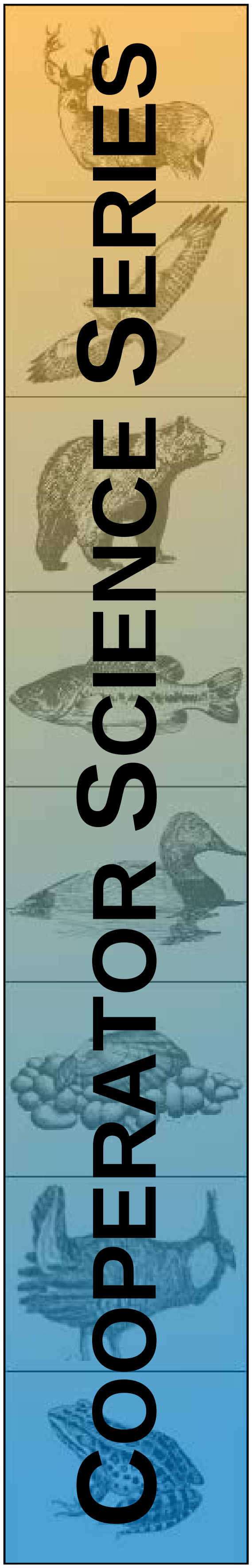

Incorporating an approach to aid river and reservoir fisheries in an altered landscape

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FINAL REPORT

Incorporating an approach to aid river and reservoir fisheries in an altered landscape

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Summary

Reservoir construction for human-use services alters connected riverine flow patterns and influences fish production. We sampled two pelagic fishes from two rivers and two reservoirs and related seasonal and annual hydrology patterns to the recruitment and growth of each species. River and reservoir populations of Freshwater Drum *Aplodinotus grunniens* reached similar ages (32 and 31, respectively). Likewise, longevity of Gizzard Shad *Dorosoma cepedianum* between the two systems was also similar (7 and 8 years, respectively). However, both species grew larger in the rivers compared to reservoir residents. Recruitment of Freshwater Drum in reservoirs was negatively related to water retention time (r^2=0.59) suggesting moving water through the reservoir was beneficial. Riverine recruitment of Freshwater Drum populations was negatively related to the annual number of flow reversals and positively related to prespawn discharge (r^2 = 0.33). Unlike Freshwater Drum, there was no relationship between flow metrics and Gizzard Shad recruitment in reservoirs. However, recruitment of riverine Gizzard Shad was positively related to high flow pulses during the prespawn and spawning seasons (r^2 = 0.48). The growth of both species in reservoirs was positively related to the number of days each year that water levels were above the conservation pool. Growth of Freshwater Drum was also negatively related to minimum reservoir summer water levels (r^2 = 0.84). Growth of both Freshwater Drum and Gizzard Shad occupying lotic systems was positively related to May (r^2 = 0.86) and July discharge (r^2 = 0.84), respectively. In general, growth and recruitment of the reservoir populations was more related to annual water patterns, whereas riverine fishes responded more to seasonal flow patterns. Results of this study provide important information on the relationship between hydrology and pelagic fish production in both rivers and reservoirs. This information is useful if agencies are interested in developing holistic river-reservoir water-allocation plans.

Background

One of the major challenges of environmental flow protection and enhancement is identifying quantifiable objectives, such as key ecological targets and flow requirements needed to sustain those targets (Richter et al. 2003). These flow requirements may represent adequate ranges of sustainability (Richter 2009) or thresholds, beyond which, ecological impairment is expected (Richter et al. 2012). The natural flow regime has been used as the primary objective, with the assumption that this represents ecological needs. However, identifying ecosystem needs requires intimate knowledge of the dependency of ecosystem function on flows in altered and unaltered systems, and this knowledge gap has been addressed in various settings through workshops based on regional expertise (King et al. 1998). In the absence of such information, Richter et al. (2012) proposed a presumptive standard ranging from 10-20% hydrologic alteration, beyond which ecological functions may be impaired. This is highly suitable for regional planning in areas of limited a priori exploitation; however, it still relies on the natural flow regime as the baseline to measure the level of alteration. Highly altered landscapes, however, may already exceed the presumptive standard, as evidenced by a large number of streams with >25% hydrologic alteration in the US (Carlisle et al. 2011). Under these conditions, two options exist: 1) either landscape conditions are improved and/or dams are removed, or 2) environmental flows must be identified that relate to the sustainability of a few fundamental ecosystem components, indicative of functioning ecosystems (Brewer et al. 2016).

One of the important water needs that may be affected by flow alteration is the ecosystem service of fish production. Fish are an important resource in Oklahoma and surrounding states. Oklahomans spend over 8 million angler days fishing every year, many as a means for sustenance (USDI 2014). These fishing trips generate approximately three quarters of a billion dollars in direct expenditures, much of this in rural economies of the state (USDI 2014). A given rural fishery can generate tens of millions of dollars annually into the local economy (Schorr et al. 1995; Chen et al. 2003; Allen et al. 2014). Further, fish play important roles within aquatic systems that ensure proper ecosystem function. For example, changes in the fish community can lead to changes in nutrient dynamics (Schaus et al. 1997; Mehner et al. 1998) or trophic cascades (Benndorf et al. 1984; Carpenter et al. 1985; Vanni and Findlay 1990) that alter phytoplankton abundance. Fish also provide critical food sources that maintain adjacent terrestrial food webs (Spencer et al. 1991). Therefore, it is important to understand how factors that are likely to alter flows (e.g., urbanization, general water use, climate change) and management actions designed to adapt to these changes, affect fish populations.

Previous research suggests changes in hydrology (i.e., discharge patterns of lotic systems or water level and residence time in lentic systems) can influence recruitment (Miranda et al. 1984; Mitzner 1991; Ozen and Noble 2005; Smith et al. 2005) and growth rates (Miranda et al. 1984; De Graaf 2003; Dutterer et al. 2013) of some fishes. Many of the relationships between hydrology and juvenile or adult fish abundance are exponential rather than linear, suggesting the effects could be quite strong with only moderate changes in hydrology (Ozen and Noble 2005). However, many important fish species have not been well studied in this regard, and different groups of fishes respond differently to changes in hydrology (Miranda et al. 1984; Quist et al. 2003), necessitating a more thorough study to cover major ecological groups of fishes.

Objective

The goal of this project was to examine the tradeoff between water management of connected reservoir and river systems. Our specific study objective was to examine how hydrology related to both year-class strength and annual growth rates of fishes. We chose Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum* as focal species, because of their important ecological roles in both river and reservoir ecosystems. Freshwater Drum play an important role in the persistence of many freshwater mussels. Over 70% of North America's freshwater mussels are considered endangered, threatened or of special concern (Williams et al. 1993; (https://www.fws.gov/midwest/endangered/clams/mussels.html). Freshwater Drum serve as a primary glochidia host facilitating freshwater mussel reproduction (Price et al. 2012). In fact, Freshwater Drum is the only host for many freshwater mussels (Lyons et al. 2007); therefore, maintaining healthy populations of Freshwater Drum is critical to protecting these threatened invertebrates. Gizzard Shad are the dominant prey species in many reservoirs (Michaletz 1997), are often stocked as supplemental prey in reservoirs (Noble 1981; Michaletz 1998), and contribute many bottom-up trophic level effects (Noble 1981). This information will allow us to better understand how fish production relates to water-management practices.

Methods

Study Area

Both the Ozark Highlands and Ouachita Mountain ecoregions have similar precipitation patterns (Ozark Highlands: 104-122 cm/year, Ouachita Mountains: 109-142 cm/year; Woods et al. 2005), and both have major rivers that have been impounded for flood control, recreation, and water storage (Figure 1). The Ozark Highlands ecoregion is characterized by limestone lithology, karst topography and associated groundwater influences, and streams in this ecoregion are relatively clear during baseflow conditions. The Elk River is a fifth order river (i.e., Strahler stream order) that terminates in Grand Lake O' the Cherokee's (hereafter referred to as Grand Lake), an 18,800-ha eutrophic reservoir with a conservation pool level of 227 m. The Elk River is one of three major tributaries to Grand Lake and accounts for ~ 12% of Grand Lake's hydrologic budget (Grand Lake Watershed Plan 2008). The Ouachita Mountain ecoregion has a different lithology that is dominated by chert, shale, and dolostone. Many streams in this ecoregion carry higher suspended sediment loads and flow is typically dominated by surface runoff. The Kiamichi River is also a fifth order stream and a major tributary of the Red River that flows west from Arkansas until it is redirected south near the confluence of Jack Fork Creek. Jack Fork Creek is impounded by Sardis Reservoir. Sardis Reservoirs is a 5,500-ha reservoir that has a conservation pool level of 213 m. Sardis reservoir is classified as eutrophic and releases from the Sardis Dam controls ~24% of the historic flows in the downstream Kiamichi River (Vaughn et al. 2015). The Kiamichi River has been designated as an ecological hotspot because of its diversity (Master et al. 1998). The Kiamichi River hosts over 100 freshwater fish species (Master et al. 1998). Additionally, more than 30 freshwater mussel species are found in the Kiamichi River, including three species that are federally listed (Vaughn et al. 2015).

Species descriptions

Flow alteration is perceived as a threat to many broadcast-spawning species though much less is known about the larger-bodied fishes within this group. Worthington et al. (2017) reviewed the threats to broadcast-spawning minnow species in the Great Plains rivers of North American and found altered hydrology was one of the primary threats. Less is known about the relationship between hydrology and larger-bodied broadcast spawners; thus, we chose two of these larger-bodied fishes as the focus of this study. Based on existing evidence, we hypothesize that both Freshwater Drum and Gizzard Shad recruitment and growth would be strongly related to flow patterns.

Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum* have similar spawning strategies, but different early life histories. Freshwater Drum is a pelagophil (Balon 1975), initiates spawning activities in May or June and has been observed spawning through July (Priegel 1969). Freshwater Drum eggs and larvae drift with changes in flow patterns because they are buoyant (Balon 1975). Egg and larvae of many broadcast spawners rely on current for development, distribution, and survival (Lechner et al. 2016). Once Freshwater Drum develop swimming abilities (~25-mm TL), they move to nursery habitat in calm backwater pools of rivers and benthic regions of reservoirs. (Holland 1986; Sheaffer and Nickum 1986). During the May spawn, adult Gizzard Shad occupy low-current backwaters of rivers and nearshore reservoir environments (Miller and Robinson 2004). Gizzard Shad is a litho-pelagophil spawner and once their adhesive eggs hatch, semi-buoyant larvae move in an upward twitching and downward settling pattern, making it easy for flows to drift them away from spawning substrate (Holland 1986). Gizzard Shad typically remain in backwater nursery areas until swimming abilities fully develop and then move to open water and initiate schooling behavior

(Pflieger 1997). Because these species are vulnerable to current at early life stages, recruitment variability is likely related to hydrology.

Defining life-history periods for recruitment analysis

We referred to regional taxonomic references to define the timing of the prespawn, spawn, nursery and over-winter periods for each species (Pflieger 1997). For Freshwater Drum, the prespawn period is March to April, the spawning period May through July, the nursery period August through October, and the overwinter period is December through February. For Gizzard Shad, the prespawn period is approximately March through April, the fish spawn during late April and May, June through November is a nursery period, and the overwinter period is typically December through February (Pflieger 1997).

Species longevity, spatial distribution, and diet

Certain characteristics of Freshwater Drum and Gizzard Shad make them model species for studying how hydrology influence fish growth. Freshwater Drum is a slow-growing, long-lived species; this allows for extensive time-series analysis, as they are exposed to long durations of hydrological variability (Winemiller and Rose 1992; Rypel et al. 2006). Freshwater Drum may live over 30 years (Rypel et al. 2006), a length of time that likely captures rare and extreme weather events (severe droughts or floods). In contrast, Gizzard Shad is a relatively short-lived, fast-growing species (Dicenzo et al. 1996), which allows for more fine-scaled relationships to be observed (e.g., influence of inter-annual hydrological variability on growth).

