

# Relationships between Hydrology and Largemouth Bass Growth in the Ouachita River, Arkansas

**Kyler B. Hecke**, Aquaculture/Fisheries Center, University of Arkansas at Pine Bluff, 1200 N. University, Box 4912, Pine Bluff, AR 71601

**Eric L. Brinkman**, Arkansas Game and Fish Commission, 7004 Highway 67 East, Perrytown, AR 71801

**Brett A. Timmons**, Arkansas Game and Fish Commission, 600-B E. Lawson Road, Jonesboro, AR 72404

**Jason A. Olive**, Arkansas Game and Fish Commission, 500 Ben Lane, Camden, AR 71701

**Michael A. Eggleton**, Aquaculture/Fisheries Center, University of Arkansas at Pine Bluff, 1200 N. University, Box 4912, Pine Bluff, AR 71601

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**Abstract:** We explored whether increased river flows negatively affected growth of largemouth bass (*Micropterus salmoides*) in the lower Ouachita River, Arkansas. To test this hypothesis, largemouth bass ( $n=460$ ) were collected during 2008–2010 from the Felsenthal Reservoir region of the river. Largemouth bass were aged and annual growth increments were calculated using standard back-calculation techniques. Growth of largemouth bass was relatively rapid in the Ouachita River, with von Bertalanffy growth model parameters determined as  $L_{\infty} = 513$  mm,  $K=0.324$ , and  $t_0 = -0.314$ ; catch-curve analysis estimated that total annual mortality of the population averaged 48% (95% CL 42%–54%). Back-calculated growth increments of largemouth bass were compared across years classified as “high-flow,” “low-flow,” and “average-flow” based on analysis of historical June–October hydrology (i.e., corresponding with the largemouth bass growing season). Two-way factorial ANOVA analyses indicated that largemouth bass growth was lower during high-flow years, with the effect most pronounced for the age 2–4 cohorts. Results suggested that high-flow periods typically beneficial to fishes in large river-floodplain systems may not always result in increased growth rates in more highly regulated river systems such as the Ouachita River. Better understanding of fish growth-hydrology relationships will become increasingly important in light of predicted future effects of climate change, which include increased frequencies of hydrologic extremes.

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**Key words:** population dynamics, hydrology, incremental growth, recruitment variability

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Hydrology is an important driving force with regard to river and reservoir fisheries (Maceina and Bettoli 1998). In rivers, seasonal flood pulses serve as spawning cues for many fishes, while also making available terrestrial resources inundated by floodwaters (Junk et al. 1989). In lakes and reservoirs, high waters coinciding with fish spawning are often associated with strong year classes of certain species (Sammons and Bettoli 2000). On the other hand, hydrologic “extremes” can cause direct mortality of juvenile and adult fishes and serve as ecosystem disturbances that play major roles in the structuring of stream and river fish assemblages (Poff and Allan 1995). Because water quantity affects aquatic habitat quality and quantity (Poff et al. 1997), better understanding of fish-hydrology relationships can assist fisheries managers with development of appropriate strategies to achieve fisheries management objectives.

Largemouth bass (*Micropterus salmoides*) are the primary sport fishery in southern U.S. waters (Noble 2002); thus, better understanding of fish-hydrology relationships for this species is especially important. When examining largemouth bass in the context of hydrology, previous research has emphasized reproductive success and survival of juvenile bass (e.g., Fisher and Zale 1991, Kohler et al. 1993). Because these factors collectively affect largemouth bass

recruitment, previous studies have attempted to quantify links between hydrology and some measure reflecting year-class strength (e.g., Reinert et al. 1995, Maceina and Bettoli 1998, Sammons and Bettoli 2000, Bonvechio and Allen 2005, Siepker and Michaletz 2013). Collectively, studies on largemouth bass have produced mixed results.

Few studies have examined the direct role that hydrology may play on largemouth bass growth, and how those influences also may affect year-class strength. Maceina and Bettoli (1998) suggested that weak largemouth bass year-classes in four Tennessee River reservoirs were attributable to higher discharges. Although largemouth bass growth was not reported, they speculated that juvenile bass survival had decreased in response to lower prey fish production during higher-flow years. Lack of forage would undoubtedly affect first-year growth of juvenile largemouth bass, which has been linked to rates of overwinter survival and eventual year-class strength in other studies (e.g., Adams et al. 1982). Raibley et al. (1997) provided compelling evidence that size distributions of largemouth bass varied with annual hydrologic regimes over several years in the Illinois River. Peacock (2011) further reported that hydrology might affect largemouth bass age classes differentially. In this study on the lower

Arkansas River, younger cohorts (ages 1–3) of largemouth bass experienced significant reductions in annual growth coincident with years of extremely high flow, while older cohorts (ages 4–6) experienced growth increases during the same years.

