Predicting Long-Term Genetic Integration Following Stocking of Florida Bass (*Micropterus salmoides*) into an Arkansas Reservoir

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Abstract: Management agencies within native largemouth bass (LMB; *Micropterus nigricans*) range across the United States regularly stock non-native pure Florida bass (FLB; *Micropterus salmoides*) or reciprocal LMB × FLB F1 hybrids to enhance angling opportunities based on public demand. Often, these stocked fish are introduced into waterbodies already occupied by LMB, which readily hybridize with FLB. This hybridization and resulting genetic integration of FLB alleles into the population is often considered the goal of stocking programs. However, managers have little available information to help them determine stocking rates and durations that will allow them to meet management goals associated with the introgression of FLB alleles. To inform such stocking decisions, we created an individual-based model and parameterized it based on the results of a recent FLB stocking program in Lake Ouachita, Arkansas. The model closely predicted lakewide genetic integration empirically observed in Lake Ouachita following stocking goals. Model results indicate that when management agencies are stocking at low rates, such as the rate utilized in Lake Ouachita (6.2 fish ha⁻¹), they should consider committing to a long time frame (e.g., multi-decade) to integrate FLB alleles at a high level. Alternatively, greater stocking rates can yield much faster results but may be resource prohibitive. This model provides information on how agencies could allocate limited resources to best achieve FLB stocking goals in states such as Arkansas where FLB are non-native and are stocked to change the genetic composition of an existing LMB population.

Key words: evaluation, management, Micropterus, modeling introgression

Journal of the Southeastern Association of Fish and Wildlife Agencies 12:1-9

Florida bass (FLB; Micropterus salmoides) are popular recreational game fish widely stocked outside their native range in the U.S. and internationally (e.g., Neal and Noble 2002, Lamothe et al. 2016, Khosa et al. 2022). These stockings often aim to increase the size potential of existing largemouth bass (LMB; Micropterus nigricans) fisheries into which they are being stocked (e.g., Wilson and DiCenzo 2002). Stocking programs may lead to the presence of trophy-sized individuals in the population. Indeed, FLB, reciprocal LMB \times FLB F1 hybrids, and other hybrids with >50% FLB alleles often dominate trophy catch records in locations where stocking has taken place and genetic information is available for fish in large size classes (e.g., Lamothe and Johnson 2013, Acy 2017). However, stocking programs frequently lead to populations containing many later-generation FX-LMB hybrids, or backcrosses, that have low levels of FLB alleles (<50%). These hybrids become abundant in the population, often exceeding native LMB in abundance (e.g., Acy 2017, Hargrove et al. 2019, Khosa et al. 2022, Lusk et al. 2023). In locations with extensive stocking histories, the majority of hybrids may possess ≥50% FLB alleles, as observed in some Texas

reservoirs (Lutz-Carrillo et al. 2023). Notably, even in locations with minimal or no history of agency stocking in the southeastern U.S., introgression frequency can be high (Hargrove et al. 2019) likely due to angler introductions or other undocumented stockings and subsequent fish movement.

Agencies often initiate stocking programs due to angler demand for improved opportunities to catch larger fish. However, stockings may occur without structured guidance on how to set and achieve genetic integration goals. Recent work comparing LMB, FLB, and their hybrids has found that low level of introgression is not sufficient to increase growth potential (i.e., <50% FLB alleles; Lusk et al. 2023, Lutz-Carrillo et al. 2023). Growth-associated genetic markers have been identified in aquaculture settings (Han et al. 2024, Hua et al. 2024), and selective breeding programs may also lead to enhanced growth (Baird et al. 2016), but, at least at southern latitudes, only hybrids with \geq 50% FLB alleles appear to have an increased size potential over LMB (Lusk et al. 2023, Lutz-Carrillo et al. 2023). Therefore, state agencies interested in introducing FLB alleles into a population should strive to maximize the number of

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fish with at least 50% FLB alleles upon completion of a stocking program. Unfortunately, agencies have limited guidance on how best to accomplish this objective.

To assist managers with making decisions related to FLB stocking rates and durations, we created an individual-based model (IBM) informed based on a prior stocking program in Lake Ouachita, Arkansas (Lusk et al. 2022). The IBM predicts genetic integration from stocking FLB into a simulated LMB population based on the number of years stocked, years elapsed since stocking, and stocking rate. We used the model to provide insight into how agencies could allocate limited resources to most effectively and efficiently achieve FLB stocking goals.

