

Spatial Patterns of Florida Largemouth Bass Genetic Introgression into a Northern Largemouth Bass Population after Stocking

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Abstract: To enhance trophy potential of largemouth bass (*Micropterus salmoides*) fisheries, state agencies across the southeastern United States commonly stock Florida largemouth bass (FLMB, *M. s. floridanus*) outside of their native range into native northern largemouth bass (NLMB, *M. s. salmoides*) populations. This practice has been ongoing for decades but spatial patterns associated with the spread of FLMB alleles in a reservoir after stocking are not well understood. From 2007–2015 the Arkansas Game and Fish Commission stocked 250 FLMB fingerlings ha⁻¹ into two embayments of Lake Ouachita, a 16,200-ha highland reservoir in western Arkansas. In 2019, we collected 1000 largemouth bass from throughout the reservoir to examine spatial patterns of FLMB introgression using a panel of 35 species-diagnostic single-nucleotide polymorphisms (SNPs). We determined that 30.4% of individuals were NLMB and 69.6% were hybrids of NLMB and FLMB, with no FLMB collected. Average % FLMB alleles across all individuals collected was 11.4%. Spatial analyses found that FLMB alleles were greater in individuals collected in close proximity to stocking areas and then eastward through the main body of the reservoir. Conversely, FLMB alleles were lower in the western half of the reservoir. Our results provide evidence that localized stocking of FLMB at high densities into a resident NLMB population can lead to widespread genetic shifts even in very large systems, but that most individuals in those systems contain low levels of FLMB alleles.

Key words: stocking evaluation, hybrid, single-nucleotide polymorphisms, genetic admixture

Journal of the Southeastern Association of Fish and Wildlife Agencies 9: 17–24

Largemouth bass (*Micropterus salmoides*) support economically valuable and recreationally important fisheries across North America (USFWS and USCB 2018). Genetic evidence indicates that largemouth bass has two separate subspecies (Fields et al. 1987, Koppleman et al. 1988, Isely et al. 1987, Kassler et al. 2002, Near et al. 2003): the northern largemouth bass (NLMB; *M. s. salmoides*) and the Florida largemouth bass (FLMB; *M. s. floridanus*). The Arkansas Game and Fish Commission (AGFC) has a long history of stocking FLMB, primarily in smaller waterbodies in the southern portion of the state (Dennis et al. 2017), to accommodate angler preferences for trophy fishing opportunities. Evaluations on these systems have found varying levels of successful introgression of FLMB alleles into existing NLMB populations after stocking events (Allen et al. 2009, Lamothe et al. 2012, Lamothe et al. 2016).

Although survival of stocked largemouth bass into established wild populations is typically low (Buckmeier and Betsill 2002, Jackson et al. 2002, Hoffman and Bettoli 2005), survival of stocked FLMB is apparently high enough that FLMB alleles are consistent-

ly found in subsequent generations of largemouth bass years after stocking (Dunham et al. 1992, Fries 2010, Lamothe et al. 2016, Acy 2017, Walsh 2021). Numerous factors have been found to influence the level of genetic introgression into a population, including stocking rate and environmental characteristics such as depth, temperature regime, water-level fluctuation, shoreline development, secchi disk depth, and vegetation (Gilliland and Whitaker 1989, Dunham et al. 1992, Buckmeier et al. 2003, Fries 2010, Acy 2017, Hargrove et al. 2019, Walsh 2021), but no clear consensus exists on specific factors mediating the amount of genetic introgression.

Two embayments of Lake Ouachita, Arkansas, were stocked with FLMB during 2007–2015 with the goal of introgressing FLMB alleles into the local largemouth bass population. Localized stocking is an effective strategy in terms of increasing survival of stocked fish and genetic introgression into a resident population (Dunham et al. 1992, Buckmeier et al. 2003, Lusk et al. 2022); however, there is uncertainty regarding the effectiveness of this strategy for altering lake-wide genetic composition of largemouth bass

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within a large reservoir system. No basin-wide evaluation of admixture following intensive stocking has been conducted in a large reservoir to examine spatial patterns of genetic introgression. The objectives of the present study were to 1) evaluate the basin-wide genetics of largemouth bass to determine if localized stocking successfully introgressed FLMB genetics into the population beyond the local scale, and 2) determine any apparent spatial patterns associated with the spread of the FLMB genetics into the reservoir as a whole.

