ARTICLE

Flow Dynamics Influence Fish Recruitment in Hydrologically Connected River–Reservoir Landscapes

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Abstract
Hydrologic processes are often important determinants of successful recruitment of native fishes. However, water management practices can result in abnormal changes in daily and seasonal hydrology patterns. Rarely has fish recruitment across river–reservoir landscapes been considered in relation to flow management, despite the direct relationship between reservoir water management and the resulting upstream and downstream hydrology. We evaluated the relationships between lotic and lentic hydrology and recruitment of two native broadcast-spawning fishes, Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum*. Four seasonal periods for each species were identified that related to the species' spawning biology, from which we derived our remaining hydrology variables. Annual hydrology variables were also considered in our analysis. We developed regression models in conjunction with a model-selection procedure for each species and habitat type based on the catch-curve residuals from fish populations in hydrologically connected river–reservoir systems in the Ozark Highland and Ouachita Mountain ecoregions, USA. Our results indicated that recruitment of reservoir Freshwater Drum was negatively correlated to annual reservoir retention time. In lotic habitats, Freshwater Drum recruitment was positively correlated with prespawn discharge conditions and negatively correlated with annual flow variability. Similarly, riverine Gizzard Shad recruitment was positively correlated to the frequency of high-flow pulses during the spawning period. Our results indicate that releasing reservoir water to best mimic relatively natural flow patterns may benefit some broadcast-spawning species that occupy both lentic and downstream lotic environments, especially during the spring. This information, combined with future efforts on additional spawning guilds, will provide a foundation for developing holistic river–reservoir water-allocation plans.

Managing fisheries in hydrologically connected river and reservoir complexes necessitates an understanding of flow-ecology relationships in each ecosystem. In response to consistent increases in river regulation and fragmentation (Sakaris 2013; Grill et al. 2015), there has been an increased emphasis on environmental flows and ecosystem

conservation (Richter 2009; Poff and Zimmerman 2010; Richter et al. 2012; Arthington et al. 2018). It is simple to conceptualize that the components of a river's flow regime (e.g., magnitude of a flow event) could have a substantial influence on fish spawning, eggs, and larvae (Balon 1975); however, for some reproductive guilds, it is unclear how reservoir hydrology influences fish recruitment (i.e., the number of fish that survive from the time of hatching to a reproductive period, a harvestable size, or size vulnerable to sampling gears; Reynolds and Kolz 2012). Although reservoir "flow" is more difficult to conceptualize, often referenced as "drawdowns" or considered "water-level changes" or "fluctuations" (Beam 1983), clearly, water moves to create those hydrologic changes (i.e., largely determined by rain, floods, and reservoir outflow). Moreover, when reservoirs are held at unusually high levels, they affect the available habitat and hydrologic characteristics of the upstream river section, thereby affecting fish behavior (e.g., Smallmouth Bass *Micropterus dolomieu* moving further upstream; Brewer and Miller, in press). Understanding the factors that contribute to strong fish recruitment in both riverine and reservoir populations and quantifying recruitment–hydrology relationships would aid in the development of more holistic management plans for fishes across increasingly fragmented landscapes.

Recruitment is commonly examined by fisheries managers, but recruitment drivers are rarely examined in river-reservoir ecosystems. Hydrologic conditions in both rivers and reservoirs can influence recruitment success (Bonvechio and Allen 2005; Dutterer et al. 2013; Rolls et al. 2013); however, few studies examine the relationship between hydrology and fish recruitment for populations residing in rivers and associated impoundments (Sakaris 2013). Additionally, most recruitment studies include economically valued species, such as sport fish (Hansen et al. 1998; Maceina and Bettoli 1998; Maceina and Stimpert 1998; Bonvechio and Allen 2005; Smith et al. 2005). However, many sport fish species have a common spawning biology, where they build nests in shallow water and guard eggs (i.e., guarders; Balon 1975). Species that exhibit active parental care may be able to tolerate a broad range of flow alteration scenarios and still have successful recruitment. We hypothesize that broadcast-spawning fishes (i.e., typified by buoyant eggs and larvae that rely on some water movement; Balon 1975) will require specific flows for successful egg hatch and larval development, particularly higher flows that keep water moving through the river–reservoir complex. The factors driving the recruitment of broadcast spawners have received little attention when compared with other fish guilds, despite their ecological importance.

Our study objective was to determine how river and reservoir hydrology influences recruitment of two broadcast spawning fishes, Freshwater Drum *Aplodinotus grunniens* and Gizzard Shad *Dorosoma cepedianum*. The ecological importance of these species is often overlooked. Freshwater Drum serve as a primary glochidial host that facilitates freshwater mussel reproduction and distribution (Price et al. 2012). With over 70% of North America's freshwater mussels considered endangered, threatened, or of special concern (Williams et al. 1993; USFWS 2017), Freshwater Drum play an important role in their persistence. 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 frequently limit piscivore production (Evans et al. 2014). Gizzard Shad are also responsible for many bottom-up trophic-level effects (Noble 1981), but they can have negative effects on economically important species of sport fish through competition or complex, indirect pathways (Stein et al. 1995; Garvey and Stein 1998; Aday et al. 2005).

