



Genetic Integrity, Population Status, and Long-Term Viability of Isolated Populations of Shoal Bass in the Upper Chattahoochee River Basin, Georgia

Natural Resource Report NPS/CHAT/NRR—2018/1620



**ON THIS PAGE**

Multi-agency sampling effort to assess Shoal Bass (*Micropterus catarractae*) population status in Big Creek
Photograph by Andrew Taylor, Oklahoma State University

ON THE COVER

Shoal Bass (*Micropterus catarractae*) sampled from Big Creek, Roswell, Georgia, in October 2014
Photograph by Trevor Starks, Oklahoma State University

Genetic Integrity, Population Status, and Long-Term Viability of Isolated Populations of Shoal Bass in the Upper Chattahoochee River Basin, Georgia

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April 2018

U.S. Department of the Interior
National Park Service
Natural Resource Stewardship and Science
Fort Collins, Colorado

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Please cite this publication as:

Taylor, A. T., and J. M. Long. 2018. Genetic integrity, population status, and long-term viability of isolated populations of shoal bass in the Upper Chattahoochee River Basin, Georgia. Natural Resource Report NPS/CHAT/NRR—2018/1620. National Park Service, Fort Collins, Colorado.

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Executive Summary

This report characterizes the status of multiple isolated Shoal Bass (*Micropterus cataractae*) populations in the upper Chattahoochee River basin (UCRB), Georgia. The Shoal Bass, a sport fish endemic to the Apalachicola-Chattahoochee-Flint River (ACF) basin, is a fluvial-specialist species considered vulnerable to local extirpations and extinction due to habitat fragmentation and introgression with non-native congeners. Perhaps one of the most isolated populations of Shoal Bass exists in a 2-km reach of Big Creek, a tributary of the Chattahoochee River located near Roswell, Georgia. Big Creek is partially contained within the Chattahoochee River National Recreation Area, although the Big Creek watershed is riddled with urban land cover. Roswell Mill Dam limits the upstream extent of the Shoal Bass population at Big Creek, and the downstream extent is presumably limited to the confluence of Big Creek and the Chattahoochee River. This reach of the Chattahoochee River is thermally depressed because of coldwater releases from Lake Lanier, and is considered unsuitable for Shoal Bass.

Herein, we examine the genetic integrity, population status, and long-term viability of the Shoal Bass population in Big Creek. We also examine two additional Shoal Bass populations that occur in the UCRB, specifically the Chestatee River and the upper Chattahoochee River, both of which are impounded at Lake Lanier. Together, the Shoal Bass inhabiting these three stream systems comprise a distinct genetic stock of Shoal Bass (Taylor 2017), underscoring the importance of conserving these populations towards maintaining the overall diversity and adaptive potential of the species. We assessed genetic diversity and estimated effective population sizes within these three rivers by genotyping fish with 16 microsatellite DNA markers. Results demonstrated that the Shoal Bass population in Big Creek has experienced high rates of introgression with non-native Smallmouth Bass (*M. dolomieu*), purportedly introduced into the Chattahoochee River in the past 10-15 years. Alarming, only 24% (15 of 62) of putative Shoal Bass collected from Big Creek were genetically pure Shoal Bass, whereas the majority of fish were first-filial (F1) generation hybrids and unidirectional backcrosses towards Shoal Bass. Fleeting opportunity may remain to conserve the native genome of the Shoal Bass population in Big Creek. High hybridization rates prevented genetic diversity analysis for the Big Creek population. Shoal Bass populations in the Chestatee and Chattahoochee rivers displayed levels of genetic diversity similar to populations that persist in other rivers in the ACF basin, namely the Flint and Chipola rivers. Effective population sizes of 93.8–197.4 for the Chestatee and Chattahoochee rivers (combined) suggest that the conservation status of these populations is stable for the short-term, but may be at risk of losing genetic diversity and adaptive potential in the long-term.

To estimate age and mortality of the three populations, we used fish scales and capture-mark-recapture (CMR) as complementary, non-lethal methods for age estimation. Estimated ages of phenotypic Shoal Bass ranged from 1-12 years in all three populations, demonstrating increased longevity compared to populations elsewhere within the native range. Catch-curve estimates of annual mortality ranged from 18.4-23.7%, which are markedly lower than those observed in other Shoal Bass populations in the ACF basin. These differences in life-history characteristics underscore

the need for the development of population-specific management and conservation strategies for Shoal Bass in the UCRB.

The lowest recruitment variability (i.e., the variation in year-class strength) was observed in the Chestatee River, a forested watershed, whereas the highest variability was observed in Big Creek, an urbanized watershed. Recruitment strength in Big Creek was negatively influenced by discharge variability in the summer months, suggesting that flashy, sediment-laden flows hinder survival of recently hatched young. Other statistically significant models from Big Creek and the Chattahoochee River indicated that over-winter survival could be an important pinch-point for recruitment in UCRB populations.

A multi-agency sampling effort was conducted from May 2013-May 2016 to estimate the population size of Shoal Bass occupying the 1-km of wadeable shoal habitats in Big Creek. Using CMR models, we estimated that approximately 219-348 Shoal Bass (≥ 70 mm total length) occupied the area throughout the duration of our study. These estimates largely reflect abundance of individuals aged 0-2 years, as only 9% (36 of 408) tagged fish were aged ≥ 7 years. Local abundance appeared similar to that reported for a population that inhabited Little Uchee Creek, a similar-sized tributary of the Chattahoochee River, prior to its recent functional extirpation. The low abundance of large, adult Shoal Bass further suggests the long-term viability of the Big Creek population may be in jeopardy. Perhaps most importantly, CMR estimates reflect abundance of phenotypic Shoal Bass – genetic analyses suggest the abundance of pure Shoal Bass could be an order of magnitude smaller.

To evaluate the potential for adult Shoal Bass to emigrate from Big Creek into the mainstem Chattahoochee River, we tagged eight adults with acoustic telemetry tags and assessed their seasonal residency at two stationary receiver locations located in increasing proximity to the confluence with the Chattahoochee River. Fish took up residency near the confluence during the fall and winter months, during which time water temperatures in Big Creek were periodically colder than the Chattahoochee River. Although we were unable to document emigration, we conclude that the potential for emigration is highest during the winter months when the Chattahoochee River may be warmer than Big Creek. Two of the tagged fish were caught by anglers near the confluence, suggesting that angling pressure at Big Creek may be higher than previously suspected.

Overall, this study observed unique life-history characteristics and characterized the population status of multiple Shoal Bass populations in the UCRB. Populations in the Chestatee and Chattahoochee rivers appear stable at present and likely represent the last remaining strongholds for pure Shoal Bass in the UCRB. Efforts to preserve forested watershed conditions, natural hydrology, and shoal habitats would contribute to the long-term persistence of Shoal Bass populations in these two rivers. Additionally, the detection of non-native Alabama Bass and their associated hybrids in both rivers is cause for concern. Diligent monitoring of hybridization dynamics between Alabama Bass and Shoal Bass is warranted, along with an assessment of Alabama Bass invasion extent upstream of Lake Lanier.

The Shoal Bass population in Big Creek is threatened by elevated levels of introgression with non-native Smallmouth Bass, recruitment variability, low abundance of adults, and isolation from other

populations. Conservation intervention is urgently needed to restore and preserve this genetically distinct population, which would contribute to preservation of range wide genetic diversity and adaptability of the species. Additionally, an urban sport fishery for Shoal Bass at Big Creek has the potential to serve as a tool for increasing public awareness, engagement, and support of Shoal Bass conservation efforts in the UCRB. We suggest strategies for conservation of the remnant shoal habitats and Shoal Bass population in Big Creek, including potential development of a supplemental stocking program, selective removal of non-native congeners, and delivery of environmental education programs that could bolster awareness and appreciation.

Acknowledgments

This research represents a collaborative effort among the U.S. Geological Survey, Oklahoma State University, the Georgia Department of Natural Resources, Georgia Power Company, and the National Park Service. In particular, we thank P. O'Rourke and C. Looney for their assistance with field sampling, as well as J. Jarquin and S. Duquette for their help maintaining telemetry receivers. Additional funding was provided by the Otto S. Cox Graduate Fellowship for Genetics Research at Oklahoma State University awarded to A. Taylor. Genotyping was performed by the Florida Fish and Wildlife Conservation Commission's Fish and Wildlife Research Institute. This study was performed under the auspices of Oklahoma State University's Institutional Animal Care and Use Committee, protocol #AG-13-8. The Oklahoma Cooperative Fish and Wildlife Research Unit is supported by the Oklahoma Department of Wildlife Conservation, U.S. Geological Survey, the Wildlife Management Institute, and the U.S. Fish and Wildlife Service. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.



Multi-agency sampling team in Big Creek, Georgia.

Introduction

A popular sportfish, the Shoal Bass (*Micropterus cataractae*) is a fluvial-specialist species endemic to the Apalachicola-Chattahoochee-Flint (ACF) basin of the southeastern U.S. Shoal Bass historically inhabited many of the larger mainstem rivers and tributaries of the ACF basin, but populations have since been confined to smaller, isolated areas because of extensive damming, concomitant fragmentation of rivers, and loss of shoal habitats (Williams and Burgess 1999; Taylor et al. 2018). The introduction of several non-native congeners, including Spotted Bass (*M. punctulatus*), Alabama Bass (*M. henshalli*), and Smallmouth Bass (*M. dolomieu*), has led to introgressive hybridization across much of the native range of the Shoal Bass (Taylor and Peterson 2014; Sammons et al. 2015). Because of these anthropogenic-related threats, the American Fisheries Society Endangered Species Committee has recognized the Shoal Bass as vulnerable to local extirpations and overall extinction (Jelks et al. 2008). State fish and wildlife management agencies in Alabama, Florida, and Georgia have variously recognized the Shoal Bass as a species of conservation interest, but the Shoal Bass has not been petitioned for protections under the federal Endangered Species Act (Taylor and Peterson 2014; Sammons et al. 2015).

The lack of population-level assessments of abundance and genetic integrity has hindered conservation efforts directed at restoration or preservation of Shoal Bass populations (Williams and Burgess 1999; Birdsong et al. 2010; Taylor and Peterson 2014). Within the last decade, however, a number of studies have characterized local abundance, population dynamics, individual movement patterns, and genetic integrity of Shoal Bass populations in portions of the native range, specifically the Flint River, Georgia, and the Chipola River, Florida (see Tringali et al. 2015a).