Study Area

Lake Ouachita is an oligotrophic, highland reservoir in a region of the state that receives less than 3400 heating degree days, which is viewed as the northern limit of stocking FLMB by the AGFC (Gilliland 1992, Dennis et al. 2017). At 16,200 ha, it is also the largest reservoir within the state. Between 2007 and 2015, approximately 100,000 Florida largemouth bass fingerlings were stocked

annually into two adjacent embayments (Buckville and Rabbittail; Figure 1) of Lake Ouachita at a rate of 250 fingerlings ha⁻¹ in the embayments (6.2 fingerlings ha⁻¹ for the entire reservoir). Control samples were taken from broodstock used for stocking. More details on the stocking program can be found in Lamothe et al. (2012) and Lusk et al. (2022). Initial genetic evaluations of this stocking program took place immediately after the stocking program in 2016 and indicated that FLMB alleles had substantially increased in the fish collected at the stocking sites as well as near several high-use boat ramps around the reservoir (Lusk et al. 2022).

Methods

Fish Collection

To collect fish as evenly as possible across the entire shoreline to evaluate spatial patterns in FLMB allele distribution, we selected sampling sites based on a stratified random design. The reservoir was divided into four quadrants (Northwest, Northeast, South-

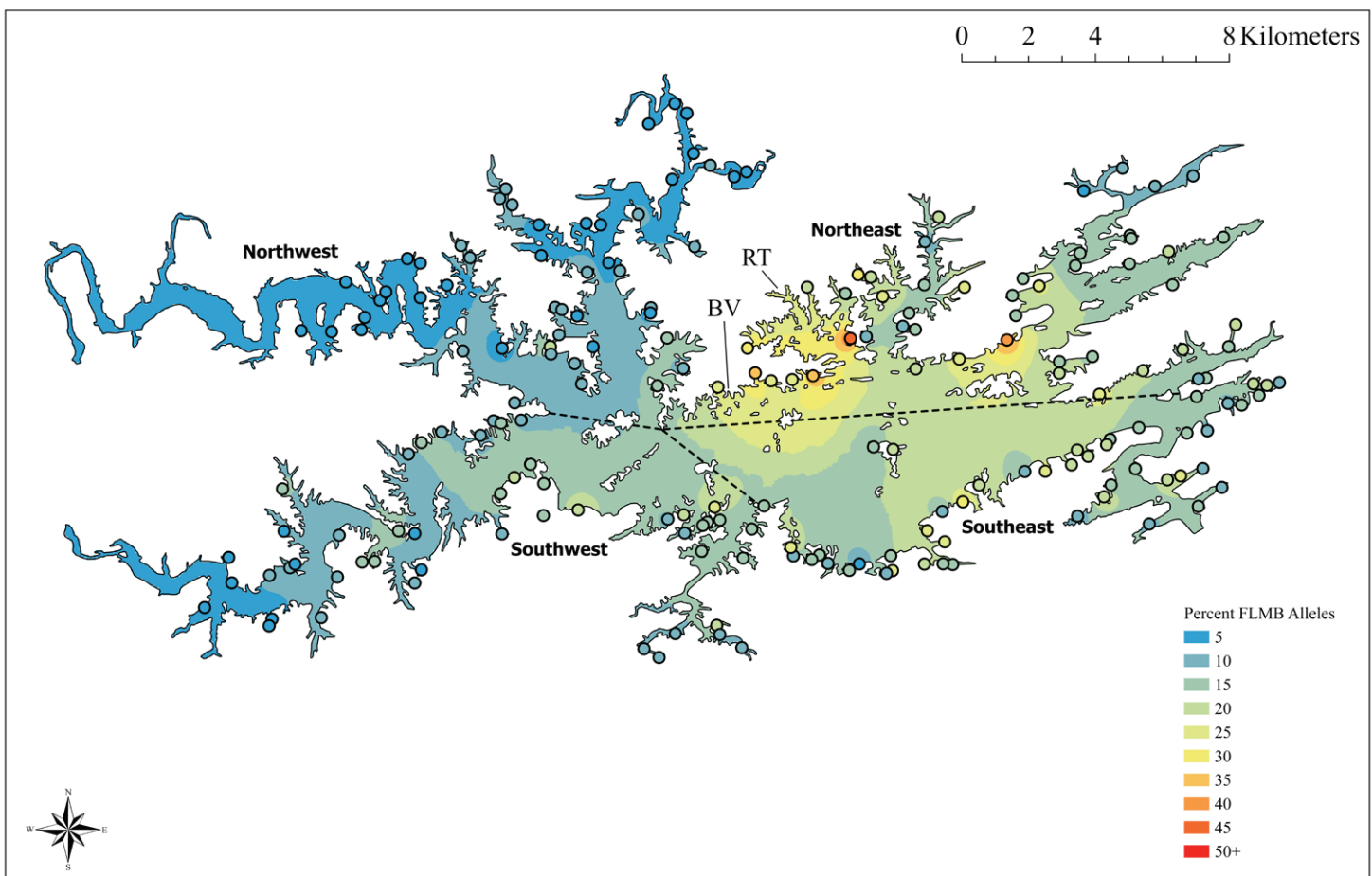


Figure 1. Stocking embayments (RT = Rabbittail; BV = Buckville) and percent of Florida largemouth bass (FLMB) alleles in fish collected during spring 2019 in Lake Ouachita, Arkansas. Location of sample collection is indicated by O markers and the color of each represents the mean % FLMB alleles of the five fish collected in that location. Colors in the reservoir body are interpolated among sampling points using an Inverse Distance Weighted analysis. Dashed lines separate quadrants of the reservoir.

west, and Southeast; Figure 1) based on logistical considerations: every quadrant contained a similar, but not an identical, shoreline distance due primarily to the dendritic nature of the reservoir. Each quadrant was further subdivided into five similarly sized segments based on shoreline distance. Within each segment, potential sample locations were created at regular 600-m intervals along the shoreline of the reservoir and major islands. Ten sampling locations were randomly chosen within each segment with the exception that the selection of adjacent sites was not allowed.