METHODS

Study area.— We selected two rivers and two associated reservoirs based on the availability of historical hydrologic data (i.e., discharge), the abundance of our study species, and the relative similarities in climate conditions. Gizzard Shad do not typically live longer than 10 years, but Freshwater Drum can reach ages >30 years old. Thus, each river–reservoir site required a minimum of 20 years of available hydrology data to match to our year-classes. Additionally, 15–20 years of flow data are considered a reasonable record for representing flow conditions (e.g., Falcone et al. 2010; Leasure et al. 2016; Worthington et al. 2016). We chose two rivers (Elk and Kiamichi rivers) and two associated reservoirs (Grand Lake O' the Cherokee, hereafter "Grand Lake", and Sardis Reservoir) for our study sites (Figure 1). Our study species were abundant enough at these sites to construct catch curves and have sufficient replication in year-classes. The Elk River, located within the Ozark Highlands ecoregion, flows from southwestern Missouri into northeastern Oklahoma where it is impounded by Grand Lake, an 18,800-ha reservoir that is located on the main stem of the Grand River (lower Neosho River). We sampled fish from approximately 2 km downstream of the U.S. Geological Survey (USGS) stream gauge to ~38 km upriver (Figure 1). The Kiamichi River, a major tributary of the Red River, drains the Ouachita Mountain ecoregion of southwestern Oklahoma and flows west from Arkansas until it is redirected south near the confluence of Jack Fork Creek. Jack Fork Creek is a 4-km-long tributary that is fed directly by dam releases from Sardis Reservoir, a 5,500-ha reservoir. Sardis Reservoir controls approximately 24% of the historical flows in the Kiamichi downriver of the Jack Fork Creek confluence (Vaughn et al.
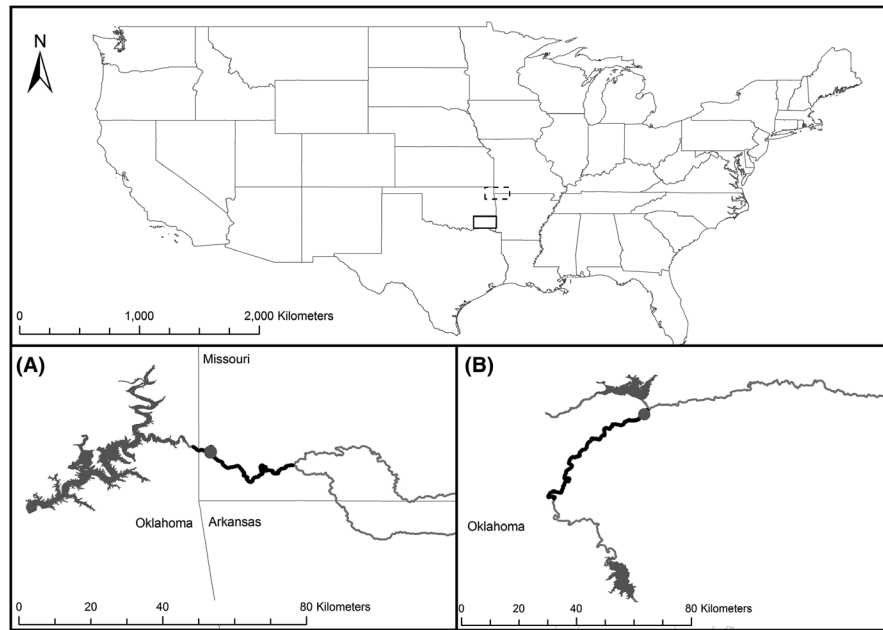
FIGURE 1. Two river–reservoir landscapes of the Ozark Highlands (dashed box) and Ouachita Mountain (solid box) ecoregions. Freshwater Drum and Gizzard Shad were sampled from each system (Elk River and Grand Lake of the Cherokees; Sardis Reservoir and Kiamichi River) during summer through autumn 2016 and summer 2017 with boat electrofishing. Each river sample reach was 40–50 km and located adjacent to a U.S. Geological Survey (USGS) stream gauge (gray dots indicate the gauge locations; **(A)** Elk River, USGS stream gauge 07189000 and Grand Lake; **(B)** Kiamichi River, USGS stream gauge 07335790, with Sardis Reservoir upstream. The state and U.S. border data were obtained by the authors from the U.S. Department of Agriculture, Natural Resources Conservation Service Geospatial Data Gateway (https://datagateway.nrcs.usda.gov/GDGHome.aspx).

2015). We sampled fish from approximately 50 km of the Kiamichi River starting at the confluence of Jack Fork Creek. The two ecoregions are considered uplands (Woods et al. 2005) and each receives approximately 115 cm of annual precipitation. Both ecoregions are dominated by limestone and dolostone lithologies, but the Ozark Highlands has higher groundwater contributions (Zhou et al. 2018).