Limited research has been directed toward Shoal Bass populations in the upper Chattahoochee River basin (UCRB), which represents the northernmost extent of the species' native range. The UCRB is fragmented by dams, and Shoal Bass have suffered functional extirpation in approximately 77 km of the mainstem Chattahoochee River because of the thermally depressed tailwaters of Lake Lanier (Long and Martin 2008). Thus, the UCRB supports four extant Shoal Bass populations in the following locations: the Chestatee River, the Chattahoochee River upstream of Lake Lanier, Big Creek, and the Chattahoochee River downstream of Morgan Falls Dam (Long and Martin 2008). Collectively, these populations represent a unique genetic stock of Shoal Bass within their native range (Taylor 2017), increasing their importance to conserving the overall genetic diversity and adaptive potential of the species. Previous genetic studies in the UCRB demonstrated that dams have isolated these populations to varying degrees (Dakin et al. 2007, 2015). Supplemental stocking successfully restored Shoal Bass abundance downstream of Morgan Falls Dam (Porta and Long 2015). However, hybridization between Shoal Bass and non-native Smallmouth Bass was detected downstream of Morgan Falls Dam following illegal introductions that purportedly occurred 10-15 years ago (Dakin et al. 2007, 2015), which has jeopardized the conservation of the native Shoal Bass population below Morgan Falls Dam. The three other Shoal Bass populations in the UCRB (i.e., Big Creek, Chestatee River, and the Chattahoochee River downstream of Lake Lanier) all appear to exist in relative isolation, with very little known of their population status, genetic integrity, or long-term viability.

Objectives

With the goal of characterizing the status and informing the long-term preservation of extant Shoal Bass populations in the UCRB, this study addressed the following objectives:

1. In Big Creek, the Chestatee River, and the Chattahoochee River upstream of Lake Lanier:
 - a. Determine effective population size and other measures of genetic diversity by genotyping 50 individuals of each population with 16 microsatellite DNA markers;
 - b. Estimate age and mortality through analysis of phenotypic Shoal Bass scale samples taken from each population; and
 - c. Determine variables influencing recruitment through catch-curve residual analysis.
2. In Big Creek:
 - a. Estimate population size of phenotypic Shoal Bass by capturing, marking, and recapturing individuals over a three-year period; and
 - b. Determine potential emigration from Big Creek into the Chattahoochee River by tagging adults with 9-month ultrasonic telemetry tags and deploying a submersible ultrasonic receiver at the confluence of Big Creek and the Chattahoochee River.

Methods

Study Areas and Sampling

Big Creek

Study Area

Big Creek is located within the Piedmont ecoregion of northern Georgia. It is a fourth-order stream that has a total drainage area of approximately 250 km². Lower portions of the Big Creek watershed are situated within the Atlanta metropolitan area and feature relatively high levels of development and impervious surfaces, contributing to increased sediment loads and altered streamflow regimes (Rose and Peters 2001; Long and Martin 2008). Shoal Bass are known to occur in a 2-km reach of Big Creek from its confluence with the Chattahoochee River upstream to Roswell Mill Dam, which was constructed in the 1830's (Long and Martin 2008). This 2-km reach of Big Creek is partially contained within the Vickery Creek Unit of the Chattahoochee River National Recreation Area. The lower 1 km is a slow-moving, channelized reach influenced by water levels in the Chattahoochee River and the operation of Morgan Falls Dam, which impounds Bull Sluice Lake just downstream of the Big Creek confluence (Graf and Plewa 2006). As a result, the lower 1 km of Big Creek has suffered bank slumping, with accumulation of silt deposits and large woody debris in the channel (Graf and Plewa 2006). In contrast, the upper 1 km of Big Creek features a series of intact shoal habitats (Graf and Plewa 2006).

Sampling

We focused our sampling efforts on roughly 950 m of wadeable shoal habitats within the upper 1 km of Big Creek, given the known affinity of Shoal Bass for these habitats (Taylor and Peterson 2014; Table 1; Figures 1 and 2). We used 4-6 backpack electrofishers and a team of approximately 10 additional netters to span the stream's width. Sampling teams proceeded methodically upstream, sampling all wadeable shoal habitats and the edges of a few deeper pools. Backpack electrofisher settings were adjusted to obtain an average output of approximately 0.35-0.40 amps. Effort (min) was recorded as the total on-time averaged across the number of backpack electrofishers deployed on a given sampling day. Multi-agency sampling teams consisted of personnel from Oklahoma State University (OSU), National Park Service (NPS), Georgia Department of Natural Resources (GADNR), U.S. Fish and Wildlife Service (USFWS), U.S. Geological Survey (USGS), Georgia Power Company, U.S. Environmental Protection Agency, and students from nearby universities (Figure 2).

Chestatee and Chattahoochee Rivers

Study Area

The headwaters of the Chestatee and Chattahoochee rivers originate in the mountainous Blue Ridge ecoregion of northern Georgia and proceed southward through the Piedmont ecoregion to their confluence, now impounded at Lake Lanier. The Chestatee River is a fourth-order stream that drains approximately 600 km², situated within a forested watershed with one of the lowest human population densities in the UCRB (Rose and Peters 2001). A gold rush in the 1830's and 1840's exposed the Chestatee River to mercury and other heavy metal contaminants still present in

sediments (Leigh 1997), but associated effects to Shoal Bass and other fishes are unknown. Where the Chattahoochee River is impounded at Lake Lanier, it is a fifth-order stream that drains approximately 970 km². The upper Chattahoochee River watershed is moderately forested, but poultry farming and housing developments have contributed to increased sediment and nutrient inputs (Zeng and Rasmussen 2005). At higher elevations, the Chestatee and Chattahoochee rivers and their cool water tributaries support seasonal trout fisheries. Shoal Bass occur downstream of those trout fisheries in the lower-elevation reaches of both rivers immediately upstream of Lake Lanier.

Sampling

In cooperation with GADNR fisheries biologists, we established four sampling sites in each river from the impoundment interface with Lake Lanier to the farthest upstream shoal habitat accessible by jet-drive boat electrofisher (Table 1; Figure 3). Each sampling site was approximately 350 m in length and was sampled with a standardized effort of 15 min of pulsed-DC electrofishing. Two upstream-to-downstream passes were made at each sampling site, electrofishing each side of the river sporadically from riverbank to mid-channel.

Table 1. Shoal Bass (*Micropterus cataractae*) sampling locations, geospatial coordinates (decimal degrees), distance upstream from interface with Lake Lanier (river kilometers; rkm), and elevation (m) of each site. Site numbers correspond to Figure 1.

Site #	Stream	Location	Latitude	Longitude	Rkm.	Elev. (m)
1	Big Creek	Big Creek	34.010574°	-84.356091°	NA	263
2	Chestatee R.	Hwy. 60	34.504223°	-83.968851°	14.56	338
3	Chestatee R.	Horseshoe Bend	34.492659°	-83.997084°	9.33	333
4	Chestatee R.	Canoe Launch	34.471844°	-83.979555°	5.77	329
5	Chestatee R.	Big Rock	34.458609°	-83.966767°	2.96	328
6	Chattahoochee R.	Buck Shoals	34.563347°	-83.628713°	23.95	361
7	Chattahoochee R.	Crow Island	34.503651°	-83.666475°	11.65	334
8	Chattahoochee R.	Bull Shoals	34.482440°	-83.680216°	8.77	330
9	Chattahoochee R.	Flat Rock	34.466399°	-83.686461°	6.43	329

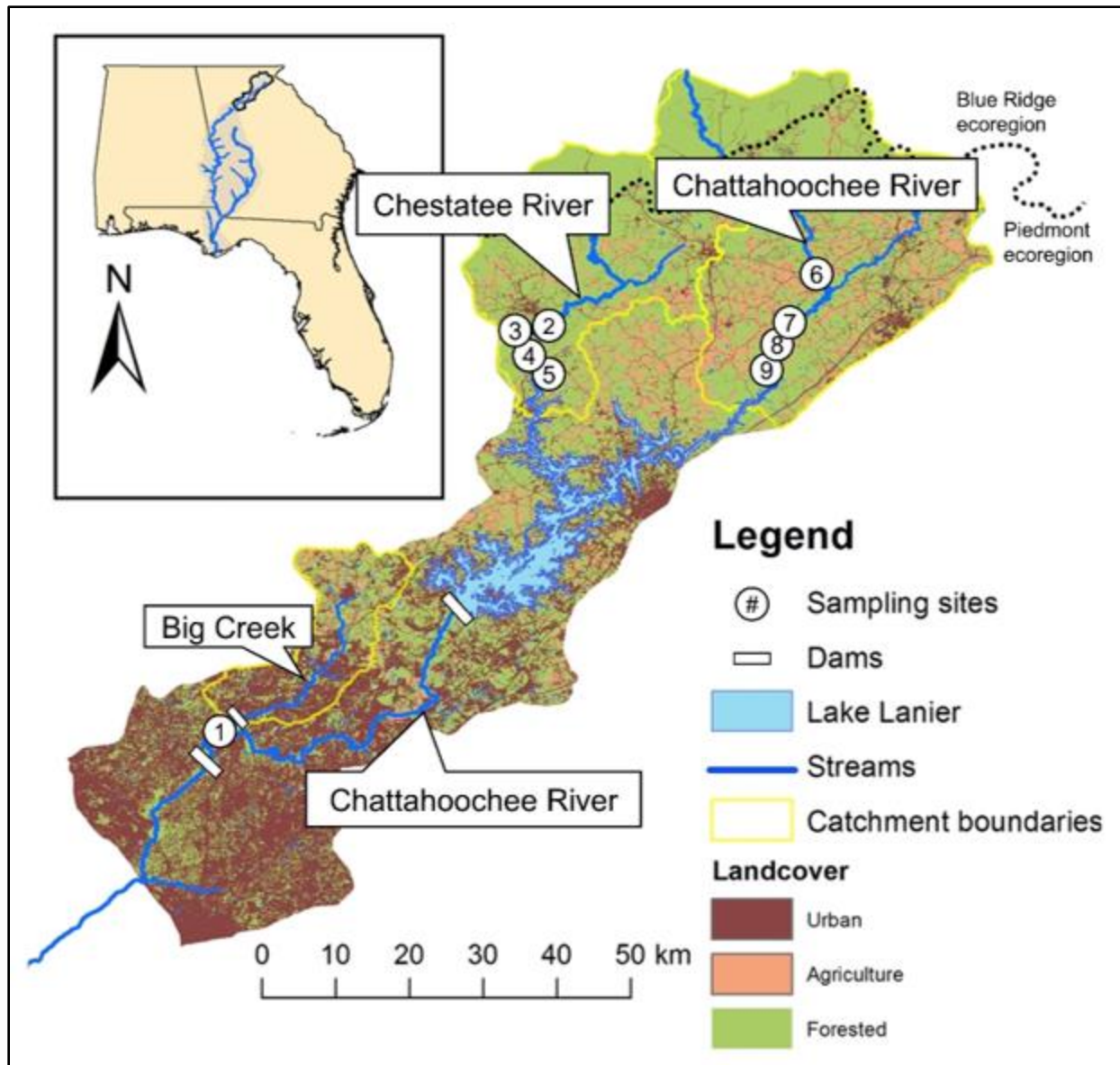


Figure 1. Study area in the upper Chattahoochee River basin (UCRB) of northern Georgia, U.S., including sites sampled to study Shoal Bass (*Micropterus cataractae*). Sampling site numbers correspond with descriptions in Table 1.