Freshwater Drum and Gizzard Shad have different diet composition and different distributions. Freshwater Drum exhibit temporal variation among habitat use, occupying deep waters in spring (Pflieger 1997), and moving to shallower habitats in summer (Bur 1984); though they tend to remain in the benthic region throughout the year. Gizzard Shad use schooling behaviors to avoid predation (Shoup and Wahl 2009), spending most of their time consistently swimming in open water, remaining near the surface (Pflieger 1997). Freshwater Drum typically feeds in benthic areas, eating freshwater mussels, crayfishes, fishes, and other invertebrates, such as insects (Bur 1982; Pflieger 1997). Gizzard Shad passively filter feeds on zooplankton, algae, and detritus, but will also actively prey on insects and larger zooplankton (Dicenzo et al. 1996; Pflieger 1997; Sampson et al. 2009).

Although they have different distribution and diets, Freshwater Drum and Gizzard Shad growth could be influenced by similar hydrology metrics, albeit in different ways. For example, the amount of suspended sediments can be influenced by high flows and frequent water-level fluctuations (Mac Donagh et al. 2009). As suspended sediment settles, it covers crevices in the benthic region, limiting both the visual abilities of Freshwater Drum while the sediments are suspended, and benthic prey accessibility after the sediments settle (Lenat et al. 1981). As such, Freshwater Drum may forage more efficiently during stable flow or water-level conditions (Rutherford et al. 1995). Suspended sediment levels are often correlated with turbidity (Bednarek 2001), and could potentially limit Gizzard Shad growth by reducing both filter-feeding and sight-feeding efficiency (Wilber and Clarke 2001; Reid et al. 1999). Reservoir volume could influence both species, as less habitat concentrates prey and benefits Freshwater Drum, but would be predicted to negatively affect Gizzard Shad because they would spend more energy avoiding predators. Hydrological variability might influence growth of these species via influences on physicochemical properties, volume of available habitats, or availability or concentrations of their food supplies.

Fish sampling and processing

We sampled fishes via boat electrofishing from May to December 2016 and May to June 2017 and collected demographic data after collection. Fishes were sampled from two rivers (Elk and Kiamichi rivers) and two reservoirs (Sardis Reservoir and Grand Lake O' the Cherokee) using boat-mounted electrofishing. We sampled reservoirs using a boat equipped with a Smith-Root 7.5 generator-powered pulsator and two boom-mounted anodes using pulsed-DC electricity. Both rivers were sampled using a 4.3-m boat equipped with a Smith-Root 5.0 generator-powered pulsator and a single boom-mounted anode using pulsed-DC electricity. Percent of range (power applied to water) was adjusted for conductivity differences at each site. We sampled rivers downstream with the current, moving from bank to bank to incorporate all habitat types (e.g., rip-rap, brush, and standing timber). Reservoirs were also sampled to incorporate available habitat types, and sampling locations ranged from the dam to the river-reservoir interface.

All captured Gizzard Shad were measured (±1 mm, TL), and the first 10 fish in each 15-mm length bin were euthanized, individually bagged, labeled, and placed on ice for transportation to the laboratory for further processing (i.e., otolith extraction). Additional fish collected after reaching the 10-fish limit were quickly released after being measured. To assign ages to Gizzard Shad that were not euthanized, we developed an age-length key. We extracted otoliths from ten fish in each bin size to construct the age-length key and assigned ages to unaged fish based on their total length (Coggins et al. 2013). The bin size was set as the average asymptotic length (L_∞) divided by 30. If < 10 individuals were collected for a bin range, then all individuals in that bin were used for aging (Tetzlaff et al. 2011). The combined total sample size of aged and unaged fish is recommended at 500-1,000 to achieve the best accuracy and precision when using this method (Coggins et al. 2013).

Methods were slightly different for Freshwater Drum because they can exhibit sexual dimorphic growth (Rypel 2007). We identified each fish as male, female or immature based on macroscopic observations of the gonads. We made an incision from the anus to the pectoral fins, then spread the incision apart to identify ovaries, testes, or undeveloped gonads. Because sex had to be determined, no age-length key was developed, and all Freshwater Drum were humanely euthanized via overdose of MS-222 using 270mg per liter of water and used for age analysis.

For both species, otoliths were extracted from euthanized fishes, cleaned by removing all tissue, and aged via two individuals. After drying for at least 24-h, whole Gizzard Shad otoliths were mounted in epoxy resin and 0.5-mm thick, transverse sections were cut across the dorso-ventral plane using a low-speed IsoMet® saw. Freshwater Drum otoliths were sectioned without epoxy mounting because they were large enough and there was no risk of fracture during the sectioning process (Figure 2). Otolith sections were polished and viewed under a microscope where annuli were counted. Two readers independently aged each fish. Any discrepancies between the two readers were discussed until a consensus was reached (Edwards et al. 2011).

Catch curves and incremental growth

Catch curves were developed to index year-class strength. Catch curves are a regression between the log of abundance and age. We used the ‘FSA’ package in program R (version 3.2.2, R Core

Development Team) to construct catch curves (Ogle 2017). This package was used to develop a weighted catch curve that assigned less weight to older age fish, which are less abundant and therefore more likely to produce outlying data (Maceina and Bettoli 1998). We used studentized residuals from the weighted catch curves to simultaneously index year-class strength of all cohorts in the population (Maceina 1997). Studentized residuals have a t-distribution where 95% of the observations fall between -1.96 and 1.96, regardless of sample size or the model fit (r^2); thus, allowing comparisons to be made between regression equations (Maceina 1997). Deviations from the catch-curve regression line were used as an index for quantifying weaker (negative residuals) or stronger (positive residuals) year classes (Maceina 1997).

Year-class strengths are a standardized and implicit measure of recruitment variation, but only age classes fully recruited to the gear can be used in this approach. With this method, recruitment does not need to be observed each year. Recruitment estimates were only assigned to age classes that were fully recruited to the sampling gear (Allen and Hightower 2010). The age that fishes were considered fully recruited to our sampling gear was assessed using abundance-at-age histograms for each site (Allen and Hightower 2010). This method assumes that abundance of individuals in younger age classes should always be greater than older age classes. The peaks in abundance-at-age histograms determined the first age vulnerable to the gear (Allen and Hightower 2010). We obtained catch curve residuals using regressions of $\log_e$(abundance at age +1) as a function of age. We included all age classes that had at least two fish present; however, age classes with less than two fish were included if subsequent age-classes contained at least two fish (Isermann et al. 2002).

Incremental growth of individual fishes was estimated using the Weisberg back-calculation method (Weisberg et al. 2010). Growth of otoliths and other aging structures are often assumed to be directly proportional to growth of the fish (Ricker 1992); thus, we used the incremental distances (0.001 mm) between each annulus to estimate annual growth. We mounted sectioned otoliths onto glass slides, viewed them under a microscope (30X/22), and captured pictures of each otolith using DinoCapture® software (Torrence CA, Dunwell Tech, Inc.). We calibrated the software to the magnification used to capture pictures, and measured distances between annuli with the measurement tool included in the software program. We measured incremental distances from approximately the same region of the otolith for all individuals. Measurements were placed at the outer edge of each successive annulus to ensure measurements represented the full year of growth. If an otolith had incremental growth beyond the last complete ring, that measurement was not included in the analysis because it did not represent a full year of growth (Campana and Thorrold 2001). To examine relationships between hydrology and incremental growth, we developed general linear mixed-effect models similar to Weisberg et al. (2010). This approach is recommended over the Dahl-Lea model when estimating growth because it accounts for growth effects arising from individual fish and years, rather than just accounting for age effects.

Recruitment and growth hydrology metrics

To analyze relationships between hydrology and recruitment, we quantified 16 hydrology variables for our river systems using Indicators of Hydrologic Alteration (IHA) software (Table 1) or Microsoft Excel (Table 2). IHA uses daily discharge data to calculate a total of 67 statistical parameters. This software was developed to easily calculate characteristics of both natural and altered flow regimes, using many environmental flow components. Daily riverine discharge data were obtained from the U.S. Geological Survey gages for the Kiamichi and Elk rivers (gages 07335790 and 07189000, respectively). All fish sampling took place within 50 river kilometers of the Kiamichi and Elk River gage sites. We analyzed daily discharge data from the years 1995 to 2016 for the Elk River and 1998 to 2016 for the Kiamichi River. We summarized percentile-based flow metrics (e.g., discharge above the 75th percentile of daily flows) using data from 1980-2016 because at least 20 years of hydrologic data are recommended to represent historical flow patterns (Richter et al. 1997). However, some IHA metrics are not calculated in this way (e.g., 90-day minimum flows), in which case only data from years corresponding to years with represented year classes were used. We used IHA to calculate six variables that summarized annual hydrologic conditions (Table 1). We also used IHA to calculate the 30-day maximum and minimum daily discharge during the spawning and nursery periods each year. We calculated median daily discharge for the four periods each year using Microsoft Excel. We chose median daily discharge because mean discharge could be strongly influenced by one extremely high flow day. We also estimated flow variability using the coefficient of variation of daily discharge for the prespawn and spawning periods.

We calculated reservoir hydrology metrics (Table 3) using daily water-level data for both Sardis Reservoir and Grand Lake. Water data were obtained from the U.S. Army Corps of Engineers monitoring website (http://www.swt-wc.usace.army.mil/), which contains the past 20 years of daily data that are recorded as follows: daily pool elevations (ft), storage (ac-ft), reservoir releases, inflow, and rainfall (in). We converted data to metric units. Our parameters were calculated from 1998 to 2015 for Sardis Reservoir, and 1995 to 2015 for Grand Lake.

We calculated 10 hydrologic metrics for our reservoirs. We calculated the average water storage (ha) and the coefficient of variation of water storage for each of the four periods (prespawn, spawn, nursery, and overwinter) each year. We calculated the total number of days per year that pool elevations were above conservation pool levels (213 m for Sardis Reservoir and 227 m for Grand Lake) in each reservoir. We also calculated annual storage variability using the annual coefficient of variation of water storage. The final variable we calculated in reservoirs was annual retention time (annual average water storage divided by the annual total releases), which represents the estimated mean time a particle of water spends in the reservoir. Reservoirs with short retention times are often considered more ‘lotic’ in character (Soares et al. 2008), whereas longer retention times are often associated with increases in primary productivity and phytoplankton biomass (Soares et al. 2008).

To analyze relationships between hydrology and growth, we calculated hydrologic metrics that we hypothesized would coincide with the ecology of both Freshwater Drum and Gizzard Shad (Table 4). We summarized annual flow metrics that influence volume of habitat (e.g., annual 90-day maximum flows and annual maximum storage), and physicochemical conditions (e.g., river reversals, reservoir retention-time, high-flow pulses and number days above conservation pool). Seasonal flow metrics were calculated that might influence either accessibility of diet items (e.g., fall rate or minimum water storages) or abundance of diet items (e.g., river reversals or maximum water storage). Finally, we summarized hydrologic conditions during each month of the growing season (March through September). We summarized riverine flow metrics (Table 5) and reservoir metrics (Table 6) as described in the recruitment section, albeit different metrics were calculated for growth.