To further examine relationships between largemouth bass growth and hydrology, the lower Ouachita River, Arkansas, was selected for this study. Largemouth bass are the most popular sport fishery in the Ouachita River system, with most of the angling effort occurring in the river's most downstream impoundment, Felsenthal Reservoir. The objectives of this study were to 1) quantify largemouth bass age and growth in the lower Ouachita River, and 2) examine relationships between largemouth bass growth and river hydrology. Results of this study will help better refine fish-hydrology relationships for largemouth bass and support fisheries managers involved in largemouth bass management.

## Methods

### Study Area

The study area for this research was the lower Ouachita River system in south-central Arkansas. Most of the study occurred in Felsenthal Reservoir, which is one of the most popular largemouth bass fisheries in southern Arkansas. Felsenthal Reservoir is a 6070-ha impoundment created by the completion of Felsenthal Lock and Dam in 1985. This reservoir is part of the U.S. Army Corps of Engineers' Ouachita-Black River Navigation Project, which includes four locks and dams and maintains a minimum 2.74-m navigation channel upstream to Camden, Arkansas (Olive et al. 2010). The reservoir is located approximately 5 km upstream of the Arkansas-Louisiana border and just downstream of the confluence of the Ouachita and Saline rivers. Felsenthal Reservoir is eutrophic and located entirely within the 26,304-ha Felsenthal National Wildlife Refuge (Olive et al. 2010). Due to the flat terrain of this region, Felsenthal Reservoir more than doubles in surface area to 14,570 ha during winter, when water levels are increased approximately 3 m for waterfowl management. Felsenthal Reservoir and the refuge are bisected by the Ouachita River main channel and contain most of the floodplain and backwater habitats for the entire river system. These floodplain habitats include numerous interconnected creeks, sloughs, swamps, and shallow lakes (Timmons 2012). In 2009, the Arkansas Game and Fish Commission (AGFC) implemented a 330-mm minimum-length limit on largemouth bass in the Felsenthal Reservoir portion of the river (excluding selected floodplain lakes).

### Fish Collections

Largemouth bass ( $n = 304$ ; total length [TL] = 131–557 mm; ages 1–7) were collected from 21 random locations throughout Felsen-

thal Reservoir during May–June from 2008–2010 by University of Arkansas at Pine Bluff (UAPB) biologists. Additional largemouth bass also were collected by AGFC biologists during April–July 2010 from 10 locations between Camden and Felsenthal Dam ( $n = 156$ ; TL = 160–512 mm; ages 1–8). Largemouth bass mean TL was similar between UAPB (298, SE = 5) and AGFC (317, SE = 7) collections, with overlapping 95% confidence limits. However, mean ages did exhibit slight differences between the two collections (UAPB mean 2.2 yrs, SE = 0.1; AGFC mean 2.7 yrs, SE = 0.2), with 95% confidence limits separated by only 0.1 yrs. We decided this age difference was not biologically significant; thus, the UAPB and AGFC largemouth bass collections ( $n = 460$ ) were pooled and used in further analyses. Overall, 87% of the fish included in this study were collected from the Felsenthal Reservoir portion of the study area. All bass were collected with boat-mounted electrofishing using a Smith-Root Model 5.0 or 7.5 GPP (Smith-Root, Inc., Vancouver, Washington). Electrofishing was conducted during daytime using settings of 500–1000 V / 60-hz pulsed-DC which achieved currents of 2–4 A, dependent on local conductivity. All largemouth bass collected were returned to the laboratory on ice and frozen for later processing.

In the laboratory, individual largemouth bass were thawed, measured (TL, mm), and weighed (g). Sagittal otoliths were extracted for age estimation following standard procedures. Whole otoliths were processed using procedures identical to those described in Fernando et al. (2014). Digital images were taken of each whole-view otolith using Spot Advanced imaging software (Diagnostic Instruments, Inc., Sterling Heights, Michigan). Otoliths determined to be older than age 3 by whole-view reading were transverse sectioned, imaged, and re-aged following Buckmeier and Howells (2003). Ages determined from the sectioned otoliths were considered to be the true age of the fish and were used in further analyses. All otolith images were read double-blind by 2–3 independent readers; between-reader discrepancies were resolved either through consultation between the readers or by a third reader who served as a tie-breaker. The third reader had > 20 yrs experience reading otoliths and further re-read every individual whole-view and sectioned otolith as a quality assurance/control measure.