Figure 2. Multi-agency backpack electrofishing team sampling Shoal Bass (*Micropterus cataractae*) in Big Creek, Georgia.



Figure 3. Jet-drive boat electrofisher sampling Shoal Bass (*Micropterus cataractae*) in the Chattahoochee River upstream of Lake Lanier, Georgia.

Data Collection

Data collection methods were consistent across the study area. Black bass of all species and sizes were collected and identified. For each specimen identified as a Shoal Bass, the following data were obtained: total length (TL; mm), weight (g), and a sample of 3-5 scales from the dorsal region. A subset of Shoal Bass were also fin-clipped for genetic analysis. Fin clips were stored in individually labeled vials of 95% ethanol at room temperature.

All sampling events that occurred after May 2013 incorporated a capture-mark-recapture (CMR) study design (*for details, see Objective 2a – Population Size*), wherein passive integrated transponder (PIT) tags (Oregon RFID 8mm FDX-B glass tags in Big Creek; 12.5mm FDX-B plastic-encapsulated tags in the Chattahoochee and Chestatee rivers) provided individual identification over time. Upon capture, each fish was scanned for a PIT tag with a handheld reader (Agrident APR350), and if not already tagged and ≥ 70 mm TL, a tag was injected into the coelomic cavity immediately posterior to the pectoral fin. Similar tagging methods have typically yielded 80-100% post-tagging survival and 95-100% tag retention (Siepker et al. 2012; Clark 2016). Tagged fish were released near original capture locations following data collection.

Objective 1a – Genetic Diversity

Approximately 50 putative Shoal Bass were fin-clipped for genetic analyses from each of the three populations. Fish were genotyped using 16 di-nucleotide microsatellite markers (*Msa*f 05, 06, 08, 09, 10, 12, 13, 17, 22, 24, 25, 27, 28, 29, 31, and 32; Seyoum et al. 2013) following the procedures of Alvarez et al. (2015). These microsatellite markers amplify *Micropterus* species and conform to Hardy-Weinberg expectations (Seyoum et al. 2013).

To ensure that non-native congeners and hybrids did not influence estimates of effective population size or genetic diversity, we first performed a taxonomic assignment of putative Shoal Bass genotypes using a Bayesian clustering approach implemented in programs STRUCTURE v. 2.3.4 (Pritchard et al. 2000), STRUCTURE HARVESTER web v. 0.6.94 (Earl and vonHoldt 2012), and CLUMPP v. 1.1.2 (Jakobsson and Rosenberg 2007). Within STRUCTURE, we assumed the admixture model and independent allele frequencies. We employed the ‘PopFlag’ option to estimate individual taxonomic proportions of putative Shoal Bass genotypes using allele frequencies from reference samples for seven black bass taxa (provided by the Florida Fish and Wildlife Conservation Commission’s Fish and Wildlife Research Institute): Largemouth Bass (*M. salmoides*) x Florida Bass (*M. floridanus*) intergrades, Alabama Bass, Spotted Bass, “Choctaw Bass” (*M. sp. cf. punctulatus*), “Bartram’s Bass” (*M. sp. cf. cataractae*), Smallmouth Bass, and Shoal Bass. We assumed *a priori* the number of genetic clusters (K) = 7 to match the number of black bass taxa included, and we used a burn-in of 20,000 and 200,000 Markov-chain Monte Carlo repetitions per 10 independent iterations (Tringali et al. 2015b). We used CLUMPP to permute STRUCTURE runs and produce final proportional assignments of putative Shoal Bass genotypes (Tringali et al. 2015b). Because uncertainty in STRUCTURE’s individual taxonomic assignments often generates small proportions of false assignments, we used the following thresholds to classify individuals into hybridization categories: ‘pure’ species were $\geq 90\%$ assignment to one respective group, ‘backcrosses’ were 75–90% assignment to one respective group, and all remaining individuals were considered first filial generation (F1) or later-generation hybrids (Dakin et al. 2015). In addition to individual proportional assignments and threshold classification, an overall genomic proportion of each taxon was also calculated to characterize the overall proportion of each taxon’s alleles in the putative Shoal Bass samples.

We calculated the following measures of genetic diversity by locus using the pure Shoal Bass genotypes identified in each stream system. We calculated the following measures using GenALEx v. 6.501 (Peakall and Smouse 2012): number of alleles observed (A), effective number of alleles (A_e), expected heterozygosity (H_e), observed heterozygosity (H_o), and the number of individuals genotyped (n). We reported both A and A_e because A_e is less sensitive to the inclusion of rare alleles (Kimura and Crow 1964). Observed heterozygosity (H_o) is the observed proportion of individuals that have two unique alleles at a specific locus, whereas H_e is the proportion of individuals that would be expected to be heterozygous at a specific locus in a large, idealized population. Comparisons of H_o and H_e can yield insight into population-level processes; for example, H_o values less than H_e values can be indicative of inbreeding. We also calculated allelic richness (AR) using Program FSTAT v. 2.9.3 (Goudet 2001); AR accounts for variation in sample sizes among

populations to represent the number of alleles that would be expected from equal sample sizes in all populations.

To estimate effective population sizes, we again used the pure Shoal Bass genotypes identified during taxonomic screening. We also used the hierarchical population genetic boundaries reported by Taylor (2017) to organize our samples for analysis. Specifically, Taylor (2017) determined that Shoal Bass populations in the Chestatee and Chattahoochee rivers upstream of Lake Lanier are genetically unique as compared to other populations within the species' native range, but also that weaker substructure exists between the populations in these two rivers. We employed several single-sample estimators in Program NeEstimator v. 2.01 (Do et al. 2014): the linkage disequilibrium estimator of Burrows (Hill 1981; Waples 2006; Waples and Do 2008), the heterozygote excess method (Pudovkin et al. 1996; Zhadanova et al. 2008; Pudovkin et al. 2010), and the molecular co-ancestry method (Nomura 2008). These methodologies produce effective population size estimates inherently related to the contributing parents in the generations sampled, and are indicative of any contemporaneous inbreeding (Waples and Do 2010). Because low-frequency alleles can upwardly bias estimates using the linkage disequilibrium and the heterozygote excess methods, we removed any rare alleles that occurred at frequencies $< 5\%$, $< 2\%$, and $< 1\%$ prior to computing estimates and their associated 95% confidence intervals (Waples and Do 2010). The linkage disequilibrium method estimates effective population size (N_e), which reflects the number of reproducing adults in an ideal population that would lose genetic variation at the same rate as the number of reproducing adults in the sampled population(s) (Hallerman 2003). The heterozygote excess and molecular co-ancestry methods both estimate effective number of breeders (N_{eb}), a similar estimate of the number of breeders in an idealized population that would contribute the same amount of dispersion in allele frequencies as those in the sampled population(s).

Objective 1b – Age and Mortality

Otoliths are widely accepted as the structure providing the most accurate age estimates for black bass (Maceina et al. 2007), but the lethality of their use limits their applicability to populations of conservation concern. Scales are perhaps the most common non-lethal structure used for aging (Maceina et al. 2007), although scale regeneration, scale resorption, and decreased discernibility of annuli are known to affect the reliability of scale-based age estimates (Simkiss 1974; Quist et al. 2012; Maceina et al. 2007). Because the populations of interest were of conservation concern, we estimated age (in years) for all phenotypic Shoal Bass encountered, using non-lethal scale samples and a consensus-based aging method (Long et al. *in review*). Briefly, two readers independently estimated annuli count from a scale sample without consideration of capture date or fish size. If the final annuli counts matched for both readers, they were adopted as the consensus count; if not, an independent concert read provided a consensus count. Because season-at-capture can influence age estimation (i.e., annulus form during spring months), a final consensus estimation of age was made with consideration of consensus annuli counts and capture date. The reliability of this aging method was assessed by several different methods. First, we examined the precision of age estimates. Second, we used CMR data to verify the timing of first annulus formation and to verify annulus periodicity across all ages by comparing age estimates of recaptured fish to known times-at-large, which together can provide *in situ* validation (Campana 2001). Third, we compared age-independent

von Bertalanffy growth models to models built with estimated ages to assess reliability of age estimates to inform management (Long et al. *in review*). Results showed that precision was high (mean coefficient of variation [CV] = 5.4%), but there was only 57% agreement between estimated age and expected increment formation with time at large. However, no age estimation error was detected for fish < 140 mm TL and, for fish > 140 mm TL, age estimation errors were unbiased (approximately equal amounts of over- and under-estimates of age). Differences among mean estimated length-at-age from age-dependent and age-independent von Bertalanffy growth models varied minimally for ages 3-8. Overall, these non-lethal age estimates could be useful for informing fisheries management (Long et al. *in review*).

Fish that lacked an age estimate (i.e., regenerated scales or missing samples) were proportionally assigned an age using age-length keys constructed in the FSA package for Program R (Isermann and Knight 2005; Ogle 2015). Age-length keys were built with 25-mm TL bins, and fish were assigned an age based on keys built for each stream system and sampling month combination to avoid potential bias introduced by variation in growth among stream systems or sampling seasons (Ogle 2015). To visualize differences in catch among stream systems (May events only, for consistency), we plotted length-frequency with the following age categories superimposed: young age classes (ages 1 and 2), non-harvestable size adults (< 355 mm TL; ages 3-6), and harvestable size adults ($\geq$ 355 mm TL; ages 7+).

We estimated annual mortality in each stream system using raw catch data and estimated ages. For consistency in mortality estimates among stream systems, we used only May sampling events. We performed linear regression of catch-curves using the FSA package in Program R (Ogle 2015), wherein we used weighted regression to reduce the influence of older, under-represented age classes (Maceina and Bettoli 1998). We pooled catch data by age (i.e., not year-class) in each stream system across sample years to dampen the potential effects of recruitment variation (Ogle 2015). We only included ages that recruited to the gear in each stream system by excluding ages in the ascending limbs of the catch-curves (Ogle 2015).

