

ARTICLE

# Age and Growth of Freshwater Drum and Gizzard Shad Occupying Two Reservoir-River Complexes with Different Groundwater Contributions

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## Abstract

Restoring groundwater flow is a management option that improves water temperature regimes and benefits fishes. Although this strategy applies more readily to river systems, the thermal character of reservoirs is heavily influenced by inflowing rivers. We examined differences in age, structure, and growth of both Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum* that occupy catchments with varying groundwater contributions in the south-central United States. Seepage run data indicated that the Kiamichi River was losing surface water to groundwater in summer 2016, whereas groundwater inflows were apparent in the Elk River basin. Summer 2016 data showed that the Elk River had cooler water temperatures than the Kiamichi River and Grand Lake O' the Cherokees water temperatures were similar to those in the incoming Elk River. We found higher densities of older Freshwater Drum and Gizzard Shad (maximums of 32 and 8 years old, respectively) in samples from the Grand basin than among fish that were sampled from the Kiamichi River basin (21 and 6 years old, respectively). Freshwater Drum grew at similar rates in both basins even though they reached larger maximum lengths in the Grand basin (649 mm TL) than in the Kiamichi River basin (600 mm). The average asymptotic length was greater for the Kiamichi population ( $L_{\infty} = 613$  mm) than for the Grand population ( $L_{\infty} = 557$  mm). Gizzard Shad from the Grand basin were larger than those from the Kiamichi River basin, though the latter population grew faster initially (Brody growth coefficient:  $K = 0.787$  versus  $K = 0.179$ , respectively), but they had smaller asymptotic length ( $L_{\infty} = 206$  mm versus  $L_{\infty} = 343$  mm). The role that groundwater plays in temperature regulation in these basins partially explains the observed differences. Our results suggest that the metabolic theory of ecology can be applied to fisheries management at a finer spatial scale.

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For widely distributed species, latitude is an important driver of demographic differences between both river and reservoir fish populations (Quist et al. 2003; Weber et al. 2015). Populations at lower latitudes typically have faster growth and higher mortality than higher-latitude

populations (Weber et al. 2015). A primary driver of these coarse spatiotemporal growth trends is temperature (Power et al. 2005; Rypel 2014), which can influence the growth, survival, and development rates of fish (Shoup and Wahl 2011; Mueller et al. 2017). However, even different

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Received May 9, 2019; accepted August 6, 2019

catchments with similar atmospheric conditions have different thermal patterns that may be driven by other landscape factors.

Average water temperatures among catchments are regulated by a combination of landscape features including climate, topography, stream discharge, interactions with the hyporheic zone, and geology (e.g., groundwater, Caissie 2006). Climate conditions vary with coarse-scale latitudinal changes. Topography, stream discharge, and groundwater inputs generally vary among ecoregions, influencing the thermal regime at finer scales (Woods et al. 2005). Geologic conditions affect connectivity between surface and groundwater (e.g., limestone and karst regions, Vineyard 1997). Seasonally, groundwater contributions can be the most important component to the regulation of water temperature, which then influences fish population demographics (Whitledge et al. 2006; Harstad et al. 2018). Water temperatures in groundwater-dominated basins are less variable because they are buffered from high fluctuations during seasonal extremes, creating thermal refuges for fish in both summer and winter seasons (Power et al. 1999; Caissie 2006; Brewer et al. 2016). Additionally, the thermal regimes of reservoirs are influenced by the temperature of inflowing lotic water (Soares et al. 2008) and by the direct discharge of groundwater into the waterbody (Rudnick et al. 2014). Groundwater contribution not only moderates temperature variations but also other temperature-dependent processes (Holmes 2000). The effects of groundwater contributions on the population demographics of coldwater fishes such as salmonids are well documented (see review by Power et al. 1999), but their effects on warmwater fish populations are less understood (Whitledge et al. 2006). Across river basins, differences in the fish population demographics in warmwater fisheries could be driven primarily by groundwater contributions that influence annual thermal patterns.

As the global climate warms, both water withdrawals and surface water temperatures are expected to increase (Shen et al. 2008) and new questions will likely arise about how groundwater further influences aquatic biota. In the United States, approximately 280 million m<sup>3</sup> of groundwater are consumed annually for public, domestic, agricultural, and industrial uses (Maupin et al. 2014). The withdrawal of both groundwater and surface water reduces stream flows (Xenopoulos et al. 2005) and increases stream temperatures (Caissie 2006). Improving our understanding of the effects of groundwater on warmwater fishes can be useful information for developing effective conservation and management actions. Although there has been a time lag between acknowledging the linkages between surface and groundwater and restoration responses (see Boulton 2007), restoring these connections is a management strategy where human actions have historically disrupted these linkages (Harper et al. 1999; Boulton 2000; Kasahara and Hill 2006; Loheide and Gorelick 2006). It is possible to restore

groundwater flow (Kasahara and Hill 2006; Boulton 2007; Suthersan et al. 2013) to facilitate thermal regimes that benefit species of interest. Although this strategy applies more readily to river systems, the thermal character of reservoirs is heavily influenced by the physicochemical characteristics of the inflowing rivers (Soares et al. 2008). Additionally, the growth and longevity of different fish populations are important parameters that are needed to model the response of fish to management interventions (Evans et al. 2014; Stewart et al. 2015) and they are useful for understanding the potential for restoration of important ecosystem processes that are influenced by fish populations (e.g., fish hosts and filtration by freshwater mussels, Vaughn et al. 2015). The objective of our study was to determine how fish age distributions and growth varied between two populations of fish that occupy river-reservoir complexes that have different relative groundwater contributions. We selected Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum* as our target species because their life histories are representative of two extremes: a long-lived and slow-growing species (Freshwater Drum) and a short-lived but fast-growing species (Gizzard Shad).