### Population Metrics

Age-frequency data were used to characterize largemouth bass recruitment with the Recruitment Variability Index (RVI). Values for RVI were calculated following Guy and Willis (1995) as:

$$RVI = [S_N / (N_m + N_p)] - (N_m / N_p),$$

where  $S_N$  = the summation of the cumulative relative frequencies of all age classes used in analyses,  $N_m$  = the number of age-groups

missing from the sample that should be present, and  $N_p$  = the number of age-groups present in the sample. The RVI provided a general index of largemouth bass recruitment stability for the lower Ouachita River during the years prior to sampling which included the life spans of all age classes collected. Instantaneous total mortality ( $Z$ ) and total annual mortality ( $A$ ) of age 2–8 largemouth bass were estimated using a standard weighted catch-curve analysis (Miranda and Bettoli 2007). Largemouth bass younger than age 2 were excluded due to underrepresentation of these ages from electrofishing. Upper and lower 95% confidence limits on  $A$  estimates were generated by nonparametric bootstrapping of the regression residuals (Fernando et al. 2014). Additionally, recruitment variation was assessed using residual analysis conducted on the catch-curve regressions (Maceina 1997). Growth was assessed by fitting a von Bertalanffy model to TL and age data using standard nonlinear modeling procedures (SAS Institute 2008).

**Growth Increment Determination**

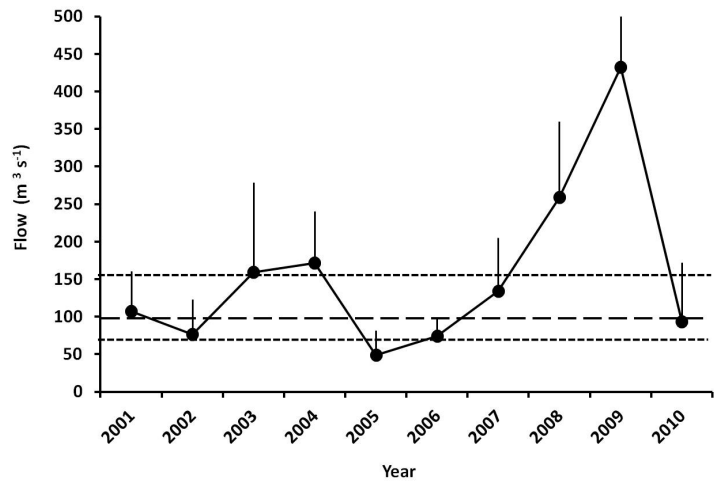
Age and growth analysis was conducted for all largemouth bass using the direct proportion (“Dahl-Lea”) method (Schramm et al. 1992, Maceina et al. 2007). From the digitized otolith images, ages were determined by counting individual annuli, with total length at age and annual growth increments calculated using the direct proportion method as:

$$L_i = \frac{A_i}{A_c} \times L_c$$

where  $L_i$  = length at age  $i$ ,  $L_c$  = length at time of capture,  $A_i$  = distance from otolith nucleus to annuli  $i$ , and  $A_c$  = distance from otolith nucleus to the otolith edge. Annual growth increments (GI) were computed as the differences between successive  $L_i$  measurements (i.e.,  $GI_{(i-1)-i} = L_i - L_{i-1}$ ). In this study, growth increments were referenced to the two ages they occurred between. For example, GI 1–2 referred to the growth increment in mm that occurred for largemouth bass between ages 1 and 2, and so forth for GI 2–3, GI 3–4, GI 4–5, GI 5–6, GI 6–7, and GI 7–8. For all otoliths that were transverse sectioned (i.e., age  $\geq 4$ ), growth increments were calculated from the sectioned images. Incremental growth that occurred during the years of sampling (i.e., between the time of annuli formation and date of fish collections) was excluded from these analyses.