Largemouth bass were collected from Lake Ouachita in early spring 2019 to coincide with the initiation of spawning activity. Because previous work has indicated that the timing of spawn can be affected by size and genetics of a fish (Maceina et al. 1988), we designated two sampling periods intended to encompass the majority of the spawning period in Lake Ouachita (period 1: 18 March–1 April; period 2: 8 April–25 April). Half of the selected sites within each segment were randomly assigned to a time period and segments were electrofished in a different order each period.

Each site was sampled using a boat-mounted DC electrofisher (7.5 GPP, Smith-Root Inc., Vancouver, Washington) moving in a single direction along the shoreline beginning at the selected point until five largemouth bass of any size were collected. Each fish was tagged, labeled by sample location, and immediately put on ice; all collected fish were transported back to the lab for processing generally the next day but at most three days after collection. At the lab, each fish was weighed (g), measured (TL; mm), and had a fin clip removed and preserved in 95% non-denatured ethanol. The genotype of each individual was established using 35 species-diagnostic single-nucleotide polymorphisms (SNPs) previously used to differentiate FLMB and NLMB alleles (Li et al. 2015, Zhao et al. 2018, Johnson 2019, Fewell 2020). This technique provides a cost-effective method with higher resolution than microsatellite techniques that were previously used in Lake Ouachita (Lamothe et al. 2012; Lusk et al. 2022). Genotyping was conducted by the Auburn Genetic and Genomics Laboratory at the School of Fisheries, Aquaculture, and Aquatic Sciences at Auburn University following previously published methodologies (e.g., Davis 2018, Hargrove et al. 2019, Johnson 2019, Fewell 2020).

The percentage of FLMB alleles within an individual's genotype was determined by dividing the total number of FLMB alleles observed by the total number of alleles amplified as described in previous work (e.g., Davis 2018, Johnson 2019, Hargrove et al. 2019) for use in spatial analyses as described below. We classified fish into one of three groups, FLMB, NLMB, or hybrid based on the % NLMB and % FLMB measured: fish with at least 95% alleles of either subspecies were classified as that subspecies, all others were

classified as hybrids (Davis 2018, Johnson 2019). Initial examinations of the raw SNP data indicated that the majority of fish collected contained relatively few FLMB alleles, and patterns of heterozygosity revealed that very few fish would be classified as F_1 or F_2 . Therefore, we chose to group individuals into three categories and did not attempt to further classify individuals by genealogical class.

