental variability, particularly in river ecosystems, often are the primary drivers of recruitment (Pitchford et al. 2005; Cardinale et al. 2009; Morrongiello et al. 2014).

Evaluating the relationship between environmental conditions and reproductive success is useful for developing management actions in regulated river ecosystems. In lotic ecosystems, fishes often use changes in environmental conditions as cues to determine spawning timing (Jackson 1989; Humphries and Lake 2000). However, environmental cues mediating successful hatches of fishes are poorly understood for many species. Identifying relationships between fluctuating environmental conditions and successful hatching by fishes may provide insight into the mechanisms affecting adult abundances (i.e., assuming a stock-recruit relationship which has been demonstrated for several species: Pacific Salmon, Striped Bass, and Threadfin Shad, Michielsens and McAllister 2004; Feyrer et al. 2007; Fleischman et al. 2013, but not others, McClatchie et al. 2010; Kell et al. 2016). These mechanisms can be used to inform river regulations and promote conditions beneficial to native species or difficult for invasive species. Specifically, successful spawning and juvenile growth are often affected by flow (Humphries et al. 1999; King et al. 2003, 2010) and water temperature (Preece and Jones 2002; Humphries et al. 2013; Tornabene et al. 2020) regimes.

Growth rates vary among life stages of fishes and are affected by a myriad of physicochemical conditions. Age-0 fish have higher growth rates than adults, and display intraspecific variation that is influenced by both environmental conditions (e.g., discharge and temperature) and spawn timing (Weatherley 1990; Campana and Thorrold 2001). Growth rates of conspecifics can vary among habitats that experience variable environmental conditions (Wilson et al. 2019). For example, Tonkin et al. (2011) found that Australian Smelt *Retropinna semoni* in the Ovens River, Australia experienced variable growth in response to discharge conditions. Further, protracted spawning can influence growth of some fishes (Bogner et al. 2016). For example, an earlier-hatched cohort could switch to piscivory faster than a later-hatched cohort, and therefore, gain growth advantage over their later-hatched conspecifics (Maceina and Isely 1986; Ludsin and Devries 1997). Alternatively, later hatched fish may experience higher growth rates due to the increasing water temperatures of summer (Coutant 1975), resulting in similar growth by multiple cohorts (e.g., Smallmouth Bass *Micropterus dolomieu*, Sabo and Orth 1994). Regardless, an important first step is to understand both hatch timing and growth of young fishes as related to environmental conditions.

Centrarchidae are a diverse family of warmwater fishes native to North America, but our understanding of their early life history is lacking for many species. This family of fishes represents numerous popular sportfishes including fishes belonging to *Micropterus*, *Lepomis, Pomoxis*, and *Ambloplites*. The life histories of many popular members within the family (e.g., Largemouth Bass *Micropterus salmoides* and Bluegill *Lepomis macrochirus*) are well studied, particularly in reservoir and lake ecosystems. However, species typically associated with lotic ecosystems, including Spotted Bass *Micropterus punctulatus,* Longear Sunfish *Lepomis megalotis*, and Orangespotted Sunfish *Lepomis humilis* do not have well described early life histories. All three species are nest spawners who typically guard their offspring for a period of time after hatching (Witt and Marzolf 1954; Rasmus et al. 2008). However, knowledge of the environmental cues and pre-spawning conditions that lead to successful hatches by these more riverine fishes is lacking.

An understanding of the relationships between environmental variability and successful hatching and growth of centrarchid fishes would be beneficial to managers. Water withdrawals and warming temperatures due to climate change may influence the natural reproductive responses of fishes within lotic ecosystems (Xenopoulos et al. 2005). Further, analysis of environmental conditions associated with successful hatch of young and their growth would provide managers with valuable information on how altering dam releases and flow regimes can sustain or disrupt completion of their life history. Therefore, my second study objective was to estimate the spatial and temporal variation in hatch dates and growth of Spotted Bass (hereafter SPB), Longear Sunfish (hereafter LES), and Orangespotted Sunfish (hereafter OSS). Specifically, I examined relationships between successful hatching and growth with discharge, temperature, precipitations, and calendar date of the three centrarchid fishes.

Methods

Site Selection

I selected seven sample sites in the lower Red River catchment distributed across both the mainstem Red River (three sites) and major tributaries: Blue River, Muddy Boggy Creek, Kiamichi River, Bois D'Arc Creek (Figure 1, see also study area description in Chapter I). Sites were selected based on river access, proximity to USGS stream gages, and detection of my target species. Each site had relatively homogenous discharge and temperature conditions (i.e., no springs). My sample sites (10 – 15 km in length) comprised a combination of diverse slackwater habitats (i.e., forewaters, backwaters, side channels, sandbar and pool complexes). These slackwater habitats are thought to be important nursery areas for a variety of age-0 fishes, including many centrarchids (Humphries et al. 2006).

Fish Collection and Preservation

I sampled age-0 SPB, LES, and OSS before they achieved a size where enumerating daily bands would be difficult to impossible, generally fishes >100 days old (Long and Grabowski 2017). Therefore, I collected age-0 SPB, LES and OSS until they reached approximately 110 mm, 45 mm, and 40 mm total length (TL), respectively (Delp et al. 2000; Rasmus et al. 2008).

I sampled at each site approximately once every 2 weeks during my sampling seasons (mid-May through September 2020 and 2021). At each site, I sampled as described for Objective 1 using a combination of mini-fyke nets, larval tows, and seining.

All captured target species were enumerated and measured for TL; however, for catches on each sample visit with more than 50 individuals, I took five haphazardly selected individuals from 5-mm TL bins. If my catches on each visit were less than 50 individuals, then I kept all of them for ageing. Collected individuals were euthanized using an overdose of tricane methanesulphonate (MS-222) (300 mg/L, Neiffer and Stamper 2009), then preserved in 1-L bottles containing 70% ethanol for future laboratory processing.

Otolith Extraction, Processing, and Ageing

I removed and mounted sagittal otoliths from age-0 SPB, LES, and OSS to estimate hatch dates. Daily band deposition on sagittal otoliths has been validated in Spotted Bass (DiCenzo and Bettoli 1995), and several other centrarchid species (e.g., Largemouth Bass, Green Sunfish, Pumpkinseed, Redspotted Sunfish, and Bluegill). However, use of sagittal otoliths for ageing has not been validated for either LES or OSS. Based on validation studies in the *Lepomis* family (Taubert and Coble 1977; Hales and Belk 1992; Roberts et al. 2004), I assumed a similar developmental timing of daily bands for both *Lepomis* species.

I removed otoliths from the collected fishes and mounted them for later reading. I removed the sagittal otoliths under a stereo dissection microscope using fine-tipped probing needle and forceps to cut the optic capsule located towards the posterior end at the base of the inside skull (VanderKooy 2009). Both otoliths were removed and placed into a petri dish. I then mounted the otoliths to slides convex side up (i.e., sulcus ascousticus facing upwards) using thermoplastic cement (Lakeside No. 70C, Monee, IL). I melted the cement on the slide until it pooled. Then, the otoliths were placed convex side up in the cement and allowed to cool at ambient temperature.

The mounted otoliths were polished in a circular pattern to allow band enumeration. I polished the otoliths by hand using 800-, 1000-, 1500-, and 2000-grit sandpaper (Wetordry, 3M, St. Paul, MN), and 1-, and 3-μm diamond lapping papers (Diamond Lapping Film, 8" diameter, plain backing, Electron Microscopy Sciences, Hatfield, PA). I began polishing the otoliths with the coarsest paper (smaller otoliths started with a finer grit sandpaper) and moved to finer grains as the nucleus becomes visible. I regularly checked the otolith under the microscope to ensure that surface quality was not compromised (i.e., bands were visible but not over polished). For LES and OSS, polishing was complete once the daily bands became visible at the nucleus (Campana and Neilson 1985). However, for SPB otoliths, I also polished the convex side using the same methods described above. After the convex side was polished, the cement was remelted and the otolith was then flipped following the methods of Miller and Storck (1982). After flipping, the concave side was again polished using a similar approach until the bands on the outer edge were clear. The otolith was considered complete once all bands were visible.

I enumerated daily bands to estimate hatch dates. Otolith microstructure (i.e., formation of daily growth bands) analysis is a proven method for estimation of both hatch dates and growth of many fishes (Stevenson and Campana 1993). I enumerated daily bands using a Nikon Eclipse E400 compound microscope at a 10X magnification. Mineral oil was applied as needed for clarification. Daily bands were counted from the outer edge toward the center to enhance accuracy (Campana and Moksness 1991, Figure 2). Two independent readers counted bands and recorded estimates. Readers had no prior information about fish size or previous reads. Band counts within 10% difference between readers were averaged; if >10% difference existed, then readers attempted to reconcile the disagreements to reach a consensus. If a consensus was not reached, then the otolith was removed from the dataset.

I estimated hatch dates by subtracting the daily band counts from the date of capture, and then subtracting an additional 5 days to account for the timing of first band formation. Spotted Bass otoliths form at the time of swim up, which in typical warm-water ecosystems is 5 days (Miller and Storck 1982; DiCenzo and Bettoli 1995; Sammons et al. 2021). Although timing of the otolith formation for LES and OSS is unknown, I also assumed that the first daily ring would form at swim-up (i.e., 5 days) based on similar *Lepomis* species (Taubert and Coble 1977). Because first band formation can vary (Campana and Neilson 1985), and to account for any discrepancies in band enumeration, I grouped hatch counts into 7-day periods, allowing evaluation of coarser environmental measurements (i.e., conditions on the day of hatch likely do not dictate hatch). Lastly, average growth (1.00 mm/day) rates were calculated by dividing TL (1.00 mm) by the estimated age (1.0 days) (Sammons et al. 2021).

Environmental Measurements

I quantified the environmental conditions that I hypothesized would be associated with successful hatches and growth of SPB, LES, and OSS (Table 1). Successful reproduction in centrarchid fishes is affected by environmental factors including discharge (Cooke and Philipp 2009; Sammons et al. 2021) and water temperature (Noltie and Keenleyside 1986; Sammons et al. 2001). Therefore, I obtained average daily discharge (1.0 m^3/s) from the USGS stream gages located nearest to my study sites (i.e., Blue River 07332500, Muddy Boggy 07335300, Arthur City 07335500, Kiamichi River

HGLO2 (Army Corps), Bois D'Arc 07332622, Fulton 07341500, Spring Bank 07344370, Table 2). To ensure these discharge data accurately represented the distance between the gage and my sites, I compared Acoustic Doppler Current Profiler discharge measurements at each site with the stream gage measurements. My results supported that I could use the stream gage data to represent conditions at my study sites (i.e., on average +/- 1.3 m^3/s compared to the gages). Further, I scaled (i.e., divided) discharge data by drainage area thereby making it comparable across my sites (e.g., high discharge in a tributary was comparable to high discharge in the mainstem).

I obtained air temperature and precipitation from the nearest weather station to each site. I used daily average air temperature from the nearest weather station to each of my sites (Oklahoma Mesonet and NOAA National Centers for Environmental Data, Table 2) as a surrogate for water temperature ($| r | = 0.96$, Figure 3). I attempted to collect daily water temperature for each site using continuous temperature loggers (Onset Hobo MX2201, Bourne, MA). However, the loggers were placed late during the 2021 season due to extremely high discharge conditions and many were stolen or exposed to air when the water receded. I also collected daily precipitation data (1.00 mm) from the weather stations. I included precipitation data because climate patterns may affect fish recruitment (King et al. 2003; Perkin et al. 2019). Lastly, I included a measure of date within the season by including calendar day (i.e., March 1st is 1, May 31st is 92, September 1st is 185) to indicate changes in photoperiod (Wedgeworth et al. 2022) and other trends that could not be measured directly (e.g., number of predators associated with their hatch dates).

Hatch Analyses

My observed hatches were grouped into 7-day periods beginning in February (i.e., when hatches were first observed) and ending in September because daily environmental changes may not capture the time period required to elicit spawning (e.g., lag effect; Forsythe et al. 2012; Vine et al. 2019). The average air temperature and scaled discharge were calculated for seven days prior to the grouped hatch week to represent changes in conditions occurring prior to a successful hatch. Additionally, the coefficient of variation (CV) of scaled discharge was calculated for the same time period. Because of many days of zero precipitation within the season, I summed rainfall during the week prior to the hatch week.

I transformed my covariates and checked for multicollinearity to ensure I met the assumptions of multiple regression, and I standardized my data. I log-transformed average scaled discharge, CV of discharge, and precipitation due to their right skewedness. I tested for multicollinearity as described in Chapter 2 (Table 3). Briefly, I used the Pearson correlation coefficients ($| r | < 0.50$) to retain orthogonal covariates for modeling. Average air temperature and calendar week were multicollinear ($| r | = 0.79$); therefore, I retained only air temperature. Lastly, I standardized all variables to a mean of zero and a standard deviation of one to aid in model interpretation and convergence (Gelman and Hill 2007).

I analyzed successful hatches related to environmental conditions using a hurdle model framework. I chose this framework for two reasons: 1) to consider both the factors that relate to the probability of hatch and hatch frequency; and 2) because of the zero inflation and overdispersion of hatch dates during the spawning season. It is important to account for both zero inflation and overdispersion during statistical analyses, because failure to accommodate them can introduce statistical biases in my results (Blasco-Moreno et al. 2019). Both hurdle models and zero-inflation (ZI) models account for excessive zeros while including overdispersion (Mullahy 1986; Greene 1994). An advantage of a hurdle model over a ZI model is that hatch (bimodal) and count data can be modeled separately (Hofstetter et al. 2016). A hurdle model framework is used to fit zeros and ones as separate processes (i.e., zero model and count model), whereas a ZI model is a mixture of the two processes (i.e., binomial process and count process, Zuur et al. 2007). I chose the hurdle model framework to analyze my data because once the hurdle is crossed, the model does not discriminate between true and false zeros, resulting in more informed relationships (Blasco-Moreno et al. 2019).

My hurdle model framework comprised two separate models (parts) to account for random effects. First, I built a model focused on the probability of a successful hatch (hereafter zero model) which consisted of a binomial outcome (i.e., 0 or 1) of a binary logit (logistic regression). A "hurdle" was then crossed once a successful hatch occurred (i.e., 1), and I built a zero-truncated negative binomial model (hereafter count model). A negative binomial distribution extends a Poisson model and can capture more of the true zeros than a traditional Poisson distribution (Hofstetter et al. 2016). I built the zero and count models separately, allowing me to analyze the relationships between successful hatch and the number of hatch events occurring as separate events. Although these models could be modeled simultaneously using an existing R package, it does not allow for the inclusion of random effects (see below).

I built my zero and count models, for each species, using fixed and random effects to analyze the variation in reproductive success. Year (2021 and 2022) was included as a fixed categorical effect in all Spotted Bass candidate models (where 2021 was the reference) to account for seasonal variation. Additionally, I included a random effect for site (i.e., stream) to account for the unequal sample sizes and spatial correlation (Wagner et al. 2006). I built the zero model (i.e., probability of hatch) using the package *lme4* (Bates et al. 2015) in the statistical computing software R (Version 4.2.2, R Core Team 2022). The mathematical expression of the zero model is expressed as:

$$logit(p_{it}) = \ln\left({}^{p}/_{1-p}\right)$$

$$= \beta_0 + \alpha_1 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \gamma_t \sim N(0, \sigma) + e_{it} \sim N(0, \sigma)$$

for i = 1 – # observations; y_i = (0,1)

Where:
p = probability of a hatch event for observation i and site t
i = observation i
t = site t
β_0 = prime intercept
α_1 = fixed effect for year where 2021 was the reference
β_i = intercept for environmental predictor variable X
X_i = environmental predictor variable
γ = random intercept for site t
e = error term that is normally distributed with a mean of 0 and sd of σ

I built the count model (i.e., frequency of hatch) using the package *glmmTMB* (Brooks et al. 2017) in the statistical computing software R (Version 4.2.2, R Core Team 2022). The mathematical expression of the count model is expressed as:

$$\log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_3{}^2 + \gamma_t \sim N(0, \sigma) + e_{it} \sim N(0, \sigma)$$

for i = 1 – # observations; $y_i \geq 1$

Where:
Y= calculated number of hatches during observation i and site t
i = probability of a hatch event for observation i
t = site t
β_0 = prime intercept
α_1 = fixed effect for year where 2021 was the reference
β_i = intercept for environmental predictor variable X
X_i = environmental predictor variable
γ = random intercept for site t
e = error term that is normally distributed with a mean of 0 and sd of 1

I built my candidate models using relationships I hypothesized would affect hatch success for each species. My models were ranked using Akaike's Information Criteria (AICc) adjusted for small sample size (*n*/*K* <40) (Anderson et al. 2000). I determined which models had the most support using AICc differences (ΔAICc) (Burnham and Anderson 2002). Models with a ΔAICc < 2 are considered to have equal support (Burnham and Anderson 2002); therefore, I reported all models with a ΔAICc < 2 for each of the species. Further, I calculated Akaike weights (w_i) (ΔAICc < 2) to evaluate the relative candidate model support (Burnham and Anderson 2002; Symonds and Moussalli 2011). Of models with equal support, I considered my top models to be the most parsimonious (i.e., < 2 ΔAICc with the highest model weights, Arnold 2010).

