Size of age-0 crappies (Pomoxis spp.) relative to reservoir habitats and water levels

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Variable year-class strength is common in crappie *Pomoxis* spp. populations in many reservoirs, yet the mechanisms behind this variability are poorly understood. Size-dependent mortality of age-0 fishes has long been recognized in the population ecology literature; however, investigations about the effects of environmental factors on age-0 crappie size are lacking. The objective of this study was to determine if differences existed in total length of age-0 crappies between embayment and floodplain habitats in reservoirs, while accounting for potential confounding effects of water level and crappie species. To this end, we examined size of age-0 crappies in four flood-control reservoirs in northwest Mississippi over 4 years. Age-0 crappies inhabiting uplake floodplain habitats grew to a larger size than fish in downlake embayments, but this trend depended on species, length of time a reservoir was dewatered in the months preceding spawning, and reservoir water level in the months following spawning. The results from our study indicate that water-level management may focus not only on allowing access to quality nursery habitat, but that alternating water levels on a multiyear schedule could increase the quality of degraded littoral habitats.

**Keywords:** reservoir habitat; water level; *Pomoxis*; age-0; size distribution

Introduction

Crappie *Pomoxis* spp. populations are dynamic, often influenced by many factors that affect recruitment, such as hatching success, larval and juvenile growth, and size entering their first winter of life (Sammons et al. 2001; McCollum et al. 2003; Sogard 2007). Various studies have examined inter-annual variability of abundance of age-0 crappies relative to environmental factors. Some of the factors considered include water quality variables such as turbidity (Spier & Heidinger 2002), temperature (St. John & Black 2004), and dissolved oxygen (Hale 1998), although none of these have produced consistent results. Water regime has also often been studied relative to year-class strength (Mitzner 1981; Maceina & Stimpert 1998; Sammons et al. 2002; Dagel & Miranda 2012). Abundances of age-0 crappies have generally been linked to high water levels during spawning and low water levels in the preceding year, a water regime that can allow for growth and flooding of vegetation in substrates that enhance spawning success as well as cover and food for juveniles (Siefert 1968). Despite the foci of past studies investigating variable crappie recruitment, pre-winter body size of age-0 crappies is likely an influential factor in subsequent survival, and thus, recruitment. Other than Sammons et al.
(2001), the published literature has given only limited attention to factors that produce variability in size of age-0 crappies. Large body size for age-0 fishes may provide survival advantages over their smaller bodied conspecifics. High overwinter mortality among smaller age-0 fish has been attributed to depletion of energy reserves during extended periods of cold water temperature (Oliver et al. 1979; Gutreuter & Anderson 1985; Miranda & Hubbard 1994). More recently, predator—prey interactions have been used to explain size-specific survival in age-0 fishes as a function of predator gape limitations (Nilsson & Brönmark 2000) and increased predator avoidance by larger fish (Lundvall et al. 1999). The rather extensive amount of literature recognizing size-specific mortality of age-0 fishes supports the value of studies that seek to better understand factors affecting size attainment during the first year of life (reviewed by Sogard 2007).

Availability of suitable habitat may also play an important role in shaping body size of age-0 fish (Tupper & Boutiller 1995). Reservoirs impounded over floodplain rivers are unique because they may include in their upper reaches extensive shallow water representing the exposed floodplain of the impounded river (Miranda 2008). Reservoirs that experience large seasonal water-level fluctuations as part of their operational objective (i.e., flood control) mimic, to an extent, the natural seasonal inundation of upstream floodplain areas. This seasonal flooding likely benefits crappies, which have evolved to rely on seasonal access to floodplains to complete their life cycle (Hocutt & Wiley 1986). In years when floodplains are not inundated, rearing areas in reservoirs may be restricted to shallow waters in embayments. Embayments of aging reservoirs are characterized as having high gradient, eroded banks, often including broad bands of mudflats with no or little vegetation (Fujita 1977; Kaczka & Miranda 2013) and, therefore, provide inferior littoral habitat for juvenile crappies.

Timing of flooding is also a likely factor in determining habitat quality for age-0 fishes. Water levels in flood control reservoirs are often drawn down during the late summer or early fall and the dewatered period until the first frost represents a window for vegetative growth in exposed substrates. Although water levels in flood control reservoirs are often managed by a guide curve (Mower & Miranda 2013), the hydrograph in any given year is partly influenced by the amount of precipitation in that year. Thus, the length of the dewatered period during the late summer/early fall may vary from year to year, resulting in differing amounts of vegetation and, therefore, spawning and nursery habitat, available the following year.

Given this background, continued research on the interactions of habitat availability, water regime, and age-0 crappie size may improve understanding of how to enhance potential control over year-class strength in reservoirs. Thus, the objective of this study was to determine if differences existed in total length of age-0 crappies between embayment and floodplain habitats, while considering the effects of water level and crappie species.