Relating hydrology to recruitment and growth

To analyze recruitment relationships, we used multiple regression to test for relationships between studentized residuals from the catch curves (response variable) and river and reservoir hydrological variables occurring during the cohort's birth year using multiple regression analysis (dependent variables). To assess trends across systems, we followed the methods of Bonvechio and Allen (2005). Briefly, studentized residuals were standardized as percent frequencies for all systems and hydrological variables were standardized and centered to zero for each system. This allowed us to combine the two rivers and the two reservoirs into the same models (one model for each species and system type [river or reservoir]), despite differences in hydrology of each replicate system. We developed four candidate model groups to describe growth patterns using each species and systems combination. For example, one candidate model group included Freshwater Drum from reservoirs and another candidate model set contained Freshwater Drum from rivers.

To determine the most parsimonious regression model for each species and system type, we used a forward-selection selection process with the SigAIC information criterion (Jamil et al. 2012). SigAIC is a variant of Akaike Information Criterion (AIC) (Burnham and Anderson 2002). The added benefit of SigAIC over AIC is that it introduces a higher penalty factor (3.84) for increased model complexity which is sized based on the chi-square distribution and guarantees that the addition of a new factor will result in a lower SigAIC if and only if the factor is significant at the alpha=0.05 level. Additionally, forward selection allowed correlated predictors ($r \geq 0.65$ where r is Pearson's correlation coefficient), to be removed as model complexity increased rather than prior to model fitting. The first step in the model selection process compared SigAIC from our null models that contained only intercepts (i.e., year-class strength) to our initial single-predictor hydrology models. If SigAIC from a hydrology model resulted in a lower SigAIC (SigAIC values within 1 unit were not considered different), it was considered more parsimonious and we selected the single-predictor model with the lowest SigAIC to become our new null model for step two. The selection process continued with the addition of the remaining predictor variables to the top model one at a time (e.g., year-class strength = x + y; year-class strength = x + z; etc), and so on until SigAIC stopped decreasing by at least 1 unit, indicating that adding more factors would not improve parsimony. A fixed site effect was then added to the top model to examine if differences among sites explained additional variation. Residual plots and quantile-quantile plots were constructed to check that constant variance and normality assumptions were reasonably met. All models and regressions were run using the lme4 package in the statistical software R (version 3.2.2, R Core Team 2016).

Similar to the recruitment analysis, we developed four candidate model groups to describe growth patterns using each species and system combination. The independent variables used in our null models were age, year, individual fish, and site:

$$Y_{ijkl} = \beta_0 + \beta_1 X_{i1} + Z_j + Z_k + Z_l$$

where Y is the growth increment *i* for fish *j* of growth year *k* in river or reservoir *l*. β_0 is the grand intercept, X is the age for which increment *i* was measured for each fish. Z_j is the random fish intercept, Z_k is the random year intercept, and Z_l is the random river or reservoir intercept for each model. We also tested whether including a fixed effect reflecting fish sex improved model fit for Freshwater Drum. Age and sex were fixed effects, whereas year, individual fish, and site were random effects. Age accounted for variation in fish growth at each measured increment, as young fish typically have faster growth than older fish in that same year (Weisberg et al. 2010). Year accounted for growth differences occurring among years that was related to unmeasured factors (e.g., climate). An individual fish factor was included so that incremental measurements were directly proportional to growth of that specific fish because fish may have differences in growth due to genetics or other unmeasured factors (Weisberg et al. 2010). Additionally, site was considered a random variable to account for environmental differences between sites. To determine the most parsimonious model for each species and system, we used a similar forward-selection process to what was used for recruitment models, using the information criterion SigAIC (Jamil et al. 2012).

Results

Hydrology

Despite similar precipitation patterns, flow patterns during the observed years differed substantially in these basins. The Kiamichi River is a flashier system that has more frequent annual peaks, but also more reversals due to lithology, topography and basin drainage patterns. There is a greater range of flows (both high and low) in the Elk River, though, rise and fall rates in the Kiamichi River are more pronounced. Additionally, long periods of low flow occurred in the Kiamichi River, likely because estimated groundwater flux in the Ozark Highlands ecoregion is generally higher than those in the Ouachita Mountain ecoregion (Zhou et al. In Review).

The functional purpose the two reservoirs serve (hydropower vs. flood control/water storage) is reflected in their dissimilar hydrology. Annual water levels fluctuated more in Grand Lake where water is typically released every month of every year, whereas Sardis Reservoir often goes months without releasing. As such, annual water retention time in Grand Lake is much shorter.

Differences in topography between the Kiamichi and Elk rivers contributed to substantial differences in hydrology observed throughout the years for which we calculated metrics. Over our analysis period (1998 - 2015), monthly median discharge from March through June in the Kiamichi River was > 5 m^3/s in over 50% of years. However, in July, August, and September, median discharge was > 5 m^3/s in less than 20% of years, with more than 75% of years having a median discharge < 1 m^3/s from July through September. The Elk River maintained a median discharge > 5 m^3/s in over 75% of years for all spring and summer months except September (> 5 m^3/s, 37% of years). The low flows in the Kiamichi River during summer corresponded to limited rise rates in > 50% of years; three summers on record indicated rise rates were much greater in the Kiamichi River compared to the Elk River during those years. Additionally, 90-day minimum and maximums, and flow reversals of the Kiamichi River were often higher when compared to the Elk River.

Sardis Reservoir was built for water storage and does not have regularly planned releases; however, Grand Lake is a hydropower reservoir that generates electricity via frequent dam releases. As such, summer water levels fluctuated more in Grand Lake, and water was typically released every month of every year, whereas Sardis Reservoir often went months without releasing any water. Annual water retention time in Grand Lake was much shorter. Sardis Reservoir only had a few days a year where pool levels were over conservation pool, whereas Grand Lake remained above conservation pool for most of the year.

Fish collection

We collected 779 Freshwater Drum and 3,467 Gizzard Shad from four river and reservoir sites (Table 7), but not all the sampled fish were included in our analyses. Some fish were omitted due to large age gaps between older individuals. Gizzard Shad from the Kiamichi River were omitted from catch-curve and growth analyses because we were only able to sample fish up to age 4.

Recruitment

Year-classes strengths and ages of Freshwater Drum varied among years and sites, but showed some regional trends (Tables 7 and 8). Longer-lived fishes were more abundant at Grand Lake and the Elk River. The 1995-year class was the oldest included from these sites, whereas the oldest for Sardis Reservoir and the Kiamichi River was 1998. Young fishes were more abundant in samples from the Kiamichi River and Sardis Reservoir, and the youngest year-classes included were 2016 and 2014, respectively. The youngest year classes we included from the Elk River and Grand Lake were 2014 and 2010, respectively. Year-class strength typically varied each year between sites; however, some years appeared to show regional trends. For example, 1999 had a strong year classes at all four sites, and 2006 and 2007 were apparently poor recruitment years for most Freshwater Drum, as three of four sites had weak year classes in these years.

Recruitment of Gizzard Shad was also variable among years and sites, with fishes collected from the Ozark Highland sites reaching older ages than Ouachita Mountain sites (Tables 7 and 8). The 2008-year class was the oldest included for analysis (from Grand Lake population). The 2011-year class in Grand Lake was particularly strong. The 2010-year class was the earliest included for both Sardis Reservoir and the Elk River. However, the Elk River was sampled a year after Sardis and fishes from the 2010-year class were age seven at the time of capture, whereas they were age six in Sardis. No apparent regional trends were noticeable between years.

Freshwater Drum and Gizzard Shad recruitment to boat electrofishing (assessed by observations of age-frequency histograms; Figures 3 and 4) varied among systems. Freshwater Drum were considered recruited to our sampling gear at age one in the Kiamichi River, age two in Sardis Reservoir, and age four in the Elk River, respectively. In Grand Lake, the age-frequency histogram peak occurred at age eight. Because this was atypically late and average lengths-at-ages six and seven were similar to those at age eight, it was possible that age-six and seven fish were recruited to our gear but had weaker year-class strength than age eight; therefore, we compared the recruitment coefficient of determination (r^2) from two age-frequency regressions, one that included individuals from ages 6- 20, and one with ages 8- 20 (Isermann 2002). The recruitment coefficient of determination ranges from zero to one, with numbers approaching one indicative of more stable recruitment (Isermann 2002); constant recruitment over time is an assumption of catch-curve analysis (Maceina 1997). The recruitment coefficient of determination was higher for the regression containing ages six through 20, which indicated recruitment over time was more stable when these fish are included. Therefore, we assumed Freshwater Drum in Grand Lake were recruited to our gear at age six. Gizzard Shad were recruited to our sampling gear at age one in Grand Lake and Sardis Reservoir, and at age two in the Elk River.

Catch-curve analysis assumes that all fishes that are vulnerable to the sampling gear have the same capture probability (Maceina 1997). Although age-0 Gizzard Shad in Sardis Reservoir represented the peak abundance-at-age in our histogram, these fish were still larvae at the time that we began sampling Sardis Reservoir and were not vulnerable to capture for these earlier samples. Thus, we did not include age-zero Gizzard Shad from Sardis Reservoir because they did not meet the assumption of equal capture probability.

Preliminary model diagnostics suggested the top selected models met assumptions of normality and constant variance, even with a few influential points. We determined that these influential points were not the result of data entry error, so they were included in the final models.

In our study rivers, recruitment of Freshwater Drum was negatively related to the number of annual reversals and positively related to prespawn median discharge (Figure 5AB). While holding prespawn median discharge constant, a one unit increase in annual river reversals decreased average year-class strength by 0.63 (Table 9). A one unit increase in prespawn median discharge increased average year-class strength by 0.59, while holding annual river reversals constant (Table 9). The top model included both variables and explained 33% of the variation in Freshwater Drum recruitment in these rivers. Including a fixed river effect did not improve model fit.

Freshwater Drum recruitment in our reservoirs was negatively related to annual retention time (Figure 6AB). Annual retention time explained 48% of Freshwater Drum recruitment variation in these two reservoirs. Adding an interaction term between reservoir and retention time explained an additional 11% of the variation (*adjusted* $r^2 = 0.59$). A one unit increase in retention time decrease the average year-class strength by 1.40 within a given reservoir (Table 10). The interaction coefficient occurred because the effect of water retention time was stronger in Grand Lake than Sardis Reservoir.

Although no effects were detected of hydrology on Gizzard Shad recruitment in reservoirs, model fit did improve with the inclusion of hydrology variables in the recruitment model for Gizzard Shad in the Elk River. Recruitment of Gizzard Shad in the Elk River was positively related to the frequency of high pulses during the prespawn and spawning periods (Figure 7). Gizzard Shad benefitted from more peaks in discharge during these two periods. A one unit increase in high pulses led to a 0.98 increase in average year-class strength (*adjusted* r^2 = 0.48) (Table 11).

Age and Growth

The lengths and ages of Freshwater Drum analyzed for growth varied between rivers, though average growth estimates were relatively similar. We observed a maximum age of 32 years from the Elk River, whereas we only sampled 21-year-old fish from the Kiamichi River. The oldest age included in our analysis was 18 from both rivers. The average age of all Freshwater Drum sampled was 7.2 years in the Elk River and 6.1 years in the Kiamichi River. The average TL of Freshwater Drum was also quite similar between the Elk and Kiamichi rivers (319-mm TL and 307-mm TL respectively). The maximum observed TL of riverine Freshwater Drum was 649 mm (Figure 8). We included 387 Freshwater Drum, consisting of 2,230 incremental measurements in the incremental analysis for river fish.

Freshwater Drum measured for growth increments were typically larger, older fish from Grand Lake and smaller, younger fish from Sardis Reservoir. The oldest age we were able to include in analysis was 21 from Grand Lake and 17 from Sardis Reservoir. The average age of all Freshwater Drum sampled in Grand Lake was 12.3, whereas it was only 5 years in Sardis Reservoir. The maximum observed TL of reservoir Freshwater Drum was 580 mm (Figure 8). Freshwater Drum in Sardis Reservoir did not have a complete annulus for the current year at the time of sampling, and that last increment measurement from all Sardis fish was omitted from analysis. We included 269 Freshwater Drum, consisting of 1,998 incremental measurements, in the incremental analysis for reservoir fish.