## METHODS

*Study site description.*—Managers are increasingly faced with managing fisheries from connected riverine–reservoir environments (Buckmeier and Schlechte 2009; Buckmeier et al. 2014); therefore, we selected two river–reservoir complexes from both a basin that is thermally influenced by groundwater contributions and a basin with similar climate conditions but primarily influenced by surface waters. The two river–reservoir complexes were located in the Ozark Highlands ecoregion and the Ouachita Mountain ecoregion (Figure 1). Both ecoregions are ecologically diverse and have similar precipitation patterns (Ozark Highlands: 104–122 cm/year, Ouachita Mountains: 109–142 cm/year; Woods et al. 2005). The two ecoregions are separated by <200 km and have similar seasonal ambient air temperatures (Ozark Highlands: mean January min/max –3.3/8.8°C and mean July min/max 20/32.7°C, Ouachita Mountains: mean January min/max –3.3/11.1°C and mean July min/max 19.4/34.4°C, Woods et al. 2005). However, the river basins have quite different groundwater contributions; springflow contributes to many reaches of Ozark Highland streams (Nigh and Schroeder 2002; Zhou et al. 2018), but many streams of the Ouachita Mountains lose surface water to groundwater during most summers (Orth and Maughan 1982; Zhou et al. 2018). The rivers of the Ozark Highlands ecoregion are emblematic of karst topography, with a prevalence of springs and relatively clear waters during baseflow conditions (Nigh and Schroeder 2002). Conversely, the rivers of the Ouachita Mountain ecoregion are characterized primarily by surface runoff. They typically

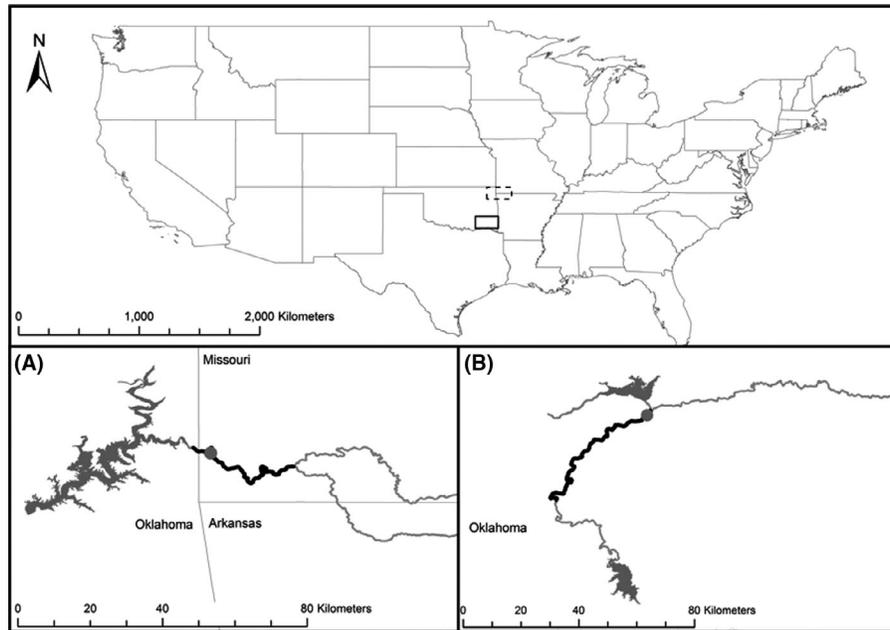


FIGURE 1. Study site locations where we compared the growth and age distributions of Freshwater Drum and Gizzard Shad that were sampled from rivers and reservoirs that are influenced by different contributions from surface and groundwater flows. The two basins are the Grand basin (dashed box), which includes Elk River and Grand Lake O' the Cherokees, and the Kiamichi basin (solid box), which includes Sardis Reservoir and the Kiamichi River. Each riverine sample reach was 40–50 km in length and adjacent to the gray dots; (A) Elk River, (B) Kiamichi River.

have flashy hydrographs and lower pH, and they carry slightly higher suspended sediment loads during baseflow conditions. We chose one large river (fifth-order) in each ecoregion from which to sample: Elk River in the Ozark Highlands and the Kiamichi River in the Ouachita Mountains. We also sampled fish from reservoirs with similar trophic states (Oklahoma Water Resources Board 2015) that were adjacent to each river: Sardis Reservoir, a 5,500-ha reservoir with a conservation pool level of 213 m that is located on Jack Fork Creek (a major tributary to the Kiamichi River) that regulates 25% of the annual discharge of the Kiamichi River; and Grand Lake O' the Cherokees (hereafter referenced as “Grand Lake”), an 18,800-ha main-stem reservoir, with a conservation pool level of 227 m that impounds the Elk River. Summer water temperatures in the Kiamichi River basin are reported to be as high as 40°C (Vaughn et al. 2015). Collectively, our study sites within the Ozark Highlands have cooler water temperatures during the summer months due to groundwater recharge (Grand Lake O' the Cherokees Watershed Alliance Foundation 2008; see also Results).