**Methods**

**Study sites**

This study was carried out within embayments and inundated upstream floodplain areas of Arkabutla (34° 45’ 26” N, 90° 07’ 28” W), Enid (34° 09’ 28” N, 89° 54’ 14” W), Grenada (33° 48’ 32” N, 89° 46’ 14” W), and Sardis (34° 24’ 21” N, 89° 47’ 25” W) reservoirs in northwest Mississippi. The four reservoirs were constructed in the 1940s and 1950s,
and at normal (i.e., summer) pool differs in area from 4800 to 14,500 ha and in mean depth from 2.9 to 5.6 m. The primary use of these reservoirs is for floodwater storage; as such, these systems experience extreme annual water-level fluctuations (3.3–7.3 m) following guide curves established by the US Army Corps of Engineers. However, variation in annual precipitation may cause water levels to exceed or fall below the guide curve.

All four reservoirs have similar characteristics due to their close geographic proximity (within a 50 km radius), age, and large water-level fluctuations. Annual fluctuations over the past 60–70 years have caused degradation of habitat in littoral zones, habitat that is valuable to a reservoir’s fish community (Meals & Miranda 1991). However, habitat degradation is not uniform throughout these reservoirs. Downstream embayments are often characterized as having high gradient, eroded shorelines that are devoid of vegetation due to wind and wave action and continual water-level fluctuations (Miranda et al. 2014). Conversely, upstream reaches of the study reservoirs are typified by low-gradient bottom profiles and wetland habitats as the wide floodplains of tributary rivers meet the reservoirs. These upper reaches are flooded during April–August in over 90% of years to provide seasonal fish habitat valued as spawning and rearing grounds for floodplain-oriented species (Miranda et al. 2014). Due to their morphometric differences, embayment and floodplain habitats are affected by water-level increases differently. Depending on reservoir, floodplains become inundated when water levels are as low as 2–3 m below normal pool, whereas ample vegetation in embayments does not become inundated until water levels are at or above the normal pool.

**Fish collections**

Age-0 crappies were collected from embayments and floodplains in the four study reservoirs using trap nets (i.e., modified fyke nets), in late-July to mid-August (day of year 205–230), during 2009–2013. Boxrucker and Ploskey (1988) reported that trap nets effectively sampled age-0 crappies and provided adequate data for making spatial and temporal comparisons. Sampling in late summer addressed two concerns: (1) sampling was carried out before scheduled decreases in water level that would limit motorboat access to sampling sites, and (2) age-0 fish were large enough to be retained by the net’s mesh and small enough to easily separate from age-1 fish based on their length–frequency distributions. Trap nets had 0.9 m × 1.8 m rectangular frames spaced 0.6 m apart, a 0.9 m × 30 m lead equipped with a float line and lead line, and a 13-mm nylon bar mesh (Miranda & Boxrucker 2009). At least 10 nets were fished over a 24-h period (i.e., a collection) in one embayment and the upstream floodplain in each reservoir and each year, for a total of 32 collections (i.e., two habitats, four reservoirs, and 4 years). Embayments and floodplain areas sampled remained fixed over the course of the study, but individual net locations within these two habitat types were chosen haphazardly and changed year to year. Embayments ranged from 115–440 ha in surface area, and floodplains ranging 970–1815 ha. Netted crappies were preserved on ice and later identified to species and measured for total length (nearest 0.5 mm) at a laboratory.

**Water levels**

We downloaded daily water levels in the study reservoirs from www.rivergages.com, administered by the US Army Corps of Engineers. These data were used to estimate two water-level-related metrics: (1) average water level during the post-spawn season, and (2) number of frost-free days the reservoir was dewatered below normal pool during the
pre-spawn period. The first metric indexed the extent of flooding and the second, the length of time the reservoir was dewatered to allow plant growth in the regulated zone. Post-spawn average water level was quantified as mean deviation (m) from normal pool during mid-May through mid-August (day of year 136–230). Because normal pool in the study reservoirs occurs at different elevations, describing water level as the mean deviation from normal pool in each reservoir provided a standardized metric for analyses. The number of pre-spawn, dewatered, frost-free days was computed as the number of days between the day of year when water level dropped below normal pool elevation and day-of-year 319 (i.e., average day of year when the first frost occurs in northwest Mississippi; www.weather.com).