Although Gizzard Shad did not live long enough in the Kiamichi River to complete a valid growth analysis, we were able to analyze Gizzard Shad growth from the Elk River. The average age of all Gizzard Shad we sampled in the Elk River was 4 years. The longest Gizzard Shad we sampled (420-mm TL) came from the Elk River (a 7-yr old fish). We included 130 Gizzard Shad, consisting of 496 incremental measurements in our Elk River increment analysis.

Ages and lengths of Gizzard Shad were very different between Grand and Sardis reservoirs. The longest fish we sampled from Grand Lake was 335 mm TL, and the maximum size collected from Sardis Reservoir was 232 mm TL. Similarly, maximum observed age in Grand Lake was eight, compared to six in Sardis Reservoir. We included 216 Gizzard Shad consisted of 697 incremental measurements in the increment analysis for reservoir fish.

Growth of Freshwater Drum in the Kiamichi and Elk rivers was negatively related to median flows at the beginning of summer (May). Inclusion of May median discharge in our model reduced SigAIC by 12.59 (Table 12). The overall explanatory power of this model was high, with a marginal R^2 of 0.87 (Table 12), and the slope coefficient estimate for May median discharge was fairly precise (Table 13). The variance components associated with the random year, fish, and river effects were minimal (Table 14).

Growth of Freshwater Drum in Grand Lake and Sardis Reservoir was negatively related to minimum summer water storage and positively related to total number of days above conservation pool level. The inclusion of these two hydrologic variables reduced SigAIC by 71.39, and marginal R^2 of this model was 0.85 (Table 12). The slope coefficient estimates for these two variables were reasonably precise (Table 13). These two variables partitioned part of the variance associated with random year effect in the null model (Table 14).

Incremental growth of Gizzard Shad in the Elk River was positively related to July median discharge. The top model (including July median discharge) resulted in a decrease in SigAIC by 8.2 compared to the null model (Table 12). The overall explanatory power of this model was high, with a marginal R^2 of 0.84 (Table 12), and the slope coefficient estimate for July median discharge was fairly precise (Table 13). The variance components associated with the random year, fish, and river effects were minimal (Table 14).

Similar to Freshwater Drum, growth of Gizzard Shad in Sardis Lake and Grand Reservoir was also positively related to number of days above conservation pool, and this was the top model. This model had a marginal R^2 of 0.84 and reduced SigAIC by 11.28 relative to the null model (Table 12). The slope coefficient estimate for the model was precise (Table 13).

Discussion

Recruitment of riverine fishes is typically associated with flow; however, we also found moving water to be important for reservoir fish recruitment. In rivers, flow is considered the master variable, driving the dynamic nature of these systems and influencing fish community structure (Power et al. 1995; Richter et al. 1996; Poff et al. 1997). In reservoirs, water-level fluctuations are often used to summarize variation in hydrology that shapes habitat and fish community structure (Gelwick and Mathews 1990; Fischer and Ohl 2005). However, the importance of moving water in relation to completion of the life history of reservoir fishes has received considerably less attention, despite the strong association between reservoir flow and water-level fluctuations (Hill and Cichra 2002). We found recruitment of select broadcast spawning fishes that occupy both river and reservoir environments was related to hydrology, even though the direction of these relationships differed in each system. The observed relationship was a novel finding for reservoir fishes, likely because recruitment research in reservoirs does not typically focus on the broadcast-spawning guild.

We found higher annual reservoir levels increased growth of Freshwater Drum, whereas regular reservoir releases increased recruitment. Unlike many reservoir fishes, Freshwater Drum is a broadcast spawner, meaning their eggs and larvae are dependent on directional flow and currents (Balon 1975). Reservoir retention time is a measure of how long water remains in a reservoir (i.e., duration), where shorter retention times resemble more lotic conditions (Rypel et al. 2006). The riverine origin of most reservoir species (Fernando and Holcik 1991) suggests moving water would be important to their life cycles; however, long reservoir retention time has been correlated with recruitment of more commonly-studied sportfishes (e.g., Largemouth Bass *Micropterus salmoides*, Wrenn et al. 1996; Maceina and Bettoli 1998; crappie spp. *Pomoxis*, Maceina and Stimpert 1998). Previous studies primarily focused on phytophil and polyphil reproductive guilds. Polyphils and phytophils both guard shallow nests, where the eggs and larvae rely on the terrestrial-aquatic ecotone to develop properly (Balon 1975; Duncan and Kubecka 1995). Alternatively, Freshwater Drum provides no parental care, and the buoyancy of eggs and larvae makes them dependent on water current (Balon 1975). Dispersal reduces the risk of cannibalism and competition for space (Lechner et al. 2016), but the eggs and larvae are vulnerable to some flow patterns (i.e., strong fluctuations). Interestingly, higher annual water levels in reservoirs were beneficial to growth of both Freshwater Drum and Gizzard Shad. High water levels and inflows increase nutrient loading and production of phytoplankton and zooplankton (Kimmel and Groeger 1984). Increased primary productivity is positively associated with Gizzard Shad growth (Michaletz 1998), which is also positively associated with growth of many reservoir piscivores (Michaletz 1997). As such, bottom-up effects increase food available for Freshwater Drum thereby benefiting growth (Mehner et al. 1988; Watkins et al. 2017). Our findings suggest that Freshwater Drum populations in reservoirs benefit via growth and recruitment in wet years when inflows keep reservoir levels high while water releases are persistent to downstream areas.

Freshwater Drum growth in reservoirs was also negatively related to higher minimum summer water levels, suggesting that conditions were more favorable for Freshwater Drum growth in years where summer water levels were lower. This may relate to the concentration of prey that is commonly associated with low water levels. Low summer water levels likely coincided with dry, hot summers. High water temperatures cause reservoirs to stratify, significantly reducing the volume of water available to fishes (Soares et al. 2008). Klobucar and Budy (2015) found that prey densities were most concentrated when summer water levels were lowest and stratified, and determined that this scenario led to the highest growth potential of predatory fish species in simulated models. Additionally, low water levels reduce the amount of littoral habitat (e.g., coarse woody debris, Gaeta et al. 2014) thereby reducing the amount of refuge habitat available to forage species, making them more susceptible to predator encounters.

The negative relationship we observed between annual reversals and riverine Freshwater Drum recruitment may be associated with food reductions or the lack of rearing habitat. River reversals indicate how frequent water conditions change. During high flows, there may be sufficient habitat to reduce competition and predation risk (Resh et al. 1988). However, as flows decrease, habitat available is reduced, thereby increasing fish densities in some habitats.

Concentrating fish in select habitats may increase both competition and predation risk (Smith et al. 2005). Walker et al. (1994) observed that accelerated reversing cycles of wetting and drying devastated sessile benthic fauna (e.g., freshwater mussels) and freshwater mussels constitute a large portion of the Freshwater Drum's diet (Lyons et al. 2007). Extreme reversal events after a peak restructures pool habitats (Resh et al. 1988) that juvenile Freshwater Drum occupy during the rearing periods (Holland 1986; Sheaffer and Nickum 1986). The frequency of river reversals downstream of dams often increases when compared to historic flow patterns (Sakaris 2013), and flow reversals are considered the most damaging to pool habitat (Resh et al. 1988).

The positive relationship we observed between Gizzard Shad growth and July median discharge in rivers may relate to changes to habitat quality and quantity. High pulses and increased discharge increase the connectivity to backwater pools (Resh et al. 1988; Junk et al. 1989) that provide flow refuges to fishes. Sheaffer and Nickum (1986) found that the relative abundance of juvenile Gizzard Shad was positively correlated with backwater areas. Future studies might benefit from investigating the possible benefit of backwater habitat to summer growth.

The importance of median flows for Freshwater Drum recruitment during the prespawn period may relate to spawning cues, or the maintenance of rearing habitat. High flows often serve as environmental cues to initiate spawning (Poff et al. 1997; Mesa and Magie 2006). As such, years when prespawn discharge was high could have triggered Freshwater Drum to spawn early, increasing first-year growth potential and overwinter survival probabilities (Hansen et al. 1998). High prespawn flows could also have created and maintained the important pool habitat used by juveniles during the nursery period, as higher flows scour pool habitats thereby preventing them from filling with sediment (Resh et al. 1988).

The negative relationship we observed between Freshwater Drum growth and riverine May discharge may be related to fish bioenergetics. First, as discharge increases, the amount of energy required for fish to maintain position in the water column also increases (Stoll et al. 2008). Second, higher May discharge could negatively affect prey availability for Freshwater Drum. Many freshwater mussels move deep into the hyporheic zone of the substratum during high flows, effectively becoming unavailable as food items (Rypel et al. 2006). If freshwater mussels are unavailable, Freshwater Drum would feed primarily on other invertebrates or fishes. However, higher flows relate to an increase in suspended sediment loads (Flotemersch et al. 2006), and it would be more difficult for Freshwater Drum to locate and capture prey because they are site feeders. Difficulty of locating food and the increased effort required to obtain adequate energy under these conditions would affect growth. Site feeding by larval and juvenile fishes is more effective during low-flow conditions (Rutherford 1995). Additionally, May encompasses the primary spawning season for many warm-water freshwater fishes (Pflieger 1997). If high May flows cue Freshwater Drum to initiate spawning activity, they may be investing more energy into gonadosomatic growth. Lastly, discharge and water temperature are often inversely related (Webb et al. 2003), and increased discharge can influence water temperature more than air temperature (van Vliet et al. 2011). Higher May discharges likely decreased water temperatures, thereby reducing overall growth potential. Increased Freshwater Drum survival has been related to growing degree days, which was attributed to increased growth (Uphoff et al. 2013).

We found no associations between recruitment of the reservoir Gizzard Shad populations and hydrology; however, we did find relationships with the riverine populations, although our statistical power was relatively low given there were only six year classes. The lack of any relationships between reservoir Gizzard Shad recruitment and hydrology could be attributed to the 2011-year class in Grand Lake being exceptionally strong. The 2011-year class strongly influenced the slope of the regression. This year class represented 18% of all Gizzard Shad sampled in Grand Lake. To put this into perspective, the total of all Gizzard Shad ages five through eight in the Elk River represented 12% and ages five through six in Sardis Lake represented less one percent of the total fish sampled. However, we found Gizzard Shad recruitment in the Elk River was positively related to the number of peak-flow events during both the prespawn and spawning periods. High-flow pulses typically increase connectivity to backwater pools (Junk et al. 1989) that are important nursery habitat for Gizzard Shad (Sheaffer and Nickum 1986).

Conservation and management efforts for lentic and lotic species require an understanding of the many different life-history aspects. Our results indicated that year classes of long-lived broadcast spawners are detectable in high relative abundance for nearly 20 years. Most reservoir-recruitment studies have focused on fishes that generally live less than 10 years (Hansen et al. 1998; Maceina and Betolli 1998; Bonvechio and Allen 2005; Smith et al. 2005; Maceina and Stimpert 1998). We focused our efforts on both a species of similar age (< 10 years), and a longer-lived conger. A persistent conflict of interest between reservoir and river fisheries management relates to water availability and use; however, sustainability of longer-lived species may be possible via water allocation that optimizes recruitment every few years. This proactive management strategy could secure the economic benefits that reservoir species provide, while managing for ecosystem health in downstream aquatic environments. Future studies should quantify the effects of altered hydrology on other non-game fishes occupying both rivers and reservoirs, to examine mutually beneficial strategies for theses ecosystems. Further, relating a population model to flow scenarios would benefit application of these relationships to flow practices and help explain the mechanisms between recruitment and hydrology.