Methods

Purpose and Entities

We describe the IBM below using a modified version of the standardized overview, design, and details protocol of Grimm et al. (2020). We created an IBM to describe the change in bass genetics due to stocking in a reservoir system. Based on number of years stocked and stocking rate, the model predicts mean level of FLB alleles in the population and percentage of the population composed of different genomic ancestry (e.g., LMB, FX-LMB). We initially parameterized the model based on Lake Ouachita, a 16,200 ha, oligotrophic highland reservoir located in the Ouachita Mountains region of Arkansas. This reservoir was stocked annually by the Arkansas Game and Fish Commission with FLB for 8 years from 2007–2014. A genetic evaluation was conducted prior to stocking and again in 2019, 5 years after final stocking (Lusk et al. 2022). The post-stocking evaluation found an increase in overall percentage of FLB alleles within the population and an increase in the number of FX-LMB individuals in the population (Lusk et al. 2022, Lusk et al. 2023). We used the data collected as part of the prior stocking study to inform the creation of an IBM. The goals of our modeling were to 1) create an IBM that effectively replicates genetic integration observed in Lake Ouachita and other reservoirs in the southeastern U.S., and 2) use the validated IBM to predict FLB stocking rates and durations needed to meet genetic integration goals set by management agencies.

Process Overview and Scheduling

The IBM tracked fish as super-individuals (SIs) to improve computation efficiency (Scheffer et al. 1995). A SI represents multiple individuals with the same demographic characteristics and functionally modeled as a single fish. We use the terms "SI" and "fish" interchangeably. Model simulations ran on an annual time step for a set number of years depending on the purpose of a simulation. Two processes that occurred annually, reproduction and

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Figure 1. Model diagram and parameter values for an individual-based model simulating Florida bass stocking and introgression. The model operates on an annual time step with an initial burn-in period of 20 years.

mortality, affected each SI. Additional SIs were introduced into the population via annual stocking and immigration (Figure 1). The model was coded in program R (R Core Team 2022) within RStudio (RStudio Team 2022). All model code is available on the corresponding author's GitHub account (https://github.com/ chrismiddaugh/Bass-Stocking-IBM).

Initialization and Input Data

The model was initialized with 500 SIs, each representing a random uniform number of individual fish between 500–1000 (Figure 1). Each SI had a value representing the %FLB alleles a fish contained (i.e., 100% would represent a pure FLB and 0% a pure LMB). The %FLB alleles a fish contained was set using a random uniform distribution with values centered on mean %FLB alleles observed in the modeled system prior to stocking (Table 1). Ages of each SI were set using a random uniform distribution from 0–10 years old. Each SI had a 50% chance of being assigned to either sex. There was an initial 20-year burn-in period where fish experienced reproduction and mortality each year. This led to a stabilization of the population at an abundance and age structure level generally maintained throughout the remainder of the simulation. No stocking or immigration occurred during the burn-in period.

Numerous model parameters were based on prior data collected in Lake Ouachita as described below in the sub-models. Genetic

Submodels

Reproduction At every annual time step, 50% of age-2 fish were randomly determined to be mature based on observed Lake Ouachita age at 50% maturity (Lusk et al. 2023) and all fish age-3+ were considered mature (Lusk et al. 2023). Each mature male fish was randomly assigned one mature female fish to reproduce with and females could reproduce more than once (DeWoody et al. 2000). The number of produced offspring individuals within the offspring SI was influenced by the number of individuals within the adult female SI and by the age of the adult female fish (Figure 1). The maximum number of individuals within an offspring SI was limited to 1000. The %FLB alleles of the offspring were determined by averaging the %FLB alleles of both parent fish. The sex of the offspring was randomly assigned.

To simulate natural variability associated with nesting success and to ensure a stable proportion of stocked fish being contributed to the population, the model randomly selected a number of offspring SIs equal to a predetermined maximum number of possible age-0 SIs added to the population (150) minus the number of stocked SIs (simulation dependent) plus the number of immigrant SIs (2; Table 1). These selected individuals represented the successful spawns and were added to the fish matrix being tracked in the model. Offspring that were not selected were considered mortalities and no longer tracked.