Hydrology.— We developed our hydrologic foundation from existing data. First, daily riverine discharge data were obtained from the USGS gauges for the Elk and Kiamichi rivers (gauges 07189000 and 07335790, respectively). We quantified 16 hydrology variables for each river system, using the Indicators of Hydrologic Alteration (The Nature Conservancy, Boulder, Colorado) software (Richter et al. 1996) for eight flow metrics (Table 1) and an additional eight metrics (medians and coefficient of variations) that were manually calculated in Microsoft Excel. Gauge height data were not available for the entire period, so they are not included in our analysis. The Indicators of Hydrologic Alteration software was developed to easily calculate characteristics of both relatively natural and altered flow regimes, based on many environmental flow components. For the annual variables, the water year was set to represent a calendar year. For the variables that were quantified over seasons corresponding to particular life history periods

(e.g., Gizzard Shad spawn period), the values were calculated by manually setting the water year in the Indicators of Hydrologic Alteration software to match those months over the entire period of record. For example, a high-pulse frequency was calculated by summing up all of the flow pulses that exceeded the 75th percentile of the season of interest (e.g., Gizzard Shad spawn period: April through May). The 90-d flow metrics for Freshwater Drum were only calculated as annual metrics, whereas we did calculate 90-d metrics specific to the Gizzard Shad seasonal periods (i.e., 90-d maximums and minimum during the nursery period) because these periods exceeded 90 d (see Supplemental Tables 2 and 3 available in the online version of this article). Next, we obtained daily historical water-level data for Grand Lake and Sardis Reservoir from the U.S. Army Corps of Engineers monitoring web site. The reservoir hydrology metrics were calculated in Microsoft Excel (average water storage [ha], the number of days that water levels were above conservation pool, coefficient of variation in water storage, and water retention time).

Our choice of seasonal and annual hydrologic variables related to the life history of each species (Table 2). For example, Freshwater Drum eggs are buoyant, whereas Gizzard Shad eggs sink and adhere to substrate or other structures. Therefore, during the spawn period, we chose the coefficient of variation in discharge and the river fall

TABLE 1. Flow metrics and calculation methods that we quantified using the Indicators of Hydrological Alteration (Richter et al. 1996) software.

Flow metric	Calculation
90-d minimum	The median of the minimum discharges that persisted for at least 90 consecutive days
90-d maximum	The median of the maximum discharges that persisted for at least 90 consecutive days
30-d minimum	The median of the minimum discharges that persisted for at least 30 consecutive days
30-d maximum	The median of the maximum discharges that persisted for at least 30 consecutive days
High-flow pulses	The frequency of high-flow pulses that exceed the 75th percentile of the entire hydrologic record
Rise rate	The median of all positive differences between consecutive daily flows
Fall rate	The median of all negative differences between consecutive daily flows
Reversal	The hydrologic record 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

TABLE 2. The ecological importance of each hydrologic variable that we hypothesized could be related to fish recruitment in our rivers and reservoirs.

Metric	Ecological importance
Rivers	
90-d minimum	Anaerobic stress on submerged aquatic vegetation habitat; lack of nutrient transport and recycling
90-d maximum	Structuring of channel morphology and habitat connectivity; long-term access to inundated terrestrial habitats
30-d minimum	Stressful conditions such as temperature extremes and low habitat availability
30-d maximum	Aeration of eggs and distribution of larvae; Structuring of physical habitat conditions; possible washout of eggs or larvae
High-flow pulses	Influences bedload transport; channel sediments and embeddedness; frequency of substrate disturbances; spawning cues
Rise rate	Possible entrapment on islands or floodplain
Fall rate	Temporal availability of inundated resources; suspended sediment deposition
Reversals	Indication of discharge variability; littoral zone and pool habitat structuring and maintenance; stress on sessile benthic organisms
Reservoirs	
Prespawn mean	Volume of resources available to adults preparing to spawn
Prespawn variability	Whether prespawning resources were consistently available or if location/amount of resources varied
Spawn mean	Volume of available spawning habitat, access to submerged substratum for adhesive egg
Spawn variability	Susceptibility of eggs and larvae to directional currents; adhesive eggs vulnerable to exposure
Nursery mean	Amount of available nursery habitat for larvae and juveniles
Nursery variability	Possible entrapment and increased stress due to nursery resource locations constantly changing
Overwinter mean	Access to temperature refuges that still provides adequate protection for predation
Over conservation pool level	How long species have access to high water levels; how long species have access to shoreline habitat and inundated terrestrial cover
Annual retention time	Retention time is often associated with primary productivity
Annual variability	Considers annual inflow, releases, rainfall events, drought in one parameter

rate for Freshwater Drum and Gizzard Shad, respectively, to reflect the hypothesized flow needs of the riverine populations of the two species (see Table 2 for an overview of metrics chosen). We used regional taxonomic references to define the timing of four seasonal periods (prespawn, spawn, nursery, and overwinter periods) that relate to

important life history stages for each species (Pflieger 1997). The prespawn period of Freshwater Drum was March through May, the spawning period was May through July, the nursery period was August through October, and the overwinter period was December through February. For Gizzard Shad, we defined the prespawn period as March, the spawn as April through May, the nursery period as June through November, and the overwinter period as December through February (Pflieger 1997). We calculated the aforementioned hydrologic variables to represent both annual values and values for the four seasonal periods for each species.