Objective 1c – Recruitment

We quantified recruitment variation with a distinct set of weighted catch-curve regressions, wherein the residuals provided an index of year-class strength (Maceina 1997; Maceina and Bettoli 1998). We used raw catch data from May samples and, again, only included ages recruited to the gear used in each stream system. Regressions were performed for each stream system and sampling year combination, while tracking the year-class represented by each age. In this manner, a given year-class in a stream system could be represented by multiple residuals derived from different sampling years. We used raw residuals for modeling environmental relationships, but used Studentized residuals to facilitate interpretation of strong (≥ 2 SD) and weak (≤ -2 SD) year-classes (Maceina 1997).

We calculated environmental variables for four biologically-relevant seasons in each year: “spring” spawning and hatching period (April-June; Taylor and Peterson 2014); “summer” post-hatch period (July-September; Sammons and Gocłowski 2012); “fall” growth period (October-December; Woodside et al. 2015); and “over-winter” survival (January-March; Suski and Ridgway 2009). For

comparability, we followed Woodside et al. (2015) in calculating seasonal hydrology variables based on mean daily discharge (m^3/s): minimum, median, average, SD, and number of days above seasonal average. Mean daily discharge values were obtained from USGS stream gauge stations immediately upstream or downstream of sampling sites that provided data through the timespan of year-classes represented in our catch (02335700 [Big Creek], 02331600 [Chattahoochee River], 0233500 [Chestatee River]). To characterize stream temperature conditions favorable for Shoal Bass growth, we also included seasonal cumulative growing degree-days and average growing degree-days. We calculated growing degree-days with a base temperature of 0°C (Schlosser et al. 2000; Chezik et al. 2013), using daily high and low air temperature records from the NOAA National Centers for Environmental Information (USW00053863 [Big Creek]; USC00093621 [Chattahoochee and Chestatee rivers]).

We investigated possible relationships among recruitment strength and environmental factors in each stream system using linear models built with a limited set of variables. Continuous variables were natural-log transformed and degree-day counts were transformed by the natural log ($x+1$) to meet normality assumptions prior to modeling. Pearson correlation coefficients (r) among variables commonly exceeded $r = |0.7|$; therefore, we conducted principal components analysis (PCA) with the transformed datasets to identify redundant linear trends among variables in each stream system. We conducted PCA analyses in PC-ORD v. 6 (McCune and Mefford 2011) to reduce the number of variables to be modeled. We retained the variable most highly correlated to each axis where the number of axes considered explained at least 10% of the variation in the dataset. Because of sample size limitations and the exploratory nature of this modeling exercise, we opted to construct univariate linear models only. We related recruitment strength (residuals) to environmental variables using linear models constructed with the 'lm' command in Program R at a significance level of $P \leq 0.05$. We evaluated the assumption of homoscedasticity with residual plots and the assumption that residuals are normally distributed with Q-Q plots.

Objective 2a – Population Size

We analyzed CMR data from all sampling events that occurred in Big Creek after May 2013 using Huggins' closed-population models (Huggins 1989) in Program MARK v. 6.0 (White and Burnham 1999). Huggins' models estimate abundance (N) as a derived parameter, along with 95% confidence intervals (CI's), based on capture (p) and recapture probabilities (c) from CMR histories. We considered sampling events that occurred within the same month to represent closed periods during which N was estimated. Sampling events within each month were conducted 1-3 days apart as dictated by weather and streamflow conditions. We parameterized models to allow p to vary over time because of heterogeneity in stream conditions and sampling teams during the closed periods.

Objective 2b – Movement

On 20 May 2014, we conducted backpack electrofishing in the wadeable shoals downstream of Roswell Mill Dam to obtain phenotypic adult Shoal Bass > 200 g (2% rule; Winter 1996) for implantation with 9-month Sonotronics IBT-96-9-I acoustic transmitters. Fish were individually immersed in an aquatic anesthetic (AquiS-20E) until they reached a deep narcosis stage for surgical transmitter implantation in the coelomic cavity. A phone number was recorded on the implanted

transmitters so that anglers could report harvest of tagged fish; however, we did not apply external markings or implement a reward system to encourage angler reporting because angling pressure for black bass species was believed to be minimal in the study area. A PIT tag (Oregon RFID 12 mm x 2.15 mm FDX-B polymer) was also inserted into the body cavity of each fish to allow for individual identification after expiration of transmitter batteries. Fish recovered from anesthesia in a tank of oxygenated ambient stream water, and were released at their original capture locations after regaining equilibrium.

Shoal habitats are characteristically noisy, which is unfavorable for acoustic telemetry methods (Koehn 2012). To ensure detectability of Shoal Bass, allow for inference into the directionality of Shoal Bass movements, and examine the potential for emigration of Shoal Bass from Big Creek into the mainstem Chattahoochee River, we placed a submersible ultrasonic receiver (SUR; Sonotronics SUR-01) at two locations on Big Creek. One receiver was placed in Big Creek 50 m upstream of the confluence with the Chattahoochee River on 02 June 2014 (“downstream SUR”) and a second was placed in a pool just downstream of the first upstream shoal habitat, approximately 1 km upstream of the confluence on 27 June 2014 (“upstream SUR”; Figure 4). Both receivers were programmed to repeatedly cycle through available tag frequencies, completing a scan every 2-3 min. We placed an active transmitter at various points from the receivers to ensure both receivers could detect nearby tagged fish and that a tagged fish near one SUR would not be detected by the other. At the downstream SUR, an active transmitter was placed across the width of the stream (approximately 20 m from SUR deployed near opposite bank) and near the confluence with the Chattahoochee River (approximately 50 m downstream from SUR). At the upstream SUR, we placed an active transmitter across the width of the stream, approximately 20 m from the SUR deployed near the opposite stream bank. Both receivers recorded detections during these trials and did not detect the transmitter while deployed near the opposite SUR. Both receivers recorded data for approximately 7 months (through 25 December 2014 for the downstream SUR and through 04 January 2015 for the upstream SUR).

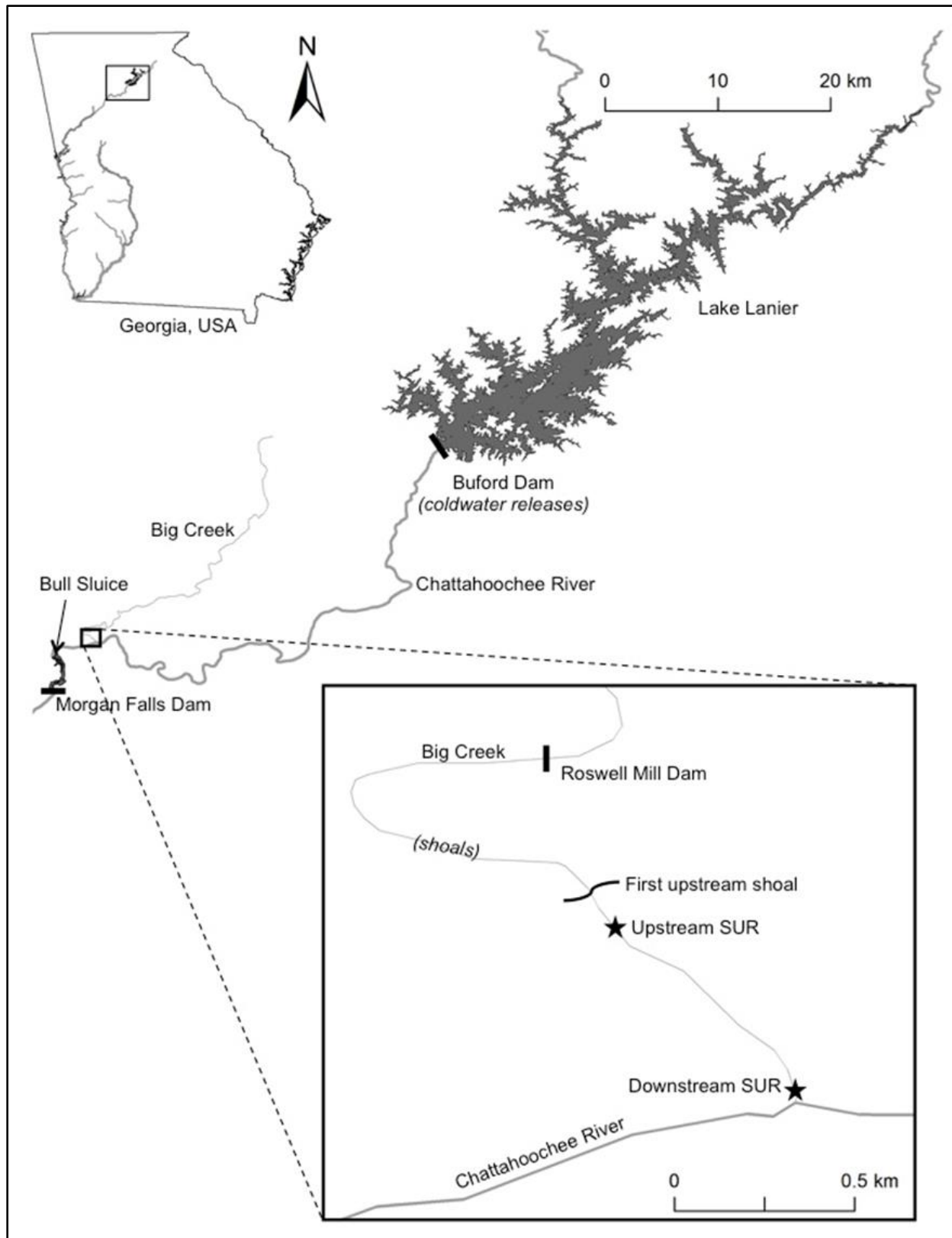


Figure 4. Telemetry study area in Big Creek, Georgia, including submersible ultrasonic receiver (SUR) locations used to detect movements of tagged adult Shoal Bass (*Micropterus cataractae*).

In addition to SUR detections, we used directed sampling efforts, opportunistic active tracking, and angler harvest reports to provide supplemental location data. CMR sampling with backpack electrofishing was performed in the upstream 1 km of wadeable shoal habitats for two days each in May 2014, Oct. 2014, May 2015, and May 2016. We also performed an opportunistic active-tracking survey on Oct. 15, 2014 with a directional hydrophone and receiver (Sonotronics USR-5W) in the lower 1 km of Big Creek. Finally, anglers that reported harvest of tagged fish were asked to provide tag number, date, and a description of capture location.