Fisheries scientists would benefit from holistic approaches that focus on system connections and functions. Reservoirs, for example, could be managed with consideration of the downstream environment. Maximizing the number of days that reservoir levels remain above conservation pool is suggested to benefit reservoir fisheries (Sammons and Bettoli 2000), and our results suggested similar trends. However, management practices in one system affect our ability to employ some management actions in another system (Sakaris 2013). Our results suggest that riverine fish production would be negatively affected by maximizing the number of days above conservation pool in the upstream reservoir. Testing these relationships through experimental releases would be beneficial. Little is known about the effects of hydrology on the growth of non-game species (Beckman and Hutson 2012), and even less about how hydrology influences them in regulated systems (Sakaris 2013). We identified important ecological relationships among growth, recruitment and hydrology that management agencies could integrate into holistic water-allocation planning.

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Table 1 Description of the hydrological variables that were calculated using Indicators of Hydrological Alterations (IHA) software. The ecological importance of each hydrologic variable was used to determine choice of hydrologic metrics calculated.

Variable	Description	Ecological Importance
30-Day Minimum	The minimum discharge that persisted for at least 30 days	Stressful conditions such as temperature and low habitat availability
30-Day Maximum	The maximum discharge that persisted for at least 30 days	Aeration of eggs and distribution of larvae; Structuring of physical habitat conditions
90-Day Minimum	The minimum discharge that persisted for at least 90 days	Anaerobic stress on submerged aquatic vegetation; Nutrient transport and recycling
90-Day Maximum	The maximum discharge that persisted for at least 90 days	Structuring of channel morphology and habitat connectivity
High-Flow Pulses	Frequency of high-flow pulses	Influences bedload transport; Channel sediments; Frequency of substrate disturbances
Rise rate	Median of all positive differences between consecutive daily flows	Possible entrapment on islands or floodplain
Fall Rate	Median of all negative differences between consecutive daily flows	Inundated resource accessibility
Reversals	The number of days that flow switches between a rising and falling period	Indication of discharge variability

Table 2 Description of riverine hydrologic predictor variables calculated using Microsoft Excel. The ecological importance of each hydrologic variable was used to determine choice of hydrologic metrics calculated.

Variable	Description	Ecological Importance
Prespawn Median	Median discharge during the prespawn period	Competition for resources among adults; connectivity and ability to find mate
Prespawn Variability	Coefficient of variation in discharge during prespawn period	Whether prespawning resources were consistently available or if location/amount of resources varied
Spawn Median	Median discharge during the spawn period	Can wash eggs away from nursery habitat if too strong; can limit oxygen to eggs if too weak
Spawn Variability	Coefficient of variation in discharge during the spawn period	Susceptibility of eggs and larvae to directional currents; can strand eggs on islands
Nursery Median	Median discharge during the nursery period	Determines available nursery habitat and if enough water is available to elude predators
Nursery Variability	Coefficient of variation in discharge during the nursery period	Possible entrapment and increased stress due to nursery resource locations constantly changing
Overwinter Median	Median discharge water during the overwinter period	Access to temperature refugees that still provides adequate protection for predation

Table 3 Description of reservoir water-level variables calculated using Microsoft Excel. The ecological importance of each variable was used to determine choice of metrics calculated.

Variable	Description	Ecological Importance
Prespawn Average	Mean water level during the prespawn period	Volume of resources available to adults preparing to spawn
Prespawn Variability	Coefficient of variation in water levels during prespawn period	Whether prespawning resources were consistently available or if location/amount of resources varied
Spawn Average	Mean water level during the spawn period	Volume of available spawning habitat, access to submerged substratum for adhesive eggs
Spawn Variability	Coefficient of variation in water levels during the spawn period	Susceptibility of eggs and larvae to directional currents; adhesive eggs vulnerable to exposure
Nursery Average	Mean water levels during the nursery period	Amount of available nursery habitat for larvae and juveniles
Nursery Variability	Coefficient of variation in water levels during the nursery period	Possible entrapment and increased stress due to nursery resource locations constantly changing
Overwinter Average	Mean water levels during the overwinter period	Access to temperature refugees that still provides adequate protection for predation
Over Conservation Pool Level	Number of days/year water levels were above conservation pool	How long species have access to high water levels; how long species subject to limited resources
Annual Retention Time	Mean annual surface area divided by total annual reservoir releases	Retention time is often associated with primary productivity
Annual Variability	Coefficient of variation in annual water levels	Considers annual inflow, releases, rainfall events, drought in one parameter

Table 4 The hydrologic variables we calculated for river and reservoir systems based on their ecological importance to both Freshwater Drum *Aplodinotus grunniens* (Drum) and Gizzard Shad *Dorosoma cepedianum* (Shad). Our hypothesized relationships between each species (Drum is listed first) and the hydrologic metric calculated are indicated as "+" as a positive relationship, and "-" as a negative relationship.

Hydrology Metric (system)	Ecological Importance: Drum	Ecological Importance: Shad	Hypothesized Relationship
90-Day Minimum (river)	Reduces pool connectivity; Suspended sediments fall, may reduce benthic prey	May increase energy spent avoiding predators; May experience oxygen stress	- , -
90-Day Maximum (river)	Ensures pool-riffle sequence and habitat connectivity between pools	Increases volume of nutrient exchange, may increase primary production and prey items	+ , +
High-Flow Pulses (river)	Maintains pool habitats; Disturbs substrate, may increase buried prey	Increases suspended sediment, may reduce filter feeding efficiency	+ , -
Rise Rate (river)	May flush invertebrates into water column, could increase prey abundance	May disturb substrate and increase suspended sediments	+ , -
Fall Rate (river)	Redistributes benthic invertebrates; Fills in pool habitat	Could trap them in isolated pools for extended periods of time	- , -
Reversals (river)	Reduces pool habitat, could reduce sessile benthic organism abundance	Increases suspended sediments and could reduce filtering efficiency	- , -
Maximum Water Storage (reservoir)	Prey is less dense, may reduce feeding efficiency	Nutrient fluxes from inflows; More area to occupy, less energy spent avoiding predators	- , +
Minimum Water Storage (reservoir)	Concentrates prey, may increase feeding efficiency	May increase energy to avoid predators	+ , -
Variability in Water Storage (reservoir)	Increases suspended sediments; sediments fall, may reduce benthic prey	Increases suspended sediment, may reduce filter feeding efficiency	- , -
Days Over Conservation Pool Level (reservoir)	Similar to maximum storage in that prey has more places to hide	Increased terrestrial inundation and nutrient cycling which may increase food	- , +
Retention Time (reservoir)	Influences thermal stratification, may reduce benthic-feeding efficiency	Associated with increases in primary productivity which may increase food	- , +

Table 5 Description of the resolution and calculation of each riverine flow metric. Flow metrics were calculated using Indicators of Hydrological Alterations and Microsoft Excel software. Each flow metric was chosen based on Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum* habitat use and diet composition.

Flow Metric (software used)	Resolution	Calculation
90-Day Minimum (IHA)	Annual	The median of the minimum discharges that persisted for at least 90 consecutive days in one year (January – December)
	Summer	The median of the minimum discharges that persisted for at least 90 consecutive days from June through September
90-Day Maximum (IHA)	Annual	The median of the maximum discharges that persisted for at least 90 consecutive days in one year (January – December)
	Summer	The median of the maximum discharges that persisted for at least 90 consecutive days from June through September
High-Flow Pulses (IHA)	Annual	The frequency of high-flow pulses in one year that exceed the 75th percentile of the entire hydrological record that was entered (January – December)
Rise rate (IHA)	Annual	The median of all positive differences between consecutive daily flows in one year (January – December)
	Summer	The median of all positive differences between consecutive daily flows from June through September
Fall Rate (IHA)	Annual	The median of all negative differences between consecutive daily flows in one year (January – December)
	Summer	The median of all negative differences between consecutive daily flows from June through September
Reversals (IHA)	Annual	The hydrological record for each year is divided into “rising” or “falling” periods, i.e., periods that daily changes in flow are positive or negative. A reversal is when flows change from one type of period to the other (January – December)
	Summer	The calculation is the same as above; from June through September
Median Discharge (Excel)	Monthly	The median daily discharge of each month, March through September

Table 6 Description of the resolution and calculation of each reservoir water-level metric hypothesized to relate to growth of Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum*. Metrics were calculated using Microsoft Excel software.

Variable	Resolution	Description and Calculation
Average Storage	Annual	The mean water storage in one year (January – December)
	Spring	The mean water storage from March through May
	Monthly	The mean water storage of each month, June through September
Maximum Storage	Summer	The highest that water storage reached from June through August
Minimum Storage	Summer	The lowest that water storage got from June through August
	Spring	The lowest that water storage got from March through May
Variability in Water Storage	Annual	The standard deviation of water storage divided by mean water storage (January – December)
Over Conservation Pool Level	Annual	The number of days where water levels were above conservation pool in a year (January – December)
Retention Time	Annual	The mean water storage divided by total reservoir releases (January – December)

Table 7 The number (N) of Gizzard Shad *Dorosoma cepedianum* and Freshwater Drum *Aplodinotus grunniens* sampled using boat electrofishing from two rivers and two reservoirs of the Ozark Highlands, Oklahoma and Missouri. Fishes were sampled to determine the relationship between water patterns of both rivers and reservoirs and fish recruitment and growth. The total length (TL) and ages varied across the two rivers and reservoirs that we sampled. All collected individuals were reported; however, we did not include all individuals sampled in the analyses. Some fish were omitted due to large age gaps between older individuals. Gizzard Shad sampled from the Kiamichi River was omitted from the catch-curve and growth increment analysis because they only lived to age four, and only one 4-yr old was sampled.

Species	Site	N	TL range (mm)	Ages (yr)
Gizzard Shad	Kiamichi River	369	87 - 338	0 - 4
	Elk River	563	129 - 420	1 - 7
	Sardis Reservoir	1,608	49 - 240	0 - 6
	Grand Lake	927	84 - 335	0 - 8
Freshwater Drum	Kiamichi River	142	120 - 600	0 - 20
	Elk River	319	156 - 649	1 - 32
	Sardis Reservoir	176	113 - 543	0 - 20
	Grand Lake	142	212 - 580	1 - 31

Table 8 The year-class strength (studentized residuals from catch curves) of Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum* from two rivers and two reservoirs in Oklahoma and Missouri. Negative values indicate weak year classes and positive values indicate strong year classes.

	Freshwater Drum				Gizzard Shad			
	Kiamichi River	Sardis Reservoir	Elk River	Grand Lake	Sardis Reservoir	Elk River	Grand Lake	
1995			0.86	0.52				1995
1996			0.43	-0.71				1996
1997			0.32	-0.37				1997
1998	0.37	0.69	0.39	-0.16				1998
1999	0.79	0.90	0.49	1.72				1999
2000	1.26	0.77	-0.29	-0.10				2000
2001	0.10	0.56	0.30	-0.20				2001
2002	-1.35	0.46	-1.12	-0.08				2002
2003	0.18	-0.61	-0.38	-0.19				2003
2004	0.05	-1.08	1.15	0.59				2004
2005	-0.47	1.19	0.57	0.61				2005
2006	0.70	-1.00	-5.10	-5.25				2006
2007	-0.84	-0.29	-0.11	0.17				2007
2008	1.16	0.48	0.44	1.20			-0.96	2008
2009	-1.27	1.27	-0.26	-0.21			-0.29	2009
2010	0.59	-1.62	1.38	0.51	0.32	-0.38	-0.66	2010
2011	-1.25	-1.19	0.97		-0.61	0.45	3.51	2011
2012	-1.09	-1.40	-0.82		1.27	-0.53	-0.05	2012
2013	-1.01	1.25	-0.02		-1.80	1.70	0.30	2013
2014	1.08	1.53			1.29	-2.09	-1.44	2014
2015	-0.74				-0.56	0.67	0.47	2015
2016	2.77							2016

Table 9 Top model estimators for Freshwater Drum *Aplodinotus grunniens* recruitment in rivers, including the associated coefficient estimates, standard errors (SE), and t-value.