**Statistical analyses**

An analysis of covariance (ANCOVA; glmselect procedure, SAS Institute 2012) was used to test if median total length of age-0 crappies differed according to habitat (class variable, fixed), species (class variable, fixed), post-spawn water level (covariate), and pre-spawn dewatered frost-free days (covariate). We analyzed average lengths rather than individual lengths to diminish the effect of a large sample, and we used median rather than mean because the median better reflected right-skewed length distributions of age-0 crappies. The main effects and all possible interactions were considered by the glmselect procedure; the model was chosen with a backward selection process that retained the model with the lowest Akaike’s Information Criterion corrected score for small sample size (AICc). This variable selection procedure does not rely on hypothesis significance testing to include or exclude variables in a model but instead focuses on the estimation of the effect and its precision (Anderson et al. 2000). An initial scatterplot of the data indicated a curvilinear relationship between median total length and post-spawn water level, so a quadratic term for post-spawn water level was made available to the glmselect procedure. We weighted each median length by its sample size under the assumption that a large collection better informed the model than a small collection. The effects of reservoir and year were not made available to the glmselect procedure as reservoirs were considered replicates because of their similarity, and year was already represented in the model by the different water levels. Adding reservoir and year into the model would likely improve the coefficient of determination of the final model but reduce the generality of our conclusions and most likely produce an overfit model.

**Results**

In all, 339 trap-net samples collected 5532 age-0 crappies over 4 years of study were included in this analysis. In 2012, water levels remained low and never inundated the floodplain; thus, no fish data for the floodplains were available to compare with data collected in the embayments and 2012 had to be left out of the analyses. Catchment of age-0 crappies per trap net ranged from 0 to 55 and averaged 16 fish. Collections from floodplains comprised 75% of the total catch. White crappies, *Pomoxis annularis* represented 77% of the total catch versus black crappies, *Pomoxis nigromaculatus* at 23%. Distribution of white crappies favored floodplain habitats, which produced 76% of the total white crappie catch versus 24% from embayments. Black crappie distribution was similar with floodplains producing 69% of the total catch versus 31% from embayments. Total length ranged from 43–106 mm for white crappies and 45–108 mm for black crappies.
Post-spawn water level and pre-spawn dewatered frost-free days varied greatly among reservoirs and years. Post-spawn water-level deviation from normal pool ranged from −0.09 to 4.12 m. Pre-spawn number of dewatered frost-free days ranged from 0 to 255 d. The observed extremes in water levels and dewatered frost-free days allowed adequate assessment of the effects of these covariates.

The ANCOVA was applied to 60 median total lengths representing lengths of black crappies and white crappies in 16 embayment collections and 16 floodplain collections made in the four reservoirs over the 4 years. However, one embayment collection (i.e., at least 10 trap nets fished concurrently for a 24-h period) collected no age-0 crappies and was excluded because no fish lengths were available. Also, one collection included only black crappie and another collection only white crappie. The backward elimination procedure with median total length as the dependent variable selected a model ($F_{22.8}; r^2 = 0.68$) that included habitat, pre-spawn dewatered frost-free days, post-spawn water level, and species (Table 1). A main effect of habitat indicated that floodplains generally produced larger age-0 crappies than embayments (Table 1, Figure 1). A main effect of dewatered frost-free days indicated that fish size increased with the number of dewatered frost-free days in the year preceding fish spawning (Figure 1). The effect of post-spawn water level × post-spawn water level indicated that the positive relationship between fish length and post-spawn water level was curved rather than linear as indicated in Figure 1. The interaction of pre-spawn dewatered frost-free days and post-spawn water level indicated that the effect of dewatered frost-free days in year $n$ on length of age-0 crappies depended on the post-spawn water level in year $n + 1$. A longer dewatered period produced larger fish at a given water level; however, the positive effect of dewatered frost-free days increased with water level for both species of crappies (Figure 1). Lastly, the selected model indicated a three-way interaction between post-spawn water level, pre-spawn dewatered frost-free days, and species. This interaction implied that the effect of water level and number of frost-free days on fish length depended on species, of which, black crappies responded more strongly to increases in post-spawn water level and pre-spawn dewatered period (Figure 1).

**Discussion**

Our study indicated differences in length of crappies occupying different habitats. While differences seemed small, they could be meaningful in survival. The difference in median
length of crappies in floodplain habitats versus embayments averaged merely 1.7 mm or 2.6% (floodplain = 66.7 mm, embayment = 65.0 mm); however, according to a length–weight equation reported by Pope and DeVries (1994), this difference in length would translate into a difference in weight of about 12%. Various studies of overwinter survival of age-0 fishes have shown that small fish depleted their energy reserves sooner than large fish (e.g., Oliver et al. 1979; Miranda & Hubbard 1994), although such effects have not been consistent (Johnson & Evans 1990; McCollum et al. 2003).