**Hydrologic Data Classification**

Daily flow data for the lower Ouachita River were obtained from the U.S. Geological Survey (USGS)—Arkansas Water Science Center in Little Rock ([waterdata.usgs.gov/usa/nwis](http://waterdata.usgs.gov/usa/nwis)). Monthly flow means were generated from daily data for the Camden gage (USGS #07362000) which was immediately upstream of the



**Figure 1.** Mean June–October flows for the lower Ouachita River, Arkansas, 2001–2010. Measurements were recorded from the Camden gage upstream of Felsenthal Reservoir. Data for 2007 were estimated from the next upstream gage (Arkadelphia) because the Camden gage was inoperable during most of that year. Vertical bars represent coefficients of variation reflecting monthly means. Horizontal lines represent the 25th percentile (bottom), 50th percentile (middle), and 75th percentile (upper) of June–October flows for each year. Years with mean flows falling above the 75th percentile line represent high-flow years (2003–2004, 2008–2009), whereas years with mean flows falling below the 25th percentile represent low-flow years (2005–2006). All other years represent average-flow years (2001–2002, 2007, 2010).

study area. For most of calendar year 2007, the Camden gage was inoperable, in which case, similar data from the next upstream gage in Arkadelphia (National Oceanographic Atmospheric Administration—National Weather Service, #AKDA4; [www.water.weather.gov/ahps](http://www.water.weather.gov/ahps)) were used for that year. Monthly flow means were further used to calculate mean flows for each year that encompassed only the largemouth bass growing season, assumed to be June through October in southern Arkansas (Carlander 1977). Based on observed age structures (up to 8 yrs) and years of sampling (2008–2010), life spans of largemouth bass used in this study encompassed the years 2001–2010.

Each year during the period 2001–2010 was categorized as “high-flow,” “average-flow,” or “low-flow” based on analysis of mean June–October flow quartiles for the period 1970–2011. Using this classification criteria, years with mean June–October flows exceeding the 75% quartile were classified as “high-flow”; whereas, years with mean June–October flows less than the 25% quartile were classified as a “low-flow” (Figure 1). All remaining years where mean June–October flows fell between the 25% and 75% quartiles were classified as “average-flow.” Using this approach for classifying the years 2001–2010, two years were classified as low-flow (2005–2006), four years were classified as high-flow (2003–2004 and 2008–2009), and four years were classified as average-flow (2001–2002, 2007, 2010) (Figure 1).

Data Analysis

Back-calculated growth increments derived from each individual largemouth bass were classified by the back-calculated age of the fish and year that the growth occurred, with years corresponding to the “high-flow,” “low-flow,” and “average-flow” categories above. Growth increments were assembled into a two-way factorial analysis of variance (ANOVA) design. In the ANOVA, “age” (i.e., back-calculated ages 1–8) and “flow” (i.e., flow classification for each year) served as the main effects, with an “age × flow” interaction term included (Isely and Grabowski 2007). Annual growth increment of individual largemouth bass was the response variable, with growth increments generated from individual largemouth bass serving as the replicates ( $n=1063$ ). Additionally, a least-squares means post-hoc test was conducted to assess the significance of pair-wise comparisons of growth increment across different combinations of flow and back-calculated age. All statistical analyses were conducted using the Statistical Analysis Software (SAS), V.9.2 (SAS Institute 2008). Statistical significance for all analyses was declared at  $P \leq 0.05$ .

Results

Population Metrics

Age structure for largemouth bass indicated that ages 1–4 comprised 93% of the population, with the oldest individual aged 8 yrs. Ages 1 and 2 represented the greatest overall percentage (63%) of the population (Figure 2). The composite RVI calculated for largemouth bass was 0.49, indicating that recruitment had been generally stable during the 2001–2010 period. RVI values calculated by individual years indicated moderately stable recruitment, with values ranging from 0.08–0.33 during 2008–2010 and no missing age classes observed. Catch-curve analysis indicated that total annual mortality ( $A$ ) of largemouth bass averaged 48% (95% CL 42%–54%) during 2008–2010, ranging from 40% (95% CL 29%–49%) in 2008 to 59% (95% CL 54%–64%) in 2010. Using residual analysis on a composite catch curve (i.e., 2008–2010 pooled), results similarly indicated stable recruitment, as did residual analyses conducted on 2009 and 2010 data. However, analysis of the 2008 catch curve indicated that the 2003 year class was weaker than expected, and the 2001 and 2006 year-classes were stronger than expected (Figure 3).