Mortality Mortality was assessed for all age-1 and older fish after reproduction took place each annual time step. Annual instantaneous mortality of LMB and FX-LMB hybrids in Lake Ouachita was previously found to be 0.4 (Lusk et al. 2023). Therefore, each SI experienced a mean of 40% annual mortality of its individuals based on a random normal distribution with a standard deviation of 0.1 to introduce variability across SIs. After removing individuals, if it was determined that a SI had \leq 5 individuals remaining alive, that SI was removed from the modeled population. No fish greater than 12 years old were observed in a recent Lake Ouachita evaluation (Lusk et al. 2023), and therefore, on the very rare occasion an SI reached 13 years of age, it was removed from the population. Age-0 fish, added to the population through reproduction, stocking, and immigration, were not included in mortality adjustments since their numbers were determined based on the assumption they had already experienced high first-year mortality and recruited to the population (i.e., overwintered).

Stocking Each year stocking took place, SIs representing stocked fingerling pure FLB were added to the population. The specific simulation determined the number of SIs added to the population (Table 1). The number of individuals within each SI was set at 1000. The number of years stocked was adjusted based on the simulation (Table 1). The model could continue to run after stocking concluded to observe changes in the population post-stocking (e.g., Lake Ouachita empirical evaluation took place 4 years after final stocking (Table 1).

Immigration Each year after the burn-in period, SIs representing immigrating pure LMB were added to the population. These fish were included to represent spawning taking place in tributary systems where populations more likely consist of pure native LMB and age-0 fish subsequently moving into the reservoir. This was consistent with empirical evaluations showing a shift in bass population %FLB alleles where newly filled reservoirs have been stocked with pure FLB, but subsequent evaluations include LMB and FX-LMB (e.g., Lamothe et al. 2016). The number of immigrants was set at a low level (two SIs). The number of individuals within each immigrant SI was set at 1000.

Model Simulations

Model Replication of Known Systems The model introduced stocked SIs as a portion of the overall population, but since the model did not include a spatial component, we did not have a way to match published stocking rates as reported in the literature (e.g., 6.2 fish ha⁻¹ in Lake Ouachita). Therefore, we conducted initial simulations based on known %FLB allele levels in Lake Ouachita prior

 Table 1. Results from an individual-based model simulating Florida bass (FLB) stocking and introgression compared to known genetic assessments in several southeastern U.S. systems. Empirical results for

 Lake Ouachita are based on Middaugh et al. (2023) with initial %FLB alleles in Lake Ouachita based on Lusk et al. (2022). Empirical results for Lake Chickamauga and Kentucky Lake are based on Hargrove et al.

 (2019) with initial %FLB alleles in both reservoirs based on O'Bara et al. (1991).

Lake Simulation	Years Stocked	Lake Size (ha)	Stocking Rate (ha ⁻¹)	Year Evaluated	Empirical %FLB Alleles	Model Mean Starting %FLB Alleles	Model SIs Stocked (SI yr ⁻¹)	Model Final %FLB alleles (SD)
Lake Ouachita	8	16,200	6	13	11.4	6	7	11.4 (0.5)
Lake Chickamauga	14	14,500	10	16	30	16	11	27.9 (0.6)
Kentucky Lake	7	65,000	1	18	16	9	4	11.8 (0.7)

to stocking as well as the number of years stocked and timing of follow-up genetic evaluation in Lake Ouachita. In these initial simulations we varied the number of stocked SIs until the final %FLB allele results were similar to those observed in the Lake Ouachita evaluation (Lusk et al. 2023). At the time of our study, there were limited other waterbodies where FLB stocking had taken place and initial %FLB alleles, stocking rates, and lakewide post-stocking genetics were known. Two relatively similar systems to Lake Ouachita were available with this information (Lake Chickamauga and Kentucky Lake). We based stocking rates, starting %FLB alleles, number of years stocked, and timing of follow-up evaluations on published information (O'Bara et al. 1991, Hargrove et al. 2019).

The model recorded the mean %FLB alleles across all SIs as well as the proportion of SIs consisting of LMB (\leq 5% FLB alleles; Lusk et al. 2023), FX-LMB hybrids (between 5–50% FLB alleles; Lusk et al. 2023), and fish with \geq 50% FLB alleles. Previous work has demonstrated that relative to LMB, hybrids with <50% FLB alleles do not have an increased maximum size potential, but hybrids with \geq 50% FLB alleles (F1, FX-FLB, and pure FLB) each have a varying, but increased size potential (Lusk et al. 2023, Lutz-Carrillo et al. 2023). Therefore, our model grouped all genotypes with \geq 50% FLB alleles (i.e., F1, FX-FLB, and FLB) into a single FX-FLB+ category to quantify all categories of fish with increased size potential.