We then explored whether Shoal Bass residency at our SUR locations was correlated with environmental factors. First, we removed false detections by filtering all SUR records by tag frequency (khz) and tag interval ($\text{ms} \pm 1 \text{ ms}$). To summarize daily detections by SUR location, we created abacus plots of daily detections of individual fish at each SUR location. To better understand trends in residence at each SUR location and elucidate whether emigration into the Chattahoochee River is plausible, we calculated daily percent residence by dividing the number of tagged fish detected at a SUR each day by the total number of tagged fish available to be detected each day. To investigate which environmental variables may have influenced residence, we calculated Pearson's product-moment correlation coefficients (r) between daily percent residence at upstream and downstream locations with several biologically relevant environmental variables using the "CORR" procedure in SAS v. 9.4 (SAS Institute, Inc.). In interpreting results, r provides indication of strength and directions of a linear relationship between two variables. We considered correlations to be significant at $P \leq 0.05$.

Environmental variables included mean daily water temperature ($^{\circ}\text{C}$) in Big Creek (USGS stream gage 02335700) and the Chattahoochee River (USGS stream gage 02335450) and mean daily discharge (m^3/s) in Big Creek (USGS gage 02335757) and the Chattahoochee River (USGS stream gage 02335450). Because daily differences in water temperature between Big Creek and the thermally altered mainstem Chattahoochee River may create a thermal barrier to Shoal Bass emigration, we calculated the difference in mean daily water temperature ($^{\circ}\text{C}$; Big Creek minus Chattahoochee River). To determine if differences in relative discharge between the two waterbodies correlated with daily residence, we standardized (mean = 0, SD = 1) mean daily discharge from each river, and then subtracted the standardized values for Big Creek from the Chattahoochee River to calculate the relative difference in discharge. Finally, because fluctuations in Bull Sluice Lake's level influence stream characteristics near Big Creek's confluence, we also included the daily mean elevation of Bull Sluice Lake's water surface above datum (m; USGS gage 02335810).

Results

Sample Collection

In Big Creek, sampling was performed on the following dates, spanning both spring and late fall/early winter seasons: 13 November 2013; 20 and 22 May 2014; 17 and 18 October 2014; 13 and 15 May 2015; and 16 and 19 May 2016. Cumulatively, we spent 3,627 minutes of sampling effort on Big Creek, where we caught 576 Shoal Bass with an overall catch-per-unit effort (CPUE) of 0.16 fish/min (Table 2). Length-frequency data for Shoal Bass in Big Creek depicted a population dominated by small, juvenile fish during all sampling events; however, large adults were more prominent in May samples compared to samples taken in October or November (Figure 5).

Table 2. Shoal Bass (*Micropterus catarractae*) catch data by date in Big Creek, Roswell, Georgia. Backpack electrofishing effort (min) was summed across all backpack electrofishing units to calculate catch-per-unit-effort (CPUE).

Date	Effort (min)	Catch	CPUE
13 Nov. 2013	292.9	27	0.10
20 May 2014	300.2	22	0.06
22 May 2014	413.6	45	0.14
17 Oct. 2014	470.3	75	0.16
18 Oct. 2014	430.9	86	0.20
13 May 2015	389.0	52	0.13
15 May 2015	456.1	69	0.15
16 May 2016	428.6	131	0.31
19 May 2016	445.3	69	0.15
All Dates	3626.8	576	0.16

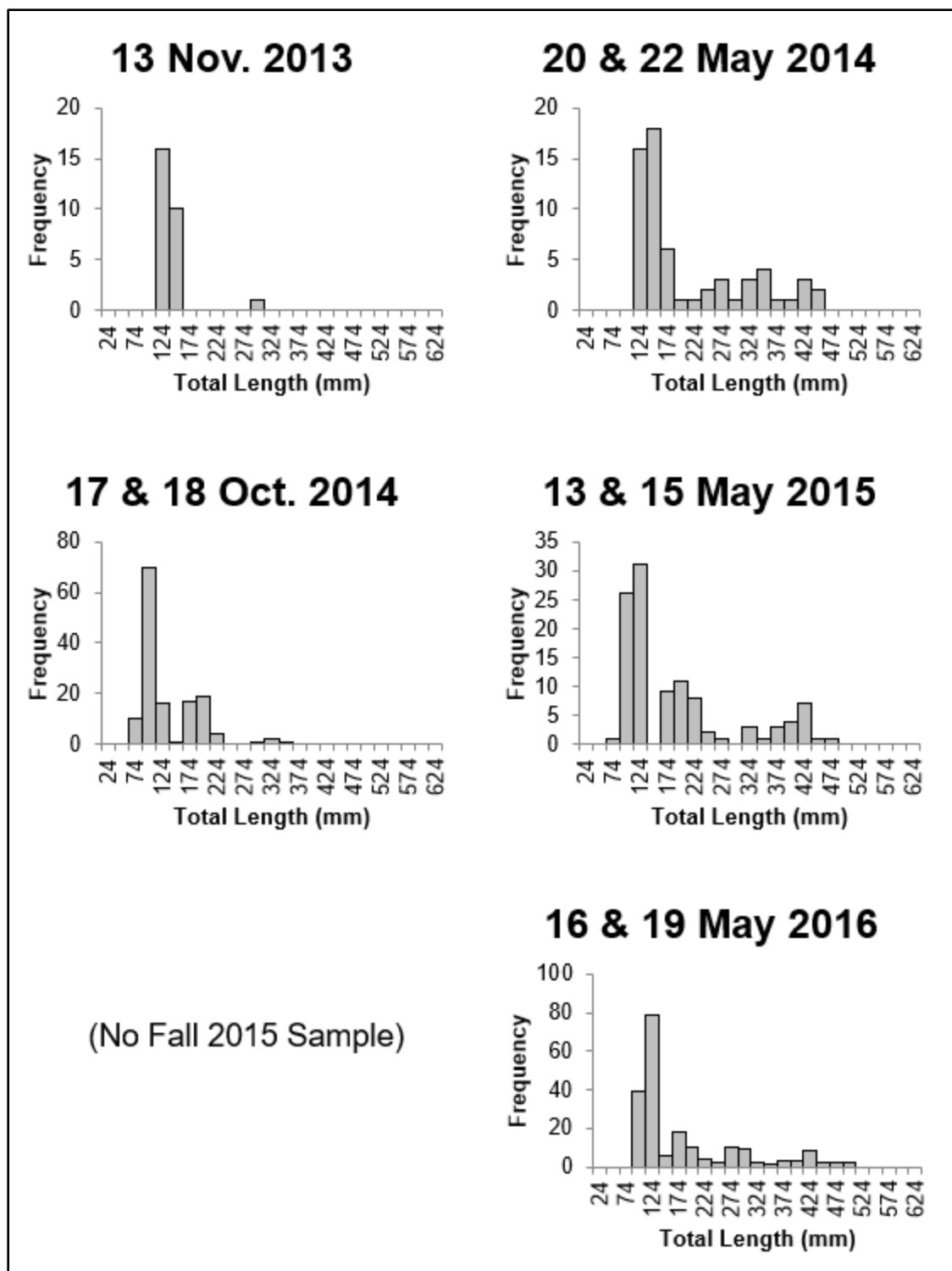


Figure 5. Length-frequency histograms of Shoal Bass (*Micropterus catarractae*) catch from Big Creek, Roswell, Georgia.

We sampled the Chestatee and Chattahoochee rivers exclusively in the spring. We sampled the Chestatee River on 29 May 2013; 19 and 21 May 2014; 12 and 14 May 2015; and 17 and 18 May 2016. Effort totaled 420 minutes in the Chestatee River and resulted in capture of 274 Shoal bass (overall CPUE of 0.65 fish/min; Table 3). We sampled the Chattahoochee River on 05 May 2013; 27 and 29 May 2014; and 18 and 20 May 2015. Sampling the Chattahoochee River in May 2016 was attempted but not completed because low discharge conditions precluded sampling. Thus, the Chattahoochee River was only sampled each spring from 2013-2015, with 270 min of effort and 182 Shoal Bass captured (overall CPUE of 0.67 fish/min; Table 4). Lengths of sampled fish from the Chestatee River (Figure 6) and Chattahoochee River (Figure 7) were more evenly distributed than those sampled from Big Creek.

Table 3. Shoal Bass (*Micropterus cataractae*) catch data by date and sampling location in the Chestatee River, Georgia.

Date	Effort (min)	Catch	CPUE
29 May 2013	60	28	0.47
19 May 2014	60	33	0.55
21 May 2014	60	37	0.62
12 May 2015	60	45	0.75
14 May 2015	60	41	0.68
17 May 2016	60	44	0.73
18 May 2016	60	46	0.77
All Dates	420	274	0.65

Table 4. Shoal Bass (*Micropterus cataractae*) catch data by date and sampling location in the Chattahoochee River, Georgia.

Date	Effort (min)	Catch	CPUE
15 May 2013	60	45	0.75
27 May 2014	60	38	0.63
29 May 2014	60	42	0.70
18 May 2015*	45	29	0.64
20 May 2015*	45	28	0.62
All Dates	270	182	0.67

* Buck Shoals (site 6) was inaccessible due to low water conditions.