Lastly, I evaluated goodness-of-fit for each top ranked zero and count models. R^2 (i.e., marginal and conditional) values for each of the species top ranked models (e.g., zero and count model) were calculated using the package *performance* (Lüdecke et al. 2021) in the statistical computing software R (Version 4.2.2, R Core Team 2022) to show the variance explained by fixed and random effects. I used binned residuals to evaluate goodness-of-fit of the top ranked zero models. A binned residual plot provides a posterior predictive check. If ~95% of binned residuals fell within the bounds, I concluded that the model had good fit (Gelman et al. 2000). To analyze goodness-of-fit of the count models, I used diagnostic plots (QQ and scatterplots of residual and fitted values) in the package *DHARMa* (Hartig 2016) within the statistical computing software R (Version 4.2.2, R Core Team 2022).

Growth Analyses

Prior to model building, I calculated environmental metrics to represent variability within the growing season and transformed my variables to meet multiple regression assumptions. I calculated cumulative precipitation (1.0 mm) from the day of hatch until each individual was collected (i.e., last day a band formed). I calculated the median temperature over the same time period to indicate general temperature trends during the growing period (Coutant 1976). I also included calendar date of hatch during the season because earlier and later-hatched cohorts can exhibit different growth rates (Ludsin and Devries 1997; Durham and Wilde 2005). I calculated both average scaled discharge (as described for the hurdle models), and the CV of discharge to describe magnitude and variation of flow. Lastly, I log-transformed scaled discharge, and discharge CV because they were right-skewed.

I tested for multicollinearity using Pearson's correlation coefficient as previously described and standardized my variables to improve model interpretation (Table 4). Hatch date and median air temperature values were highly correlated ($| r | = 0.87$); therefore, I retained temperature. Additionally, precipitation was correlated with hatch date (| r | = -0.59), scaled discharge (| r | = 0.53), and air temperature (| r | = -0.53); therefore, I removed precipitation from the dataset to avoid confounding effects. All remaining variables (| r | < 0.50) were retained for analyses. All variables were standardized to a mean of zero and standard deviation of one to improve model interpretation and promote convergence.

I analyzed the relationships between average daily growth since hatch, by species, and associated environmental conditions. I built a multiple regression model following Maceina (1992) where growth is modeled as a function of environmental covariates, but modifying the response growth variable to fit daily increments. My daily growth models were built using both fixed and random effects. Year (where 2021 was the reference) was included as a fixed effect in my Spotted Bass models. I modeled site as a random effect in all the models. I built my multiple regression models using the package *nmle* (Pinheiro et al. 2021) in the statistical computing software R (Version 4.2.2, R Core Team 2022). The growth model is expressed as:

$$Y_{it} = \beta_0 + \alpha_1 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_4 + \gamma_t \sim N(0, \sigma) + e_{it} \sim N(0, \sigma)$$

for i = 1 – # individuals; $Y_{it} > 0$

Where:
Y= estimated growth rate of individual i at site t
i = the individual of each species
t = site t
β_0 = prime intercept
α_1 = fixed effect for year where 2021 was the reference
β_i = intercept for environmental predictor variable X
X_i = environmental predictor variable
μ = random intercept for site t
e = error term that is normally distributed with a mean of 0 and sd of σ

I ranked my growth models using AICc as described for the hurdle model framework (see above). I considered my top model for each species to be the model with the most support (i.e., < 2 ΔAICc with the highest model weights, Arnold 2010) for each species. I calculated R^2 (i.e., marginal and conational) values for the top ranked models (i.e., those with ΔAICc < 2). Lastly, I evaluated goodness-of-fit using binned residual plots for my top models.

Results

Fish Collection

I completed 102 surveys (35 in 2021 and 67 in 2022) at my 7 sites during 2021 and 2022 (Table 5). I attempted to sample biweekly in 2021 but this was not possible during some periods due to flooding (see Chapter I, Figure 2 for hydrograph). In 2022, I was able to sample each site approximately every two weeks beginning in late May through mid-August. I collected 203 and 817 SPB in 2021 and 2022, respectively (Table 6). I collected 246 LES, and 342 OSS in 2022. The most individuals sampled were obtained from the mainstem Red River site at Spring Bank (Table 6). The fewest fish sampled came from my Blue River site. The fish collected covered a range of sizes for juvenile fishes: SPB TL 19 – 100 mm, OSS TL 19 – 41 mm, and LES TL 15 – 57 mm (Table 7).

Ageing and Growth

I processed 1599 otoliths from all three species to analyze hatch and growth relationships (Table 7). I retained age estimates for otoliths meeting my criteria (i.e., reader agreement and within a certain size range) for 93% (954 of 1019) of SPB, 87%

(298 of 339) of OSS, and 93% (228 of 241) of LES. Daily band estimates for all three species ranged between 22 and 125 days.

Hatch dates varied between years for SPB and spatially for all species (Table 7). SPB hatches occurred later (April 8th) and extended later (July 1st) during 2021 when compared to 2022 (March 21st- June 4th). Further, OSS hatch dates occurred between February 7th and June 23rd, and LES hatch dates between February 5th and July 7th during 2022. The earliest hatch dates varied by site for each species. SPB hatches were observed earliest in Muddy Boggy Creek during 2021 and the Kiamichi River during 2022. Additionally, the earliest OSS hatch was observed at the Fulton site on the Red River, and the earliest LES hatch was observed in Muddy Boggy Creek. I also observed the highest frequency of hatch dates within the Muddy Boggy for SPB during 2021, and LES during 2022. The highest frequency of hatch dates observed for OSS occurred at the Fulton site of the Red River with Muddy Boggy Creek in close frequency. The Blue River had the lowest frequency of observed hatch dates for SPB during both years, and OSS in 2022. Alternatively, the lowest frequency of observed LES hatches occurred at the Spring Bank site on the Red River.

Growth rates varied both by species and among sites (Table 8). SPB grew faster than the other two sunfishes. Individual SPB growth rates ranged from 0.42 – 1.20 mm/day with the highest growth rates, on average, in Bois D’Arc Creek and the mainstem Red River at Arthur City. OSS growth rates ranged from 0.30 – 0.65 mm/day with the highest growth rates occurring in Bois D’Arc Creek and the mainstem Red River at Fulton. LES growth rates ranged from 0.28 – 0.74 mm/day with the highest growth rates occurring in fish collected from Bois D'Arc Creek, Muddy Boggy Creek, and the Fulton site in the Red River.

Environmental Measurements

Environmental conditions varied both temporally and spatially (Table 9). I sampled over one relatively wet and one relatively dry season as indicated by both discharge (Chapter I, Figure 2) and precipitation patterns. Discharge conditions were, on average, higher in 2021 than the historically low discharge conditions of 2022 (~ 16.7 percentile over a 10-year average). Air temperature was much less variable than discharge and gradually increased over each sample season. Temperatures were higher, on average, during 2022 but also more variable. The mainstem Red River (Fulton) reflected the highest air temperatures, whereas the coolest air temperatures were recorded from the Muddy Boggy in 2021.

Both OSS and LES began hatching at cooler air temperatures than SPB. The earliest observed hatch by SPB occurred at 16.5 °C and 15.1 °C in 2021 and 2022, respectively. In 2022, both OSS and LES hatched at air temperatures that were 6.7 °C and 3.5 °C, respectively.

Hurdle Modeling – Zero Model

My binomial logistic regression models relating the probability of hatch to select environmental covariates had adequate model fit. The binned residual plots for the three species models showed that > 95% of residuals retained within the bounds indicating appropriate goodness of fit (Appendix 1). The fixed effects explained the most variability in my SPB model (48%), whereas less variation was explained in the models for the other two species (OSS, 16%, LES, 14%). Including the random effect of site accounted for some additional variability in my models (4%-11%), where the conditional R^2 was 0.52, 0.22, and 0.25 for the models related to hatch of SPB, OSS, and LES, respectively (Table 10).

My top hatch probability model for SPB had the additive effects of scaled discharge, CV of discharge, precipitation, temperature, and year (Table 11). The probability of successful hatch increased with increasing precipitation, discharge, and CV of discharge, and decreased with increasing temperatures. The probability of hatch was also higher in 2022, on average, compared to 2021 (Figure 9).

Like Spotted Bass, hatch probability of both sunfishes was positively related to scaled discharge (Figure 10); however, other additive effects were different. My top probability of hatch model for OSS had the additive effects of scaled discharge and precipitation (Table 11). Both fixed effects were positively associated with increasing hatch probability. The top LES model had the additive effects of scaled discharge and temperature (Table 11). Hatch success by LES was positively associated with warmer and higher discharge conditions. The random effect of site explained additional variability (6-11 % for OSS and LES, respectively) in my models. Neither of the two sunfish models had a year effect as sampling was restricted to 2022.

Hurdle Modeling – Count Model

My top ranked negative binomial count models for all species had adequate fit. The count models for all three species displayed appropriate QQ-plot distributions, and uniform distributions of the residual values in the DHARMa diagnostic plots (Appendix 2). The additive fixed effects explained the most variability in the LES hatch count model (47%), whereas the SPB (41 %) and OSS (35 %) models explained less variability.

Conditional R^2 (i.e., the variance explained by the random effect for site) values were not able to be calculated for the count models.

The top count frequency models for SPB, LES, and OSS all contained different fixed effects (Table 12). The top model for SPB included the fixed effects of precipitation and year, and a random effect for site (Table 13). The frequency of SPB hatches was positively associated with increasing precipitation; however, there was variability by site and year (Figure 11). Further, SPB hatch frequencies were higher in 2022, on average, when compared to 2021. The top ranked OSS model included the fixed effects of temperature and CV of discharge (Table 13), in addition to a random effect for site. OSS hatch frequency was positively related to increasing temperatures and decreasing CV of discharge (Figure 12). Alternatively, the top ranked LES model included the fixed effects of scaled discharge, precipitation, and temperature (Table 13), where hatch frequency increased at higher discharges, increased precipitation, and warmer temperature conditions (Figure 13).

Growth Modeling

The growth models for my three target species had adequate fit and explained a reasonable amount of variability in my data. The binned residual plots showed 95% of residuals fell within the 95% error bounds (Appendix 3). The inclusion of random effects within the model (i.e., Marginal R^2) explained the most variance in LES (38%) and OSS (29%) models. Random effects explained less variance withing the SPB accounting for 18%. Additional fixed effects (i.e., conditional R^2) increased variance explained in the OSS (56%) and LES (50%) models, whereas the SPB model explained less at 19%.

The top ranked growth models for all three species varied in the number of fixed effects within the model; however, all were positively related to warmer temperatures (Figure 14). The top ranked SPB model included the fixed effects of scaled discharge, temperature and year in addition to a random effect for site (Table 14). SPB growth was positively associated with warmer air temperatures and negatively related to increasing discharges (Table 15). Additionally, growth was lower in 2022 than in 2021. Both LES and OSS had the same top ranked model (Table 14), which included a fixed effect for temperature and a random effect for site. Growth in both species was positively related to increasing air temperatures (Table 15).

Discussion

Although centrarchid fishes have been studied for a long time, our understanding of their spatial and temporal hatch variability is limited, particularly in riverine fishes. Largemouth Bass, for example, is one of the most well described species in North America (Phillip 2002); however, much of the early life history knowledge comes from small impoundments (DeVries et al. 2009) and reservoir ecosystems (Kohler et al. 1993; Sammons et al. 1999). Likewise, spatial and temporal variability of hatching in Bluegill *Lepomis macrochirus* is well studied in Midwestern impoundments (Jolley et al. 2009; Bogner et al. 2016). Our understanding of the factors driving successful hatch of riverine centrarchids appears to be limited to Redbreast Sunfish *Lepomis auritus* in the Tallapoosa River, AL (Goar 2013), Largemouth Bass, Alabama Bass *Micropterus henshalli*, and Shoal Bass *Micropterus cataractae* in the Flint River, GA (Sammons et al. 2021), Neosho Bass *Micropterus velox* in the Ozark Highlands (Brewer and Miller 2020), and Orangespotted Sunfish from a lowland river in Ontario, Canada (Leslie and Timmins

2005). Other observations that indirectly infer hatch success by sunfishes (Longear Sunfish, Bluegill, and Smallmouth Bass) were limited to a small, second order stream in Illinois (Schlosser 1985) and then quantified later by Jennings and Philipp (1994). Available size distributions of juveniles have also been used to infer hatch success by riverine Largemouth Bass in the Hudson and Illinois rivers (Nack et al. 1993; Raibley et al. 1997). The relationship between flood pulses and levels of dissolved oxygen were related to counts of *Lepomis* spp. in the Atchafalaya River in Louisiana (Fontenot et al. 2001). Lastly, early observations that spawning in OSS typically began in April and May were made by (Barney 1923) and several other biologists interested in natural history (e.g., Pflieger 1997; Robison and Buchanan 2020). Although several of these studies covered temporal variability in spawning, they tended to be either restricted to a single site or river where temporal variability was captured but not spatial variability. It is difficult to quantify both forms of variability due to logistical challenges, but both forms of variability provide insight into how plastic the species are relative to environmental changes.

Understanding spatial and temporal variation in hatching dynamics is important to understanding how recruitment is affected by environmental variability. I show that hatch success varied spatially, between wet and dry years for SPB (Figure 4 and Figure 5). Variability in spawning success is expected and useful for populations exposed to a variety of different perturbations over time (Humphries et al. 2013). For example, periods of extreme high flows and drought are expected in riverine systems and affect hatching success in those years (Wedgeworth et al. 2022). Plasticity in spawning dynamics is a mechanism that fish populations can use to ensure spawning is successful during most years (e.g., Bluegill, Philippi and Seger 1989; Garvey et al. 2002). Both spatial and temporal differences in hatching success were observed in the lower Red River catchment in my study. In the wetter year, hatch success by SPB was lower in tributary systems, but this difference was less so in the mainstem Red River sites. Like riverine Smallmouth Bass in Virginia, Spotted Bass spawned later during the wet year compared to the dry year (Sabo and Orth 1995). The two sunfishes, however, spawned as early as February but at some sites, successful hatches were not observed for a month or two and then resumed later in the summer. In the Muddy Boggy River, however, spawning was much more consistent from March through May for both OSS and LES. Part of the spatial and temporal variability I observed was likely related both natural environmental variability and dam operations.

Dam operations in the lower Red River catchment appear to affect the hatching success of fishes at some locations. The most consistent spawning by OSS and LES was observed in the unregulated Muddy Boggy Creek in 2022 (Figures 8 -10). The Muddy Boggy also had more successful hatches observed during 2021 (i.e., wet year); however, this pattern was not observed during 2022 when there were limited flood releases from the reservoirs (i.e., except hydropower at Dennison Dam). Many species depend on flow variability, which is diminished by dam releases (Freeman et al. 2001). Rivers experiencing flow regulation have been documented with decreased abundance of age-0 fishes when compared to unregulated ecosystems (Freeman et al. 2001). Flow is the master variable affecting riverine ecosystems (Resh et al. 1988; Poff et al. 1997), and can influence temperature regimes (Caissie 2006; Hamid et al. 2020), habitat availability (Freeman et al. 2001), and salinity (Vertessy et al. 2003). Male centrarchids may abandon their nest and presumably seek refuge during higher discharge events. Without the care of the adult male, eggs and larvae in nests likely do not survive (Jennings et al. 2002). Lukas and Orth (1993) and Martin (2008) reported a decrease in nest success by Redbreast Sunfish due to discharge changes associated with hydropower generation. Although dam operations are likely to affect successful spawning, I also show a positive relationship between discharge and hatch success.