Coefficient	Estimate	SE	t-value
Intercept	0.006	0.164	0.038
Prespawn Median Discharge	0.594	0.172	3.453
Annual Reversals	-0.625	0.172	-3.630

Table 10 Top model estimators for Freshwater Drum *Aplodinotus grunniens* recruitment in reservoirs, including the associated coefficient estimates, standard errors (SE), and t-values (the intercept was fixed at zero for easier interpretation).

Coefficient	Estimate	SE	t-value
Grand Lake	-0.122	0.203	-0.599
Retention Time	-1.395	0.210	-6.650
Sardis Lake * Retention Time	0.926	0.292	3.172
Sardis Reservoir	0.112	0.197	0.571

Table 11 Top model estimators for Gizzard Shad *Dorosoma cepedianum* recruitment in the Elk River, including the associated coefficient estimates, standard errors (SE), and t-values.

Coefficient	Estimate	SE	t-value
Intercept	-0.030	0.379	-0.079
High-Pulse Frequency	0.986	0.415	2.375

Table 12 Top predictor model for fish growth (selected by SigAIC), where Y is the growth increment *i* for fish *j*, of growth year *k*, in river or reservoir *l* for each model. β_0 is the grand intercept, X_1 is the age that the increment was measured. Z_j is the random fish intercept, Z_k is the random year intercept, Z_l is the random river or reservoir intercept for each model. The fixed predictor variables for each model are as follows: Freshwater Drum *Aplodinotus grunniens* reservoir model (X_2 is minimum reservoir storage in summer, X_3 is annual number of days above conservation pool level); Freshwater Drum river model (X_2 is May median discharge); Gizzard Shad *Dorosoma cepedianum* Elk River model (X_3 is July median discharge); Gizzard Shad reservoir model (X_2 is annual number of days above conservation pool level). The number of model parameters is indicated by *K*. The information criterion score for each model is represented by SigAIC, and ΔSigAIC is the difference in SigAIC between the top model and the null model. Marginal R^2 (Mar.) is the coefficient of determination for only the fixed effects in each model. Conditional R^2 is the coefficient of determination for the whole model (i.e., both fixed and random effects).

Top Model	*K*	SigAIC	ΔSigAIC	Mar. R^2	Con. R^2
Freshwater Drum – Rivers					
$Y_{ijkl} = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + Z_j + Z_k + Z_l$	6	-1560.1	-12.59	0.868	0.898
Freshwater Drum – Reservoirs					
$Y_{ijkl} = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + \beta_3 X_{i3} + Z_j + Z_k + Z_l$	7	-998.6	-71.39	0.846	0.891
Gizzard Shad – Rivers					
$Y_{ijkl} = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + Z_j + Z_k$	5	-199.3	-8.2	0.841	0.855
Gizzard Shad - Reservoirs					
$Y_{ijkl} = \beta_0 + \beta_1 X_{i1} + \beta_2 X_{i2} + Z_j + Z_k + Z_l$	5	-237.0	-11.28	0.839	0.855

Table 13 Coefficient estimates and standard errors for the fixed hydrologic predictor variables from the top models describing the effects of hydrology on incremental growth of Freshwater Drum *Aplodinotus grunniens* (Drum) and Gizzard Shad *Dorosoma cepedianum* (Shad). Each model included a fixed age effect and three random effects representing individual fish, year, and system (i.e., river or reservoir).

Coefficient	Estimate	SE	Sp. - System
May Median Discharge	-0.0283	0.0068	Drum - Rivers
Days Above Conservation Pool	0.0538	0.0103	Drum - Reservoirs
Minimum Summer Storage	-0.0544	0.0054	
July Median Discharge	0.0605	0.0119	Shad - River
Days Above Conservation Pool	0.0469	0.0086	Shad - Reservoirs

Table 14 Standard deviation (Std. Dev.) of the random effects (year, fish, system) from the four null models that did not include hydrology variables and the top predictor models that included fixed hydrology variables.

	Null Model	Top Model	
Random Effects	Std. Dev.	Std. Dev.	Sp. - System
Year	0.0471	0.0401	Drum - Rivers
Fish	0.0599	0.0606	
River	0.0362	0.045	
Residual	0.1592	0.1587	
Year	0.0837	0.0706	Drum - Reservoirs
Fish	0.0879	0.0845	
Reservoir	0.0000	0.0121	
Residual	0.1744	0.1715	
Year	0.0658	0.0147	Shad - Rivers
Fish	0.0517	0.0514	
Residual	0.1692	0.1692	
Year	0.0975	0.1134	Shad - Reservoirs
Fish	0.0875	0.0854	
Reservoir	0.0747	0.0000	
Residual	0.1501	0.1496	

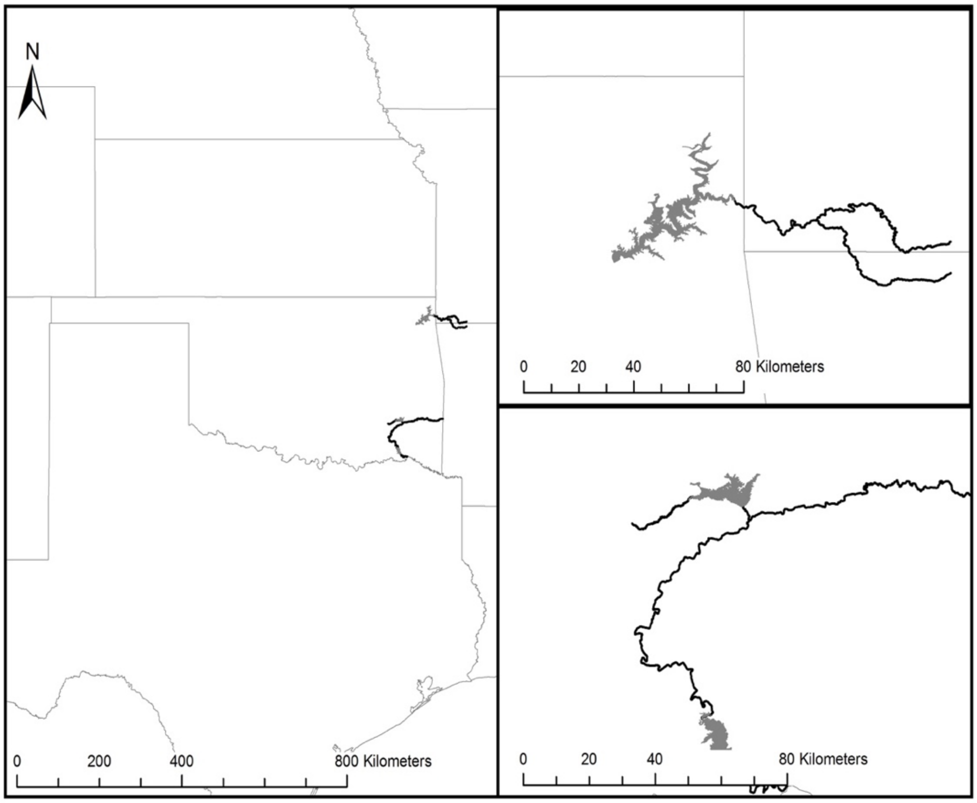

Figure 1 The Elk River and Grand Lake (top right) of the Ozark Highlands ecoregion. The bottom right shows Jack Fork Creek (flowing south from the northern-most reservoir, Sardis) of the Ouachita Mountain ecoregion, and the Kiamichi River that continues to flow southward, terminating in Lake Hugo, Oklahoma.

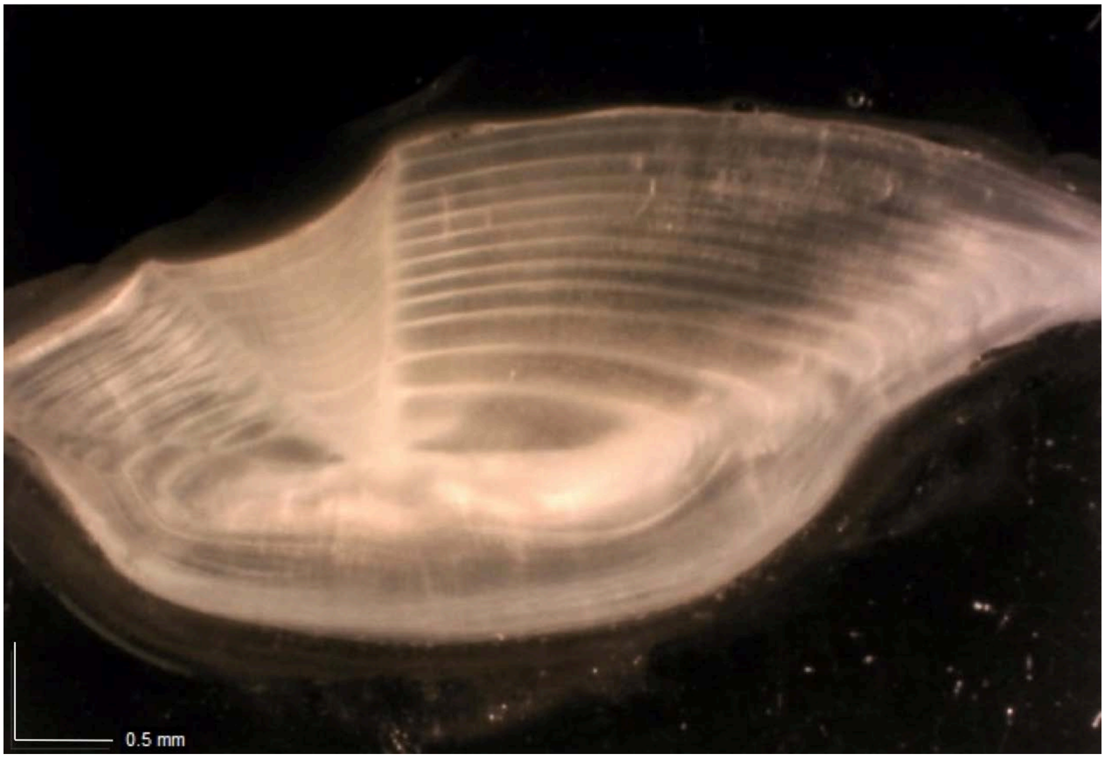

Figure 2 Sectioned otolith from an 11-yr old Freshwater Drum *Aplodinotus grunniens*. The otolith was sectioned to 0.5-mm thick. Transverse sections were cut across the dorso-ventral plane using a low-speed IsoMet® saw. The section was viewed under a microscope (30X/22), and the image was captured using DinoCapture® software (Torrence CA, Dunwell Tech, Inc.).