Growth of largemouth bass based on mean back-calculated lengths was initially fast but leveled off by age 5 (Table 1). Von Bertalanffy growth model parameters of 513 mm for  $L_{\infty}$ , 0.324 for  $K$ , and  $-0.314$  for  $t_0$  were computed from mean back-calculated lengths at age. Growth model results indicated that largemouth bass reached 300, 380, and 430 mm TL in 2.5, 3.9, and 5.3 yrs, respectively. These estimates indicated that approximately 57% and 18% of the population were composed of quality-sized fish (i.e.,  $\geq$

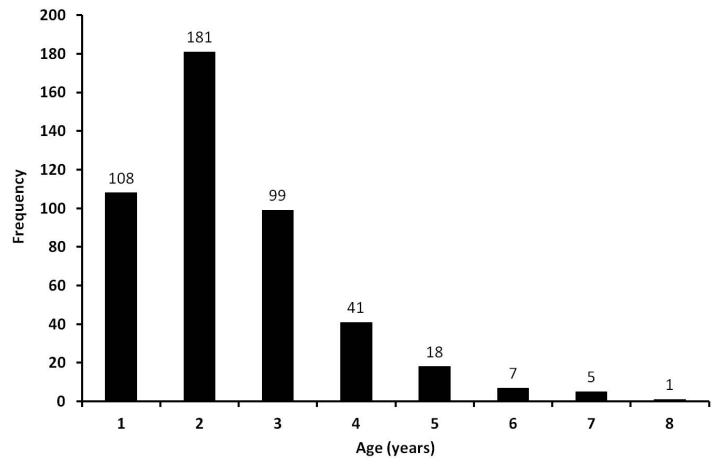


Figure 2. Age-frequency distribution of largemouth bass ( $n = 460$ ) collected from the lower Ouachita River, Arkansas, 2008–2010. Numbers above each bar represent sample sizes for each age.

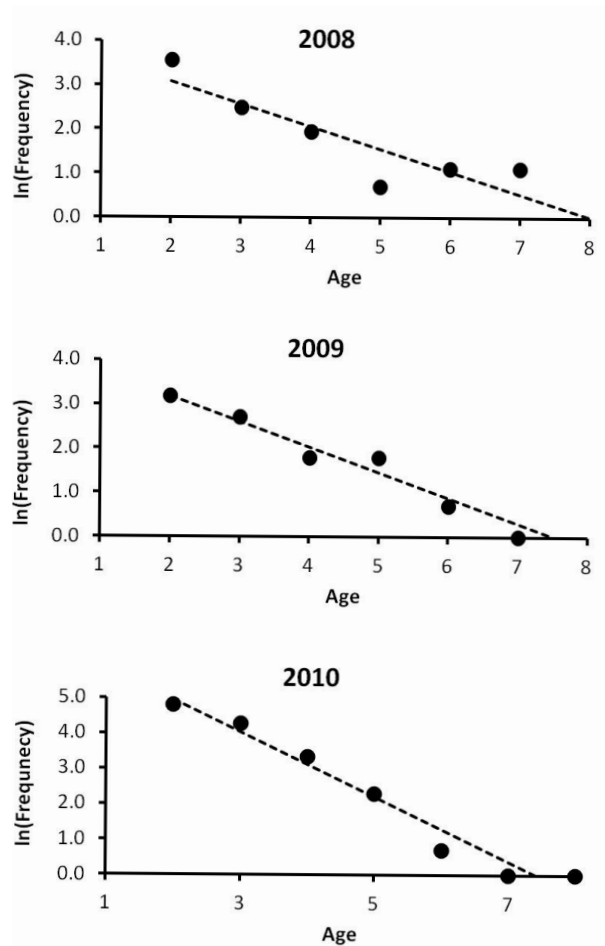


Figure 3. Catch curves from largemouth bass collected from the lower Ouachita River, Arkansas, 2008–2010. Vertical distances between data points and line represent ordinary regression residuals following Maceina (1997).



**Table 1.** Mean backcalculated lengths at age for largemouth bass ( $n = 460$ ) from the lower Ouachita River, Arkansas, collected during 2008–2010. Numbers in parentheses represent standard errors.