Increasing discharge is a common cue used by fishes to initiate spawning, but the timing and duration of higher flows and how they coincide with water temperature are likely important to overall hatch success. I show that spawning occurs much earlier (February) than has been found for OSS and LES in other ecosystems (typically, April through June, Barney 1923; Bietz 1981) Spawning early in the season can provide a longer period for growth which can benefit overwinter survival (Maceina and Isely 1986; Phillips et al. 1995). However, spawning early may also be a bet hedging strategy to deal with environmental perturbations as I observed major disruption in spawning success at some locations which is likely why the probability of hatching increased with warmer water temperatures. Colder water temperatures during the early spawning season can result in greater mortality of offspring (Sabo and Orth 1995; Mion et al. 1998; Garvey et al. 2002) though may benefit the overall population when harsh conditions occur later in the year. Although discharge is important to hatching success, there is likely a threshold where spawning is disrupted (e.g., Spotted Bass at sites in 2021). Interestingly, Sammons et al. (2021) indicate that Largemouth Bass, Shoal Bass, and Redeye Bass *Micropterus coosae* successfully spawned from March-June, typically on the descending limb of the hydrograph. The nest-spawning reproductive strategy (Simon 2020) exhibited by all three species typically requires bed spawning in lower velocity habitats to prevent washout (Leonard and Orth 1988). Although increased discharge can washout beds adjacent to the main channel (Harnish et al. 2014), some amount of elevated discharge may allow access to more off-channel slackwater habitats that can be unavailable at lower flows (Junk et al. 1989; e.g., Largemouth Bass spawning, Nack et al. 1993; Raibley et al. 1997). In 2022, my study streams were warmer than 2022 which may have allowed for earlier reproduction by these species (Humphries et al. 2002). Warmer climates may allow for an earlier and more protracted spawning season that can lead to increased recruitment (Humphries et al. 2013). For example, reproduction in black bass species in the Florida Everglades was documented as early as January (Clugston 1966) leading to a stronger recruitment class during that year. Moreover, my findings indicate that both OSS and LES can reproduce in temperatures much lower than other species in the same genera (OSS - 6.7 °C and LES - 3.5 °C). For example, Mischke and Morris (1997) reported spawning of Bluegill initiating after water temperatures reach 21°C. The success of the earlier (i.e., colder water temperatures) and later (i.e., water temperatures) hatches may influence recruitment trends (Ludsin and DeVries 1997). The interaction between water temperature and discharge may be more important to OSS and LES rather than each variable independently. Future studies examining overwinter survival may provide insight into the advantage of spawning earlier in the season. Such insights could be important if flow regulations are exacerbated in the catchment as water demands increase in major metropolitan areas.

Although extremely wet years may create difficult spawning conditions for some fishes, they are likely important for maintaining habitat important to fishes in the catchment. Nursery habitats of the lower Red River rely on connectivity with important off-channel, slackwater habitats and the presence of deep pools (see Chapter II Discussion). Even though extreme high flows may influence reduced nascent survival (e.g., SPB during 2021), these events are responsible for the creation and maintenance of deep pools that occur within reaches important to juvenile fishes. For example, after peak flows during 2021, SPB experienced a decline in reproductive success (Figure 4 and Figure 5); however, the timing of these extreme flows (> 2,000 m^3/s) can create more heterogeneity in habitat including the formation of important oxbow lake nursery grounds (Zinger et al. 2011; Hudson et al. 2012), and deep pool habitat (Giller 1998). The formation of these habitats, while not conducive to reproduction during the event year, may positively influence success over time (e.g., over 10 year period) through the creation of nurseries that improve survival and recruitment (Pease et al. 2006). The frequency of these formative flows are important, as an extended period of flooding may be problematic for shorter lived species (e.g., pelagophils, Perkin et al. 2015).

Unregulated tributaries (i.e., Muddy Boggy Creek) may provide recruitment consistency during wetter years because of habitat resiliency and buffer from the flow extremes caused by upstream impoundments. Humphries et al. (2013) proposed a window-of-opportunity hypothesis where temporally fluctuating environmental conditions allow protracted spawning species to gain a recruitment advantage over those only spawning for a short period of time. Unregulated rivers may maintain habitats (i.e., nurseries), promoting optimal conditions for a longer time (Chen and Olden 2017) via a more natural flow regime (Poff et al. 1997). Moreover, breaks in spawning success for all three Centrarchid fishes in my study indicate that releases from dams during extremely wet years may inhibit survival, whereas not providing any releases downstream during dry periods may place long term limits on habitats need (Jager and Smith 2008). For example, daily releases from Denison Dam provide some connectivity to the floodplain (Newcomer 2017); however, releases may not be sustained long enough for fish to continually spawn throughout the season and the timing may actually disrupt spawning cues. Additionally, precipitation and its frequency may also play an important role in providing reasonable flows, particularly within tributaries.

The importance of precipitation events to successful hatching may relate to finer scale changes in discharge and spatially to local conditions. Although discharge and precipitation were not highly correlated, precipitation patterns in the Great Plains can be discrete events that are not captured by major changes at gauge locations (Worthington et al. 2019). For example, Espírito-Santo et al. (2013) found that hydrological fluctuations primarily controlled by precipitation in the Negro and Solimoes rivers, Brazil, influenced Amazonian fishes reproductive strategies including timing and frequency. Smaller changes in discharge caused by rainfall can also affect local conditions including water quality. Moreover, organic nutrients (e.g., nitrogen, phosphorous, silica, and iron) often enter smaller tributaries through runoff during storm events (Allan et al. 1997; Hamid et al. 2020). Increased nutrients can enhance higher order streams within the watershed by promoting higher zooplankton concentrations (Hitchcock et al. 2010), although there may be loading limitations negatively affecting reproduction (Wehr and Descy 1998; Jeppesen et al. 2010). Precipitation can also be indicative of local barometric pressure which can affect fish reproductive behavior (Lennox et al. 2018). For example, Dedual and Jowett (1999) found increased spawning movements of Rainbow Trout *Oncorhynchus mykiss* in the Tongariro River, New Zealand was influenced by barometric pressure. The relationship between precipitation and successful hatches in centrarchid fishes suggests the influence of a variety of environmental conditions.

Successful reproduction by sunfishes appears to be influenced by a variety of conditions, including those that I did not quantify. The low R^2 values associated with OSS and LES hatching models indicate that there are other biotic and/or abiotic factors affecting the probability of hatch and hatch frequency. Fish can use biotic signals including the presence of the opposite sex (Tornabene et al. 2020), and semiochemical (i.e., chemical substances produced by organisms) cues (Sorensen and Wisenden 2015). Sunfishes, in particular, exhibit social behaviors that are particularly relevant to spawning. LES spawning success has been found to be related to several behavioral factors such as group size, nest size, and the location of the nest within an aggregate of sunfish (Dupuis and Keenleyside 1988). Moreover, courtship behaviors by a variety of riverine fishes may vary with photoperiod length (Wildhaber 2006). Environmental factors interact to determine phenology and successful hatching. Additionally, other abiotic factors such as acoustic noises (Slabbekoorn et al. 2010), nutrient concentrations (Volkoff and London 2018), and sublethal exposure to wastewater (Petersen 1979) may affect spawning behaviors and therefore reproductive success. Understanding the variability in spawning by aggregate and social animals is complicated; it is interesting that the variability of growth by these same species was somewhat well explained.

Warmer temperatures typically increase growth of many warmwater fishes. Riverine fish are poikilothermic (Wolf and Mann 1980; Provancha et al. 1986; Brannon et al. 2004), where optimal growth occurs at the same optimal metabolic temperature

(Coutant 1976). Juvenile fishes exhibit higher growth when compared to their adult conspecifics (Sibly et al. 2015). The highest growth rates for all species in my study were associated with warmer median temperatures (e.g., SPB (27°C), OSS (30°C), and LES (31°C)). The median temperature used for the analysis was highly correlated with hatch date where earlier hatched fish experienced a lower median temperature than later hatched fish. Fish that hatch earlier may grow slower but could have an advantage relative to time and likely dependent on when they switch to piscivory (~50-100-mm TL, see overview by Churchill and Bettoli 2015). Alternatively, later hatched fish may exhibit compensatory responses and be as large as earlier hatches by the end of the growing season (Vonesh and Bolker 2005).

The variability in growth rates by all three species indicates a tradeoff between successful hatching and growth between years for Spotted Bass and spatially for all species. My growth rates for Spotted Bass ranged from 0.42 – 1.20 mm/day. The variability in growth rates is both lower and higher than other populations of riverine basses (e.g., 0.61-.088 mm/day, Sammons et al. 2021). Interestingly, Spotted Bass grew faster in 2021 when hatching success (i.e., counts) was lower across the catchment. Prey availability for opportunistic sunfishes (Kaemingk et al. 2012) may be higher during wet years. Increased growth rates of adult Redbreast Sunfish in Georgia coastal plain rivers have been found during wet years (Sammons and Maceina 2009).

I found growth of Spotted Bass was negatively related to increasing discharge even though hatch probability was positively related to discharge. However, there was no relationship between hatch counts and discharge which indicates spawning was more common, but the frequency of hatch events had no relationship. This is interesting because several authors indicate bass species as fluvial specialists or generalists, which is probably dependent on which aspect of their life history is being examined and how. For example, although we found no relationship between hatch frequency and discharge for Spotted Bass, spawning by the species was clearly affected by repeated high flows in 2021. Therefore, it would be incorrect to indicate that black bass are not affected by variable discharge conditions (e.g., Sammons et al. 2021). However, there does appear to be a trade-off in the conditions associated with higher hatching than those that promote faster growth. I also observed this trend spatially where the highest OSS growth rates were associated with sites that were not particularly strong locations for reproductive success. It is possible that locations that are more suitable as nursery habitats are not located in close proximity to ideal spawning habitats. Alternatively, density-dependent mechanisms that regulate growth may also be related to these observations. Regardless, the heterogeneity of the riverscape functions to accommodate trade-offs in success associated with reproduction and growth of juvenile fishes.

Spatial and temporal variability is essential within ecosystems, and promotes successful coexistence among species (Strong 1983). Having specific management recommendations that benefit an assemblage of species is difficult particularly with limited funding (Kinsolving and Bain 1993; Brussard et al. 1998). Ensuring relatively natural variability in both flow and thermal regimes (i.e., less habitat fragmentation and damming) is the solution that would have assemblage-wide benefits for species occupying different ecological niches. Moreover, changes in existing flow operations would benefit from consideration of species phenology. Preventing riverscape fragmentation that disrupts the plasticity that fish use to maintain populations when environmental conditions vary would be very advantageous.

Table 1. Environmental covariates that influence successful fish hatches and growth with their associated resolution and a description of the ecological importance (Justification).

Covariate	Resolution	Justification
Discharge	1.00 m^3/s	Successful hatches in riverine fishes can be positively influenced by discharge.[1,2,3]
Temperature	1.0 °C	Egg development is positively related to water temperature.[4,5,6]
Precipitation	1.00 mm	Precipitation can be indicative of general climate conditions that may influence successful hatches.[7,8,9]
Calendar Day	24 hr	Fish spawning may be influenced by timing or photoperiod during season.[2,10,11]

1. (Sammons et al. 2021) 2. (Wedgeworth et al. 2022) 3. (Craven et al. 2010) 4. (Humphries and Lake 2000) 5. (Coutant 1976) 6. (Sternecker et al. 2013) 7. (King et al. 2003) 8. (Perkin et al. 2019) 9. (Graham and Harrod 2009) 10. (Bogner et al. 2016) 11. (Schiemer et al. 2002)

Table 2. Environmental data sources used to obtain discharge and water air temperature data for each of the 7 hatch site locations (Site). All discharge data were collected from either the USGS stream gages network (gage provided below) or the Tulsa District US Army Corps of Engineers (Army Corp). Precipitation and air temperature data were collected from either (Source) the Oklahoma Mesonet or National Centers for Environmental Information – National Oceanic and Atmospheric Administration (NOAA). Location indicates the location of the weather station, whereas Station indicates the name.

Site	USGS stream gage	Location	Station	Source
Blue River	07332500	Durant, OK	DURA	Oklahoma Mesonet
Muddy Boggy Creek	07335300	Antlers, OK	ANT2	Oklahoma Mesonet
Red River (Arthur City)	07335500	Valliant, OK	VALL	Oklahoma Mesonet
Kiamichi River	HGLO2 (Army Corp)	Hugo, OK	HUGO	Oklahoma Mesonet
Bois D'Arc Creek	07332622	Bonham, TX	USC00410923	NOAA
Red River (Fulton)	07341500	Texarkana Webb Airfield, AR	USW00013977	NOAA
Red River (Spring Bank)	07344370	Atlanta, TX	USC00410408	NOAA

Table 3. Pearson's Correlation matrix for weekly environmental covariates used for hatch analyses. Collected discharge measurements were scaled to each site's respective drainage area. Included covariates represent calendar week within the season (Week), scaled mean discharge (Scaled Q), coefficient of variation of discharge (CV Q), cumulative precipitation (Rain), and average temperature (Temp). Discharge and temperature data were calculated 7 days prior to the hatch. Rain represented the sum of precipitation (1 mm) for 7 days prior to hatch. Correlations were examined after necessary transformations were made (see methods).

	Week	Scaled Q	CV Q	Rain	Temp
Week	1.00				
Scaled Q	-0.33	1.00			
CV Q	-0.35	0.10	1.00		
Rain	-0.35	0.23	0.22	1.00	
Temp	0.79	-0.22	-0.30	-0.30	1.00

Table 4. Pearson's Correlation matrix for weekly environmental covariates used for growth analyses. Collected discharge measurements were scaled to each site's respective drainage area. Included covariates represent date of hatch within the season (Hatch), scaled mean discharge (Scaled Q), coefficient of variation of discharge (CV Q), cumulative precipitation (Rain), and median temperature (Temp). All covariates used for growth analysis were calculated for the total period during each individual's growth. Correlations were examined after necessary transformations were made (see methods).

	Hatch	Scaled Q	CV Q	Rain	Temp
Hatch	1.00				
Scaled Q	-0.26	1.00			
CV Q	-0.01	0.01	1.00		
Rain	-0.59	0.53	-0.03	1.00	
Temp	0.87	-0.31	-0.01	-0.53	1.00

Table 5. Number of fish surveys completed at each site (10-15 km long) during 2021 and 2022. Fish were sampled using mini-fyke nets, seining, and larval tows.

Site	2021	2022	Total
Blue River	3	6	9
Muddy Boggy Creek	4	9	13
Red River (Arthur City)	6	12	18
Kiamichi River	7	7	14
Bois D'Arc Creek	1	9	10
Red River (Fulton)	8	12	20
Red River (Spring Bank)	6	12	18

Table 6. The number of juvenile Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES) collected from each of the 7 hatch sites (Site) during the 2021 and 2022 sample seasons. Totals sum both 2021 and 2022 counts. Orangespotted Sunfish and Longear Sunfish were not collected during 2021 and are therefore, only reported for 2022.

Species	Site	2021	2022	Total
SPB	Blue River	4	38	42
	Muddy Boggy Creek	59	78	133
	Red River (Arthur City)	14	172	184
	Kiamichi River	3	80	83
	Bois D'Arc Creek	NA	214	214
	Red River (Fulton)	37	94	128
	Red River (Spring Bank)	90	141	228
OSS	Blue River	-	9	9
	Muddy Boggy Creek	-	33	33
	Red River (Arthur City)	-	51	51
	Kiamichi River	-	24	24
	Bois D'Arc Creek	-	17	17
	Red River (Fulton)	-	147	147
	Red River (Spring Bank)	-	61	61
LES	Blue River	-	34	34
	Muddy Boggy Creek	-	42	42
	Red River (Arthur City)	-	14	14
	Kiamichi River	-	46	46
	Bois D'Arc Creek	-	51	51
	Red River (Fulton)	-	38	38
	Red River (Spring Bank)	-	20	20

Table 7. Age and hatch date estimates for Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES) collected from sites in the lower Red River catchment during summer 2021 and 2022. Spotted Bass were sampled but not collected from Bois D'Arc Creek in 2021.Orangespotted Sunfish and Longear Sunfish were not collected in 2021. The location of hatch (Site), the number of otoliths aged in 2021 (R: retained otoliths meeting between reader agreement criteria in parentheses), otoliths aged in 2022 (R), the number of weeks during which a hatch occurred in 2021 (HW2021) and 2022 (HW2022), average total length (TL) of each species, daily age (Ages), and range of hatch dates in 2021 (HD2021) and 2022 (HD2022). Orangespotted Sunfish and Longear Sunfish were not collected during 2021 and are therefore, only reported for 2022.