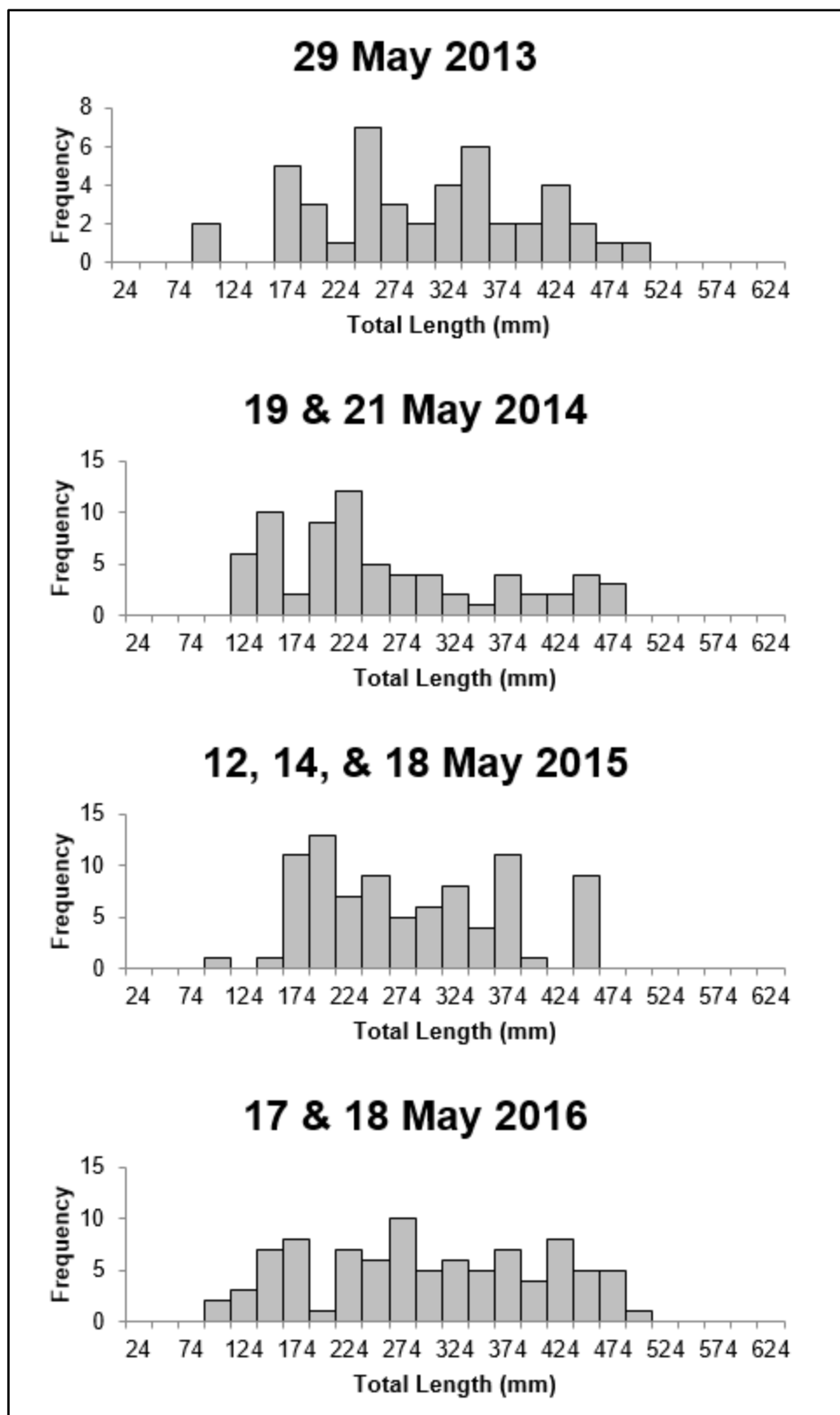


Figure 6. Length-frequency histograms of phenotypic Shoal Bass (*Micropterus cataractae*) catch from the Chestatee River, Georgia.

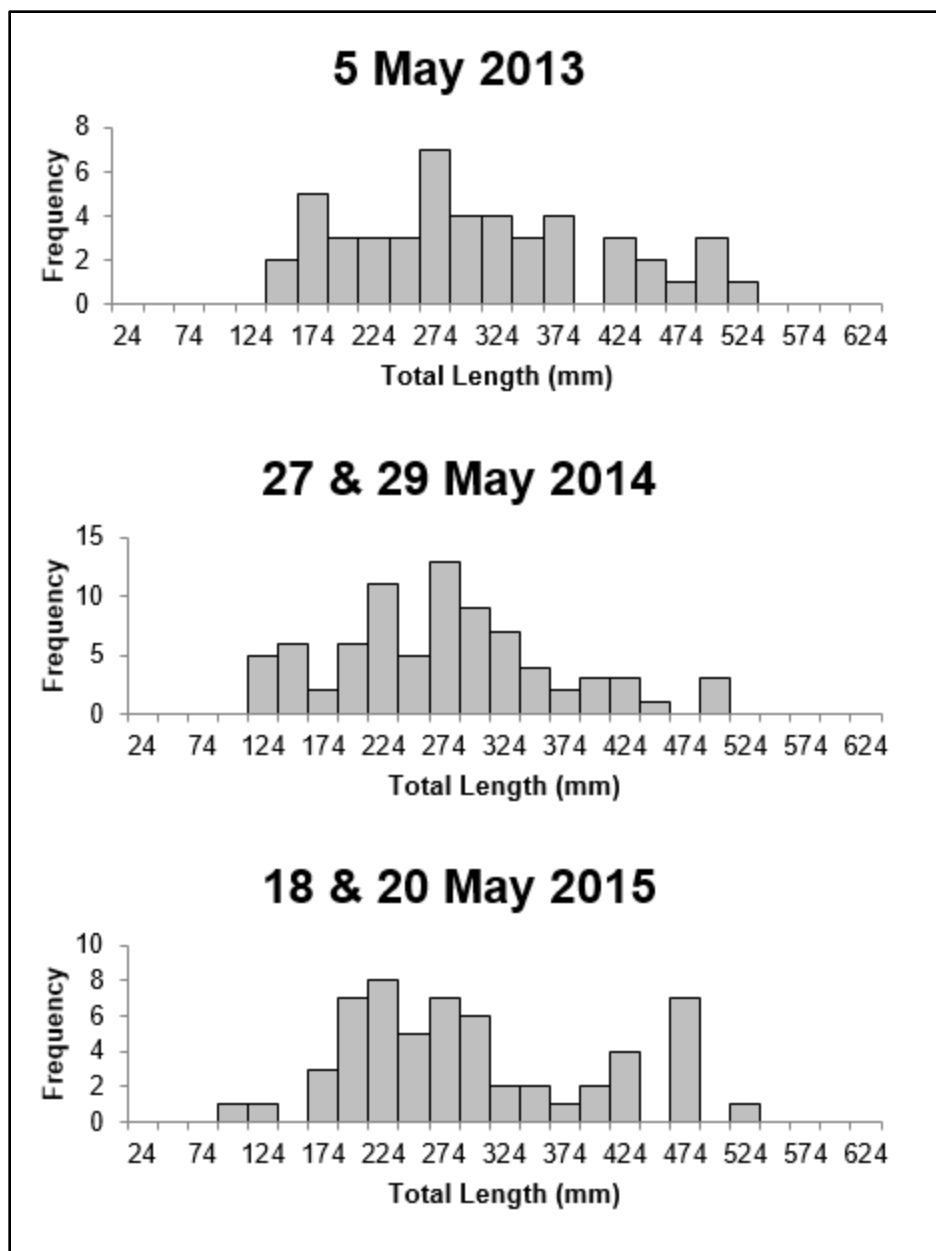


Figure 7. Length-frequency histograms of phenotypic Shoal Bass (*Micropterus catarractae*) catch from the Chattahoochee River upstream of Lake Lanier, Georgia.

Objective 1a – Genetic Diversity

We collected 62 fin-clips from putative Shoal Bass sampled in Big Creek on 13 and 15 May 2015. Fifty fin-clips were collected from putative Shoal Bass in the Chattahoochee River on 05 May 2013, and 45 fin-clips were collected from the Chestatee River on 29 May 2013.

Taxonomic assignment of 62 putative Shoal Bass genotypes from Big Creek illustrated that introgressive hybridization was widespread, particularly with non-native Smallmouth Bass. Individual proportional assignments illustrated the majority of individuals were Shoal Bass x Smallmouth Bass hybrids (Figure 8), and taxonomic classification resulted in 15 (24%) pure Shoal Bass, 21 (34%) backcrosses towards Shoal Bass, and 26 (42%) F1 or later-generation hybrids. Several hybrid individuals also contained appreciable amounts (14%-39%) of Alabama Bass alleles. Introgression with Smallmouth Bass appears to have proceeded as unidirectional backcrossing towards native Shoal Bass. Overall genomic proportions for the population were 77% Shoal Bass, 20% Smallmouth Bass, 2% Alabama Bass, and negligible amounts of other black bass taxa (Figure 9). Low sample size of pure Shoal Bass genotypes in Big Creek precluded genetic diversity analysis and N_e estimation.

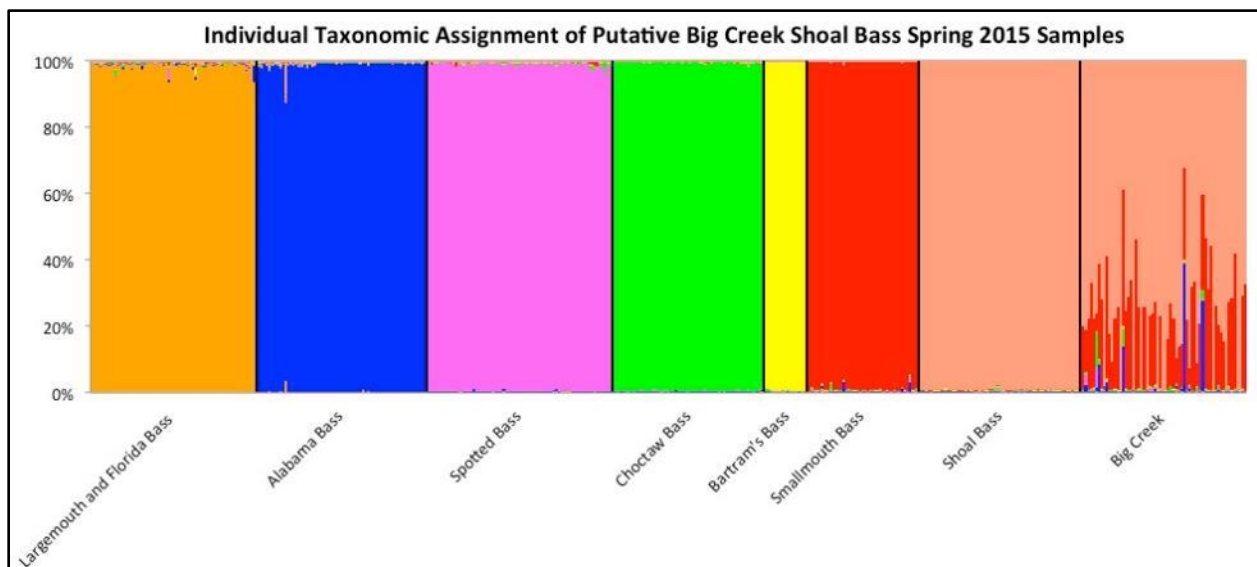


Figure 8. Taxonomic assignment of 62 putative Shoal Bass (*Micropterus cataractae*) collected in Big Creek, Roswell, Georgia, in spring 2015. Reference genotypes of seven reference black bass taxa were used to proportionally assign individuals from Big Creek genotypes.