Age $i$	$n$	Mean back-calculated length at age $i$ (mm)	GI from age $i-1$ to age $i$	Mean growth increment (mm) from age $i-1$ to age $i$
1	460	173 (2)	0–1	173 (2)
2	352	274 (2)	1–2	99 (2)
3	171	345 (3)	2–3	60 (2)
4	72	384 (3)	3–4	34 (2)
5	31	415 (5)	4–5	28 (3)
6	13	441 (13)	5–6	22 (3)
7	5	461 (28)	6–7	16 (3)
8	1	488	7–8	14

**Table 2.** Mean growth increments for largemouth bass ( $n = 454$ ) from the lower Ouachita River, Arkansas collected during 2008–2010. Growth increments presented by back-calculated age and flow category. Numbers in parentheses represent standard errors. Ages 7–8 excluded from this analysis; means with common letters are not significantly different ( $P > 0.05$ ).

GI from age $i-1$ to age $i$	$n$	Low flow < 65 m <sup>3</sup> sec <sup>-1</sup>	Average flow 65–153 m <sup>3</sup> sec <sup>-1</sup>	High flow > 153 m <sup>3</sup> sec <sup>-1</sup>
0–1	454	170 (4)	175 (3)	174 (3)
1–2	346	111 (3) a	105 (3) b	94 (2) c
2–3	165	70 (4) a	64 (4) ab	57 (2) b
3–4	66	46 (7) a	36 (4) ab	30 (2) b
4–5	25	29 (4)	28 (7)	29 (4)
5–6	7	–	28 (1)	28 (9)

300-mm TL) and preferred-sized fish (i.e.,  $\geq 380$ -mm TL), respectively, though neither figure was adjusted for the underrepresentation of age-1 fish from sampling.

**Growth-Hydrology Relationships**

As expected, largemouth bass growth increments declined with fish age. Six largemouth bass aged 7–8 yrs old were excluded from this analysis due to low sample sizes that caused the flow main effect to be incompletely crossed within the ANOVA. First-year growth increment (i.e., GI 0-1) of Ouachita River largemouth bass averaged 173 (SE = 2) mm but declined with age from 99 (SE = 2) mm for GI 1–2 to less than 20 (SE = 3) mm for GI 6–7 and GI 7–8 (Table 1). Two-way factorial ANOVA results indicated largemouth bass growth was significantly affected by age ( $F = 384.2$ ,  $df = 5$ ,  $P < 0.0001$ ) but not flow ( $F = 1.12$ ,  $df = 2$ ,  $P = 0.3265$ ), with the age  $\times$  flow interaction also not significant ( $F = 1.57$ ,  $df = 9$ ,  $P = 0.1196$ ). The analysis was re-run without the age  $\times$  flow interaction term, in which case effects were significant for age ( $F = 546.6$ ,  $df = 5$ ,  $P < 0.0001$ ) and flow ( $F = 3.78$ ,  $df = 2$ ,  $P = 0.0231$ ). From the least-squares means post-hoc test, flow significantly affected largemouth bass growth increment for most ages, though the effect was most pronounced for ages 2–4. In particular, age 2–4 largemouth bass

grew significantly faster during low-flow years compared to years with high-flow conditions (Table 2). Additionally, growth of age-2 largemouth bass was significantly greater during average-flow years compared to high-flow years. Largemouth bass growth during average-flow years was similar to both high-flow and low-flow years for age-3 (i.e., GI 2–3) and age-4 (i.e., GI 3–4) largemouth bass (Table 2). Growth increment of age-1 (i.e., GI 0–1) and older age 5–6 (i.e., GI 4–5 and 5–6) largemouth bass exhibited no flow effects ( $P > 0.05$ ). Sample sizes were large for age-1 bass ( $n = 454$ ) and likely did not lack statistical power but were much lower for the age-4 and age-5 fish ( $n = 32$ ).

**Discussion**

**Population Metrics**

Growth of largemouth bass in the lower Ouachita River was above average in comparison to similar populations in other systems, many of which were from reservoirs or river mainstem lock and dam systems. In general, largemouth bass lengths at age from the lower Ouachita River exceeded national averages and other Arkansas populations by 10%–15% at ages 1–8 (Beamesderfer and North 1995). The von Bertalanffy growth coefficient ( $K$ ) also suggested above-average growth compared to other populations. The  $K$  coefficient of 0.32 exceeded the Arkansas average (0.29) and the North American average (0.21) reported by Beamesderfer and North (1995), but was similar to an earlier value from Felsenthal Reservoir (0.36; Turman and Olive 2007). Largemouth bass in the lower Ouachita River reached quality size in 2.5 yrs, faster than the 3.6-yr average reported by Beamesderfer and North (1995), but slower than the Arkansas River average (2.0 yrs) reported by Eggleton et al. (2010). However, theoretical maximum size ( $L_{\infty}$ ) of the lower Ouachita River population was only 513-mm TL. Although this parameter approximated only the 25th percentile of values reported in Beamesderfer and North (1995), it was similar to two earlier estimates from the system, both of which were < 500-mm TL (Turman and Olive 2007, Olive and Yung 2014). The lower Ouachita River largemouth bass population appears to be reaching quality size faster than other populations though may not be reaching the large sizes found in other systems. Although largemouth bass exploitation in Felsenthal Reservoir has historically always exceeded statewide averages (32%; Olive and Yung 2014), excessive angling mortality was not suspected to be influencing the lack of larger bass > 500-mm TL.