Model Predictions We conducted two prediction scenarios based on Lake Ouachita parameters to provide insight into various stocking durations and rates. First, we modeled a hypothetical scenario where Lake Ouachita was stocked for 100 years at a stable stocking rate in order to observe the changes in the overall lake %FLB as well as the change in proportions of different genotypes. We next conducted a series of simulations in which the number of SIs stocked varied from 1-50, which, based on initial model validation of Lake Ouachita, corresponds to a stocking rate of 0.7–34.4 fish ha⁻¹. For each stocking rate, the model ran until both the %FLB lakewide alleles reached 25% and the proportion of FX-FLB+ fish in the population reached 25%. These values were selected to represent realistic stocking goals that a management agency may select when initiating a stocking program and to demonstrate any differences in timing between reaching a lakewide average %FLB allele level versus a corresponding level for the percentage of the fish population with the potential for increased maximum size.

Results

Model Replication of Known Systems

We closely matched the final lakewide mean %FLB allele level empirically observed in Lake Ouachita (11.4%; Middaugh et al. 2022) using a stocking rate of 7 SIs annually (Table 1). At this stocking rate, the model predicted a final value of 11.4% lakewide FLB alleles 5 years post-stocking (Table 1). The model also predicted similar proportions of genomic ancestry to those observed by Middaugh et al. (2022) with FX-LMB being most abundant (empirical: 30% LMB, 3% FX-FLB+, 67% FX-LMB; model: 32% LMB, 8% FX-FLB+, 60% FX-LMB; Figure 2).

We also modeled Lakes Chickamauga and Kentucky based on published information (Table 1). We adjusted the number stocked in each simulation based on the relative stocking rate compared to Lake Ouachita (Table 1). The model predicted a final value of 27.9% lakewide FLB alleles in Lake Chickamauga, which was close to the 30% reported by Hargrove et al. (2019). The model predicted a final value of 11.8% in Kentucky Lake compared to an average value of 16% reported by Hargrove et al. (2019). Due to differences in how genotypes were determined, we did not compare our simulated genotypes against those reported by Hargrove et al. (2019).

Model Predictions

Because the model closely matched reported values in both Lake Ouachita and Lake Chickamauga, we conducted several predictive simulations. First was a scenario where Lake Ouachita was stocked at a stable rate of seven SIs (6.2 ha⁻¹) for 100 years. At the end of the 100-year period, the model predicted a final value of 51.9% lakewide FLB alleles (Figure 3). It predicted that at year 100, the population will comprise 1.5% LMB, 46.4% FX-FLB+, and 52.1% FX-LMB (Figure 3).

Model results based on reaching set stocking goals indicated an exponential relationship between number of years stocked, the stocking rate, and length of time to reach a stocking goal. We set arbitrary goals of 25% FLB alleles in the population or 25% of the population being FX-FLB+. At the Lake Ouachita stocking rate (6.2 ha⁻¹), it took 31 years to reach a mean of 25% lakewide FLB alleles but it took 71 years to reach 25% FX-FLB+ in the population (Figure 4). These results indicate that at moderate to low stocking levels, it takes fewer years to reach an average of 25% lakewide FLB alleles than to reach a goal of >25% FX-FLB+ in the population (Figure 4).





Figure 2. Individual-based model simulation results for replicating the Lake Ouachita Florida bass (FLB) stocking program and subsequent genetic assessment. Simulated stocking took place from year 1 to year 8, and the simulation ended 5 years after the final stocking event to replicate results described in Middaugh et al. (2023). Lines indicate the reservoir-wide mean %FLB alleles in the population (A) and the proportion of different genotypes present in the population (B). The FX-FLB+ genotype represents all fish with \geq 50% FLB alleles, fish with between 5–50% FLB alleles are considered to be FX-LMB, and fish with \leq 5% are considered LMB. Each line represents a mean of 10 replicated simulations with error bars representing standard deviation across simulations.