Species	Site	2021 aged (R)	2022 aged (R)	HW2021	HW2022	TL	Ages	HD2021	HD2022
SPB	Blue River	4 (3)	38 (38)	3	8	25.9 - 94.2	45 - 114	5/1 - 5/16	3/31 - 5/19
	Muddy Boggy Creek	59 (55)	78 (71)	11	9	22.8 - 88.0	39 - 115	4/8 - 6/15	3/28 - 5/17
	Red River (Arthur City)	14 (12)	172 (157)	6	8	25.4 - 99.9	27 - 118	4/28 - 7/1	3/31 - 5/21
	Kiamichi River	3 (3)	80 (77)	2	12	31.6 - 98.0	41 - 120	6/20 - 6/21	3/21 - 6/4
	Bois D'Arc Creek	NA	214 (200)	NA	9	29.3 - 100.1	35 - 110	NA	3/24 - 5/20

	Red River (Fulton)	37 (36)	111 (94)	9	7	19.5 - 89.8	22 - 109	5/1 - 6/23	3/24 - 5/6
	Red River (Spring Bank)	90 (87)	141 (121)	10	8	22.7 - 92.3	33 - 118	4/24 - 6/25	3/18 - 5/4
OSS	Blue River	-	9 (5)	-	2	27.2 - 36.7	58 - 72	-	5/19 - 5/27
	Muddy Boggy Creek	-	33 (33)	-	9	19.9 - 39.2	44 - 99	-	3/11 - 5/16
	Red River (Arthur City)	-	51 (50)	-	7	18.7 - 39.6	38 - 81	-	4/19 - 6/8
	Kiamichi River	-	24 (17)	-	7	20.0 - 39.9	38 - 89	-	2/25 - 6/15
	Bois D'Arc Creek	-	17 (13)	-	4	24.0 - 41.0	39 - 89	-	3/16 - 6/23
	Red River (Fulton)	-	147 (123)	-	15	22.5 - 39.9	39 - 110	-	2/7 - 6/23
	Red River (Spring Bank)	-	61 (57)	-	8	21.7 - 39.8	46 - 121	-	2/22 - 6/03
LES	Blue River	-	34 (31)	-	10	17.8 - 38.9	39 - 118	-	2/15 - 7/5
	Muddy Boggy Creek	-	42 (38)	-	15	15.5 - 57.2	35 - 137	-	2/5 - 6/28
	Red River (Arthur City)	-	14 (14)	-	8	19.1 - 40.0	32 - 93	-	2/24 - 7/7
	Kiamichi River	-	46 (43)	-	8	25.1 - 40.0	55 - 85	-	5/1 - 6/15

Bois D'Arc Creek	-	51 (45)	-	14	17.3 - 46.8	34 - 125	-	2/8 - 6/24
Red River (Fulton)	-	38 (37)	-	13	15.7 - 49.1	35 - 109	-	2/26 - 7/7
Red River (Spring Bank)	-	20 (20)	-	7	19.4 - 39.4	38 - 68	-	5/9 - 7/2

Table 8. Mean and range (in parentheses) estimates of growth (mm/day) for Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES) for each hatch site (Site), during 2021 (GR2021) and 2022 (GR2022).

Species	Site	GR2021	GR2022
SPB	Blue River	0.82 (0.74 - 0.95)	0.74 (0.56 - 0.93)
	Muddy Boggy Creek	0.72 (0.58 - 0.90)	0.67 (0.42 - 0.99)
	Red River (Arthur City)	0.81 (0.56 - 1.20)	0.76 (0.50 - 1.04)
	Kiamichi River	0.68 (0.51 - 0.82)	0.64 (0.45 - 0.84)
	Bois D'Arc Creek	NA	0.76 (0.46 - 1.15)
	Red River (Fulton)	0.79 (0.51 - 1.04)	0.73 (0.50 - 1.04)
	Red River (Spring Bank)	0.76 (0.54 - 1.08)	0.67 (0.45 - 1.13)
OSS	Blue River	-	0.51 (0.47 - 0.56)
	Muddy Boggy Creek	-	0.48 (0.35 - 0.58)
	Red River (Arthur City)	-	0.49 (0.41 - 0.57)
	Kiamichi River	-	0.45 (0.36 - 0.59)
	Bois D'Arc Creek	-	0.57 (0.46 - 0.65)
	Red River (Fulton)	-	0.47 (0.30 - 0.61)
	Red River (Spring Bank)	-	0.47 (0.32 - 0.60)
LES	Blue River	-	0.50 (0.32 - 0.65)
	Muddy Boggy Creek	-	0.41 (0.29 - 0.57)
	Red River (Arthur City)	-	0.58 (0.43 - 0.73)
	Kiamichi River	-	0.49 (0.40 - 0.58)
	Bois D'Arc Creek	-	0.51 (0.37 - 0.74)
	Red River (Fulton)	-	0.50 (0.28 - 0.73)
	Red River (Spring Bank)	-	0.56 (0.38 - 0.65)

Table 9. Environmental covariates used for hatch and growth analyses. Mean and ranges (in parentheses) of daily discharge (Discharge, 1.00 m^3/s), 10-year (2012 -2022) flow percentile over a 10-year period (%), daily air temperature (Temperature,1.0 °C), and total daily rainfall (Precipitation, 1 mm) by site during both 2021 and 2022. Discharge data were collected from the nearest USGS stream gage to each site. Air temperature and precipitation data were collected from the nearest Oklahoma Mesonet and NOAA National Centers for Environmental Data station (see Table 2). The Red River at Fulton did not have 10 years of discharge data available (the period of record was 2019 - 2023).

Year	Site	Discharge	%	Temperature	Precipitation
2021	Blue River	10.93 (0.93 - 268.44)	51	22.04 (7.98 - 30.41)	3.50 (0.00 - 92.96)
	Muddy Boggy Creek	62.51 (0.99 - 557.84)	60	21.10 (6.32 - 29.40)	3.86 (0.00 - 81.03)
	Red River (Arthur City)	313.45 (33.41 - 1364.87)	60	21.51 (7.88 - 29.29)	4.32 (0.00 - 104.65)
	Kiamichi River	84.25 (1.70 - 537.68)	50	21.93 (8.62 - 30.13)	4.54 (0.00 - 88.40)
	Bois D'Arc Creek	7.99 (0.01 - 45.97)	50	22.63 (7.20 - 31.65)	3.29 (0.00 - 109.20)
	Red River (Fulton)	806.43 (91.75 - 2803.37)	-	21.57 (5.25 - 29.75)	3.76 (0.00 - 69.10)
	Red River (Spring Bank)	1099.39 (106.75 - 3143.14)	60	22.86 (6.95 - 31.40)	4.77 (0.00 - 66.00)
2022	Blue River	4.82 (0.18 - 131.96)	20	23.53 (-0.22 - 34.07)	2.46 (0.00 - 98.55)
	Muddy Boggy Creek	36.52 (0.57 - 379.44)	40	22.30 (-0.20 - 31.61)	2.47(0.00 - 71.12)

Red River (Arthur City)	112.22 (6.46 - 1155.32)	19	22.80 (1.10 - 32.97)	2.68 (0.00 - 64.77)
Kiamichi River	55.33 (0.00 - 369.79)	10	23.27 (0.08 - 33.47)	2.86 (0.00 - 95.50)
Bois D'Arc Creek	0.89 (0.01 - 14.72)	1	23.50 (-0.10 - 34.00)	2.93 (0.00 - 72.60
Red River (Fulton)	347.29 (47.86 - 1656.52)	-	24.74 (41.15 - 35.00)	3.30 (0.00 - 100.10)
Red River (Spring Bank)	417.55 (66.54 - 1834.91)	10	23.37 (3.10 - 33.90)	3.60 (0.00 - 87.10)

Table 10. Top ranked binomial models of the probability of hatch (zero models) for Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES) and their AICc scores. The degrees of freedom (df), and log-likelihood (logLik) are indicated for each model, Akaike's information criterion correlated for small sample size (AICc), the difference of between each model and the top ranked model (ΔAICc), model weight (w_i), and the conditional (R_c^2; variance explained by fixed and random effects) and the marginal (R_m^2; variance explained by fixed effects) R^2 values are also reported.

Species	Model	df	logLik	AICc	ΔAICc	w_i	R_c^2	R_m^2
SPB	$logit(p_{it}) = \beta_0 + \alpha_1 + \beta_1 Q_1 + \beta_2 CV_2 + \beta_3 Temp_3 + \beta_4 Rain_4 + \gamma_t + e_{it}$	7	-158.02	330.34	0.00	0.51	0.52	0.48
	$logit(p_{it}) = \beta_0 + \alpha_1 + \beta_1 Q_1 + \beta_2 CV_2 + \beta_3 Temp_3 + \gamma_t + e_{it}$	6	-159.50	331.23	0.88	0.33	0.52	0.46
OSS	$logit(p_{it}) = \beta_0 + \beta_1 Rain_1 + \beta_2 Q_2 + \gamma_t + e_{it}$	4	-107.56	223.31	0.00	0.33	0.22	0.16
	$logit(p_{it}) = \beta_0 + \beta_1 Rain_1 + \beta_2 Q_2 + \beta_3 CV_3 + \gamma_t + e_{it}$	5	-107.28	224.86	1.55	0.15	0.23	0.16
	$logit(p_{it}) = \beta_0 + \beta_1 Temp_1 + \beta_2 Q_2 + \gamma_t + e_{it}$	4	-108.39	224.97	1.66	0.14	0.22	0.14
LES	$logit(p_{it}) = \beta_0 + \beta_1 Temp_1 + \beta_2 Q_2 + \gamma_t + e_{it}$	4	-128.79	265.78	0.00	0.33	0.25	0.14
	$logit(p_{it}) = \beta_0 + \beta_1 Rain_1 + \beta_2 Q_2 + \gamma_t + e_{it}$	4	-129.27	266.74	0.95	0.20	0.24	0.13
	$logit(p_{it}) = \beta_0 + \beta_1 Q_1 + \beta_2 CV_2 + \beta_3 Temp_3 + \beta_4 Rain_4 + \gamma_t + e_{it}$	6	-127.66	267.73	1.95	0.12	0.31	0.17

$logit(p_{it}) = \beta_0 + \beta_1 Temp_1 + \beta_2 Q_2 + \beta_3 CV_3 + \gamma_t + e_{it}$	5	-128.73	267.75	1.96	0.12	0.28	0.15

Table 11. Estimates (logit) of each covariate included in the top model related to the probability of successful hatch for Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES). The standard error (SE), 95% confidence interval (CI) and p-values (P) are provided for each estimate. Included covariates represent scaled mean discharge (Scaled Q), coefficient of variation of discharge (CV Q), cumulative precipitation (Rain), and average temperature (Temp). Year represents a categorical fixed effect for year were 2021 was the reference.

Species	Covariate	Estimate	SE	95% CI	P
SPB	Intercept	-2.29	0.35	(-3.10, -1.57)	< 0.01
	Scaled Q	1.20	0.25	(0.76, 1.71)	< 0.01
	CV Q	0.32	0.17	(-0.03, 0.66)	0.065
	Rain	0.29	0.17	(-0.04, 0.64)	0.089
	Temp	-0.88	0.16	(-1.20, -0.58)	< 0.01
	Year	1.29	0.32	(0.67, 1.94)	< 0.01
OSS	Intercept	-1.32	0.27	(-1.99, -0.75)	< 0.01
	Scaled Q	0.67	0.24	(0.21, 1.18)	0.005
	Rain	0.38	0.19	(0.02, 0.77)	0.04
OSS	Intercept	-0.66	0.30	(-1.39, 0.04)	0.028
	Scaled Q	0.71	0.22	(0.29, 1.17)	0.001
	Temp	-0.34	0.16	(-0.65, -0.03)	0.032

Table 12. Top ranked negative binomial models of the frequency of hatch (count models) for Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES) and their AICc scores. The degrees of freedom (df), and log-likelihood (logLik) are indicated for each model, Akaike's information criterion correlated for small sample size (AICc), the difference of between each model and the top ranked model (ΔAICc), model weight (w_i), and the conditional (R_c^2; variance explained by fixed and random effects) and the marginal (R_m^2; variance explained by fixed effects) R^2 values are also reported.

Species	Model	df	logLik	AICc	ΔAICc	w_i	R_m^2
SPB	$log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1 Rain_1 + \gamma_t + e_{it}$	5	-302.50	615.56	0.00	0.32	0.41
	$log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1 Rain_1 + \beta_2 Temp_2 + \beta_3 Temp_3^2 + \gamma_t + e_{it}$	6	-301.97	616.82	1.26	0.17	0.41
	$log(Y_{it}) = \beta_0 + \alpha_1 + \beta_1 Rain_1 + \beta_2 Q_2 + \gamma_t + e_{it}$	6	-320.16	617.21	1.65	0.14	0.39
OSS	$log(Y_{it}) = \beta_0 + \beta_1 Temp_1 + \beta_2 CV_2 + \beta_3 CV_3^2 + \gamma_t + e_{it}$	5	-130.38	272.07	0.00	0.34	0.35
	$log(Y_{it}) = \beta_0 + \beta_1 Temp_1 + \beta_2 CV_2 + \beta_3 CV_3^2 + \beta_4 Q_4 + \gamma_t + e_{it}$	6	-129.65	273.16	1.08	0.20	0.38
LES	$log(Y_{it}) = \beta_0 + \beta_1 Temp_1 + \beta_2 Rain_2 + \beta_3 Q_3 + \gamma_t + e_{it}$	6	-131.83	276.88	0	0.34	0.47
	$log(Y_{it}) = \beta_0 + \beta_1 Temp_1 + \beta_2 Q_2 + \gamma_t + e_{it}$	5	-133.11	277.09	0.21	0.30	0.41
	$log(Y_{it}) = \beta_0 + \beta_1 Temp_1 + \beta_2 CV_2 + \beta_3 CV_3^2 + \beta_4 Rain_4 + \beta_5 Q_5 + \gamma_t + e_{it}$	7	-131.48	278.63	1.74	0.14	0.46

Table 13. Estimates (log) of each covariate included in the top model related to the frequency of hatches for Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES). The standard error (SE), 95% confidence interval (CI) and p-values (P) are provided for each estimate. Included covariates represent scaled mean discharge (Scaled Q), cumulative precipitation (Rain), and average temperature (Temp). Year represents a categorical fixed effect for year were 2021 was the reference.

Species	Covariate	Estimate	SE	95% CI	P
SPB	Intercept	1.02	0.25	0.52, 1.51	< 0.01
	Rain	0.46	0.14	0.20, 0.73	0.001
	Year	1.37	0.26	0.87, 1.87	< 0.01
OSS	Intercept	1.34	0.21	0.92, 1.75	< 0.01
	Temp	0.61	0.18	0.26, 0.96	0.01
	CV (quadratic)	-0.44	0.20	-0.83, -0.05	0.03
LES	Intercept	0.39	0.26	-0.11, 0.90	0.13
	Rain	0.26	0.16	-0.06, 0.58	0.11
	Scaled Q	0.59	0.20	0.20, 0.98	0.01
	Temp	0.50	0.18	0.14, 0.86	0.01

Table 14. Top ranked linear regression models of daily growth rates for Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES) and their AICc scores. The degrees of freedom (df), and log-likelihood (logLik) are indicated for each model, Akaike's information criterion correlated for small sample size (AICc), the difference of between each model and the top ranked model (ΔAICc), model weight (w_i), and the conditional (R_c^2; variance explained by fixed and random effects) and the marginal (R_m^2; variance explained by fixed effects) R^2 values are also reported.

Species	Model	df	logLik	AICc	ΔAICc	w_i	R_c^2	R_m^2
SPB	$Y_i = \beta_0 + \alpha_1 + \beta_1 Q_1 + \beta_2 Temp_2 + \gamma_t + e_{it}$	6	728.87	-1445.65	0.00	0.98	0.19	0.18
OSS	$Y_i = \beta_0 + \beta_1 Temp_1 + \gamma_t + e_{it}$	4	463.03	-917.93	0.00	0.85	0.56	0.29
LES	$Y_i = \beta_0 + \beta_1 Temp_1 + \gamma_t + e_{it}$	4	294.13	-580.09	0.00	0.97	0.5	0.38

Table 15. Estimates of each covariate included in the top model related to growth of Spotted Bass (SPB), Orangespotted Sunfish (OSS), and Longear Sunfish (LES). The standard error (SE), 95% confidence interval (CI) and p-values (P) are provided for each estimate. Included covariates represent scaled mean discharge (Scaled Q), cumulative precipitation (Rain), and median temperature (Temp). Year represents a categorical fixed effect for year were 2021 was the reference.