Observed annual mortality was similar to multiple estimates reported for the Arkansas River population by Eggleton et al. (2010) and Peacock et al. (2011). RVI values and residual analysis further indicated the Ouachita River largemouth bass population had relatively stable recruitment. The 2008 data indicated that the 2001

and 2006 year classes may have been strong, but these data may have been compromised by small sample sizes ( $n=5$  for the two year classes combined), and thus, concluding weak or strong year-classes from these observations was unwarranted. The 2008 catch curve also indicated that the 2006 year class was strong, which was spawned in a low-flow year. However, observed abundances of this cohort in subsequent catch curves suggested average year-class strength. Thus, it seems likely that largemouth bass recruitment in the Ouachita River was relatively stable during 2001–2010, as suggested by the RVI and catch curves.

### Growth-Hydrology Relationships

High flows and associated flooding typically beneficial to fishes in large river-floodplain systems (e.g., Junk et al. 1989) may not always result in increased growth rates for largemouth bass in more highly regulated river systems such as the lower Ouachita River. Hydrology-related growth decreases have important implications for largemouth bass, which is the most important sport fish in southern U.S. waters (Noble 2002). Higher-flow conditions in most regulated river systems are associated with greater depths because rivers are impounded and floodplains are leveed, faster seasonal and annual current velocities, reduced river-floodplain connectivity, and greater turbidities due to faster flows (Bolstad and Swank 1997, Pinter et al. 2008, Schramm et al. 2015). In the lower Ouachita River, mean flows have been steadily increasing on decadal time scales. For instance, mean June–October flows were  $73.4 \text{ m}^3 \text{ sec}^{-1}$  in the 1940s,  $90.4 \text{ m}^3 \text{ sec}^{-1}$  in the 1960s,  $107.4 \text{ m}^3 \text{ sec}^{-1}$  in 1980s, and  $168.9 \text{ m}^3 \text{ sec}^{-1}$  in the 2000s. These flow increases are significant and likely related to a combination of watershed practices that have evolved in the Ouachita River basin during the past century. Although two reservoirs were built on the mainstem Ouachita River in 1924 and 1930, three additional reservoirs were constructed upstream in the basin between 1950 and 1972. All five dams are hydropower projects with managed water releases which could be expected to affect summer flows coincident with seasonal hydropower demands. Another possibility might be the widespread conversion of bottomland hardwood forests to other land uses (e.g., pine plantations) in large portions of the basin which has been shown to alter watershed hydrology to varying degrees in other systems (Harris and Gosselink 1990). Constructed levee systems isolate floodplain habitats from the main river and can alter hydrology by way of reducing flood storage capacity in floodplains (Pinter et al. 2008). However, the majority of levee construction in the Ouachita River basin has occurred downstream of Felsenthal Reservoir in Louisiana.

Inverse relationships between largemouth bass growth and river flows may not be surprising in a regulated river system such as the