Spatial Data Analyses

Spatial analyses were conducted using mean values of % FLMB alleles based on the five fish collected at each sample location. Sample locations were converted to points using the centroid and a mean % FLMB allele value was calculated for each centroid. Next, an inverse distance weighted (IDW) analysis (Watson and Phillip 1985) in ArcGIS Pro (version 2.7.0) was calculated using a default power of two and the default search radius settings. The raster was then clipped to the boundaries of the reservoir in ArcGIS. A visual inspection of the results indicated that the interpolated results appeared reasonable. A map showing interpolated % FLMB alleles across the entire reservoir was created by overlaying the centroid points and IDW raster (Figure 1). As an artifact of the analysis, interpolation results span the entirety of the reservoir, including the pelagic zone where no fish were collected.

A hot spot analysis was conducted using the Getis-Ord G_i^* tool (Getis and Ord 1992, Ord and Getis 1995) in ArcGIS Pro to test for significant differences in % FLMB alleles spatially compared to the overall reservoir mean. First, a fishnet with 500-m spacing was created over the reservoir shapefile. The extract value by point tool was then used to obtain the raster value from the IDW layer created as described above at each point location. This value was then used as the input field for the hot spot analysis. Spatial relationships were conceptualized using K nearest neighbors with a default value of eight neighbors selected which appeared reasonable for our study spatial scale. For a point to be a significant hot spot, the point needed to have a high value (high % FLMB alleles) as well as be surrounded by neighboring points with similarly high values. The % FLMB alleles for a point and its neighbors were compared to the reservoir as a whole to determine significance based on a z-score. A field calculation was executed on the hot spot analysis output to reclassify points based on statistical significance ($P \leq 0.05$) as either higher than the reservoir overall (hot spot) or lower than the reservoir overall (cold spot). Points within the Rabbitail and Buckville stocking embayments were excluded from the analysis because these were already known to have high levels of FLMB alleles present (Lusk et al. 2022). Including these points would raise the reservoir-wide mean % FLMB allele level making it

more difficult to demonstrate patterns in allele spread through the rest of the reservoir. Points within the pelagic area of the reservoir where no fish were collected were included within this analysis and in the final figure for visualization purposes and conclusions should be drawn with caution regarding these areas.

Results

A *t* test indicated no difference in average % FLMB alleles between sampling periods ($t=0.116$, $df=976.3$, $P=0.91$) and all fish were included in subsequent analyses. In total, 304 individuals were classified as NLMB, 696 classified as hybrids and no individuals were classified as FLMB (Table 1). The Northeast quadrant, containing the stocking areas, exhibited the greatest concentration of hybrids (89.6% of individuals), followed by the Southeast quadrant (83.2% of individuals). Conversely, the western half of the reservoir contained relatively few hybrid individuals with the Northwest quadrant of the reservoir the lowest at 36.8% of individuals (Table 1, Figure 2).

FLMB alleles were present in at least one fish at every sample location around the reservoir and the mean % FLMB alleles reservoir-wide was 11.4% (Table 1). Mean % FLMB alleles across hybrids was 15.4%. One hybrid individual contained 94% FLMB alleles, but all other fish contained 57% FLMB alleles or less. The Northeast quadrant of the reservoir contained the highest mean percentage of FLMB alleles followed by the Southeast portion of the reservoir (Table 1).

Although FLMB alleles remained relatively high east of the stocking locations, they were more concentrated in fish collected along the main reservoir shoreline relative to those found in the backs of coves. The FLMB allele percentage decreased rapidly west of the stocking area and most fish contained very few FLMB alleles in the Northwest portion of the reservoir (Figure 1, 2). The hot spot analysis demonstrated a significant pattern of genetic introgression to the south and east of the stocking area, but not in the western portion of the reservoir (Figure 3). Most of the main body of the reservoir that is in the immediate proximity of or to the east of the stocking location was categorized as a hot spot whereas most of the western portion of the reservoir was either not significant or was categorized as a cold spot. Many of the creek arms, even in the eastern portion of the reservoir, were either not significant or were significant cold spots.