Figure 3. Individual-based model simulation results predicting Lake Ouachita bass genotypes and mean % Florida bass (FLB) alleles if stocking took place continuously for 100 years. Lines indicate the reservoir-wide mean %FLB alleles in the population (A) and the proportion of different genotypes present in the population (B). The FX-FLB+ genotype represents all fish with \geq 50% FLB alleles, fish with between 5–50% FLB alleles are considered to be FX-LMB, and fish with \leq 5% are considered LMB. Each line represents a mean of 10 replicated simulations with error bars representing standard deviation across simulations.



Figure 4. Relationship between number of Florida bass (FLB) stocked (fish ha^{-1}) and number of years of stocking needed to reach 25% of the population containing \geq 50% FLB alleles (dashed line; FX-FLB+ genotype) or an average of 25% FLB alleles in the population (black line). Results are from individual-based model simulating FLB stocking and introgression. For reference, the horizontal line corresponds to the stocking rate of Lake Ouachita (6.2 fish ha^{-1}).

Discussion

Our results clarify the relationship between FLB stocking rates and durations in systems populated by LMB, and the resulting genotypic and phenotypic outcomes. We demonstrated that, even at low stocking rates such as in a system like Lake Ouachita, stocking FLB will quickly reduce the number of pure LMB and elevate the number of FX-LMB in the population. The proportion of FX-FLB+ fish, the category of fish most likely to provide trophy fishing opportunities for anglers, slowly increases in the population. When stocking was simulated for long periods of time in Lake Ouachita, our model predicted that there would be effectively no LMB (>95% LMB alleles) in the population after about 50 years, with FX-LMB being the dominant genotype in the population long-term. The proportion of FX-FLB+ genotype fish did not exceed 50% of the population, even after 100 years of stocking. These results indicate that over multiple decades, managers should expect a population to primarily be comprised of FX-LMB genotype fish when stocking levels are low (e.g., <10 fish ha⁻¹).

Our model can provide guidance to agencies in reaching a stocking goal based on genetic integration, but there is no clear consensus about the level at which a genetic integration goal should be set to meet stakeholders' desires. The goal of the Lake Ouachita stocking program was for 40% of fish to have some level of FLB influence (Lusk et al. 2022). However, recent work has

found that hybrids with low levels of FLB alleles do not have any maximum size potential increase over LMB (Lusk et al. 2023, Lutz-Carrillo et al. 2023). Therefore, a more appropriate goal to meet angler demands should relate to increasing number of fish with higher likelihood of large size potential (i.e., >50% FLB alleles). In this model, we select an arbitrary goal of 25% FLB alleles in the population or 25% of the population being FX-FLB+ or greater as metrics that presumably would result in a noticeable number of larger size class fish in the lake. Simulations predicting the relationship between stocking rates and years stocked indicate that agencies can achieve stocking goals either by committing to long time periods of stocking at relatively low levels or by increasing stocking rates to reach goals sooner. In large reservoir systems such as Lake Ouachita, Lake Chickamauga, Kentucky Lake, and many others in the southeastern U.S., large water body size may limit the ability of agencies to stock at high rates. Even at a stocking rate of 10 fish ha-1 like in Lake Chickamauga, we predict it would take >20 years to reach 25% of the population consisting of FX-FLB+ fish, if starting with relatively low levels of FLB alleles in the population as observed in Lake Ouachita. This indicates agencies should expect to commit to long-term (e.g., multi-decade) stocking programs in large water bodies if they desire to significantly increase FLB genetic integration.

Though our model output matched Lake Ouachita and Lake Chickamauga results well, model-predicted %FLB alleles for Kentucky Lake did not match empirical results as well. We set our stocking rate higher than what was reported by Hargrove et al. (2019) for the Kentucky Lake simulation to ensure stocking was higher than immigration, and even with the elevated stocking rate, final predicted %FLB alleles were lower than empirically observed levels. Hargrove et al. (2019) report higher levels of FLB admixture in systems upstream of Kentucky Lake (e.g., Pickwick Reservoir) and it is possible that there could be immigration from those sources. It is also possible that the survival of stocked fish may have been greater, or more undocumented introductions of FLB may have occurred in Kentucky Lake than in other systems we modeled. Finally, Hargrove et al. (2019) only evaluated genetics from the Tennessee portion of Kentucky Lake, which may have elevated the integration estimate relative to the entire reservoir. A recent evaluation of %FLB alleles in the Kentucky portion of the reservoir found an average of 8.1% FLB alleles in the population (KY DFWR 2023) compared to 16% reported in Tennessee (Hargrove et al. 2019).