*Groundwater quantification.*—During 2016, we conducted seepage runs to quantify the relative groundwater contributions in both the Kiamichi River and its major tributaries and the Elk River of the Grand basin. A seepage run is a field technique that is used to estimate net water fluxes between surface water and groundwater (see Zhou et al. 2018). During each seepage run, we measured discharge

at multiple transects along the river by using a RiverSurveyor M9 Acoustic Doppler Current Profiler (ADCP, SonTek, San Diego). The discharge difference between transects is assumed to be the result of groundwater discharge to the stream (i.e., a positive value) or loss of stream water to groundwater (a negative value). The acoustic Doppler current profiler error was minimized at  $\leq \pm 0.015 \text{ m}^3/\text{s}$ . Our transects were spaced approximately 500-m apart. We found that using three transects across a stream reach was sufficient to minimize error (error  $\leq \pm 1.5 \times 10^{-5} \text{ m}^2/\text{s}$ ) in groundwater flux across sites, but at some sites only two measurements were possible due to tributary inflows. Groundwater flux is reported as the gain or loss in discharge, normalized by reach area ( $\text{m}^2$ ).

Seepage runs were completed on several Ozark stream reaches in the Elk River catchment and on the main-stem Kiamichi River in June and July 2016 to assess groundwater contributions. Seepage runs were completed at six sites in the Elk River catchment: two sites on Big Sugar Creek, Missouri, three sites on Buffalo Creek, Oklahoma, and one site on Elk River just upstream of the Buffalo Creek confluence. We completed six seepage runs on the Kiamichi River at six locations: three locations upstream of the Jack Fork confluence, one run just downstream of the confluence, and two runs in the Kiamichi River (25 and 39 km downstream of the confluence, respectively).

*Thermal conditions.*—We obtained temperature data from a variety of sources to show the relative differences

in thermal conditions among these systems. Water temperature data were available on the Kiamichi River downstream of the Jack Fork Creek confluence. These data were collected at 1-h intervals by using data loggers (HOBO, Onset Computer Corp., Bourne, Massachusetts) that were placed in the main channel of the river in a well-mixed location (C. Vaughn, University of Oklahoma, unpublished data). As part of a separate study, we collected water temperature data on the Elk River just above the confluence with Buffalo Creek at 1-h intervals by using data loggers (HOBO) that were placed in a well-mixed area of the main channel. Reservoir water temperature data are rarely monitored in Oklahoma except when reservoir profile data are collected (Oklahoma Water Resources Board, personal communication). We obtained reservoir profile data from two stations on Grand Lake from the Grand River Dam Authority; one station was located near the dam (i.e., hereafter, “dam”) and the other was located approximately mid-reservoir in the main channel of the reservoir (i.e., hereafter, “main channel”). Four water–temperature profiles were available on Grand Lake in summer 2016, whereas no water–temperature profiles were taken in Sardis Reservoir. However, the water temperature in Sardis Reservoir should more closely match the river temperatures because the reservoir dams only one major tributary to the Kiamichi River, unlike Grand Lake, which impounds several major rivers.

*Study species.*—Certain characteristics of Freshwater Drum and Gizzard Shad make them model species for studying differences in age and growth. First, they are commonly found together in both lotic and lentic ecosystems. Freshwater Drum is a slow-growing, long-lived species (30+ years, Rypel et al. 2006; Jacquemin et al. 2014). In contrast, Gizzard Shad is a relatively short-lived, fast-growing species (Dicenzo et al. 1996), with age-0 Gizzard Shad capable of exceeding gape limits for many common predators by autumn of their first year (Michaletz 1997). Growth and age distributions of Freshwater Drum populations often differ between populations in lotic and lentic locations (Rypel et al. 2006; Jacquemin et al. 2014), but it is unknown whether interconnected systems show the same patterns. Similarly, differences in the growth and age distributions of Gizzard Shad have been related to the trophic classification and physical characteristics (i.e., mean depth) of the habitat, with more rapid first year growth in shallow eutrophic waters but larger size at older ages in deep oligotrophic waters (Dicenzo et al. 1996; Michaletz 1998). Although neither fish is considered a sportfish, both can constitute a large proportion of the fish biomass of aquatic systems such that they compete with or provide prey resources for sportfish via young-of-the-year production (Swingle 1953; Stein et al. 1995). For both species, little is known about how thermal regime influences growth and age structure. Because

both Freshwater Drum and Gizzard Shad can move between the river and reservoir system in the Grand basin and we assumed that the thermal regimes of the river–reservoir systems would be similar within each ecoregion, we combined the data from both systems in our analyses rather than assuming that these populations are distinct.

*Fish sampling.*—We sampled fish from May to December 2016 and May to June 2017. We obtained samples from the reservoirs by using a 5.5-m electrofishing boat that was equipped with a Smith-Root 7.5 generator-powered pulsator and two boom-mounted anodes that used pulsed-DC electricity. Samples from both rivers were collected by using a 4.3-m boat that was equipped with a Smith-Root 5.0 generator-powered pulsator and a single boom-mounted anode that used pulsed-DC electricity. The percentage of range (the power that was applied to the water) was adjusted for conductivity differences at each site. The power output was also adjusted based on the response of the fish, with amperage adjustments ranging from 5 to 10 and pulses per s being either 60 (Gizzard Shad sampling) or 120 (Freshwater Drum sampling). We sampled all of the major habitat types within the reservoirs (e.g., rip rap, aquatic vegetation, deep banks, shallow backwaters, and standing timber), and our sampling locations ranged from the dam to the river-reservoir interface. The rivers were sampled while navigating downstream with the current, moving from bank to bank, to incorporate all of the major navigable habitat types (e.g., rip rap, brush, and standing timber).