Fish sampling and processing.— The fish were sampled in close proximity to the stream gauges (see Figure 1) from May to December 2016 and from May to June 2017 with boat-mounted electrofishing. Both rivers were sampled with a 4.3-m boat that was equipped with a Smith-Root 5.0 generator-powered pulsator (Smith-Root, Vancouver, Washington) and a single boom-mounted anode with pulsed-DC electricity (frequency and duty cycle varied by site). We sampled the rivers in a downstream direction, incorporating all major habitat types (e.g., woody debris in pools, rocky outcrops, and fast-flowing runs). The reservoirs were sampled with a 5.5-m boat that was equipped with a Smith-Root 7.5 generator-powered pulsator and two boom-mounted anodes with pulsed-DC electricity. The reservoirs were also sampled by covering major habitat elements (e.g., coves, points of main channels, and rip-rap). Numerous sampling locations were selected from the reservoirs to cover representative habitat ranging from conditions near the dam to main channel locations, coves, and areas of the upper river–reservoir interfaces.

The captured fishes were processed differently for each species because not all of the sampled Gizzard Shad were aged. For Gizzard Shad, we measured total length (to 1.0 mm) of each fish, and the first 10 fish in each 15-mm length bin were euthanized to construct age–length keys (Ricker 1975; Coggins et al. 2013). Ages were assigned to individuals of unknown age based on their length with the age–length key. If <10 individuals were collected for a bin range, then all of the individuals in that bin were used for aging (Tetzlaff et al. 2011). No age–length key was developed for Freshwater Drum, and all of the sampled specimens were kept for aging. The euthanized fish were individually bagged, labeled, and placed on ice for transportation to the laboratory for otolith extraction and processing.

The otoliths were extracted from the euthanized fish, cleaned by removing all tissue, and stored in individually marked coin envelopes. After drying for at least 24 h, the whole otoliths were mounted in epoxy resin and 0.5-mm-thick transverse sections were cut across the dorso ventral plane with a low-speed IsoMet saw (Buehler, Lake Bluff,

Illinois). The otoliths from the Freshwater Drum were sectioned without epoxy mounting because they were larger and there was no risk of fracture during sectioning. The sections were polished and viewed under 40× magnification for annuli counts. Two readers independently aged each fish. Any discrepancies between the two readers were discussed until a consensus was reached, or the otoliths were omitted if consensus could not be reached (Edwards et al. 2011).

Catch curve.— We used regression to develop catch curves to index year-class strength and determine residuals as a function of age. Catch curves are commonly used in fisheries to estimate total instantaneous mortality, from which total annual mortality and survival can also be calculated. Traditional catch-curve analysis has been expanded to multiple regression by incorporating environmental factors as predictor variables in the equation (Maceina 1997; Sammons et al. 2002; Tetzlaff et al. 2011). The major assumption of this approach is that variation in the catch curves is entirely attributed to recruitment variation, with equal probability of capture of individuals from all the year-classes included in the analysis. We used a similar approach by incorporating hydrologic variables and excluding year in the model. We used the 'FSA' package in the statistical software R (version 3.2.2, R Core Development Team, Vienna) to develop a weighted regression of log abundance versus age, assigning less weight to older fish that are expected to be less abundant (Maceina and Bettoli 1998). Studentized residuals from the weighted catch curves were used to simultaneously index year-class strength of all cohorts in the population (Maceina 1997). The use of studentized residuals allows different regression models to be comparable because about 95% of the observations will fall between −1.96 and 1.96 (Maceina 1997). Deviations from the catch-curve regression line were attributed to weaker (negative residuals) or stronger (positive residuals) year-classes (Supplemental Figures 1 and 2). With this method, recruitment does not need to be observed each year when year-class strength is set (i.e., samples of age-0 fish are not needed annually). We used regressions of $\log_e$(abundance + 1) to obtain catch-curve residuals as a function of age.

Recruitment estimates were only assigned to age-classes that were fully recruited to the sampling gear (Allen and Hightower 2010). The age of full recruitment was assessed by examining the modes on abundance-at-age histograms for each site (Allen and Hightower 2010), which assumes that the abundance of individuals in young age-classes should always be more than that of older age-classes (Supplemental Figures 3 and 4).

Relating hydrology to recruitment.— We developed multiple regression models to examine relationships between hydrology and year-class strength. Hydrologic predictor variables were the independent variables in these models.