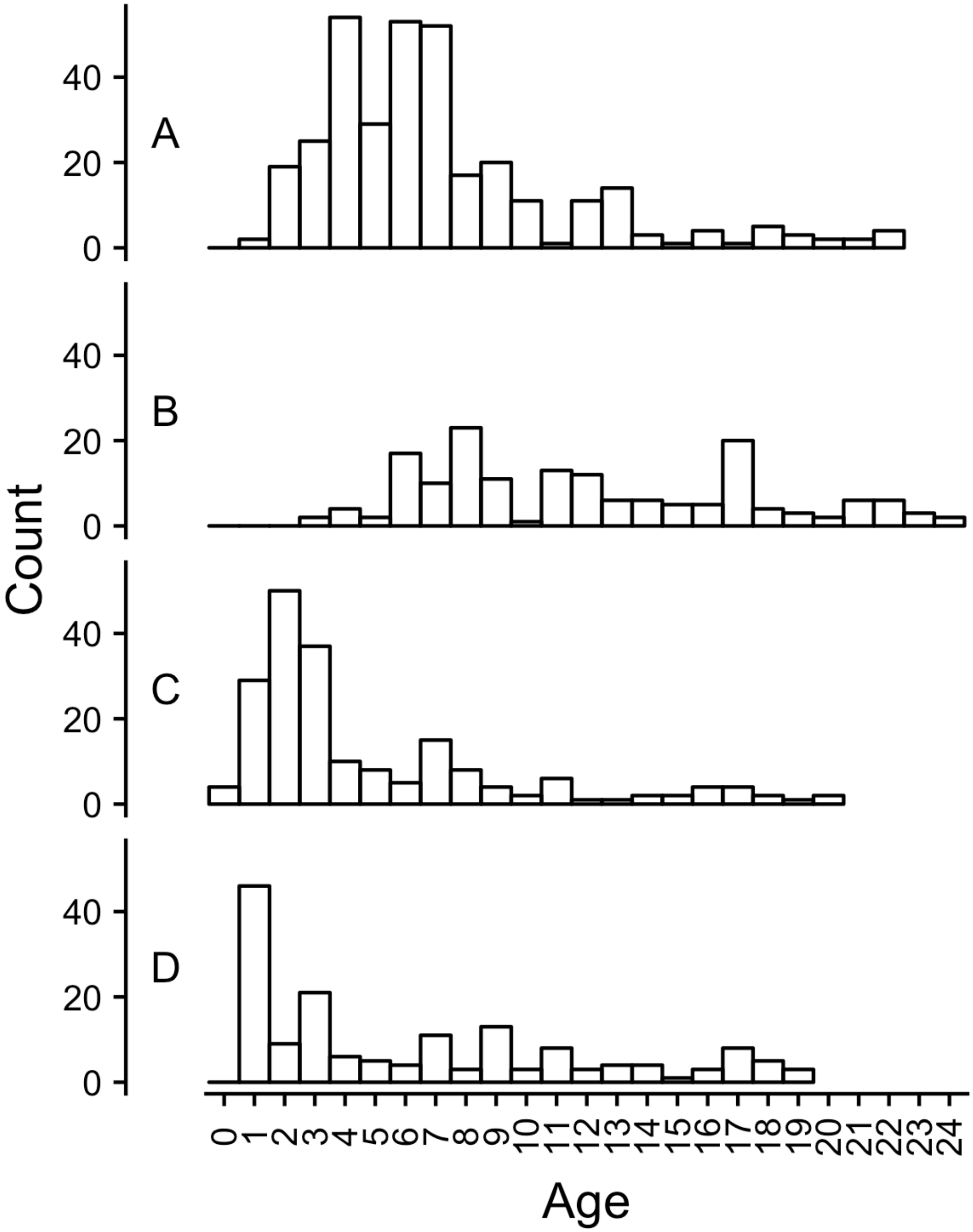

Figure 3 Age-frequency of Freshwater Drum *Aplodinotus grunniens* collected from A: Elk River, B: Grand Lake, C: Sardis Reservoir, and D: Kiamichi River. Older fish that were sampled, but not included in the analysis, are not shown (described in methods).

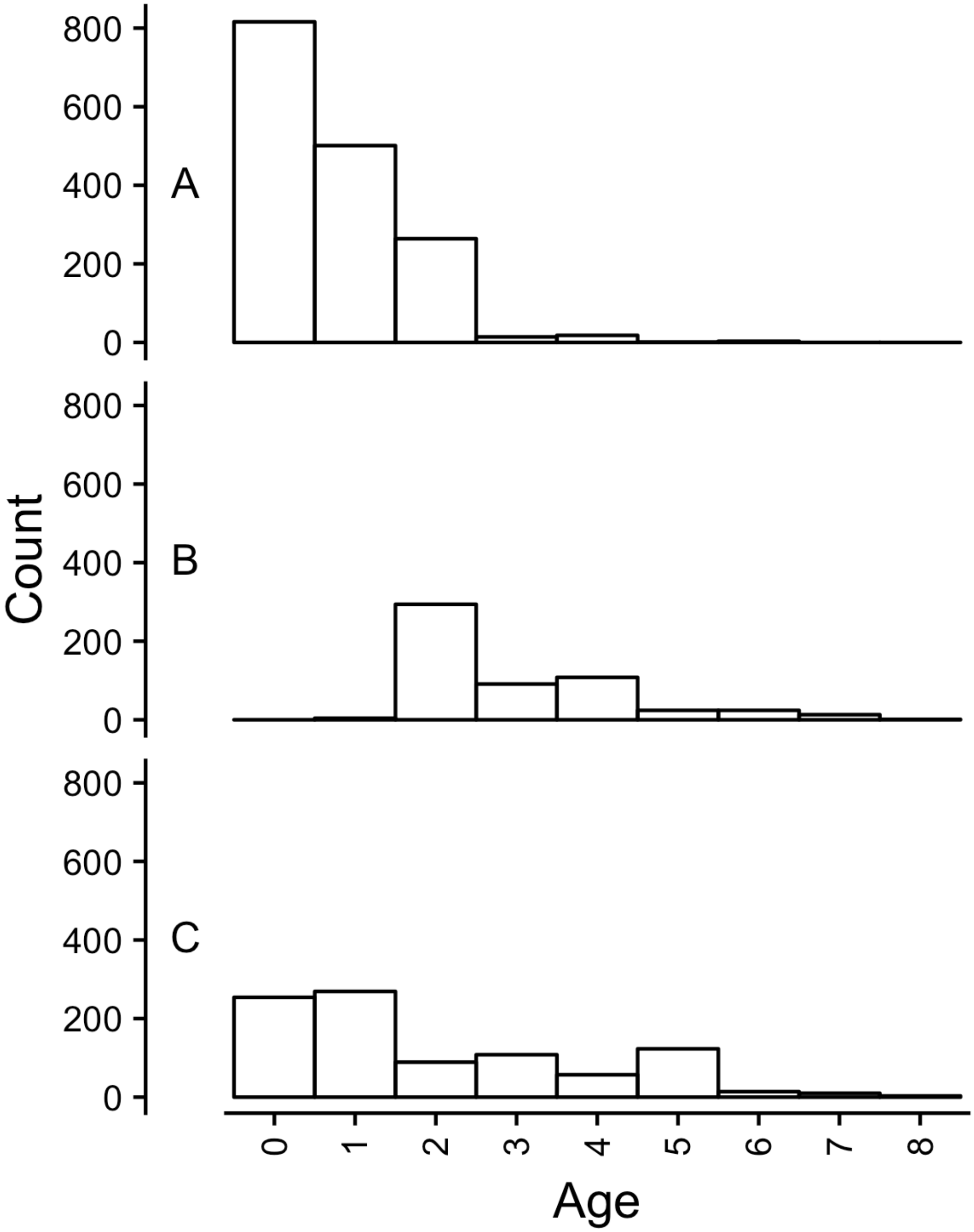

Figure 4 Age-frequency of Gizzard Shad *Dorosoma cepedianum* sampled from: A: Sardis Reservoir, B: Elk River, and C: Grand Lake.

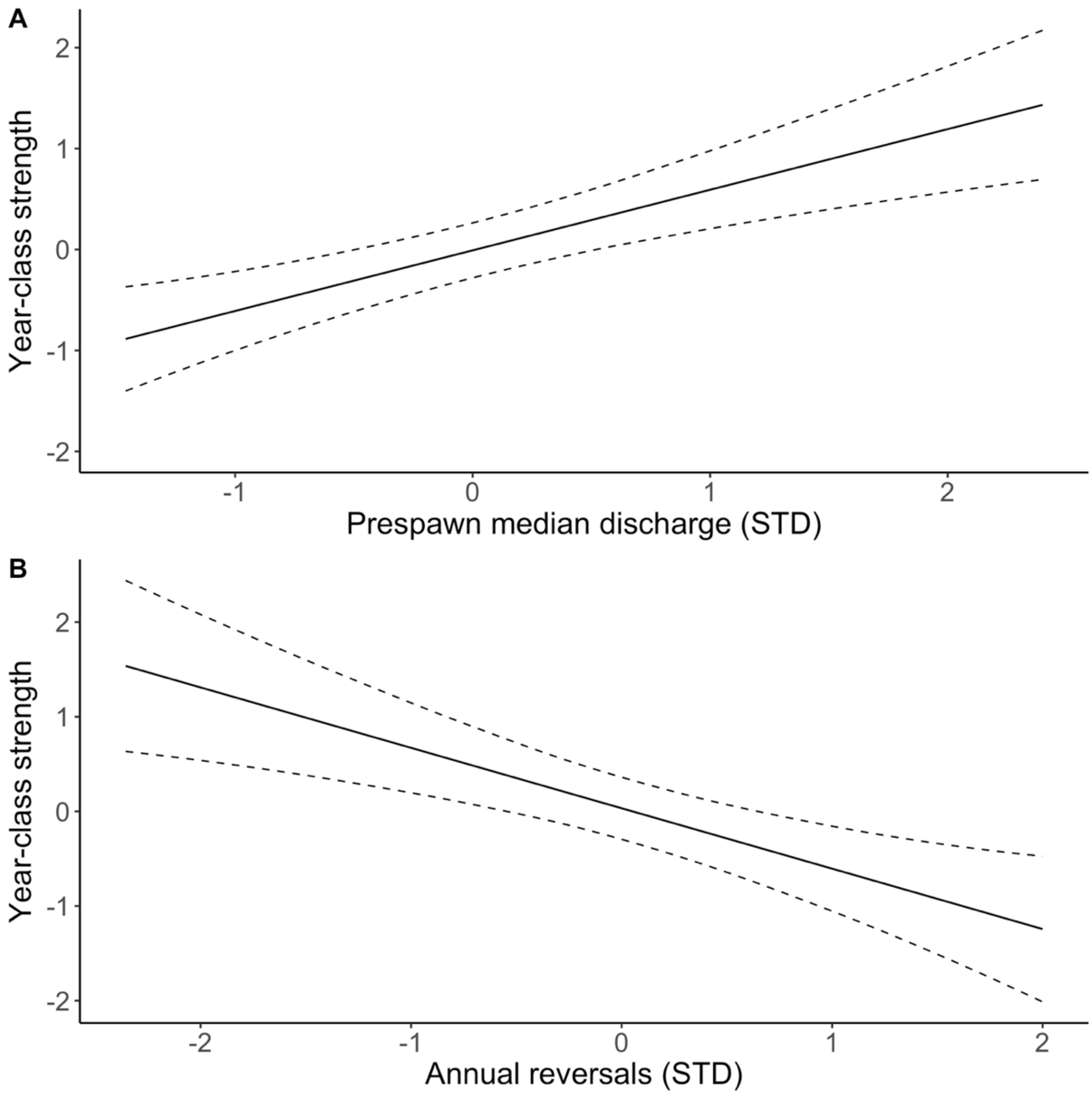

Figure 5 Relationship of the two hydrology variables selected in the top regression model for Freshwater Drum *Aplodinotus grunniens* recruitment in the Kiamichi and Elk rivers: A) prespawn median discharge (m^3/s) (shown while holding annual reversals constant at the mean), and B) the number of annual reversals (shown while holding prespawn median discharge constant at the mean). Data were standardized for each system and dashed lines indicate 95% confidence intervals.