*Fish aging.*—All of the captured Gizzard Shad were measured (to the nearest  $\pm 1.0$  mm TL), and the first 10 fish in each length bin were euthanized and placed on ice for transportation to the laboratory for aging. Additional fish that were collected after reaching the 10-fish limit were released after being measured. The bin size was set as the average asymptotic length ( $L_{\infty}$ ) divided by 30 (Coggin et al. 2013). Following Coggin et al. (2013), a 300-mm average asymptotic length was used because Gizzard Shad is a small, short-lived, and fast-growing species. If <10 individuals were collected in a bin, then all of the individuals in that bin were euthanized for later aging (Tetzlaff et al. 2011). All of the large individuals (>300 mm) were kept due to the expected variability in the age–length relationships of larger fish. Age–length keys for each population were developed using the FSA package (Ogle et al. 2017) in R (R Core Team 2018). The FSA package was also used to assign ages to unaged Gizzard Shad. Because Freshwater Drum were less abundant, all of the sampled fish were euthanized and aged.

The sagittal otoliths were extracted from the euthanized fish, cleaned of all tissue, and prepared for aging. After drying for at least 24 h, the whole Gizzard Shad otoliths were mounted in epoxy resin and 0.5-mm thick transverse

sections were cut across the dorsoventral plane by using a low-speed IsoMet saw (Buehler, Lake City, Illinois). The Freshwater Drum otoliths were sectioned (0.5-mm thick transverse sections cut across the dorsoventral plane) without epoxy mounting because they were large enough to secure in the saw and there was little risk of fracture during the sectioning process. The otolith sections were polished and viewed under a microscope where annuli were counted up to the outermost annulus. Two readers independently aged each fish. Any discrepancies between the two readers were discussed until a consensus was reached (Edwards et al. 2011). The average age of the sampled fish from each basin was calculated from our samples, and age-frequency distributions were constructed to visualize age differences between populations. Mortality was calculated from a weighted catch curve using the `catchCurve()` function of the FSA package in R (Ogle et al. 2017), and mortality rates were statistically compared using the `lm()` function in R (R Core Team 2018), with a linear model predicting the natural log of abundance from age and basin (Grand or Kiamichi) where the significance of the age by basin interaction indicated whether the two mortality slopes were significantly different.

*Fish growth.*—We examined the individual growth of the fish using two techniques. First, von Bertalanffy growth models were derived by fitting the age at capture to the length at capture and used to estimate growth parameters. The growth function is represented by

$$E(L|t) = L_{\infty} \left( 1 - e^{-K(t-t_0)} \right)$$

where  $E(L|t)$  is the expected length at time  $t$ ,  $L_{\infty}$  is the asymptotic average length,  $K$  is the growth coefficient, and  $t_0$  represents a theoretical time when the average length equals 0 mm (Cailliet et al. 2006). The growth curve parameters were statistically compared via hierarchical ratio tests (Kimura 1980) by using the nonlinear least squares function in R (R Core Team 2018). Second, to better visualize any growth patterns with respect to fish age, mean length at age from all of the sampled fish was also examined.

## RESULTS

### Groundwater Quantification

Seepage runs suggested that groundwater contributions differed across the two basins. During summer 2016, the Kiamichi River functioned as a losing stream, where surface flows were recharging groundwater. The net groundwater flux estimates were negative for all of the study reaches, indicating a loss of surface water to groundwater (i.e., losing reaches) at this time.

Seepage run data from the two major tributaries of the Elk River, Buffalo and Big Sugar creeks, and the Elk River reflected both gaining and losing stream reaches during summer 2016. Four of the reaches were gaining, including the two sites that were nearest to our fish collections within the Elk River (5.21 m/d and 0.38 m/d in lower Buffalo Creek and the Elk River, respectively). The two losing reaches were located in the upper portion of Buffalo Creek (0.16 m/d) and upstream in Big Sugar Creek (−0.55 m/d, located near FR2295 in Missouri).

### Thermal Conditions

We obtained river temperature data, collected during a similar period of summer 2016, to reflect differences in associated thermal patterns. Overlapping temperature data were collected from June 30 2016 to August 28, 2016, from both main-stem rivers of each basin: Elk River and Kiamichi River. Similar to our groundwater estimates, our temperature data indicated that Elk River receives more groundwater contributions that have cooler water temperatures (mean: 25.4°C) during the same summer period than the Kiamichi River (mean: 29.3°C, Figure 2) does.

Continuous temperature data were not available on both reservoirs, but temperature data from summer 2016 were available in Grand Lake. Four reservoir profiles on Grand Lake were taken on June 29, July 19, August 9, and August 30, 2016. The average water temperatures at each reservoir site (1.8-m deep) were similar (28.3°C and 28.8°C at the main channel and dam sites, respectively). Water temperatures ranged from 27.5°C to 29.5°C and from 27.6°C to 29.9°C at the main channel and dam, respectively.

### Fish Age and Growth

The Freshwater Drum and Gizzard Shad were well represented in our electrofishing samples from both basins. Of the 779 Freshwater Drum that were sampled across ecoregions, 461 Freshwater Drum came from the groundwater-dominated Grand basin and 318 were from the runoff-driven Kiamichi basin. Of the 3,467 Gizzard Shad that were sampled, 1,491 were sampled from Grand basin sites and 1,976 came from the Kiamichi basin sites.