Species	Covariate	Estimate	SE	95% CI	P
SPB	Intercept	0.78	0.01	(0.76, 0.81)	< 0.01
	Scaled Q	-0.05	0.01	(-0.06, -0.03)	< 0.01
	Temp	0.03	0.01	(0.02, 0.03)	< 0.01
	Year	-0.07	0.02	(-0.09, -0.04)	< 0.01
OSS	Intercept	0.49	0.02	(0.46, 0.52)	< 0.01
	Temp	0.04	0.00	(0.03, 0.05)	< 0.01
LES	Intercept	0.50	0.01	(0.48, 0.53)	< 0.01
	Temp	0.05	0.01	(0.04, 0.06)	< 0.01

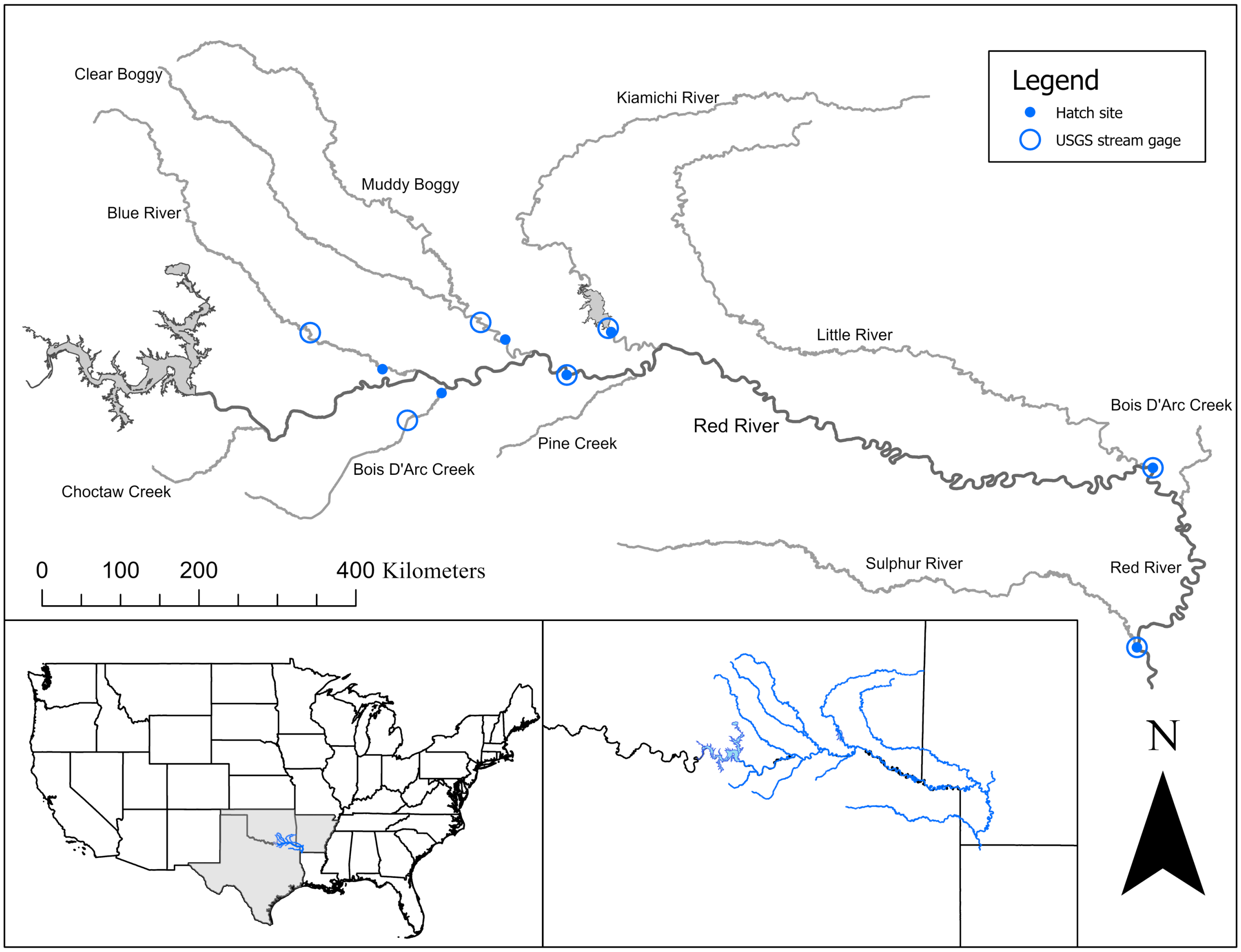


Figure 1. Sample sites in the lower Red River catchment where juvenile fishes were sampled to determine the factors related to successful hatching and growth. The solid blue circles show the 7 site locations: Blue River, Bois D'Arc Creek, Muddy Boggy Creek, Red River (Arthur City), Kiamichi River, Red River (Fulton), and Red River (Spring Bank). The open blue circles are the nearest USGS stream gages used to obtain daily discharge data: (from top left to lower right): 07332500, 07332622, 07335300, 07335500, HGLO2 (Army Corps), 07341500, 07344370.

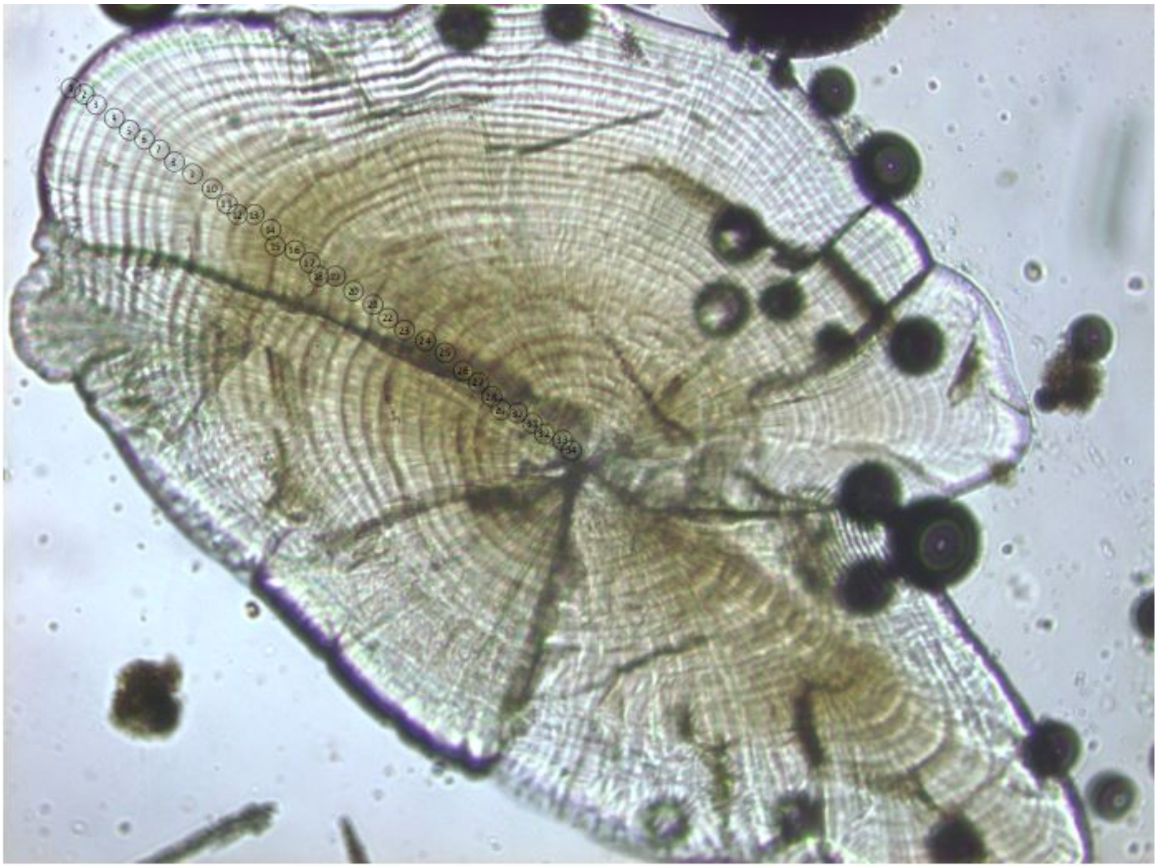


Figure 2. Daily bands of an estimated 39 day old (34 bands plus 5 days for formation of the first band) Spotted Bass *Micropterus puntulatus. S*agittal otolith viewed under a 10X magnification compound microscope (Nikon Eclipse E400 compound microscope). Bands were enumerated from the outer edge inward to reduce error until the nucleus was reached.

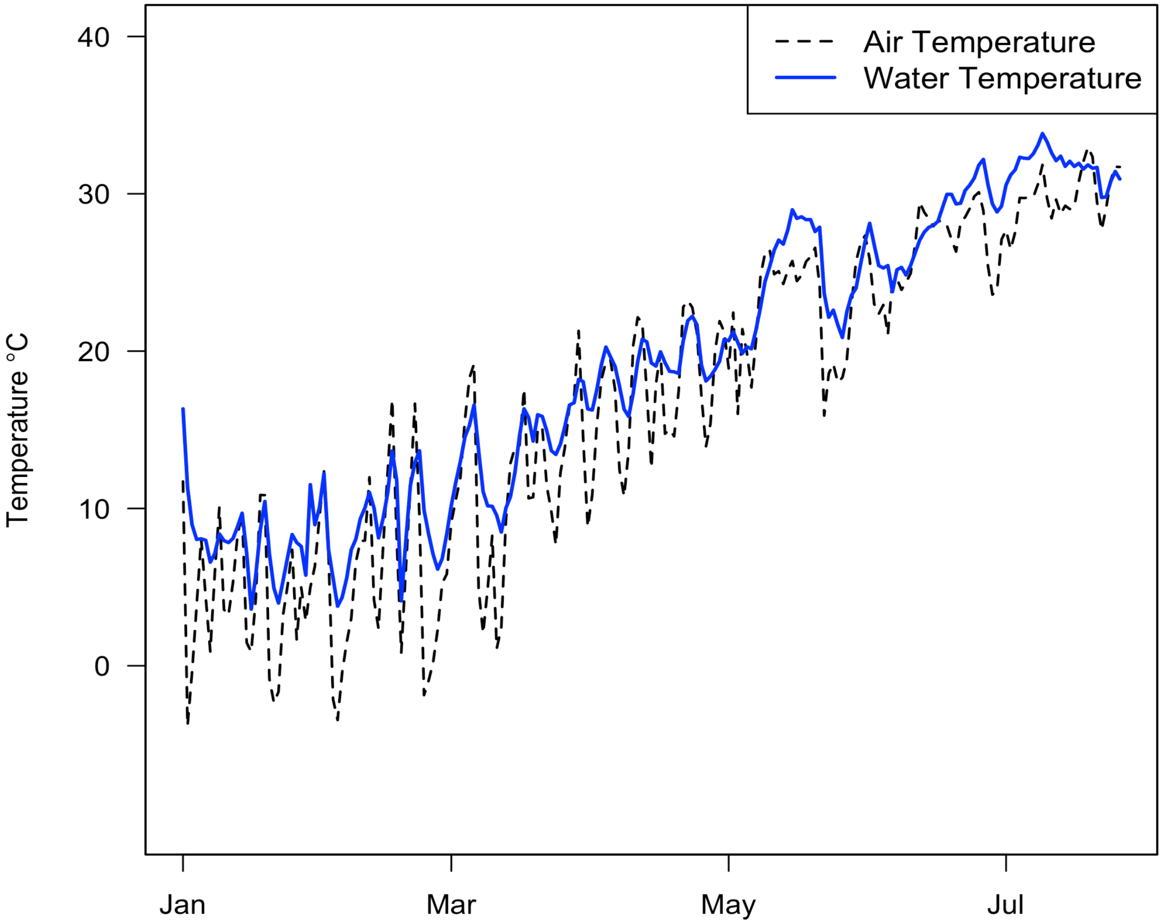


Figure 3. Daily average air temperatures and water temperatures during 2022. Air temperatures were collected from Oklahoma Mesonet weather station (VALL), and water temperatures were collected using a continuous temperature logger (Onset Hobo MX2201, Bourne, MA) from the Red River (Arthur City).

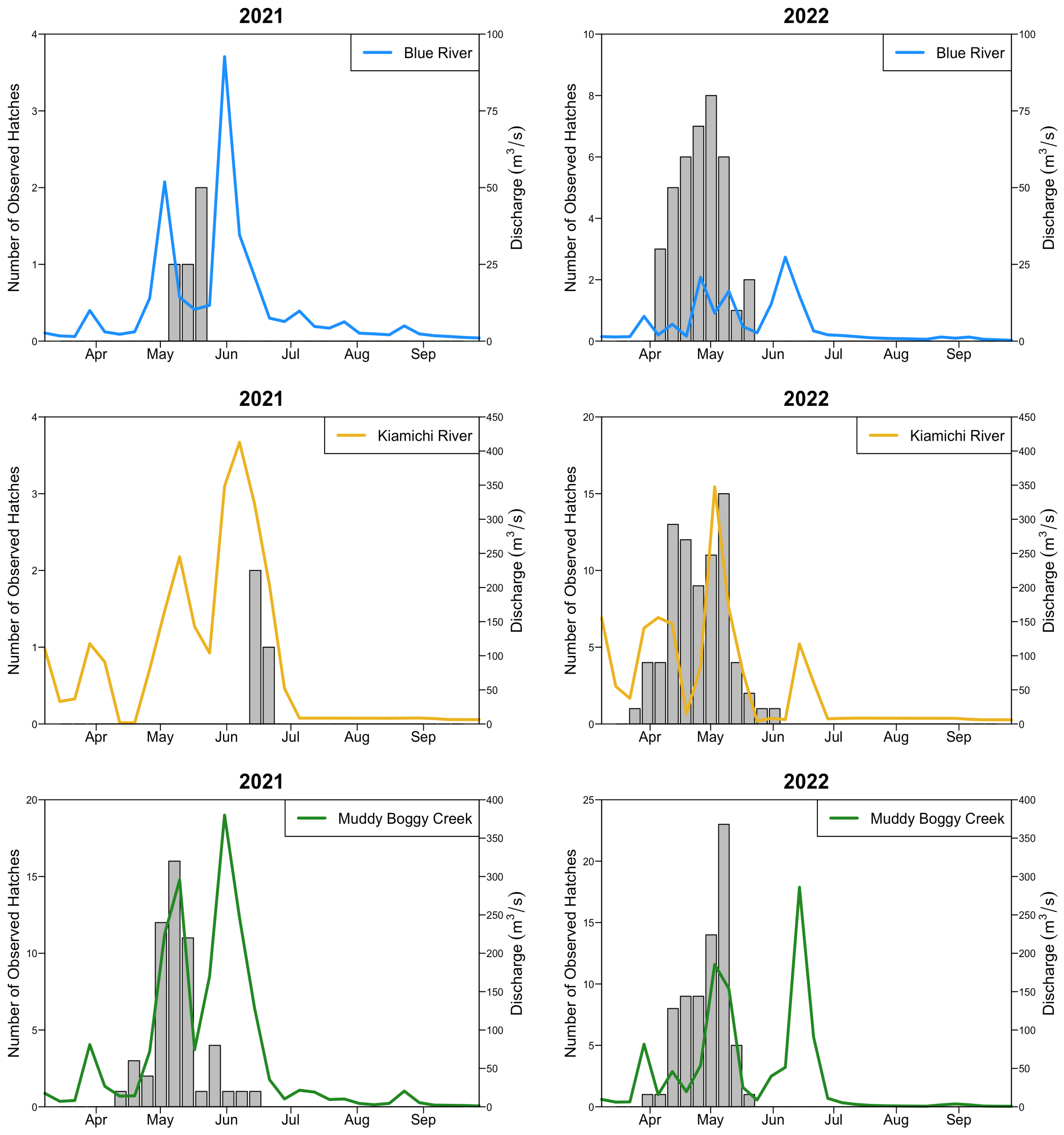


Figure 4. Summary of weekly average discharge (m^3/s) values for Spotted Bass in the Blue River, Kiamichi River, and Muddy Boggy Creek during 2021 (left panel) and 2022 (right panel). Colored lines represent the discharge hydrograph, and gray bars represent the number of observed hatches per week.