Table 1. Number (*n*) of fish sampled in each quadrant of Lake Ouachita, Arkansas, during spring 2019, and the percent of individuals of each species category (northern largemouth bass, NLMB; Florida largemouth bass, FLMB) within each reservoir quadrant. The last column displays the mean % FLMB alleles among all individuals within each reservoir quadrant.

Quadrant	<i>n</i>	% NLMB	% Hybrid	% FLMB	FLMB alleles (%)
Northeast	250	10.4	89.6	0	16.6
Southeast	250	16.8	83.2	0	14.3
Southwest	250	31.2	68.8	0	9.8
Northwest	250	63.2	36.8	0	5.1
Total	1000	30.4	69.6	0	11.4

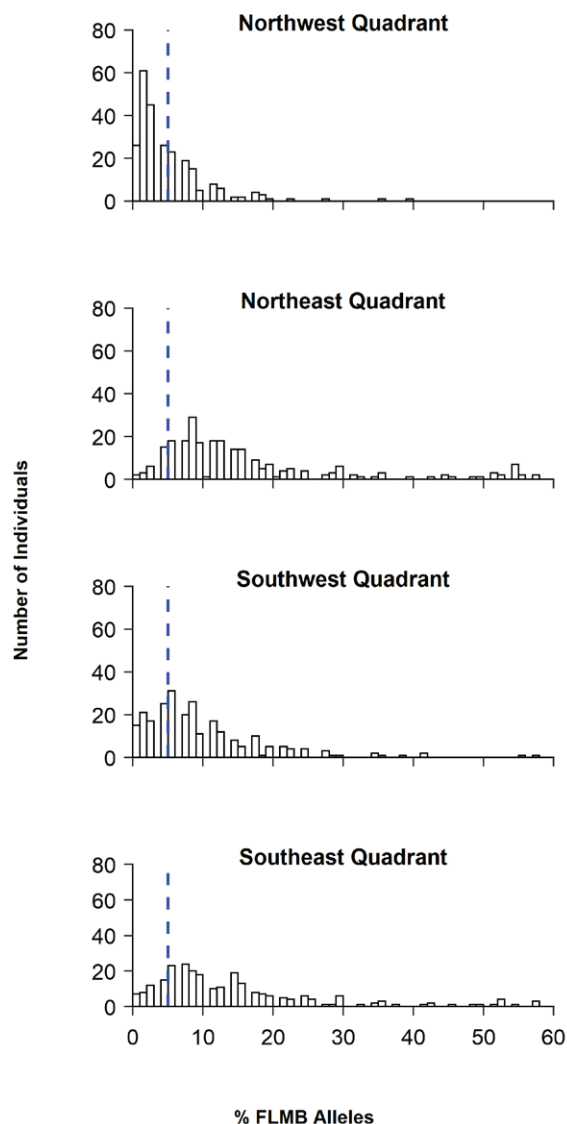


Figure 2. Distribution of % FLMB alleles within each quadrant ($n = 250$ per quadrant) of Lake Ouachita, Arkansas. The dashed blue lines indicate the cutoff in % FLMB alleles between hybrid and NLMB classification. One fish with an exceptionally high level of FLMB alleles (94%) in the Northeast quadrant was excluded from this figure. The Northeast quadrant contained the sites where FLMB were stocked.