Both fish species lived longer in the groundwater-dominated river–reservoir complex (Grand basin) than fish from the basin that were fed by surface flows (Kiamichi basin) did. The average age of Freshwater Drum was 7.3 years in the Grand basin but only 5.0 years in the Kiamichi basin. Similarly, Gizzard Shad in the Grand basin averaged 2.3 years old and only 0.8 years old from the Kiamichi basin. Freshwater Drum and Gizzard Shad in the Grand basin reached older maximum observed ages and had more consistent numbers of fish in older age classes following the first major drop in the age-frequency distribution (Figures 3 and 4). For Freshwater Drum in

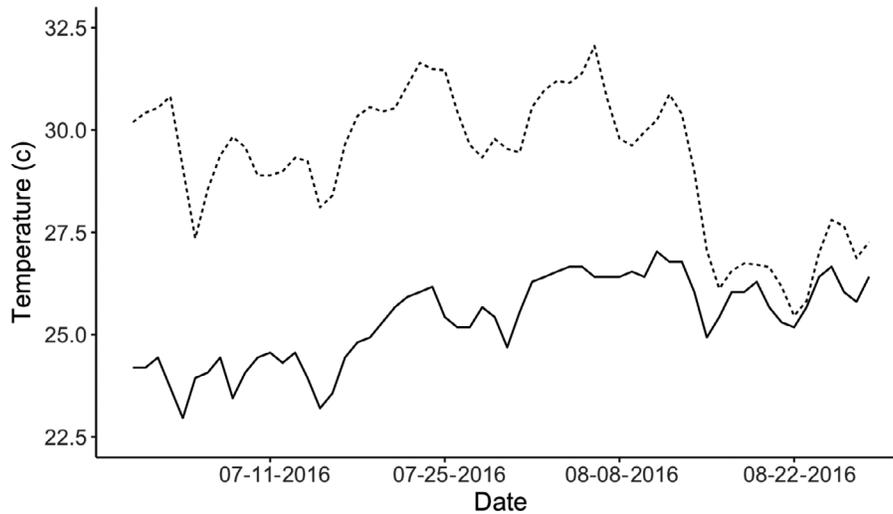


FIGURE 2. Daily water temperatures ( $^{\circ}\text{C}$ ) in the main-stem Elk (solid line) and Kiamichi (dashed line) rivers. These water temperature data are from the same period (June 30 to August 28, 2016), and they overlap with fish sampling during the first year of this study.

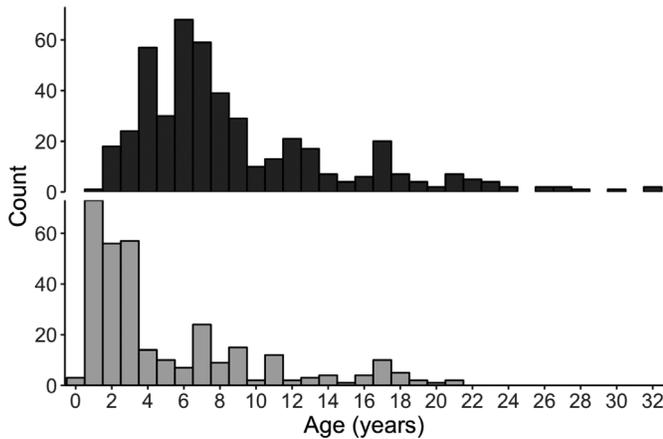


FIGURE 3. Age-frequency distributions for Freshwater Drum populations that were sampled from the Grand (dark gray bars) and Kiamichi basins (light gray bars).

the Kiamichi basin, the relative numbers of fish that were collected generally declined after age 3, and the number of older fish after this initial drop did not show the same consistency as that in the Grand basin population (Figure 3). However, instantaneous mortality rates were similar in the Grand ( $Z=0.19$ ; 17% annualized) and the Kiamichi ( $Z=0.31$ ; 27% annualized) systems ( $F_{1,39}=1.38$ ,  $P=0.25$ ). We observed a similar age-frequency pattern for Gizzard Shad, with a high frequency of fish up to age 5 in the Grand basin and very few individuals were observed that were older than age 2 in the Kiamichi basin (Figure 4). Correspondingly, the instantaneous mortality rate was significantly lower in the Grand basin ( $Z=0.66$ ; 48% annualized) than in the Kiamichi basin ( $Z=1.09$ ; 66% annualized;  $F_{1,11}=10.25$ ,  $P=0.008$ ).

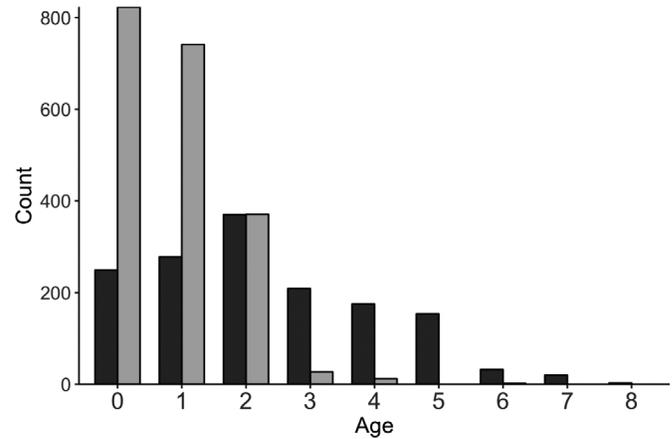


FIGURE 4. Age-frequency distributions for Gizzard Shad populations that were sampled from the Grand (dark gray bars) and Kiamichi basins (light gray bars).