To assess trends across systems, we followed the methods outlined in Bonvechio and Allen (2005). Briefly, the hydrologic variables were standardized and scaled to a mean of zero for each system (i.e., independent variable). This allowed us to develop one model for each ecosystem (river or reservoir) and species combination, despite differences in hydrology of each replicate system. The two species could not be combined into a single model because of the large discrepancies in their longevity.

We used a manual forward-selection process with the SigAIC information criterion (Jamil et al. 2012) to determine the most parsimonious regression model for each species and system (i.e., river and reservoir). SigAIC is a variant of the Akaike information criterion (Burnham and Anderson 2002) that introduces a higher penalty factor (3.84) for increased model complexity such that any variable that is added at any given step must have a significant slope, significantly reducing the potential to overfit models. Additionally, forward selection allowed correlated predictors ($r \geq 0.65$) to be removed as the model complexity increased rather than a priori (correlation coefficients are reported in Supplemental Tables 1–3). The first step in the model selection process compared the SigAICs from our null models (which contained only intercepts, i.e., year-class strength) and each single-variable model, one at a time. The SigAIC values that were within 1 unit were not considered different (Mollenhauer et al. 2017). If the SigAIC from a model containing a predictor variable resulted in a lower SigAIC, it was considered more parsimonious and we selected the single-predictor model with the lowest SigAIC as 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, and was terminated when the SigAIC values stopped decreasing by at least 1 unit. Site (i.e., Elk River and Kiamichi River) was not considered a random effect in these models, as there were only two levels for both rivers and reservoirs. Instead, a fixed site effect was added to the top predictor model to examine whether a main effect or an interaction explained additional variation in our data. Residual plots and quantile-quantile plots were constructed to check that constant variance and normality assumptions were reasonably met in all of the final models. All of the models were developed with the stats package in the statistical software R (version 3.2.2), and the compared models with SigAIC (model rankings are reported in Supplemental Tables 4–6).

RESULTS

Fish Collection

We collected 779 Freshwater Drum and 3,467 Gizzard Shad from all of the sites. Some older age-classes were omitted due to large age gaps between older individuals (Supplemental Figures 3 and 4). Additionally, some younger cohorts were omitted from our catch-curve analysis because they were not fully recruited to the sampling gear (Supplemental Figures 3 and 4). Independent readers reached a consensus age for all individuals, and no fish data were omitted due to aging discrepancies. Ages ranged from 1 to 32 years for Freshwater Drum in rivers and from 0 to 32 years in reservoirs. Gizzard Shad ranged from 0 to 7 years in rivers and from 0 to 8 years in reservoirs. However, we were only able to sample Gizzard Shad from the Kiamichi River up to age 4; thus, we were not able to include this population in our final analyses (i.e., Elk River data were used solely in our riverine Gizzard Shad model).

Hydrology and Recruitment

For riverine Freshwater Drum, our top model included both river reversals and prespawn median discharge and explained 36% of the variation in recruitment. In both the Elk and Kiamichi rivers, year-class strength of Freshwater Drum was negatively related to annual discharge variability (i.e., the number of annual reversals) and positively related to prespawn (March through May) median discharge (Figure 2). Holding prespawn median discharge constant at the mean, a one-standard-deviation increase in annual river reversals decreased average year-class strength by 0.64, whereas holding annual river reversals constant, a one-standard-deviation increase in prespawn median discharge increased average year-class strength by 0.60 (Table 3). Including a fixed site effect did not improve model fit.

For reservoir Freshwater Drum, our top model included annual retention time and explained 60% of the variation in recruitment. Year-class strength for Freshwater Drum from reservoirs was negatively related to annual retention time (Figure 3). A one-standard-deviation increase in retention time decreased the average year-class strength by 1.40 within a given reservoir (Table 3). The top model included an interaction term between reservoir and retention time. The interaction coefficient indicated that the effect of retention time was stronger in Grand Lake than in Sardis Reservoir.