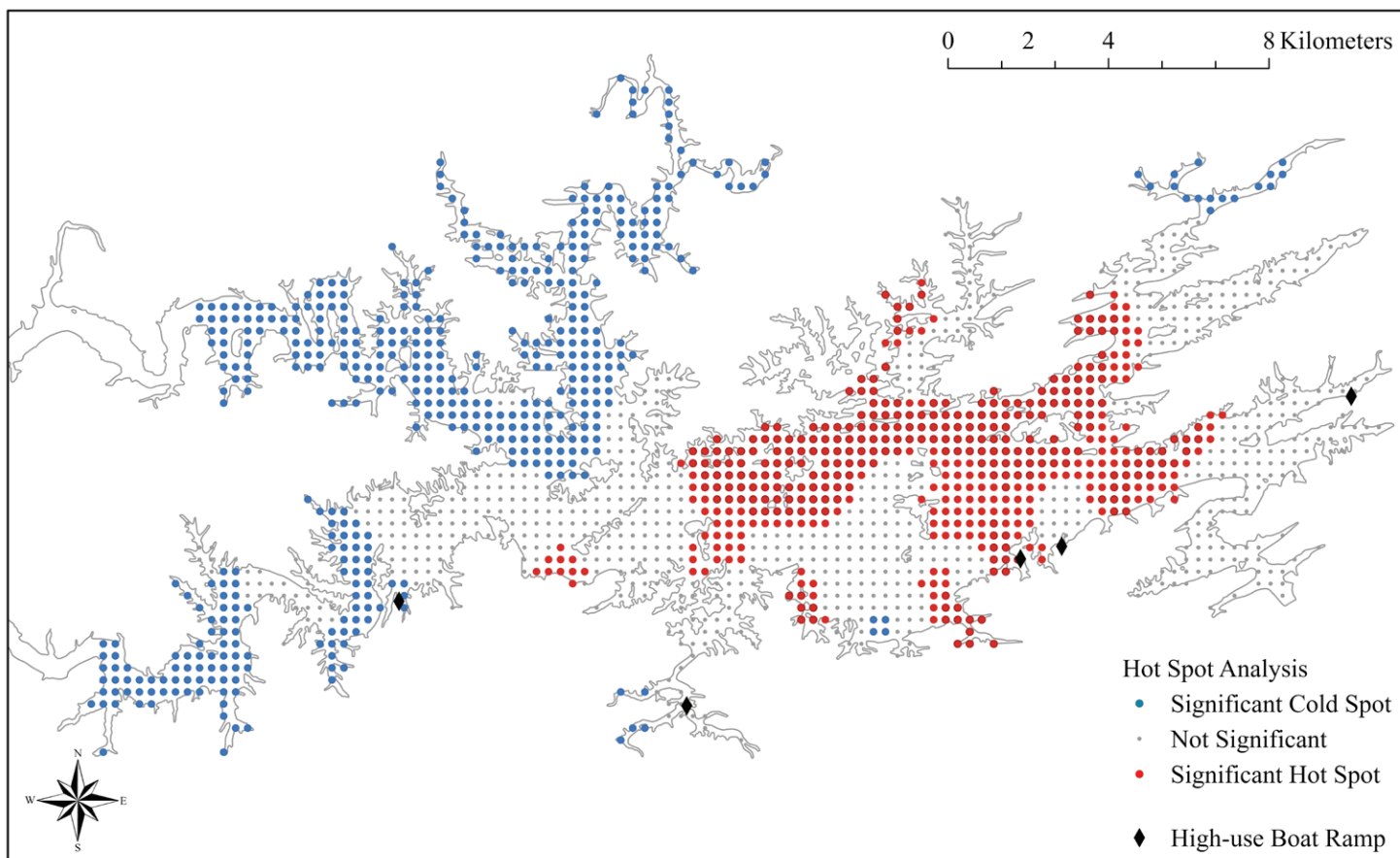


Figure 3. Hot spot analysis based on the results of the Inverse Distance Weighted analysis of % Florida largemouth bass (FLMB) alleles in Lake Ouachita, Arkansas. Significant hot spots signify higher levels of FLMB alleles in that location as well as neighboring cells as compared to the overall reservoir. Significant cold spots signify lower levels of FLMB alleles in that location as well as neighboring cells as compared to the overall reservoir. Boat ramps receiving the highest tournament angler usage in the reservoir are also shown. Cells within the stocking embayments are not included in the analysis and do not contribute to the overall reservoir mean level of FLMB alleles.

Discussion

Our results support that stocking of Florida largemouth bass in locally high densities over multiple years in a small area can lead to widespread introgression throughout the native population. Lusk et al. (2022) found changes in the genotype of fish within the stocking area, but the present study demonstrates substantial spread of FLMB alleles from the stocking area throughout at least half of the reservoir. Previous work has determined that number of years since stocking (Dunham et al. 1992), stocking rates (Dunham et al. 1992, Buckmeier et al. 2003, Acy 2017, Hargrove et al. 2019), and number of stocking events (Walsh 2021) are positively related to the introgression of FLMB alleles into a NLMB population. The Lake Ouachita stocking effort likely succeeded in introgressing FLMB alleles into a large area because it occurred over multiple years with a high local stocking density.