The largest individuals of both fish species were sampled from the Grand basin. The largest Freshwater Drum that were collected from the Grand basin and Kiamichi basin were 649 mm and 600 mm, respectively. The largest Gizzard Shad that we sampled was from the Grand basin and was 420 mm, whereas the largest from the Kiamichi basin measured 321 mm.

The average length at age of the captured Freshwater Drum was typically larger for the population that was associated with the runoff-reliant Kiamichi basin than that from the Grand basin population. Fish from the Kiamichi basin had greater mean lengths for 10 of the 22 age-classes that were present in both basins (ages 1–21; Figure 5). The mean length at age for Gizzard Shad was larger for all ages that were sampled from the Grand

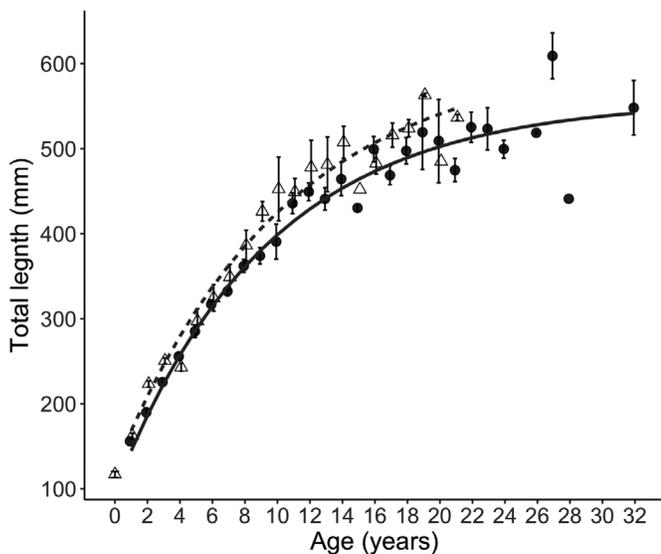


FIGURE 5. von Bertalanffy curves for the Freshwater Drum populations that were sampled from the Grand basin (solid line) and the Kiamichi basin (dashed line). We also show mean ( $\pm$ SE) length at ages for the Freshwater Drum populations that were sampled from the Grand basin (solid circles) and from the Kiamichi basin (triangles).

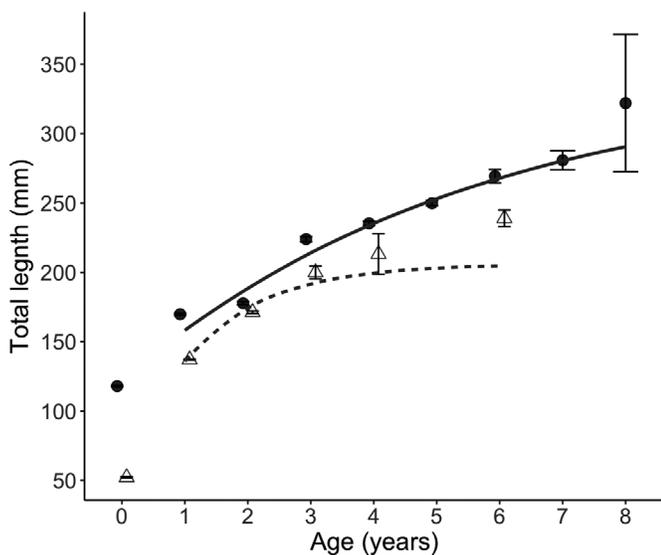


FIGURE 6. von Bertalanffy growth curves for the Gizzard Shad populations that were sampled from the Grand basin (solid line) and the Kiamichi basin (dashed line). We also show mean ( $\pm$ SE) length at ages for the Gizzard Shad populations that were sampled from the Grand basin (solid circles) and from the Kiamichi basin (triangles).

basin populations, with no overlapping standard error bars (Figure 6).

Freshwater Drum from the Kiamichi basin had a larger theoretical maximum length ( $L_{\infty}$ ) than those from the

groundwater-dominated Grand basin ( $\chi^2 = 54.1$ ,  $df = 3$ ,  $P < 0.01$ ; by comparing the models with common parameters with the models with all independent parameters, hierarchical analysis indicated that the best model had common  $K$  and  $t_0$  but independent  $L_{\infty}$  parameters; Table 1). The Brody growth coefficient ( $K$ ) and  $t_0$  were similar for both Freshwater Drum populations ( $\chi^2 = 0.7$ ,  $df = 1$ ,  $P = 0.39$ ) when comparing models with all independent parameters to the model with a common  $K$ ;  $\chi^2 = 1.6$ ,  $df = 1$ ,  $P = 0.20$  when comparing models with all independent parameters with common  $t_0$ ). In general, the von Bertalanffy curves for both Freshwater Drum populations were similar until age 10. Thereafter, shorter-lived Freshwater Drum from the Kiamichi basin maintained growth similar to that of younger fish, whereas Freshwater Drum from the Grand basin began to have a growth plateau (Figure 5).

All three of the von Bertalanffy model parameters differed for the Gizzard Shad populations in the Grand versus Kiamichi basins ( $\chi^2 = 2,331.2$ ,  $df = 3$ ,  $P < 0.01$  when comparing models with common parameters with those with all independent parameters; all of the models with one parameter in common were significantly different [ $P < 0.01$  for all 3 comparisons] from the model with all independent parameters; Table 1). Gizzard Shad from the Grand basin had a much larger theoretical maximum length than those from the Kiamichi basin (Table 1). However, Gizzard Shad from the Kiamichi basin grew faster earlier in life (i.e., showing a steep slope from ages 1 to 2; Figure 6) than those from the Grand basin population (high  $K$ , Table 1). This faster growth rate early in the Kiamichi basin population did not continue beyond age 2 (Figure 6). Gizzard Shad from the Grand basin maintained a steady growth rate through age 8 leading to a much larger average asymptotic length (Figure 6).