Recruitment of Gizzard Shad was related to hydrology in the river but not in the reservoirs (i.e., no predictor models resulted in a decrease of SigAIC by >1 relative to the null model). Recruitment of riverine Gizzard Shad was positively related to the frequency of high pulses during the spawning period (April and May; Figure 4). A one-standard-deviation increase in high pulses increased average year-class strength by 1.12 (Table 3). This model explained 70% of the variation in recruitment, though statistical power was relatively low with only six year-classes.
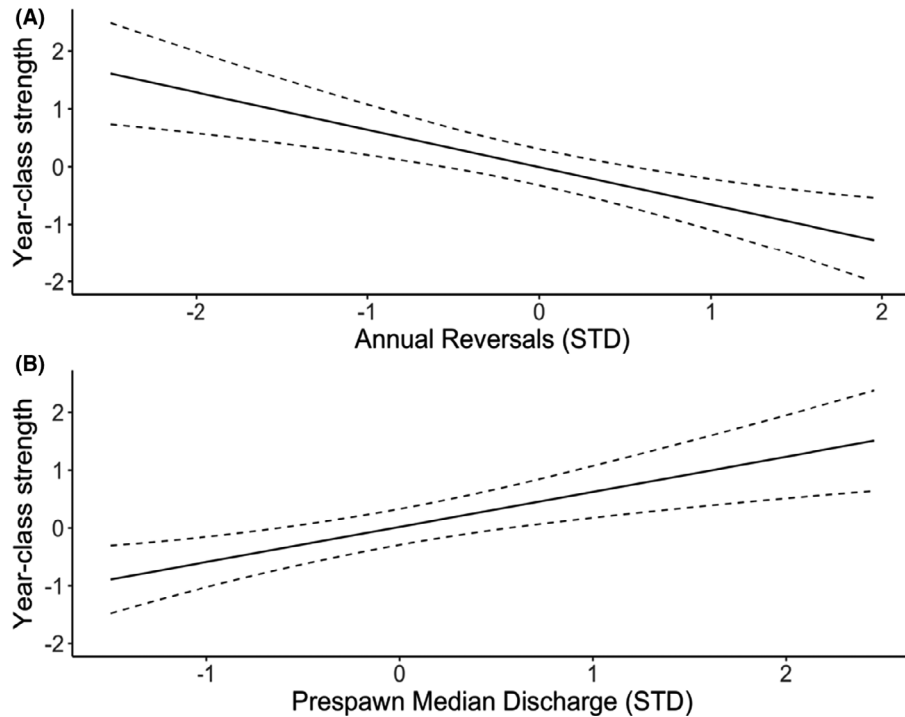
FIGURE 2. Year-class strength of Freshwater Drum across levels of prespawn median discharge and frequency of annual reversals using estimates from the top river Freshwater Drum model. Panel **(A)** shows the relationship between annual river reversals and year-class strength while holding prespawn median discharge constant at the mean, and panel **(B)** shows the relationship between prespawn median discharge while holding annual reversals constant at the mean. The hydrology metrics were standardized (STD) relative to the conditions within each river. The dashed lines indicate 95% confidence intervals.

TABLE 3. Parameter estimates from the top model (lowest SigAIC) explaining Freshwater Drum and Gizzard Shad year-class strength, by river and reservoir.

System: species	Coefficient	Estimate	SE	t-value
River: Freshwater Drum	Intercept	0.009	0.157	0.055
	Annual reversals	−0.641	0.164	−3.902
	Prespawn discharge	0.601	0.164	3.659
Reservoir: Freshwater Drum	Intercept	−0.122	0.203	−0.599
	Grand retention time slope	−1.395	0.210	−6.650
	Sardis retention time slope	−0.469	0.292	3.172
	Interaction effect	0.112	0.197	0.571
River: Gizzard Shad	Intercept	−0.030	0.288	−0.104
	High-pulse frequency	1.124	0.315	3.568

DISCUSSION

Recruitment of riverine fishes is typically associated with moving water; however, our results suggest that retention time (i.e., corresponding to water movement through the system) could influence recruitment of reservoir populations. For rivers in temperate climates, flow is considered the master variable, driving the dynamic nature of these ecosystems and influencing fish assemblage structure (Power et al. 1995; Richter et al. 1996; Poff et al. 1997). In reservoirs, water-level fluctuations are often used to summarize the variation in hydrology that shapes habitat and assemblage structure (Gelwick and Matthews 1990; Fischer and Öhl 2005). However, the importance of moving water in relation to completion of the life history of broadcast-spawning reservoir fishes has received considerably less attention, despite the strong association between reservoir flow and water-level fluctuations (Hill and Cichra 2002). We found that hydrology was an
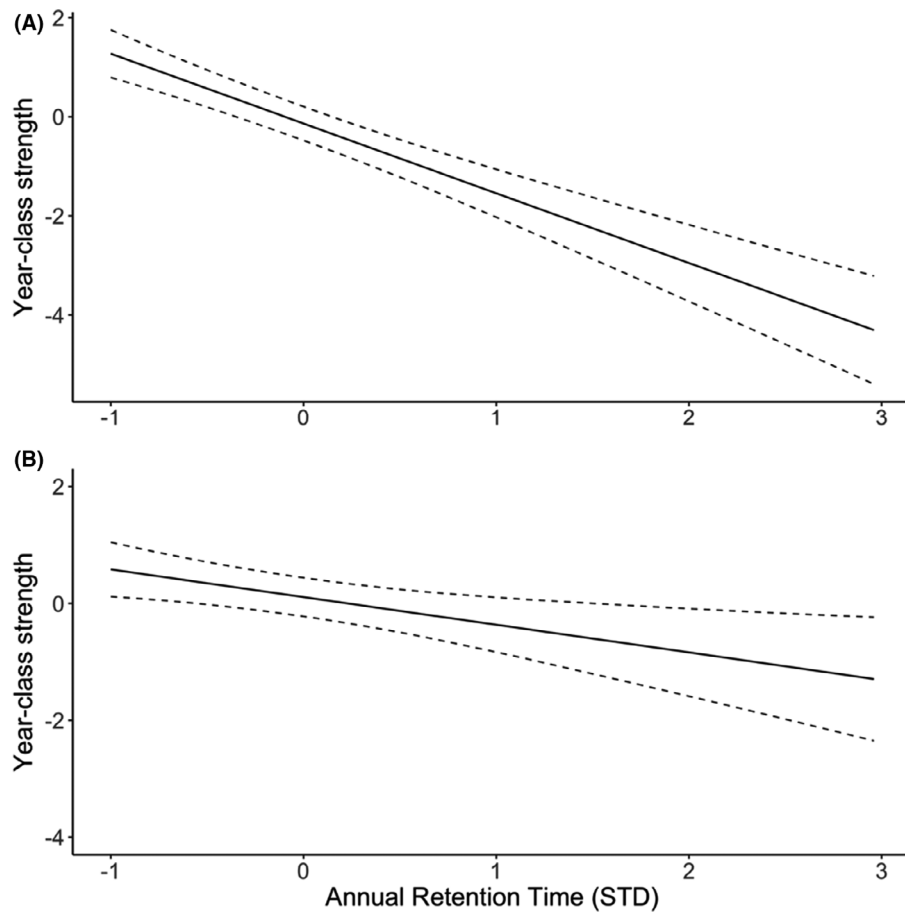
FIGURE 3. Year-class strength of Freshwater Drum across levels of retention time using estimates from the top reservoir Freshwater Drum model that included an interaction term between reservoirs. Panel **(A)** Shows the relationship between reservoir retention time and year-class strength in Grand Lake while holding the reference constant (Sardis Reservoir), and panel **(B)** shows the relationship between reservoir retention time in Sardis Reservoir while holding the reference constant (Grand Lake). The retention times were standardized (STD) relative to conditions in each reservoir. The dashed lines indicate 95% confidence intervals.