lower Ouachita River. During the past century, flow regimes in the Ouachita River have likely shifted away from the river's historical hydrograph which may have contained more optimal conditions for species like largemouth bass. Largemouth bass evolved in free-flowing river-floodplain ecosystems of the southern United States and prefer shallow, slow-moving, and clearer waters for spawning, feeding, and growth (Heidinger 1975). Largemouth bass growth reductions observed in this study could be attributed to several factors. Reductions in floodplain habitats are considered a lesser possibility, at least for the Felsenthal Reservoir area of the basin, because this area contains most of the available floodplain in the basin and is protected within a national wildlife refuge. Turbidity increases that are often associated with increases in river flow (e.g., Bariller et al. 1993) are a possibility, given that experimental studies have documented turbidity effects (e.g., lower foraging success) on sight-feeding largemouth bass (Reid et al. 1999, Shoup and Wahl 2009). While this statement is not meant to imply that high water is always “bad” for largemouth bass, it may be possible that high-water extremes could be detrimental to largemouth bass in some systems, especially if improperly timed during the year or occurring in consecutive years. For example, in the lower Ouachita River, mean June–October flows in 2008 and 2009 were 3.5-fold and 2.1-fold greater than the long-term (1970–2011) average. In the case of 2009, the mean June–October flow exceeded the long-term average by nearly four standard deviations (Figure 1). If the proposed bass growth-hydrology linkage is true, it may be more common and detectable in a system like the lower Ouachita River. This system is similar to many others in the southern United States, in that it contains multiple locks and dams, has upstream hydropower projects with managed releases, and has undergone widespread land-use changes within its watershed during the past century. It is possible that many of the effects on fishes purported under the flood-pulse concept (Junk et al. 1989) may be dampened or non-existent in more highly regulated river systems.

If largemouth bass growth decreases in response to high flows, as suggested by this study, the effect may persist in the population for extended periods of time. For example, when annual growth is hindered early in life, the effect may be compounded such that cohort mean size is reduced over several years. Recovery from this deficit may be difficult because cohort growth increments decrease with age (e.g., Ricker 1975), and maximum age of largemouth bass in this and similar systems appears to be only about 8–10 yrs (Eggleton et al. 2010, Olive and Yung 2014). In other words, above-average growth at ages 5–7 is unable to compensate for poor growth at ages 2–4 when growth potential is greater. While a 20–25 mm growth deficit may seem quite small, the cumulative effect throughout the life of the cohort may affect the size structure of

the fishery, especially if the high-flow years are consecutive. In the case of the lower Ouachita River, the growth increment differences between low-flow and high-flow years averaged 17 mm, 13 mm, and 16 mm for ages 2–4, respectively, and averaged 15 mm overall (Table 2). Assuming these growth increment figures are additive, the affected largemouth bass cohort would have been 30 mm smaller on average following two high-flow years that occurred consecutively. This scenario may not be that unusual, as the four high-flow years classified in this study contained two pairs of consecutive years. In fact, this observation was similar to what Peacock (2011) observed over a 40-yr period in the Arkansas River, where both low-flow and high-flow years occurred consecutively on decadal time scales. Winkley (1977) also reported that years of hydrologic extremes (both high and low) occurred in distinct groups over nearly 100 years in the lower Mississippi River. Both of these findings suggest that river hydrology may be regulated by larger-scale, perhaps even continental, factors. Although managing such hydrologic factors would not be possible, understanding such mechanisms would aid future largemouth bass management.

Hydrology-induced growth reductions have other management implications for largemouth bass. In the lower Arkansas River, Peacock et al. (2011) reported that largemouth bass took one additional year on average to reach the legal minimum-length limit (381 mm TL) as a result of three consecutive years (2007–2009) of high-flow conditions (i.e.,  $\geq 1$  SD above 40-yr mean flow) that appeared to significantly reduce growth of younger (i.e., age 1–3) cohorts. During this extra year that largemouth bass took to recruit into the fishery, individuals were subjected to additional natural mortality and catch-and-release mortality despite being unavailable for harvest, which likely reduced the number of fish recruiting to the fishery (Peacock et al. 2011). The importance of good growth during the early part of a fish's life history has been previously hypothesized. Adams et al. (1982) suggested that good first-year growth helped reduce overwinter mortality of juvenile largemouth bass. Similarly, Adams and DeAngelis (1987) and Ludsin and DeVries (1997) suggested that earlier largemouth bass hatch dates facilitating earlier switches to piscivory was important in affecting juvenile largemouth bass first-year growth and eventual year-class strength. If the proposed growth-hydrology mechanism for largemouth bass is valid, the combined decrease in cohort size might also affect angler satisfaction, as the smaller cohorts remain abundant in the fishery.

Our results suggested that high-flow periods typically beneficial to fishes in large river-floodplain systems may not always result in increased growth rates for largemouth bass in more highly regulated river systems such as the lower Ouachita River. Further understanding of fish growth-hydrology relationships may be vital

for future largemouth bass management in light of documented climate change (e.g., Rypel 2009), and associated predictions concerning more extreme weather patterns and increased frequencies of hydrologic extremes in many river systems (Ficke et al. 2007).

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