## DISCUSSION

We observed differences in the age and growth of two Freshwater Drum and Gizzard Shad populations that may relate to different groundwater contributions that regulate the thermal conditions in each system. Temperature is a primary driver of latitudinal trends in animal populations (Bergmann 1847). Water temperature is also associated with differences in life history traits (Magnuson et al. 1990; Power et al. 2005; Rypel 2014), with populations at lower latitudes typically growing faster but having shorter life spans (Quist et al. 2003; Weber et al. 2015). Both our seepage run data and summer water temperature data support the hypothesis that, through influences on thermal regimes, groundwater may play a role similar to that of latitude in regulating fish life history characteristics at a smaller, regional scale.

TABLE 1. von Bertalanffy growth equations for Freshwater Drum and Gizzard Shad in the groundwater-influenced Grand basin and the runoff-dominated Kiamichi basin. The models that are presented are the most parsimonious, based on ratio tests (Kimura 1980) that hierarchically compare the models with common or independent parameters for each population.

Basin	Attribute	Species	von Bertalanffy
Grand	Groundwater	Freshwater Drum	$L_{age} = 556\{1 - \exp^{[-0.10(age-2.24)]}\}$
		Gizzard Shad	$L_{age} = 343\{1 - \exp^{[-0.180(age-2.44)]}\}$
Kiamichi River	Runoff	Freshwater Drum	$L_{age} = 609\{1 - \exp^{[-0.10(age-2.24)]}\}$
		Gizzard Shad	$L_{age} = 206\{1 - \exp^{[-0.787(age-0.373)]}\}$

Groundwater and geology often covary, and both may contribute to variations in population dynamics. For example, the bedrock-dominated streams of the Ouachita Mountain ecoregion lose a substantial amount of available habitat and thermal refuge during the summer months when discharge declines (Orth and Maughan 1982), whereas the karst topography of the Ozark Highlands allow for greater connectivity between surface and groundwater. These connections with groundwater help maintain cooler water temperatures during the summer but can be disrupted during extreme drought (Power et al. 1999). Additionally, geology features can influence the geochemical characteristics of catchments, influencing water quality parameters such as pH. In the streams and reservoirs of the Ouachita Mountain ecoregion, pH is generally lower than that in the Ozark Highlands (pH = 5.04–9.31 in Ouachita Mountain ecoregion and 7.41–8.20 in the Ozark Highlands; Oklahoma Water Resources Board 2017), with values that often produce physiological stress for fish (i.e., pH < 7, Wedemeyer 2002). Stressors that are related to other water quality associations may also be a contributing factor to our growth differences.

In addition to groundwater differences among basins, there are several other factors that may have influenced fish growth. Fishing pressure, nutrient enrichment, and differences in available habitat can all influence fish growth (Power et al. 1995; Dicenzo et al. 1996; Michaletz 1998; Churchill et al. 2002; Shoup et al. 2012; Hunter et al. 2015). Neither species that was examined is considered a sportfish, so fishing pressure is not likely to have caused the growth differences. Population-level growth differences of Gizzard Shad have been related to nutrient classifications in reservoirs (Dicenzo et al. 1996; Michaletz 1998), but the reservoirs that we sampled were both classified as mesotrophic to eutrophic in recent years (Oklahoma Water Resources Board 2015). From 1999 to 2012, mean chlorophyll *a* values near our sampling site on the Elk River were 2.5 mg/m<sup>3</sup> and 10.8 mg/m<sup>3</sup> for the Kiamichi River from 1998 through present (Oklahoma Water Resources Board 2015).

Other factors that drive the fish bioenergetics (e.g., diet, food consumption, temperature tolerances) that regulate fish growth, and they may be specific to fish size. Freshwater Drum typically feed in benthic areas, and once they

reach a large enough size their diet shifts from insects to freshwater mussels, crayfish, and fish (Bur 1984; Pflieger 1997). More than 30 freshwater mussel species are found in the ecologically diverse Kiamichi River, including several that are federally listed (Vaughn et al. 2015). More than half of the freshwater mussel species in the state of Oklahoma can be found in the Kiamichi River (Master et al. 1998). However, the Elk River in Oklahoma supports fewer freshwater mussel species, though many Ozark streams have high abundances of freshwater crayfish (Brewer et al. 2009) that make up a large percentage of the diet of other fish species (e.g., Smallmouth Bass *Micropterus dolomieu*; Whitley et al. 2006). We did observe adult Freshwater Drum from both basins with crayfish and freshwater mussel remains in their stomachs. The similar growth rates in both basins suggest that food sources are adequate but the quantities that are consumed may differ based on their availability. Gizzard Shad passively filter-feed on zooplankton, algae, and detritus, but they will also actively prey on insects and larger zooplankton (Dicenzo et al. 1996; Pflieger 1997; Sampson et al. 2009). Although we did not quantify prey availability, hyporheic exchange often relates to areas of higher productivity and large invertebrate populations (Godbout and Hynes 1982; Stanford and Ward 1993; Krause et al. 2011). Because Gizzard Shad are filter feeders, the population in the Kiamichi basin may not have been able to feed as efficiently as that in the Grand Lake population due to higher turbidity conditions. Suspended sediment levels are correlated with turbidity (Bednarek 2001) and could limit the growth potential of Gizzard Shad by reducing both their filter-feeding and sight-feeding efficiency (Wilber and Clarke 2001; Reid et al. 1999). However, we found that Gizzard Shad from the Kiamichi basin grew more rapidly earlier in life than Gizzard Shad from the Grand basin. This may also be driven by thermal differences in each basin and relate to thermal tolerances at different life stages. Typically, both juvenile invertebrates (Peck et al. 2013) and fish (Comte and Olden 2017) have higher thermal tolerances than adults due to their lower oxygen demand; thus, they grow faster under warmer conditions if food is adequate. Higher juvenile thermal tolerances have been noted in both coldwater (e.g., Rainbow Trout