important driver of recruitment in both riverine and reservoir populations of select broadcast-spawning fishes, even though the direction of these relationships was system specific. The observed negative relationship between long water retention and recruitment was a novel finding for nongame reservoir fishes.

Unlike many reservoir fishes, the eggs and larvae of Freshwater Drum are dependent on directional flow and currents (Balon 1975). Reservoir retention time is the duration that water remains in a reservoir, where shorter retention times resemble more lotic conditions (Rypel et al. 2006). The riverine origin of most reservoir species suggests that moving water would be important to their life cycles (Fernando and Holčík 1991); however, long reservoir retention time has been positively correlated with recruitment of more commonly studied species of sport fish (e.g., Largemouth Bass *Micropterus salmoides*: Wrenn et al. 1996; Maceina and Bettoli 1998; crappie *Pomoxis*

spp.: 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 Kubečka 1995). Alternatively, Freshwater Drum provide no parental care, and the buoyancy of eggs and larvae makes them dependent on water current (Balon 1975). Moving water aids the dispersal of buoyant eggs and larvae, thereby reducing the risk of cannibalism and competition for space (Lechner et al. 2016). Additionally, Freshwater Drum growth in reservoirs has been negatively associated with retention time (Rypel et al. 2006). Less than optimal growing conditions could limit female fecundity in years where retention time was long, potentially limiting recruitment during those years.

The negative relationship that we observed between annual reversals and riverine Freshwater Drum recruitment
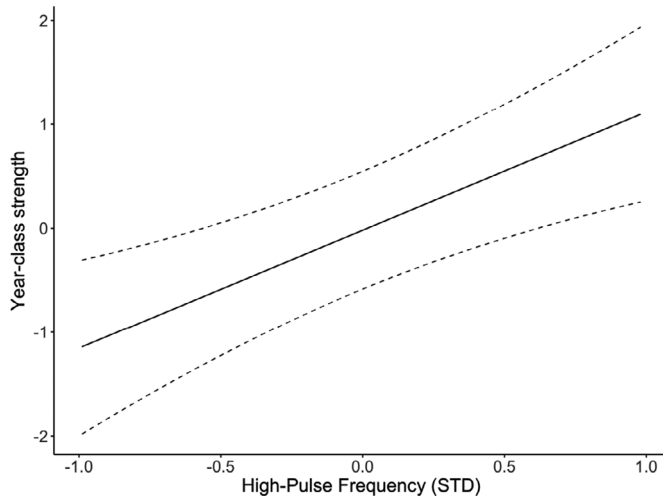
FIGURE 4. Year-class strength of Gizzard Shad across levels of high-pulse frequency during the spawning period (April–May) using the model estimate associated with Gizzard Shad in the Elk River. The high pulses during the spawning period were standardized (STD) relative to the conditions of the river. The dashed lines indicate 95% confidence intervals.