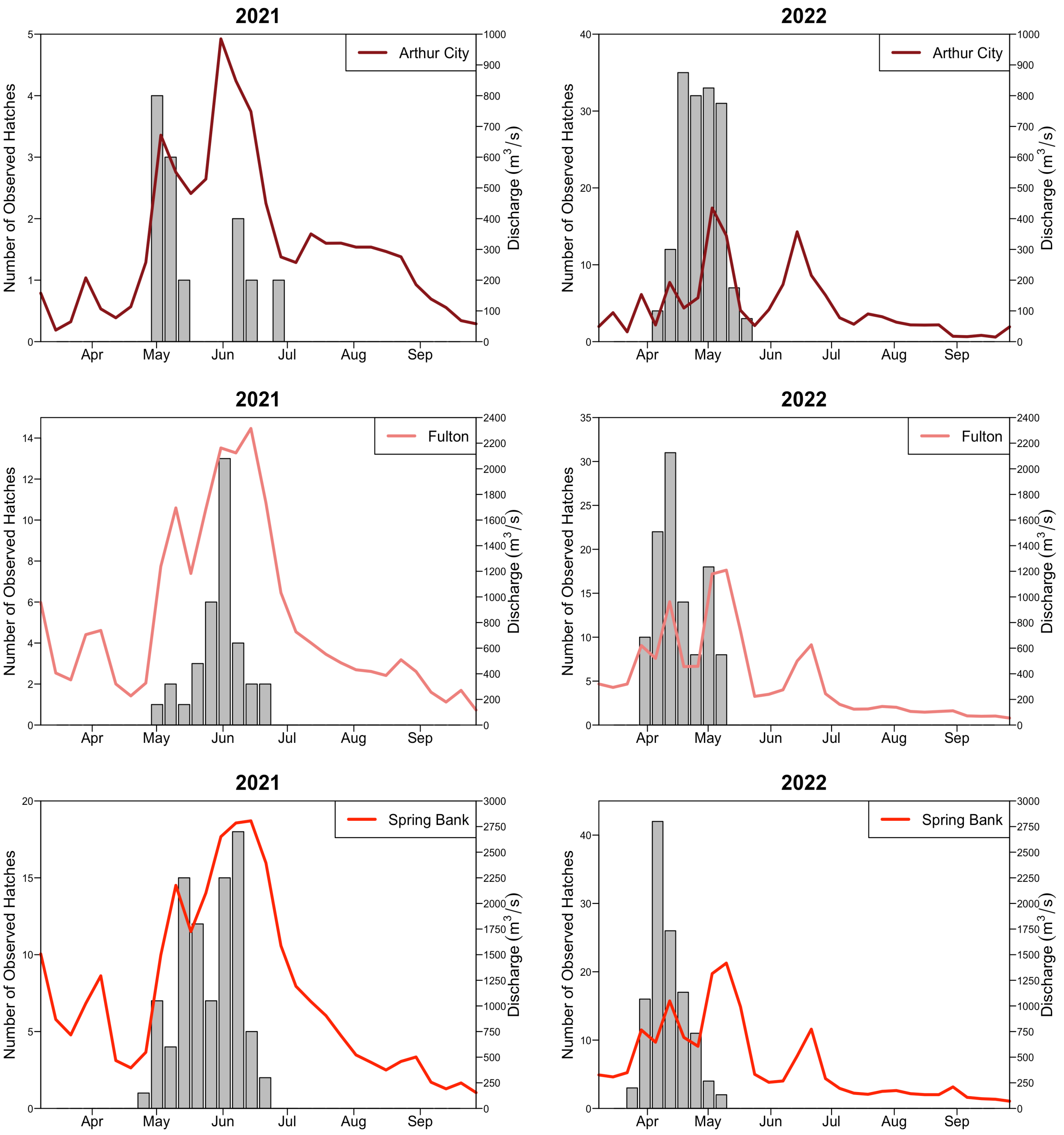


Figure 5. Summary of weekly average discharge (m^3/s) values for Spotted Bass in the Red River (Arthur City), Red River (Fulton), and Red River (Spring Bank) during 2021 (left panel) and 2022 (right panel). Colored lines represent the discharge hydrograph, and gray bars represent the number of observed hatches per week.

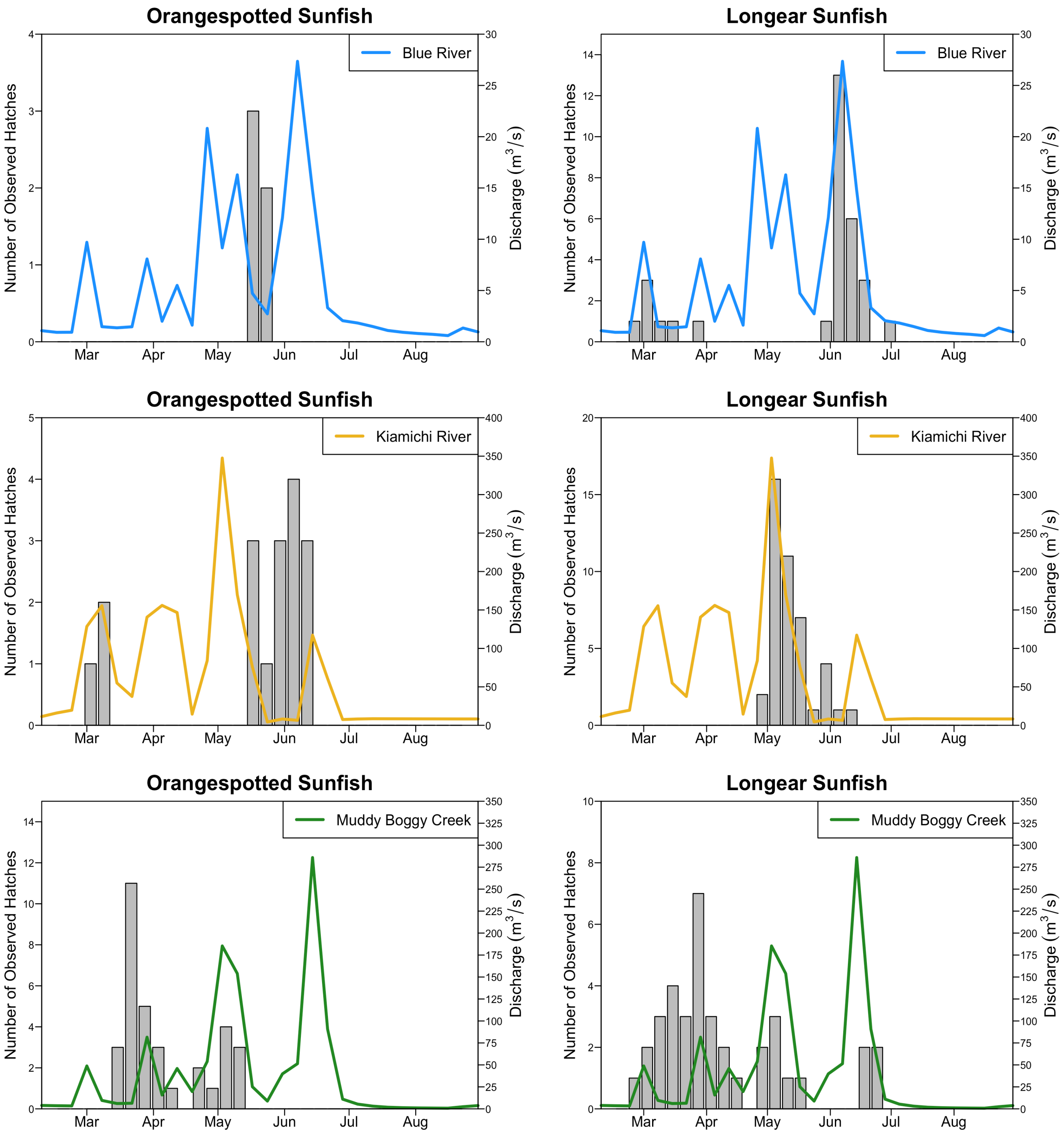


Figure 6. Summary of weekly average discharge (m^3/s) values in the Blue River, Kiamichi River, and Muddy Boggy Creek for Orangespotted Sunfish (left panel) and Longear Sunfish (right panel) during 2022. Colored lines represent the discharge hydrograph, and gray bars represent the number of observed hatches per week.

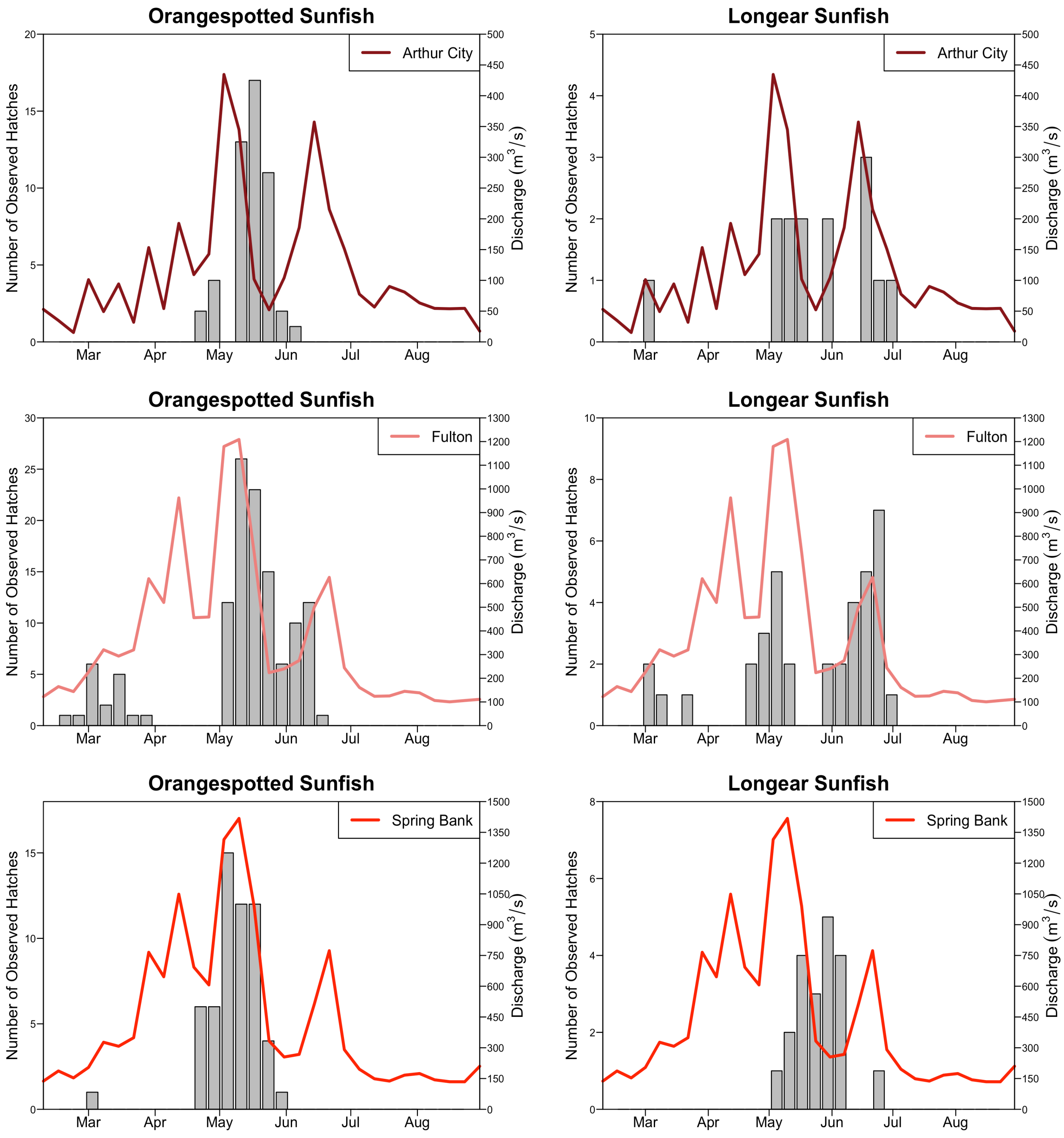


Figure 7. Summary of weekly average discharge (m^3/s) values in the Red River (Arthur City), Red River (Fulton), and Red River (Spring Bank) for Orangespotted Sunfish (left panel) and Longear Sunfish (right panel) during 2022. Colored lines represent the discharge hydrograph, and gray bars represent the number of observed hatches per week.

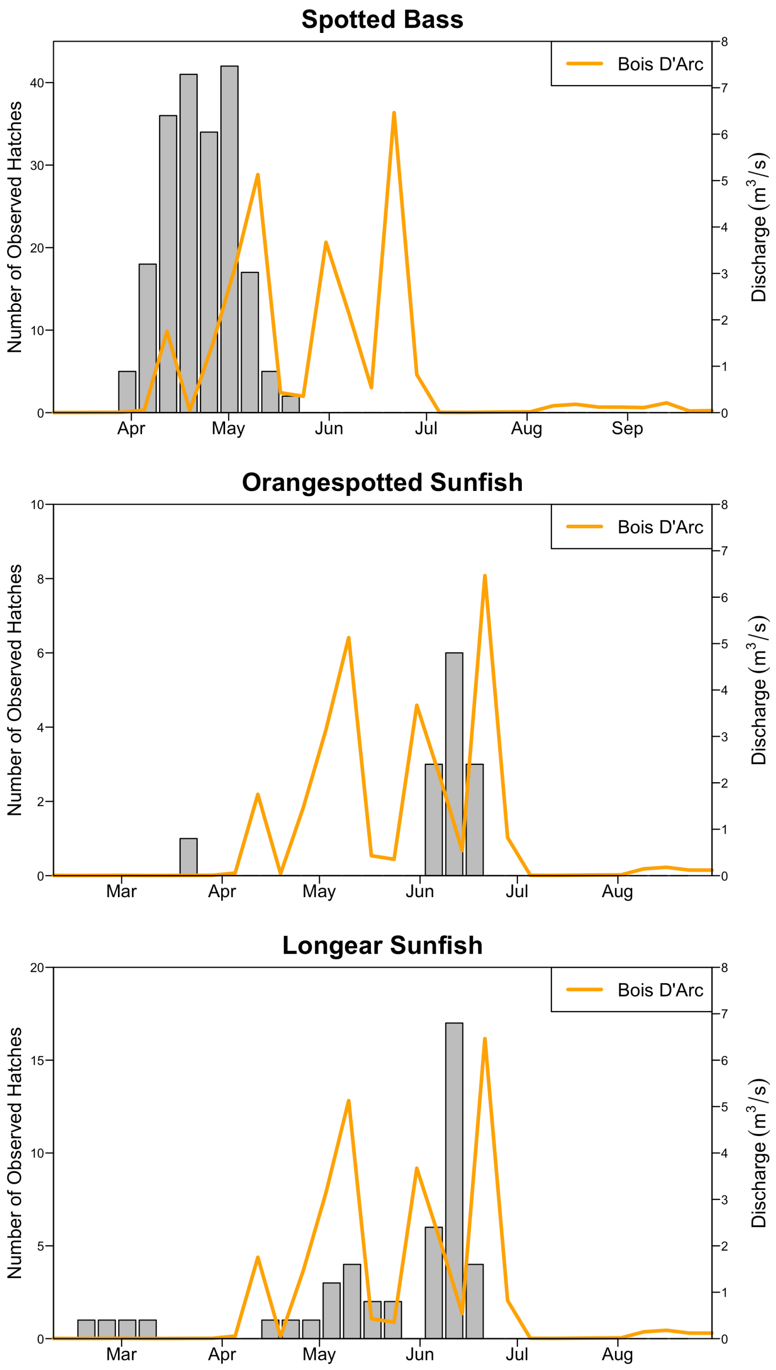


Figure 8. Summary of weekly average discharge (m^3/s) values in Bois D'Arc Creek for Spotted Bass (top), Orangespotted Sunfish (middle) and Longear Sunfish (bottom) during 2022. Colored lines represent the discharge hydrograph, and gray bars represent the number of observed hatches per week.

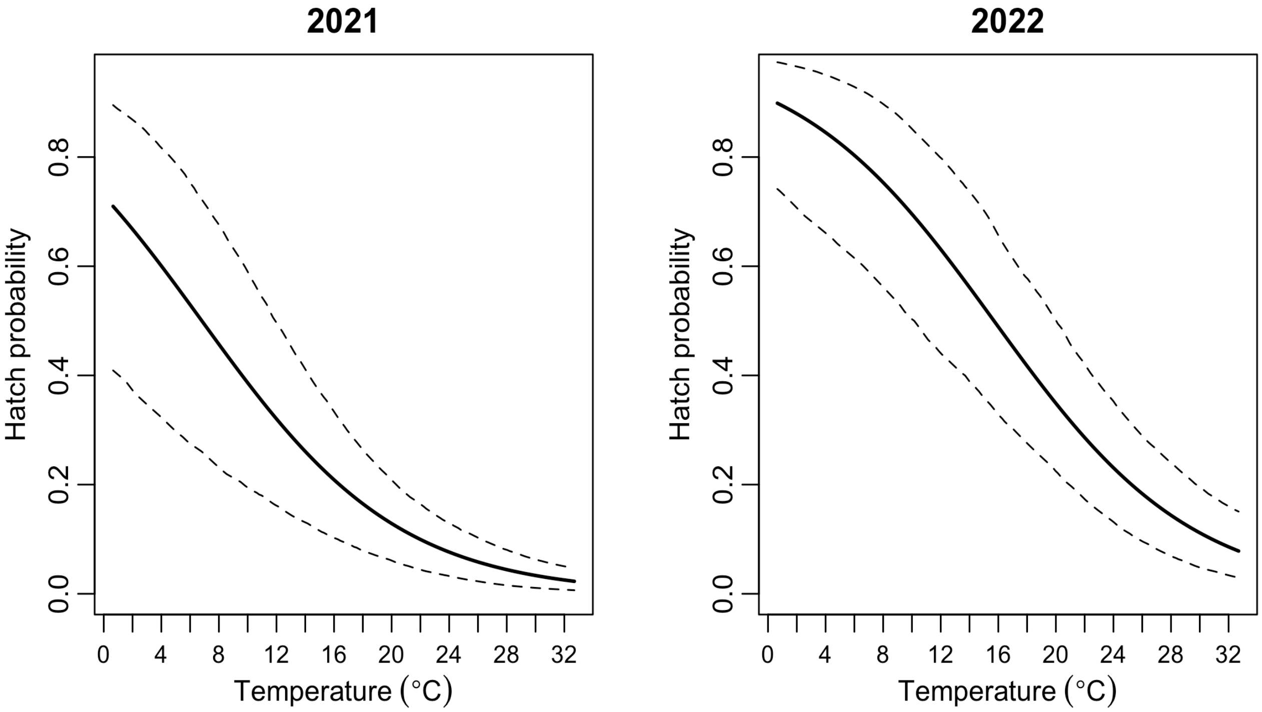


Figure 9. Plot representing the negative relationship between Spotted Bass hatch probability and air temperatures during the 2021 (left panel) and 2022 (right panel) spawning seasons. The dashed lines represent the 95% confidence intervals.