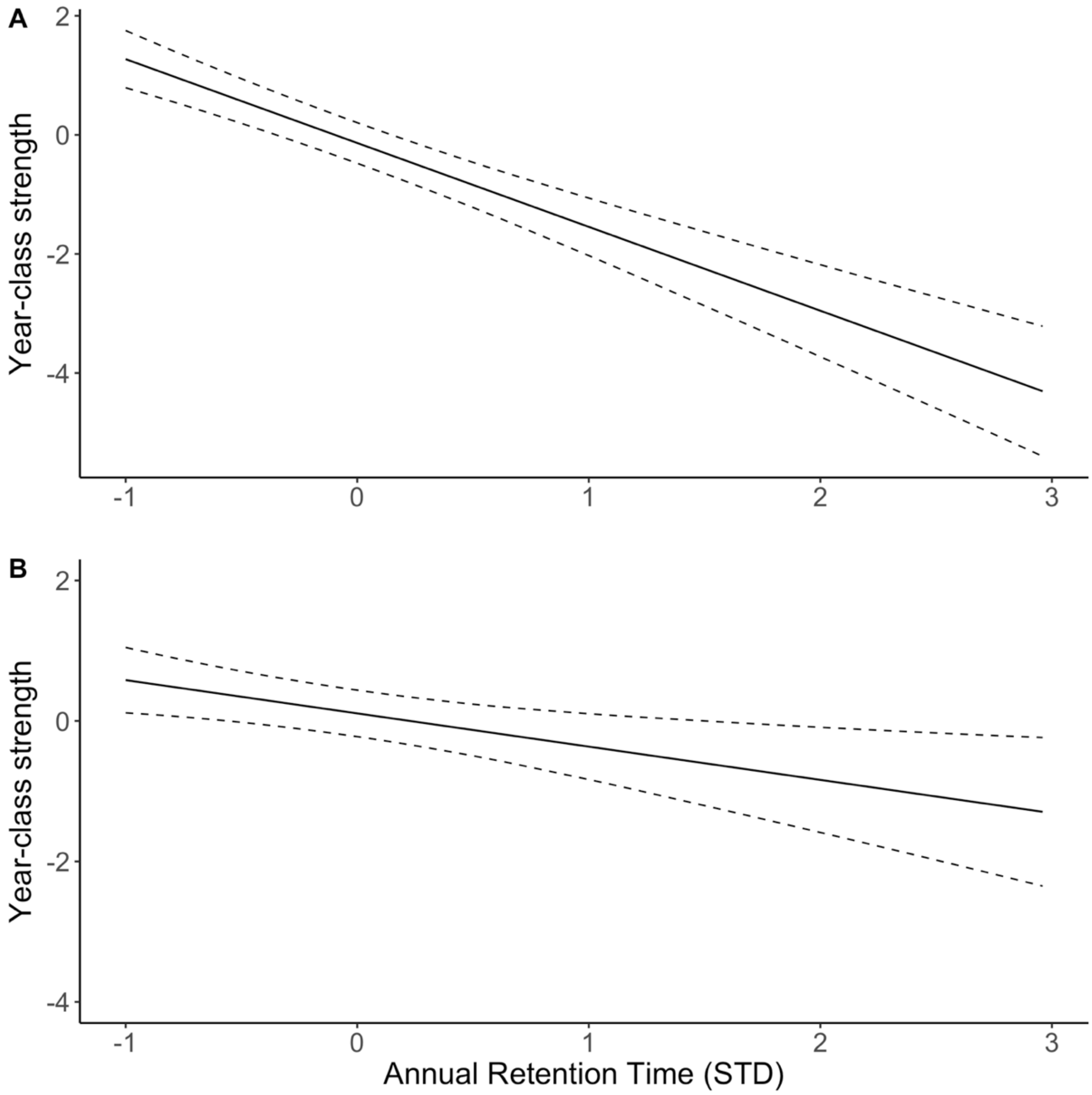

Figure 6 Relationship between annual retention time and Freshwater Drum *Aplodinotus grunniens* year-class strength in A) Grand Lake O' the Cherokee (while holding Sardis constant); and B) Sardis Reservoir (relationship shown while holding Grand constant). Individual slopes were fit for each site because of the reservoir interaction term included in the top model. Annual retention time was standardized by each system and dashed lines indicate 95% confidence intervals.

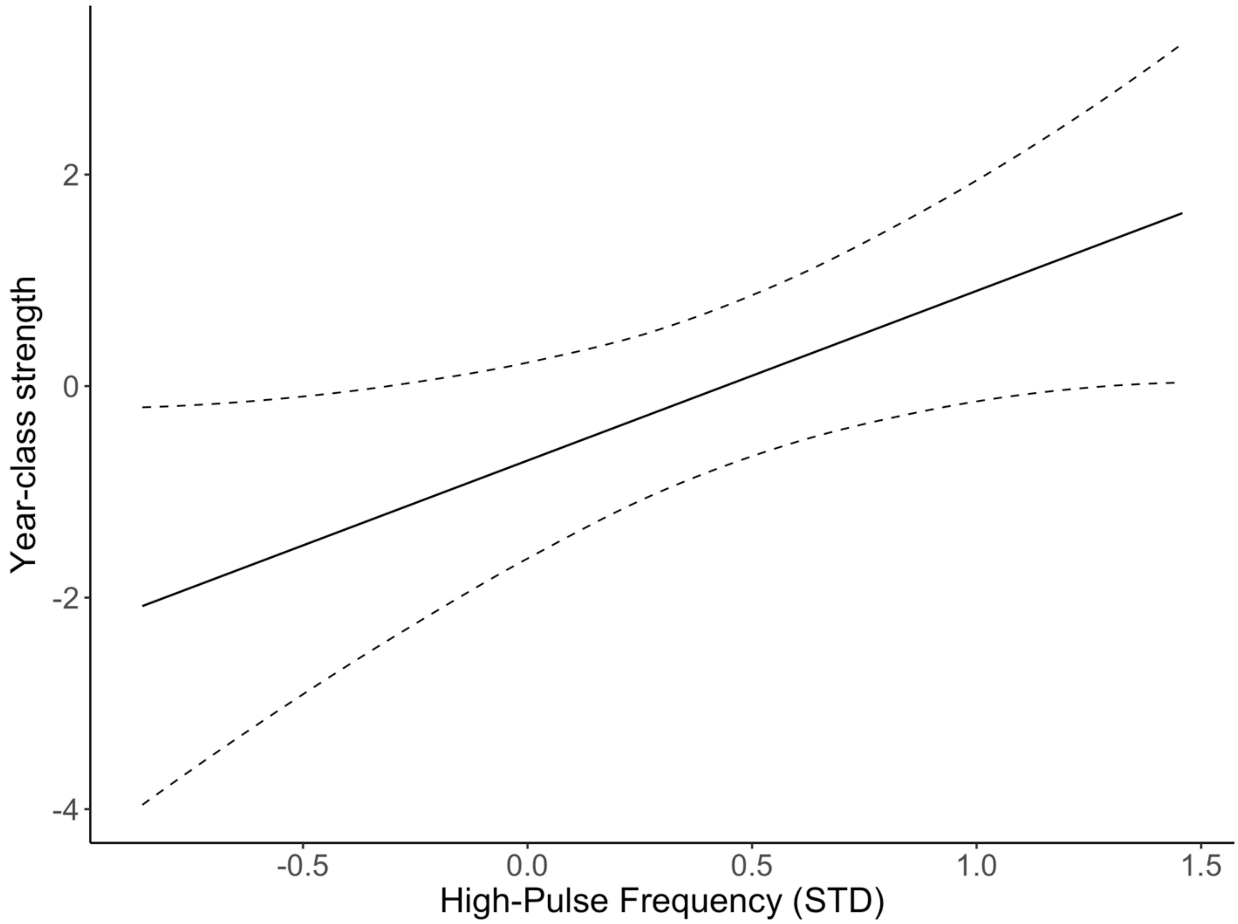

Figure 7 The relationship between Gizzard Shad *Dorosoma cepedianum* year-class strength and high-pulse frequency for the Elk River. High pulse frequency was standardized and dashed lines indicate 95% confidence intervals.

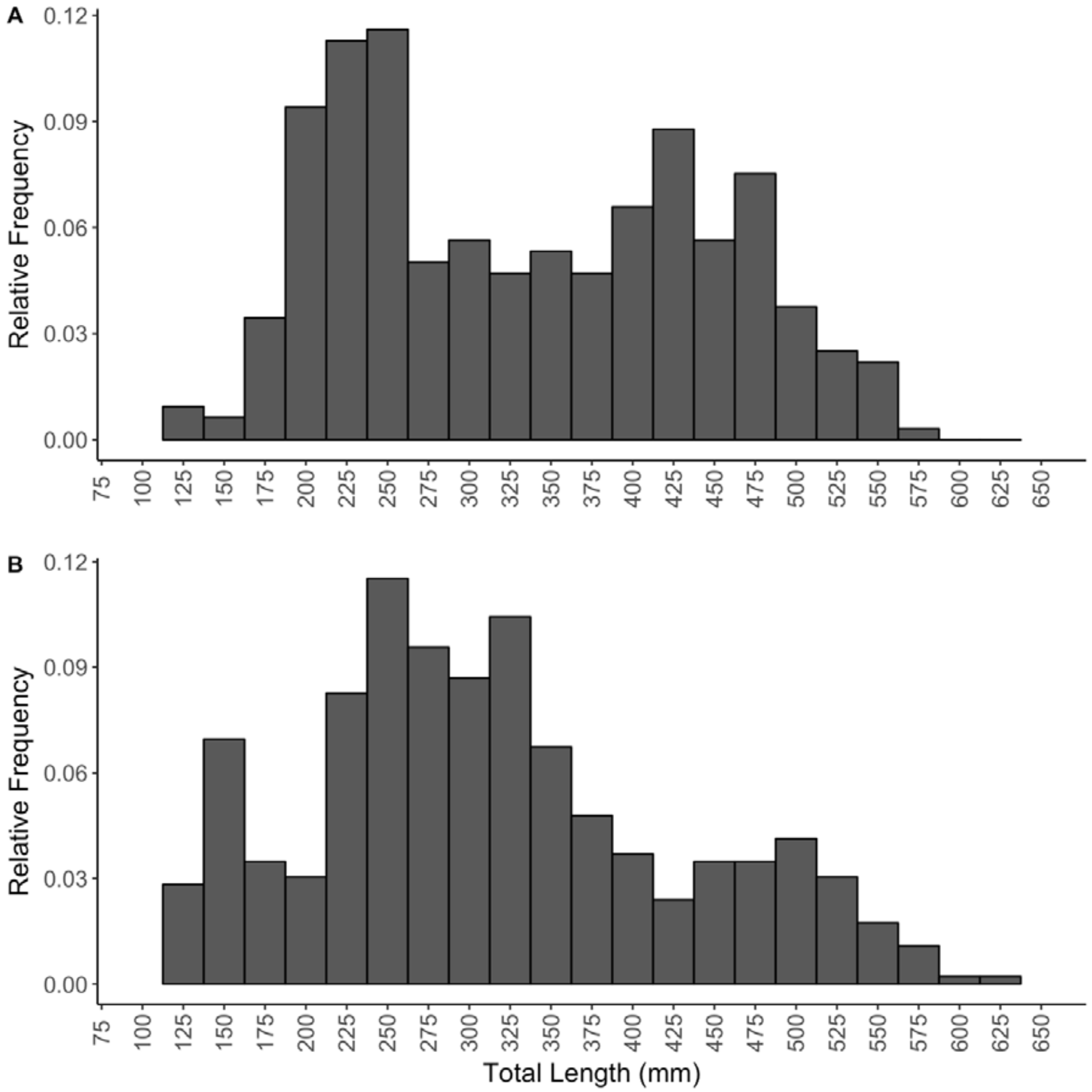

Figure 8 Relative frequency distribution of total length (mm) Freshwater Drum *Aplodinotus grunniens*: A) combined from Grand and Sardis reservoirs (*n* = 318), and B) from the Elk and Kiamichi rivers (*n* = 461).