*Oncorhynchus mykiss*; Fowler et al. 2009) and warmwater fishes (e.g., Bluegill *Lepomis macrochirus* and Golden Redhorse *Moxostoma erythrurum*; Farless and Brewer 2017). Freshwater Drum growth has been related to hydrology and growing degree days (Braaten and Guy 2002; Rypel et al. 2006; Richard and Rypel 2013; Jacquemin et al. 2014; Rypel 2014). This study did not examine relationships between growth and hydrology, but our results agree with previous findings that Freshwater Drum growth was positively associated with temperature and growing degree days (Richard and Rypel 2013; Rypel 2014). Our results suggest that the observed differences in fish growth may be attributable to the different thermal regimes that relate to groundwater contributions.

Our data were pooled to include both river and reservoir populations of fish into one data set. The average depth and trophic status of reservoirs have been associated with the age distribution and growth of Gizzard Shad, with rapid first year growth in shallow eutrophic waters but larger size at older ages in deep oligotrophic waters (Dicenzo et al. 1996; Michaletz 1998). Grand and Sardis reservoirs are each classified as eutrophic. However, Grand Lake is much deeper than Sardis reservoir, with mean depths of 10.9 m and 5.2 m, respectively. The depth of these reservoirs may relate to some of the age and growth differences that we observed between these two populations. However, because some fish can make substantial movements and Grand Lake and Elk River lack known movement barriers, we chose to combine these data and analyze our data by basin. Future efforts might examine multiple systems where (1) movements are not possible between systems and (2) additional variables could be related to growth differences (e.g., water depth, prey availability).

Although we focused on groundwater and water temperature differences in these river-reservoir complexes during summer conditions, groundwater provides thermal refugia during both winter and summer (Power et al. 1999). These basins are located far enough south that complete ice cover does not occur during winter. However, portions of the southeast United States have seen recent increases in the severity and frequency of droughts (Pederson et al. 2012). River basins that are not supplemented with groundwater are especially at risk of losing connectivity and reaching higher temperatures during the summer months that approach thermal maxima for some aquatic species (Power et al. 1999; Zhou et al. 2018). The Kiamichi basin has experienced two severe droughts within the past 25 years (Vaughn et al. 2015). The role that groundwater plays in the regulation of stream temperature regimes in these two basins is similar to that played by latitude, with higher average temperatures at lower latitudes and lower average temperatures at higher latitudes. Fish populations that live in higher latitudes often live longer than those that live in lower latitudes (Quist et al. 2003). This pattern is consistent with the metabolic theory of ecology,

which has been used to explain growth variation over large spatial scales (Weber et al. 2015).

Our results suggest that the metabolic theory of ecology may also be applicable in management scenarios where populations are not separated by large distances but do experience water temperature differences, much like populations that live at high and low latitudes. Metabolic theory explains latitudinal variations in Common Carp *Cyprinus carpio* population demographics (Weber et al. 2015), with individuals living longer and growing larger at higher latitudes (lower temperatures) but with individuals growing faster with higher mortality at lower latitudes (higher temperatures). Our hypothesis that groundwater may influence fish demographics is built on the same temperature-regulating concept that was described by Weber et al. (2015), though at a finer spatial scale. The mechanisms that drive fish growth are often of interest to management agencies. For example, high growth rates at younger ages can cause Gizzard Shad to quickly outgrow the gape limitation of many economically important sportfish (Stein et al. 1995; Michaletz 1997). The metabolic theory of ecology suggests that fish grow differently based on system latitude. Our findings suggest that managers may need to have different growth and age expectations for different thermal regimes. Using fish stocking as an example, applying our localized idea of metabolic theory could help to identify areas where thermal regime differences could affect the successful growth of the stocked species in different systems. If water temperatures increase over time due to human influences, such as groundwater pumping, the restoration of groundwater connections may be warranted. This is especially important in ecosystems that depend on species interactions to support biological diversity (e.g., Freshwater Drum is a reproductive host for many species of threatened and endangered freshwater mussels, Lyons et al. 2007). Applying the metabolic theory concept to management at the river-basin scales when temperature differences are known might offer unique restoration options under some conditions.

#### ACKNOWLEDGMENTS

This research is a contribution of the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Geological Survey, Oklahoma Department of Wildlife Conservation, Oklahoma State University, and Wildlife Management Institute cooperating). Funding was provided by the U.S. Fish and Wildlife Service, Gulf Coast Prairie Landscape Conservation Cooperative. We thank Jason Glover, Desiree Moore, and Andy Miller for technical assistance and Caryn Vaughn for providing water temperature data. This research was conducted under the auspices of Oklahoma State University's Animal Care and Use Committee (Protocol AG-1526). We thank Michael Quist and two

reviewers for providing comments that improved our manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. There is no conflict of interest declared in this article.

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