The overall reservoir % FLMB level (11.4%) was modest compared to reservoirs in another recent study using the same SNP

loci (Hargrove et al. 2019). In that study, 7 of 14 Tennessee reservoirs contained higher levels of mean % FLMB alleles than Lake Ouachita, including one with no history of state agency stocking in the reservoir (Hargrove et al. 2019). However, spatial patterns related to admixture in these systems was not examined. Our reservoir-wide stocking rate (6.2 fish ha^{-1}) was higher than that employed in Kentucky Lake, Tennessee-Kentucky ($<1 \text{ fish ha}^{-1}$), but lower than that employed in Chickamauga Reservoir, Tennessee (10 fish ha^{-1}). Both Tennessee reservoirs had higher levels of % FLMB alleles (16.3% and 30.4% FLMB, respectively) than Lake Ouachita, but the number of years of stocking and the time since stocking was initiated varied among each (Hargrove et al. 2019). Pure FLMB were only collected in Chickamauga Reservoir, and in low numbers. Similarly, we collected no pure FLMB, potentially due to mortality occurring between the last stocking event and the beginning of sampling.

Other genetic techniques have been used to assess FLMB intro-

gression across a large spatial scale. Lamothe et al. (2016) used microsatellite analysis to examine a suite of smaller reservoirs across southern Arkansas that had been stocked over multiple years with FLMB and found a high percentage of fish with low levels of FLMB alleles present and very few fish with high levels of FLMB alleles. Another study used microsatellites to assess largemouth bass genetics in Oklahoma reservoirs previously stocked with FLMB and found large numbers of fish with low levels of FLMB alleles, with 90% of fish containing at least one FLMB allele (Acy 2017). An assessment of FLMB-stocked water bodies across Louisiana found that 6%–37% of fish were NLMB x FLMB hybrids (Fries 2010). A more recent study across six Louisiana water bodies determined that FLMB alleles ranged from a mean of 13.4% at the lowest to 50.7% at the highest (Walsh 2021).

We found that FLMB alleles were present in a large portion of the main body of Lake Ouachita, even directly across the main body of the reservoir from the stocking embayments. Fingerling FLMB often disperse following stocking (Neal and Noble 2002, Hoffman and Bettoli 2005) even offshore (Thompson et al. 2016), and movement of stocked fingerlings outside of the stocking zone could account for some of the genetic distribution patterns seen. However, juvenile dispersal and survival after stocking is typically very low (e.g., Copeland and Noble 1994) and dispersal of stocked fish is unlikely to explain all spatial patterns in the present study. Our study occurred four years after the last stocking event and therefore dispersal of FLMB alleles occurred over more of a generational time scale. Spatial patterns most likely reflect successful reproduction and subsequent dispersal of wild-spawned fish over time.

Incorporation of FLMB alleles into the eastern but not western portion of the reservoir could reflect adaptation limitations of FLMB in Lake Ouachita. Lake Ouachita is at the northern extent of where AGFC stocks FLMB based on number of heating degree days (Gilliland 1992). The western, more riverine zone of the reservoir may experience wider temperature fluctuations, including colder winter temperatures (Ford 1990). The lacustrine zone of the reservoir likely provides more thermal stability for FLMB, potentially leading to seasonal habitat selection and higher levels of genetic introgression. Alternatively, the western, riverine zone of Lake Ouachita is more productive and contains higher fish abundances than the lacustrine zone of the reservoir (AGFC unpublished data) and competitive interactions with abundant native NLMB could potentially slow the spread of alleles into the western portion of the reservoir.