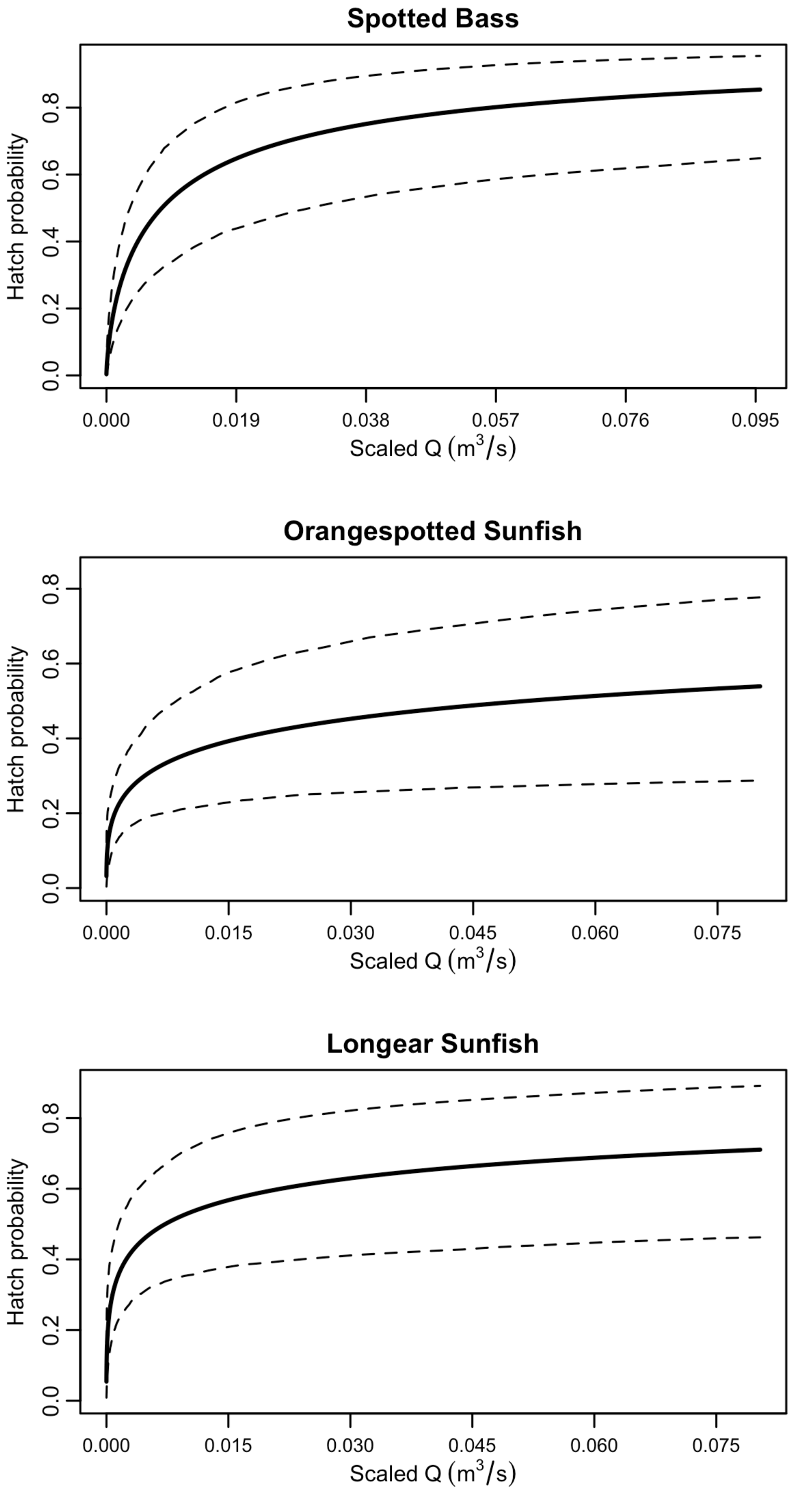


Figure 10. Plot representing the positive relationship between hatch probability and scaled discharge for Spotted Bass (top), Orangespotted Sunfish (middle), and Longear Sunfish (bottom). The dashed lines represent the 95% confidence intervals.

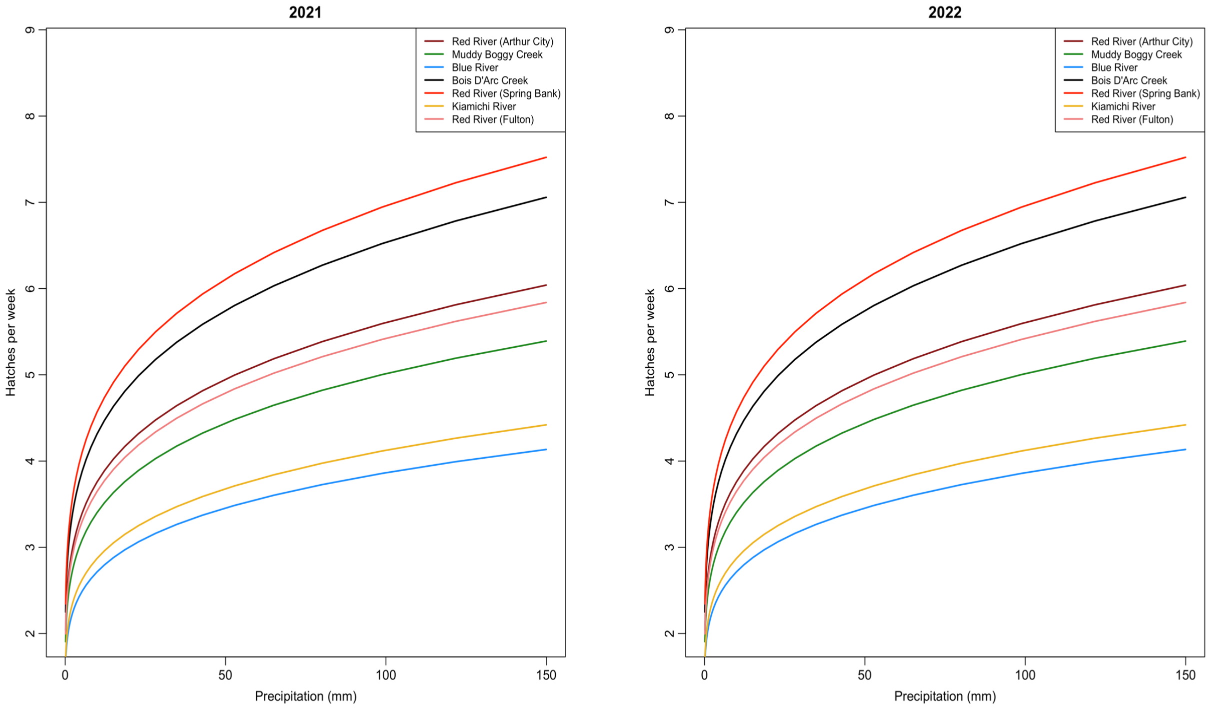


Figure 11. Plots representing the changes in the hatch frequency (negative binomial) by sample site for Spotted Bass during 2021 (left panel) and 2022 (right panel). The included sample sites are Red River (Arthur City), Muddy Boggy Creek, Blue River, Bois D’Arc Creel, Red River (Spring Bank), Kiamichi River, and the Red River (Fulton).

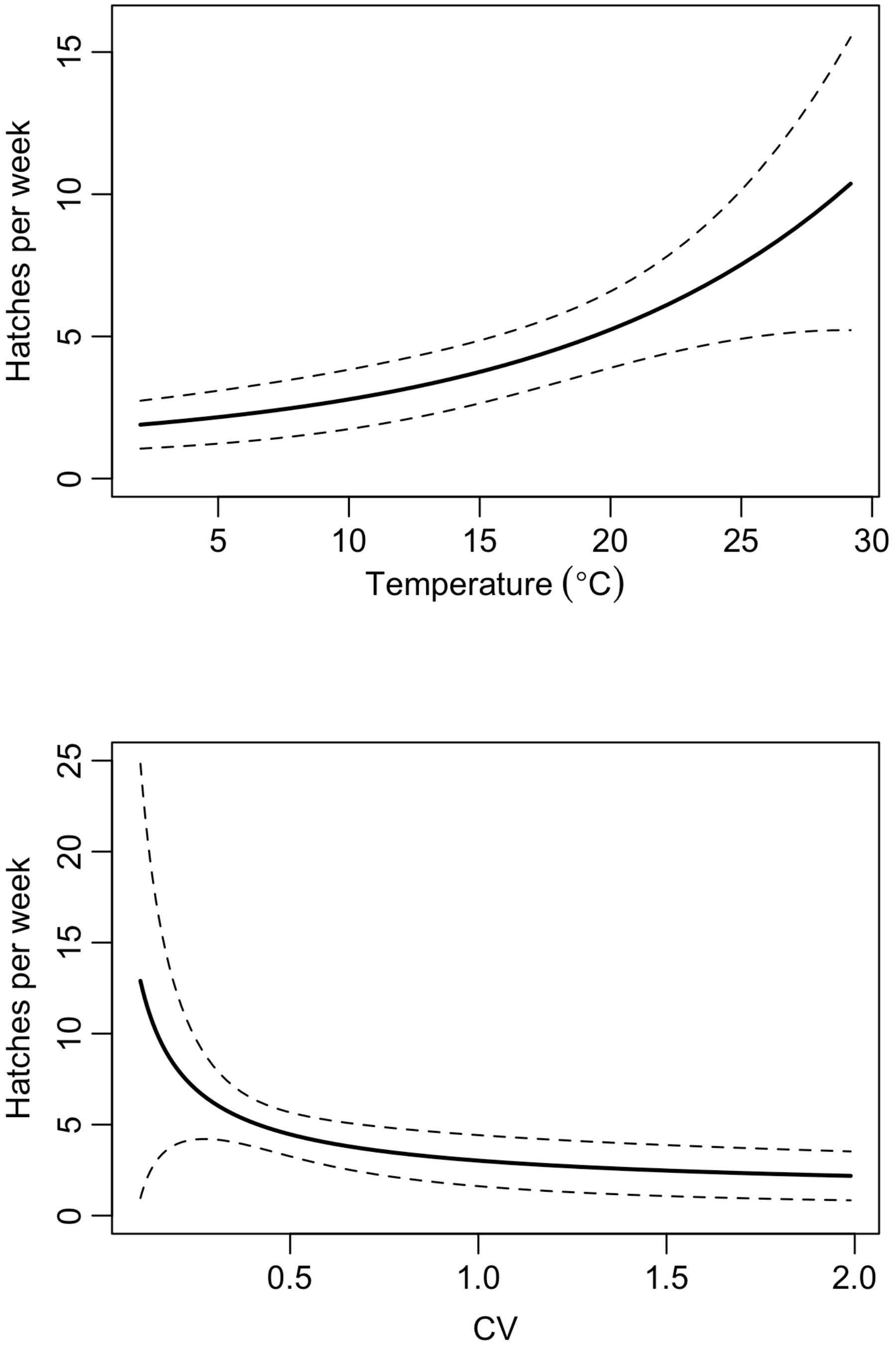


Figure 12. Plot representing positive relationship between hatch frequency and temperature (top), and the negative relationship with CV of discharge (m^3/s) (bottom) for Orangespotted Sunfish. The dashed lines represent the 95% confidence intervals.

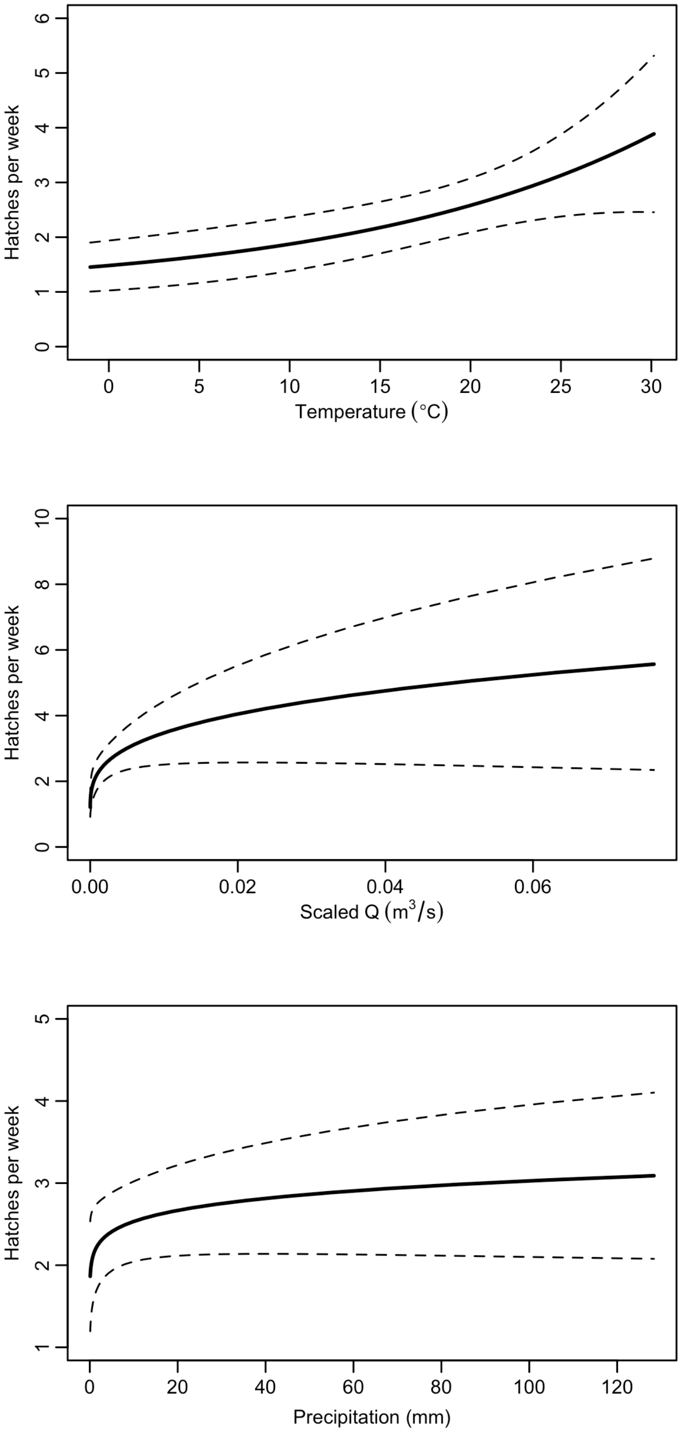


Figure 13. Plot representing positive relationships between hatch frequency and temperature (top), scaled discharge (middle), and cumulative precipitation (bottom) for Longear Sunfish. The dashed lines represent the 95% confidence intervals

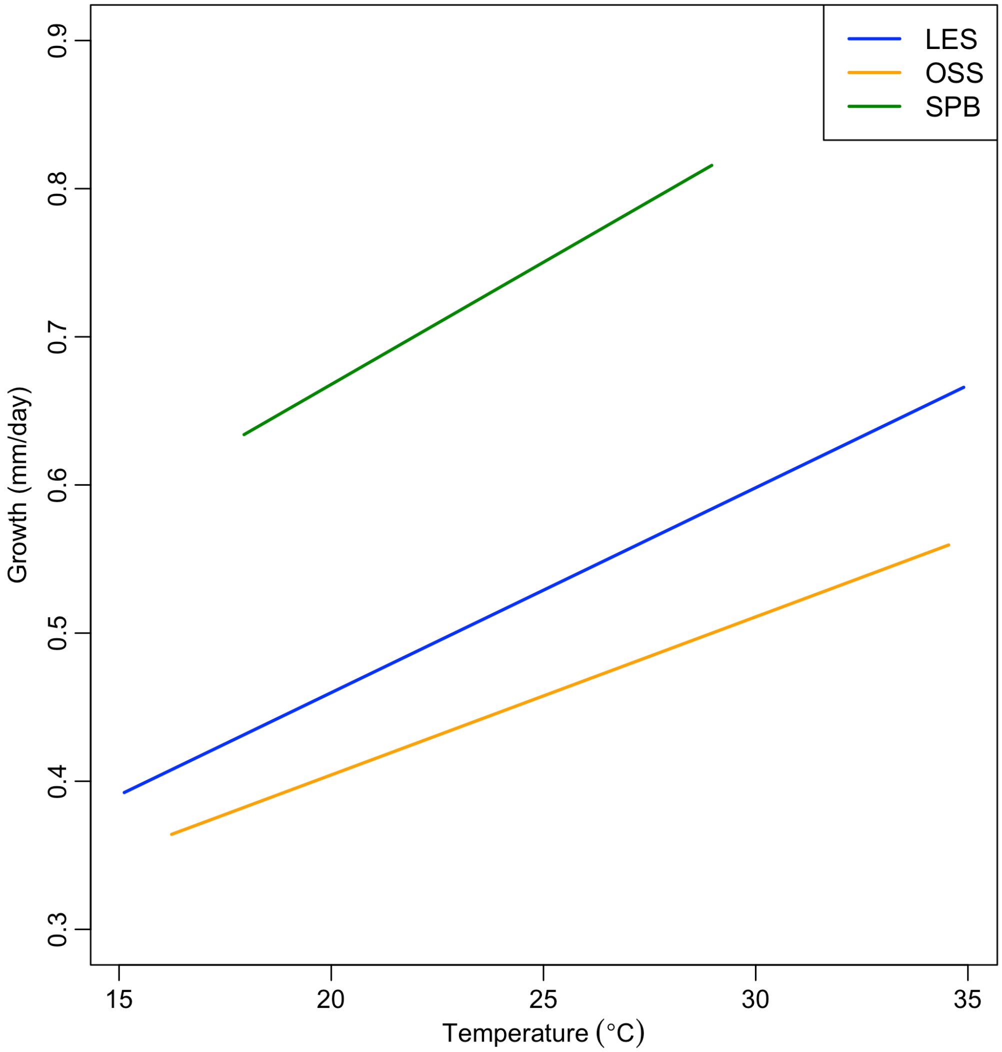


Figure 14. Plot showing the positive relationships between average daily growth and median temperature for Longear Sunfish (LES), Orangespotted Sunfish (OSS), and Spotted Bass (SPB)