Floodplains produced larger age-0 crappies. Dewatered embayments grow primarily upland vegetation maladapted to the fluctuations in water level occurring in the study reservoirs. As a result, most upland vegetation has disappeared from the regulated zone of these reservoirs over their 60–70 years of age, producing a wide band of mudflats.
between conservation and normal pool elevations (Kaczka & Miranda 2013). Only above normal pool, where flooding occurs less often and for shorter periods, upland vegetation remains that provides suitable habitat (Miranda et al. 2014). Conversely, floodplains represent lowland environments with flatter bottom profiles and an extensive seedbank of wetland plants better suited to withstand the reservoir’s water-level fluctuations. These habitats allow for a ‘moving littoral’ as described by the flood-pulse concept (Junk et al. 1989); in embayments, the moving littoral effect is essentially non-existent until water level rises above normal pool. Moreover, as water levels rise, floodplains are inundated when water levels are below normal pool, allowing spawning adults access to suitable habitat earlier than in embayments. This access may control time of spawning so that age-0 fish in floodplains may be older and larger than age-0 fish in embayments. According to Miranda, Dagel et al. (2014), adult crappies in floodplains spawned on average eight days earlier than those in embayments.

A longer dewatered interval in the year prior to hatching resulted in increased sizes of age-0 crappies. The longer dewatered interval during the frost-free period allowed for more extensive vegetative growth that, when re-flooded the following year, increased quality of nursery habitat by providing enhanced access to invertebrate prey. Mower (2013) studied a multi-year series of satellite images at Enid Reservoir (included in our study) and reported that a longer dewatered period resulted in greater vegetation development. In our study, the benefits afforded by prolonged pre-spawn dewatered frost-free periods were regulated by post-spawn water level, with the largest fish resulting from a long pre-spawn dewatered interval and a high post-spawn water level. This combination of pre-spawn and post-spawn water regime would conceivably allow for the highest abundance of food by enabling growth of vegetation and ensuring that it is flooded the following year.

During periods of prolonged dewatered frost-free days followed by years of high post-spawn water levels, black crappies might have been able to exploit resources more

Table 2. Model selection summary for an analysis of covariance model relating the predictor class variables habitat and species, and the predictor continuous variables post-spawn water level and pre-spawn number of dewatered frost-free days to the dependent variable median total length of age-0 crappies. The main effects and all possible interactions were considered by a glmsel ect procedure with a backward selection process that retained the model with the lowest Akaike’s Information Criterion corrected for small sample size (AICc).

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effectively than white crappies, as indicated by their larger sizes. The exploitative advantages displayed by age-0 black crappies may be a result of their feeding preferences. Juvenile black crappies are more insectivorous than white crappies (Sievert 1968; Ross 2001), benefitting immediately from the substrate for macroinvertebrates provided by submerged vegetation (De Szalay & Resh 2008). Thus, high post-spawn water level following a year with a long dewatered frost-free period is likely to enhance black crappie size more than white crappie size due to the increased habitat for macroinvertebrate colonization, although sizes of both species are enhanced.

We did not include density in our analyses because it was correlated with water levels as previously reported for the study reservoirs (Dagel & Miranda 2012). Like length, density increased when water level was low at the end of a year and high the following year. Increases in both length and density with high water levels suggest a lack of density-dependent effects within the range of conditions observed during the study period. Conceivably, the increases in water level that produced increases in age-0 crappie size might have also produced increases in population sizes (not measured), but the density of the population might have not changed considering that reservoir volume and area also increased. Thus, due to the increases in available space associated with increased water levels, increases in population size did not produce decreases in growth. Similarly, Sammons et al. (2001) reported strong differences in densities among white crappie year classes yet small differences in length.

Our study suggests that habitat, post-spawn reservoir water level, and pre-spawn length of the vegetation growing season interact to play important roles in determining age-0 crappie size in flood-control reservoirs. Strategies to enhance median length of a new cohort may focus on enhancing habitat and access to habitat through water-level management. Seed banks in uplake floodplains are largely comprised of wetland plants that are tolerant to prolonged inundation and can readily re-establish soon after water levels are dropped (Casanova & Brock 2000). Embayments have seed banks restricted to small floodplains of minor tributaries limited to the upper reaches of the embayment; vegetative growth in embayments is constrained mainly to upland plants whose seeds are mostly blown in by wind (Mower 2013). Water-level management that allows for late-summer drawdowns can potentially rejuvenate vegetation in floodplains and embayments, if there is sufficient rainfall to support vegetation growth or reservoir water levels are further manipulated to periodically moisten the vegetation. In the following spring, water level is raised to inundate the vegetation synchronous with the crappie spawning season. Retaining water at a high level throughout the crappie growing season may increase overall size of age-0 fish before entering their first winter, although prolonged inundation will shorten the time available for plant growth in the fall. Thus, water management policy may include a multi-year schedule that produces a large number of dewatered frost-free days followed by high post-spawn water level over the alternating years.

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