Interestingly, greater levels of FLMB alleles were found in fish collected from the shoreline around the main reservoir body than areas of the reservoir in the backs of creek arms. Largemouth

bass often select for cove habitat (Sammons and Bettoli 1999) and native NLMB in Lake Ouachita could be present in higher densities there than in main reservoir areas which typically have little vegetation and rocky, steep banks (AGFC unpublished data). Fries (2010) similarly noted that FLMB introgression was higher in waterbodies with low vegetation levels and speculated that these likely had lower natural recruitment which would allow for faster genetic introgression by stocked fish. Seasonal habitat use patterns may also affect our spatial results. We collected all samples during a single season but we may have observed different patterns in other seasons. For example, largemouth bass have been shown to exhibit migratory patterns during winter months, selecting offshore habitat and inshore habitat differently at certain times of day (Woodward and Noble 1997). It is unknown if patterns such as this may differ for FLMB as compared to NLMB or if thermal adaptations between FLMB and NLMB could affect habitat use seasonally. Few studies have examined habitat use and behavior differences between largemouth bass subspecies (but see Betsill et al. 1986) and our results could reflect these differences, changes in natural densities, or recruitment variations between hybrid and pure NLMB leading to slower dispersal of alleles into these areas.

The effects of angler-mediated translocations on our results is unknown. Angler-mediated movement of fishes among aquatic systems has been well documented (e.g., Cambrey 2003, Rahel 2004, Taylor et al. 2017) but little work has been focused on the effect of within system translocations on fish population characteristics (but see Ricks and Maceina 2008). Lake Ouachita was found to have a low level of FLMB alleles in the population prior to FLMB stocking (Lamothe et al. 2012, Lusk et al. 2022) but our results demonstrated clear patterns centered near the stocking area, indicating that it was the primary source of FLMB alleles in the reservoir presently. No patterns were apparent regarding FLMB allele presence relative to locations of high-use boat ramps around the reservoir, which may indicate little effect of angler movement of either stocked FLMB or early progeny of stocked fish. However, numerous studies have documented rapid dispersal of released fish from weigh-in areas following tournaments (e.g., Hunter and Maceina 2008, Kaintz and Bettoli 2010, Maynard et al. 2017) which could obscure our ability to observe any patterns related to boat ramps.

Management Implications

Lake Ouachita provided an excellent opportunity to examine the genetic effects of stocking FLMB into a large reservoir with an existing population of native NLMB, a practice which is commonly done throughout the southeastern United States. Some stocking strategies specify genetics goals, such as increasing population-level

frequency or the number of fish with FLMB alleles to a specified level (Churchill and Reeves 2001, Lamothe et al. 2012, Lusk et al. 2022), but genetic goals do not appear to be based on demonstrated size-based outcomes at proposed admixture proportions. Our results indicate that the evaluated stocking program was successful in meeting the objective of integrating FLMB alleles into the population on a large scale over a relatively short time period. However, this stocking created many fish with low levels of FLMB alleles, and more work remains to determine if the level of genetic admixture that we observed in this study will meet the common FLMB stocking goal of providing trophy angling opportunities. Future work is needed to give additional guidance to agencies in regards to whether stocking goals should be based on levels of FLMB introgression and whether such introgression-based criteria are adequate to meet recreational fisheries-based goals.

In a large highland reservoir, our results clearly indicate that localized stocking at a high density can have a large-scale response in terms of the presence of FLMB alleles in native northern largemouth bass populations. At least for a period of time after stocking, spatial patterns are likely established with areas of higher and areas of lower levels of % FLMB alleles. Thus, future studies evaluating genetic composition of lentic fish populations should account for prior stocking locations when collecting fish for genetic evaluation. Further work is needed to determine how spatial patterns in FLMB genetics change over time. In addition, very little is known about how largemouth bass F_x hybrids may differ from native NLMB in terms of growth, mortality, age-at-maturity, and other critical life-history parameters. Further investigations into how life-history characteristics are affected by stocking are critical for complete evaluation of FLMB stockings outside their native range. We urge managers to carefully consider their stocking program goals and long term implications of shifting genetics of an entire population.

Acknowledgments

The authors thank J. Buckingham, C. Dennis, B. Hobbs, L. Rengstorf, and K. Winningham for assistance with fieldwork and data collection. Dr. Eric Peatman and his lab at Auburn University performed all genetics work and techniques. J. Olive, S. Sammons, and three anonymous reviewers provided reviews that improved this manuscript. This research project was partially supported by Federal Aid in Sport Fish Restoration funds awarded to the AGFC. The views and opinions expressed herein are those of the authors and do not necessarily reflect the views or policies of the Arkansas Game and Fish Commission.

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