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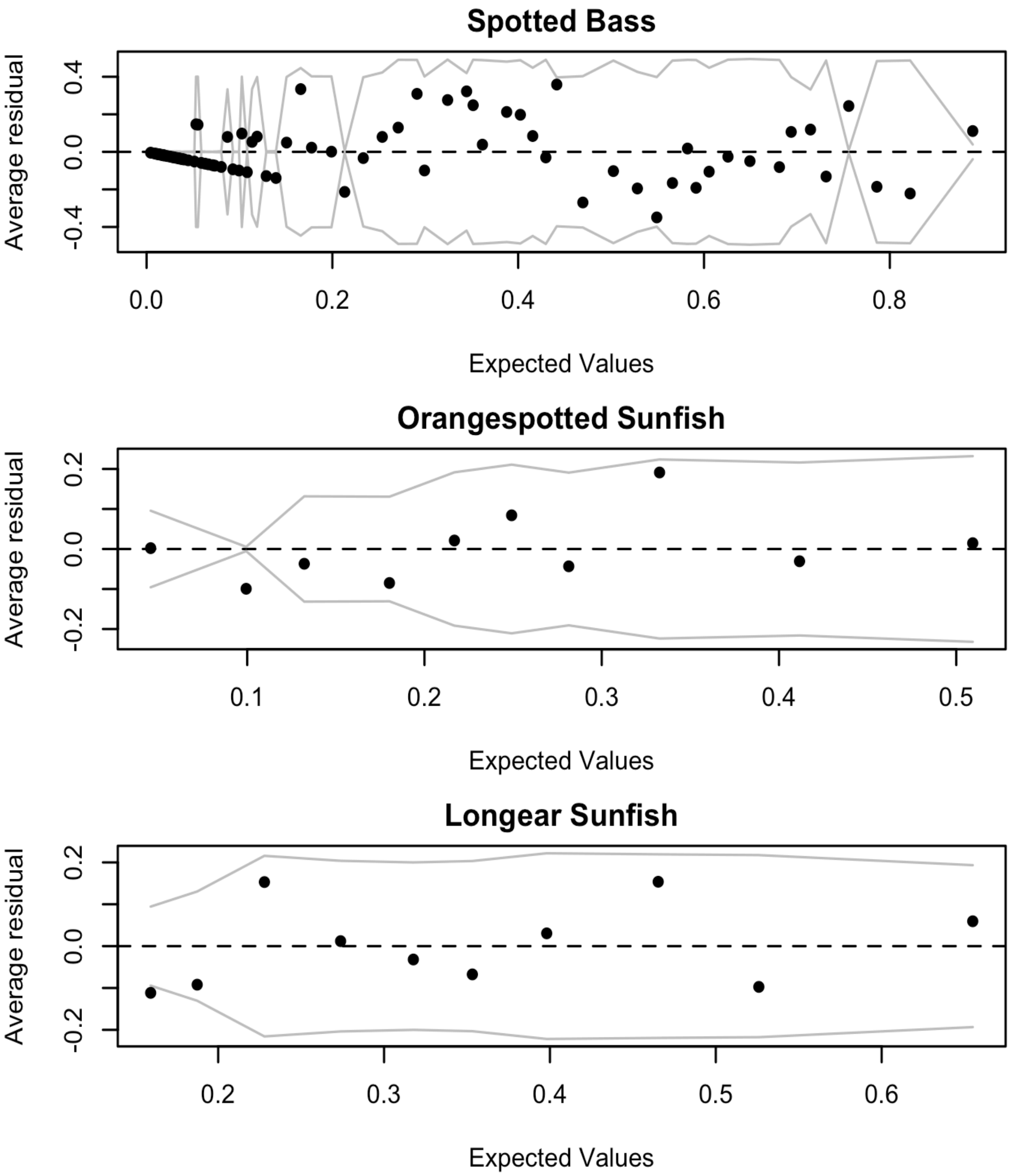
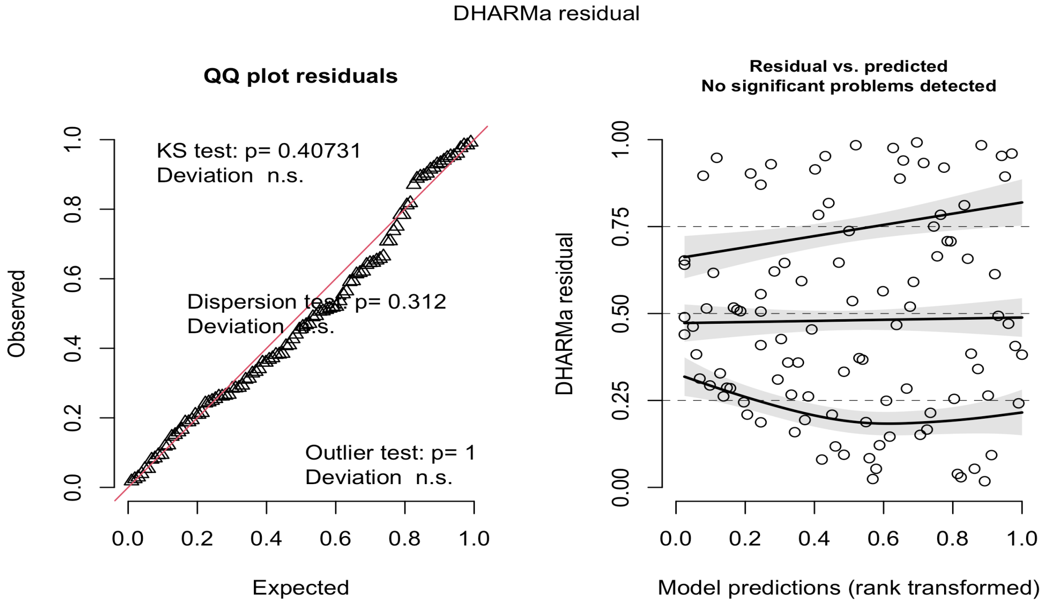
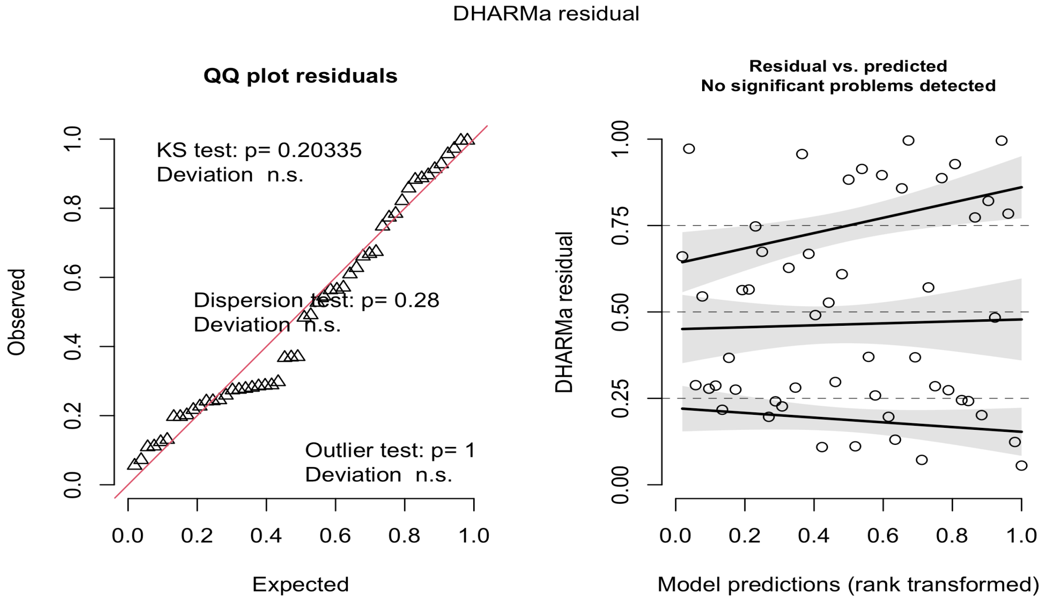
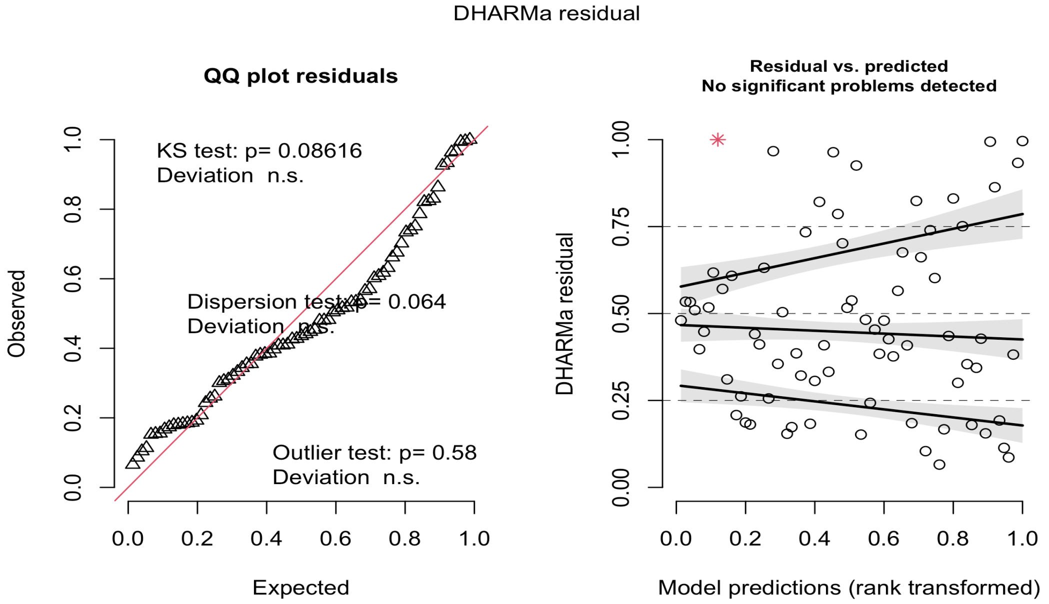
Appendices



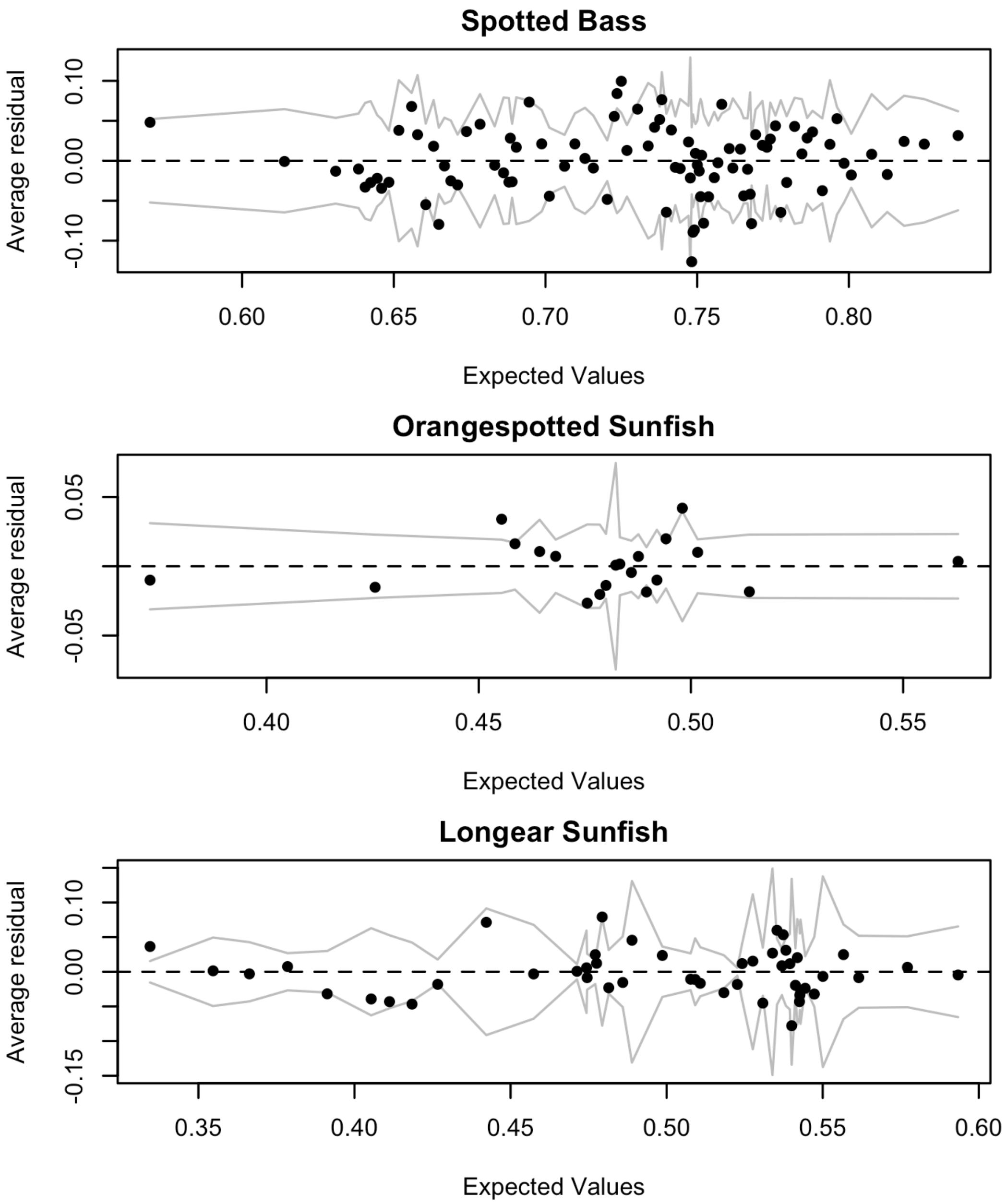
Appendix 1. Binned residual plots for the binomial logistic probability of hatch models (zero models). Black dots are the plotted residuals, and the gray lines indicate the theoretical error bounds of the model.


DHARMa residual
QQ plot residuals
KS test: p= 0.40731
Deviation n.s.
Dispersion test: p= 0.312
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
0.0
0.2
0.4
0.6
0.8
1.0
Residual vs. predicted
No significant problems detected
DHARMa residual
Model predictions (rank transformed)
0.00
0.25
0.50
0.75
1.00


DHARMa residual
QQ plot residuals
KS test: p= 0.20335
Deviation n.s.
Dispersion test: p= 0.28
Deviation n.s.
Outlier test: p= 1
Deviation n.s.
Observed
Expected
0.0
0.2
0.4
0.6
0.8
1.0
Residual vs. predicted
No significant problems detected
DHARMa residual
Model predictions (rank transformed)
0.00
0.25
0.50
0.75
1.00



Appendix 2. QQ and DHARMa plots of the negative binomial models of the frequency of hatch (count models) for each of the species. My models associated with frequency of hatch of Spotted Bass (Top), Orangespotted Sunfish (Middle), and Longear Sunfish (Bottom) had reasonable model fit. The red star represents an outlier that was retained after the datum was checked for accuracy.



Appendix 3. Binned residual plots for the growth models (linear multiple regression). Black dots are the plots residuals, and the gray lines indicate the theoretical error bounds of the model.