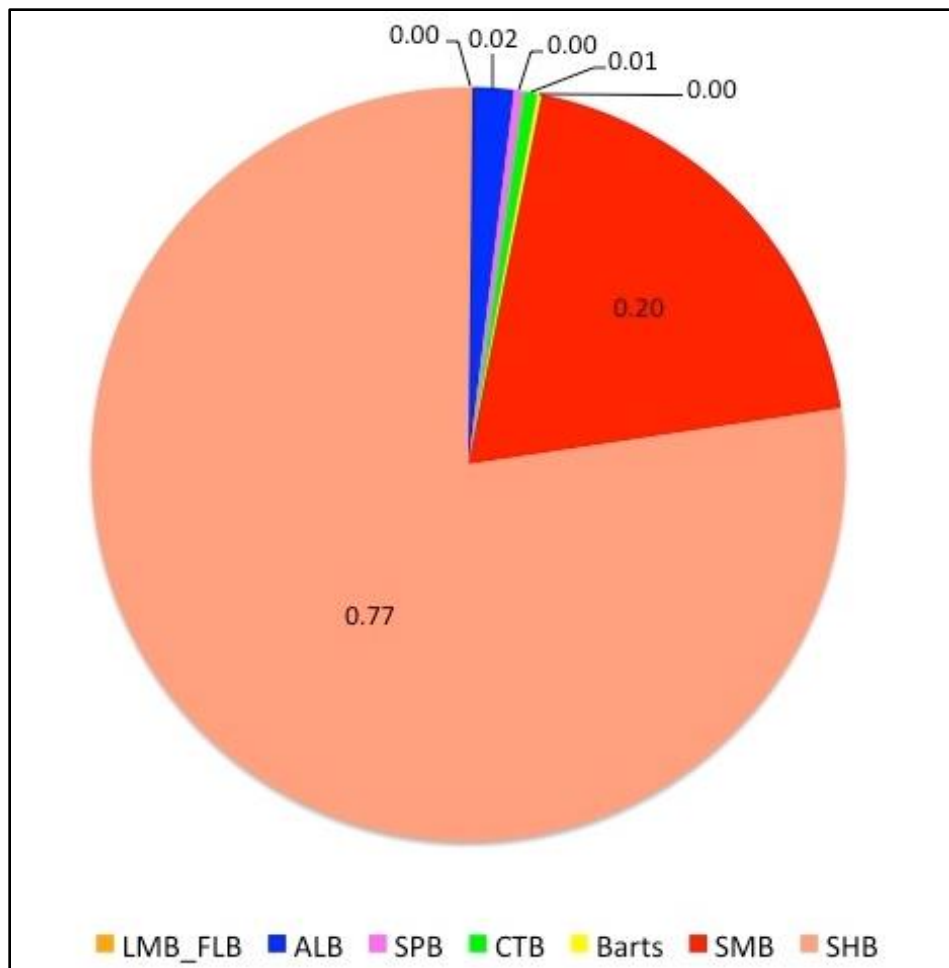


Figure 9. Overall genomic proportions for 62 putative Shoal Bass (*Micropterus cataractae*) individuals sampled in Big Creek in spring 2015. Label abbreviations are as follows: LMB_FLB = Largemouth Bass and Florida Bass intergrades, ALB = Alabama Bass, SPB = Spotted Bass, CTB = Choctaw Bass, Barts = Bartram's Bass, SMB = Smallmouth Bass, and SHB = Shoal Bass.

Taxonomic screening of putative Shoal Bass genotypes revealed that 42 of 45 (93%) from the Chestatee River and 49 of 50 (98%) from the Chattahoochee River were pure Shoal Bass; 3 fish from the Chestatee River were recent backcrosses with Alabama Bass, and 1 fish from the Chattahoochee River was an Alabama Bass. Of 16 microsatellite markers, 6 loci were fixed for one allele in all Shoal Bass from the Chestatee and Chattahoochee rivers. Shoal Bass from the Chestatee River had 3 private alleles amongst 3 loci and the Chattahoochee River had 12 private alleles amongst 5 loci; however, all private alleles occurred at low frequencies of 1.0–7.1%. Measures of allelic diversity indicated slightly higher diversity in the Chattahoochee River, as samples had higher average values for *A* and *AR* (Table 5). There were only slight discrepancies between *He* and *Ho* at specific loci in both rivers.

Table 5. Genetic diversity measures by locus for Shoal Bass (*Micropterus cataractae*) sampled in the Chestatee and Chattahoochee rivers, Georgia: number of alleles observed (A), effective number of alleles (A_e), allelic richness (A_R), expected heterozygosity (H_e), observed heterozygosity (H_o), and the number of individuals genotyped (n). Table is continued on following page.

Locus	Statistic	Chestatee River	Chattahoochee River
Msaf 05 (total 5 alleles)	A	5	5
	A_e	1.773	1.803
	A_R	4.000	4.953
	H_e	0.436	0.445
	H_o	0.381	0.490
	n	42	49
Msaf 06 (total 4 alleles)	A	4	3
	A_e	2.226	2.119
	A_R	3.996	2.999
	H_e	0.551	0.528
	H_o	0.524	0.490
	n	42	49
Msaf 10 (total 5 alleles)	A	4	5
	A_e	3.181	2.525
	A_R	4.000	4.959
	H_e	0.686	0.604
	H_o	0.595	0.592
Msaf 17 (total 9 alleles)	A	8	7
	A_e	3.585	3.249
	A_R	7.849	6.388
	H_e	0.721	0.692
	H_o	0.833	0.714
	n	42	49
Msaf 22 (total 2 alleles)	A	2	2
	A_e	1.385	1.324
	A_R	2.000	2.000
	H_e	0.278	0.245
	H_o	0.286	0.286
	n	42	49
Msaf 25 (total 2 alleles)	A	2	2
	A_e	1.800	1.534
	A_R	2.000	2.000
	H_e	0.444	0.348
	H_o	0.429	0.327
	n	42	49

* Fixed loci not shown but included in overall average: Msaf 08, 09, 12, 13, 24, and 31.

Table 5 (continued). Genetic diversity measures by locus for Shoal Bass (*Micropterus cataractae*) sampled in the Chestatee and Chattahoochee rivers, Georgia: number of alleles observed (A), effective number of alleles (A_e), allelic richness (A_R), expected heterozygosity (H_e), observed heterozygosity (H_o), and the number of individuals genotyped (n). Table is continued on following page.

Locus	Statistic	Chestatee River	Chattahoochee River
Msaf 27 (total 4 alleles)	A	4	4
	A_e	3.076	2.502
	A_R	4.000	4.000
	H_e	0.675	0.600
	H_o	0.738	0.571
	n	42	49
Msaf 28 (total 2 alleles)	A	2	2
	A_e	1.126	1.021
	A_R	2.000	1.796
	H_e	0.112	0.020
	H_o	0.119	0.020
	n	42	49
Msaf 29 (total 17 alleles)	A	9	17
	A_e	6.533	11.039
	A_R	8.995	16.526
	H_e	0.847	0.909
	H_o	0.810	0.898
	n	42	49
Msaf 32 (total 4 alleles)	A	3	4
	A_e	2.566	2.665
	A_R	3.000	3.994
	H_e	0.610	0.625
	H_o	0.500	0.625
	n	42	48
Average*	A	3.1	3.6
	A_e	2.078	2.236
	A_R	2.990	3.476
	H_e	0.335	0.314
	H_o	0.326	0.313
	n	41.8	48.9

* Fixed loci not shown but included in overall average: Msaf 08, 09, 12, 13, 24, and 31.

Following the population structure reported by Taylor (2017), we estimated N_e and N_{eb} for the Chestatee River population, the Chattahoochee River population, and a combined population of fish from both rivers (Table 6). The heterozygote excess method did not perform well with our dataset, thus we disregarded those estimates in further interpretation of our results. Linkage disequilibrium and molecular coancestry estimators suggested that the Chattahoochee River population had a larger estimated effective population size than the Chestatee River population; however, river-specific estimates were hindered by smaller sample sizes that resulted in excessive uncertainty. Point estimates for effective size of the combined population of both rivers ranged from 93.8–197.4.

Table 6. Estimates of effective population size (N_e) and effective number of breeders (N_{eb}) for Shoal Bass (*Micropterus cataractae*) populations in the Chestatee River, Chattahoochee River, and both populations combined. Thresholds (thres.) were applied to remove rare alleles at the frequencies given to account for estimate inflation.

Estimator	Thres.	Population estimates (95% C.I.'s)		
		Chestatee	Chattahoochee	Combined
Linkage Disequilibrium (N_e)	< 5%	43.8 (22.8 - 129.9)	∞ (249.2 - ∞)	111.9 (58.3 - 371.0)
Linkage Disequilibrium (N_e)	< 2%	85.5 (38.0 - 2144.2)	3670.8 (110.1 - ∞)	151.8 (85.3 - 429.2)
Linkage Disequilibrium (N_e)	< 1%	93.4 (40.6 - ∞)	∞ (202.8 - ∞)	197.4 (105.0 - 761.8)
Heterozygote Excess (N_{eb})	< 5%	∞ (16.8 - ∞)	29.5 (9.8 - ∞)	∞ (115.9 - ∞)
Heterozygote Excess (N_{eb})	< 2%	∞ (18.8 - ∞)	704.0 (13.3 - ∞)	∞ (138.0 - ∞)
Heterozygote Excess (N_{eb})	< 1%	∞ (19.5 - ∞)	2364.8 (14.9 - ∞)	∞ (173.9 - ∞)
Molecular Coancestry (N_{eb})	NA	9.4 (3.1 - 19.3)	∞ (∞ - ∞)	93.8 (0.1 - 471.0)

Objective 1b – Age and Mortality

We estimated age for 92% of scale samples and assigned ages with age-length keys to 27 samples in Big Creek, 27 in the Chattahoochee River, and 31 in the Chestatee River. Ages ranged from 1-12 years in all three rivers, and age-0 fish were only encountered in Big Creek in October 2014. Differences in raw catch were evident among rivers, with relatively more young fish captured in Big Creek (Figure 10). Harvestable-size fish (≥ 355 mm TL; GADNR regulations) comprised 10% of the catch from Big Creek compared to 18% of the combined catch from the Chestatee and Chattahoochee rivers. Maximum TL observed was 478 mm in Big Creek, 516 mm in the Chattahoochee River, and 487 mm in the Chestatee River.