Inherent to our model were numerous assumptions related to stocking rates and methods. Lake Ouachita stocking occurred in two discrete embayments with known high-quality nursery habitat (Lusk et al. 2022). In addition, stocking size was consistent throughout the stocking period (fingerlings ~50mm TL). Other studies have also indicated that stocking in discrete locations provides an effective strategy for genetic introgression into a population (Dunham et al. 1992, Buckmeier et al. 2003). Though not all stocking is conducted this way, stocking fingerlings in high-quality habitat is consistent with how the Arkansas Game and Fish Commission stocks large reservoir systems. We also assumed that stocking rate is directly related to genetic integration into the population. Previous studies indicate that both stocking and environmental conditions affect the integration of FLB alleles into stocked populations. Studies across wide geographic areas in Alabama, Louisiana, Oklahoma, and Tennessee indicate a relationship between stocking rates or stocking frequency and level of genetic integration into the population (Gilland and Whitaker 1989, Dunham et al. 1992, Acy 2017, Hargrove et al. 2019, Walsh 2021). Typically, these studies also find significant relationships with environmental characteristics such as aquatic vegetation (Walsh 2021) and water temperature (Gilliland and Whitaker 1989). Though most work indicates a relationship between stocking rate and FLB genetic integration, some studies have found limited relationships (Allen 2009, Fries 2010), emphasizing that genetic integration is not solely due to stocking levels. Finally, we modeled a large range of stocking rates, but very high stocking levels may produce diminishing returns in

terms of contribution to the year class (Buckmeier et al. 2003) and it is unknown how accurate our model predictions are for systems with high stocking rates. We acknowledge that our model incorporated a simplistic understanding of the effect of stocking rate on integrating FLB alleles into the population and that environmental conditions conducive to the survival of stocked FLB and the continued persistence of adult FLB must also be present. For example, survival and growth of stocked FLB in Oklahoma reservoirs with lower heating degree days (HDD) was lower than in reservoirs with higher HDD (Gilliland 1992).

We did not incorporate any spatial component into our model. This simplified the model and made it more generalizable across different systems. Spatial modeling of the spread of %FLB alleles in Lake Ouachita indicates widespread integration long distances from the stocking area over a short time period (e.g., across the main lake body; Middaugh et al. 2022), signifying that hybridization may take place quickly over a large spatial area. Angler movement of fish captured during tournaments and released into different lake areas (Ricks and Maceina 2008) may also contribute to quick integration. Other assumptions of our model included the use of age-at-maturity, mortality, and other parameters based on the Lake Ouachita population, which may differ from other systems.

Management Implications

This study provides insights into how stocking programs alter the overall genetics of a waterbody and the resulting proportions of different genotypes in a population. Results also provide stocking rate and duration guidance to managers as they set FLB stocking goals. To achieve high levels of genetic integration and meet angler demand for larger fish, we recommend committing to either long-term stocking programs or high stocking rates. Alternatively, agencies will be much more efficient at reaching high numbers of FX-FLB+ in the population when stocking small waterbodies or newly filled reservoirs with no existing LMB in the population. Management agencies should also consider the effect of stocking non-native FLB on native LMB genetics and whether there are systems where stocking should be prohibited so that native genetics are conserved.

Genetics are just one of several important components for creating a trophy fishery and our results likely do not pertain to systems that do not have adequate nursery habitat for juvenile fish, lack appropriate forage and adult habitat, or that otherwise are not conducive to supporting FLB. The model presented here is not intended to predict outcomes with high accuracy across a large region, but rather to provide a starting point for managers as they make long-term stocking plans. We recommend that any stocking program be accompanied by a genetic monitoring program to document the changing genetics over time and adjust stocking parameters as deemed necessary. We encourage agencies to consider available resources and to prioritize stocking a limited number of systems where resources could be most effectively used rather than stocking few FLB into a large number of systems.

Acknowledgments

This research was partially supported by Federal Aid in Sport Fish Restoration Funds. We thank T. Alfermann, V. DiCenzo, A. Martin, and E. Naas for thoughtful reviews of an earlier draft of this manuscript. M. Wegener and two anonymous reviewers provided additional reviews that improved this manuscript. We thank D. Hike for promoting conversation on this topic. The views and opinions expressed herein are those of the authors and do not necessarily reflect the views or policies of the AGFC. Product references do not constitute endorsement. There is no conflict of interest declared in this article.

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