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 (i.e., reversal) habitat availability 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). Food availability is often associated with fitness and fecundity (Sammons et al. 2002; Bonvechio and Allen 2005), and a lack of a primary diet source would likely reduce spawning potential. River reversals also influence the structure and function of instream habitat, including pools. Extreme reversal events that occur after peak flow events restructure pool habitats (Resh et al. 1988) that many species, including Freshwater Drum, occupy during the rearing periods (Holland 1986; Sheaffer and Nickum 1986). Although our results indicate a relationship between Freshwater Drum recruitment and annual river reversals, more information is needed to determine exactly how and when river reversals may influence recruitment. This would likely be best achieved by supplementing our findings with studies at finer temporal extents that pinpoint spawning activity with flow events. These finer-scale studies could then be paired with hourly discharge and water temperature data.

The importance of prespawn median flows for Freshwater Drum recruitment 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). Therefore, years when prespawn discharge is high could trigger fish 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 that is used by juveniles during the nursery period, as higher flows scour pool habitats, preventing them from filling with sediment (Resh et al. 1988).

Although we did not find any relationships between reservoir hydrology and recruitment for reservoir Gizzard Shad populations, riverine populations had strong year-classes in years with increased pulse frequency during the spawning period. There may be several reasons that we did not find a relationship in our reservoir populations. First, there may not be a relationship between the reservoir hydrology metrics we chose and year-class strength. Second, an exceptionally strong 2011 year-class in Grand Lake influenced the other year-class strength estimates from our Grand Lake catch curve and this may have been caused by size biases that are associated with electrofishing that could have made the 2011 cohort disproportionately vulnerable to our sampling methods (Reynolds and Kolz 2012). In contrast to reservoir populations, we found that Gizzard Shad recruitment in the Elk River was positively related to the number of peak-flow events during the spawning period. High-flow pulses typically increase connectivity between rivers and backwater pools (Junk et al. 1989), which are important nursery habitat for riverine Gizzard Shad (Sheaffer and Nickum 1986). High spring flows are associated with weak year-classes of some nest-building species (Bonvechio and Allen 2005; Smith et al. 2005). However, Gizzard Shad are broadcast spawners; high pulses during the spawn could have oxygenated the adhesive eggs and adequately dispersed buoyant larval fish to backwater rearing habitats, further illustrating the importance of incorporating other spawning guilds in recruitment studies.

It would be beneficial to consider the broader fish assemblage as part of the management process, and ecological trade-offs are often made to benefit some species and systems one year and others the next (depending on longevity and flow needs). High-pulse events through scheduled reservoir releases would also benefit downstream broadcast-spawning recruitment (Sakaris 2013), and shorter retention times related to reservoir releases could increase recruitment in the reservoirs for some species, such as Freshwater Drum. Additionally, reservoir releases would limit the pooling of water in the lower section of the connected upriver systems, which would also reduce water retention time. However, consideration of

riverine environments just upstream would be beneficial because the river–reservoir interface provides habitat that is used by numerous species at particular times of the year and the production of some nest-spawning sport fish benefits from long retention times (i.e., minimal releases) where water levels inundate terrestrial vegetation (Maceina and Bettoli 1998; Sammons and Bettoli 2000; Buckmeier et al. 2014; Guy et al. 2015). Additionally, high-flow pulses in rivers during the spawning season can negatively affect recruitment of nest-spawning species (Bonvechio and Allen 2005; Smith et al. 2005). There is a high economic incentive for agencies to maintain healthy sportfish populations; however, over 95% of North American fishes are nongame species and maintaining healthy populations of nongame fishes influences whole ecosystem assemblage structures (Stein et al. 1995; Michaletz 1997).

River–reservoir complexes present management agencies with the difficult task of developing a holistic management plan that incorporates the hydrology needs of numerous species, and in two very different hydrologic environments. Conservation and management efforts for lentic and lotic species require an understanding of the many different life history aspects of assemblage members. Our results indicated that year-classes of longer-lived broadcast spawners are detectable in high relative abundance for nearly 20 years. Most reservoir-recruitment studies focus on species that live <10 years (Maceina and Bettoli 1998; Maceina and Stimpert 1998; Sammons and Bettoli 2000; Bonvechio and Allen 2005). Water allocation between rivers and reservoirs is a common management problem (Zimmerman et al. 2010); however, the sustainability of longer-lived species in both habitats may be possible via water allocation that optimizes recruitment in each habitat every few years to ensure the production of some strong year-classes within the age structure of both populations (unless there are sensitive short-lived species). This proactive management strategy could secure the economic and recreational benefits that many reservoir species provide while managing for ecosystem health in riverine environments. It would be advantageous for future studies to quantify the effects of altered hydrology on other nongame fishes that occupy both rivers and reservoirs to further identify mutually beneficial management strategies for these ecosystems. Further, relating a population model to experimental flow releases or lack thereof would improve the application of these relationships to management practices. Specific studies could target possible limiting factors that are associated with different flows, including food availability and habitat quality and quantity. Last, special attention to upriver changes during reservoir releases would be beneficial to improving our understanding of how water releases affect the upstream shifting reservoir-river environment.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.