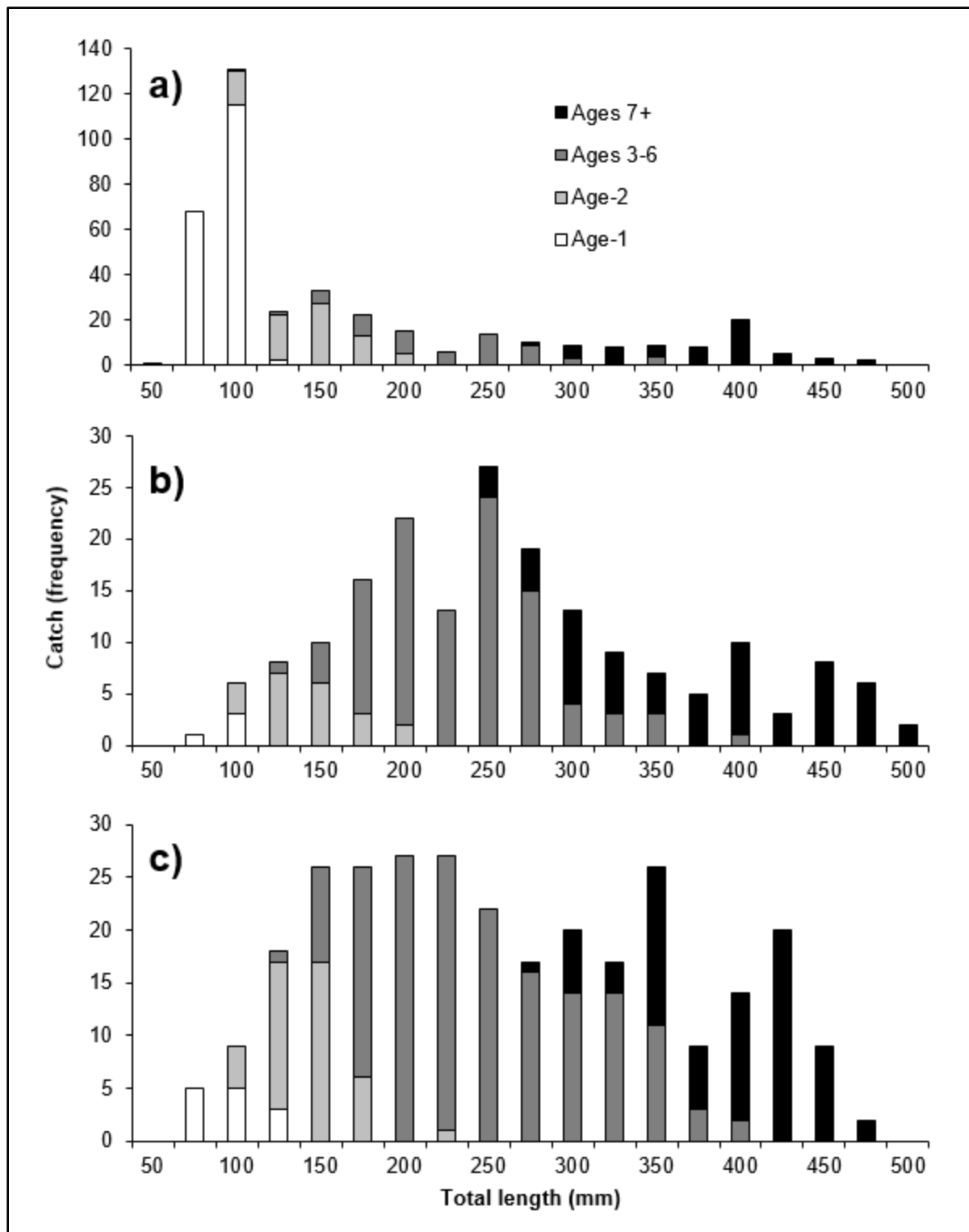


Figure 10. Length-frequency histograms, with age categories superimposed, depicting raw catch of Shoal Bass (*Micropterus cataractae*) from May sampling events in (a) Big Creek, (b) Chattahoochee River, and (c) Chestatee River.

Shoal Bass did not fully recruit to boat-electrofishing gear used in the Chattahoochee and Chestatee rivers until age-3, but recruited to backpack-electrofishing gear in Big Creek at age-0. Because catch-curve regressions assume mortality rates are equal across all ages included, we excluded younger age classes recruited to the gear in Big Creek because they may experience disproportionately higher mortality rates than older age classes. In this manner, results were more comparable across systems because mortality was estimated across same range of ages. Catch-curve estimates of annual mortality for ages 3-12 years were similar among systems: 18.4% (95% CI's: 7.8-27.8%; $R^2 = 0.65$) in Big Creek, 20.8% (95% CI's: 13.2-27.7%; $R^2 = 0.81$) in the Chattahoochee River, and 23.7% (95% CI's: 13.8-32.4%; $R^2 = 0.80$) in the Chestatee River (Figure 11).

Objective 1c – Recruitment

We used ages 3-12 years to perform weighted catch-curve regressions to investigate recruitment variation in each river. Studentized residuals indicated strong year-classes in 2006 and 2007 in Big Creek and in 2006 in the Chattahoochee River, whereas weak year-classes were evident in 2004, 2009, and 2013 in Big Creek, in 2003, 2004, and 2011 in the Chattahoochee River, and in 2007 and 2008 in the Chestatee River (Figure 12). Principal components analysis identified three axes that explained at least 10% of the variation in each river, wherein the majority of variation among environmental variables (PC-axis 1) in Big Creek was driven by summer SD of discharge (49%), compared to fall minimum discharge in the Chattahoochee (50%) and Chestatee (50%) rivers (Table 7). Two significant linear models were obtained in Big Creek, one suggesting a negative relationship between recruitment strength and summer SD of discharge ($P < 0.01$; $R^2 = 0.38$) and another indicating a positive relationship between recruitment strength and fall cumulative growing degree-days ($P = 0.04$; $R^2 = 0.15$; Table 8). We obtained a single significant model in the Chattahoochee River that suggested a positive relationship between recruitment strength and winter SD of discharge ($P = 0.04$; $R^2 = 0.16$). No significant models were obtained in the Chestatee River, likely because recruitment variation was not as pronounced as in the other rivers. No violations to linear model assumptions of homoscedasticity or normality of residuals were evident among the models examined.

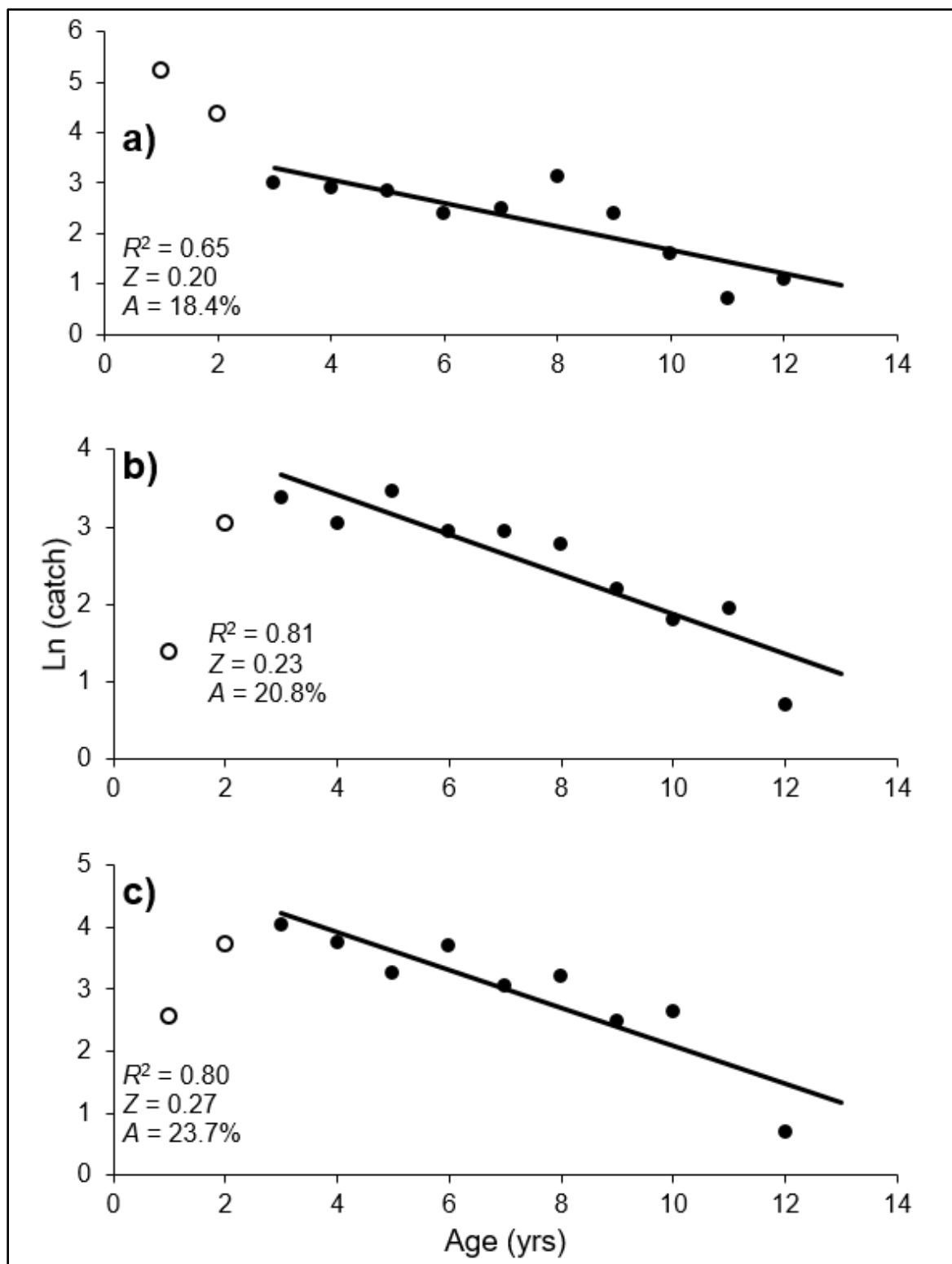


Figure 11. Catch-curve weighted regressions used to estimate annual mortality in Shoal Bass aged 3-12 years in (a) Big Creek, (b) Chattahoochee River, and (c) Chestatee River. Fish aged < 3 years (hollow data points) were not included in regressions. R^2 measures fit to the regression line, Z is the instantaneous mortality rate, and A is annual mortality.

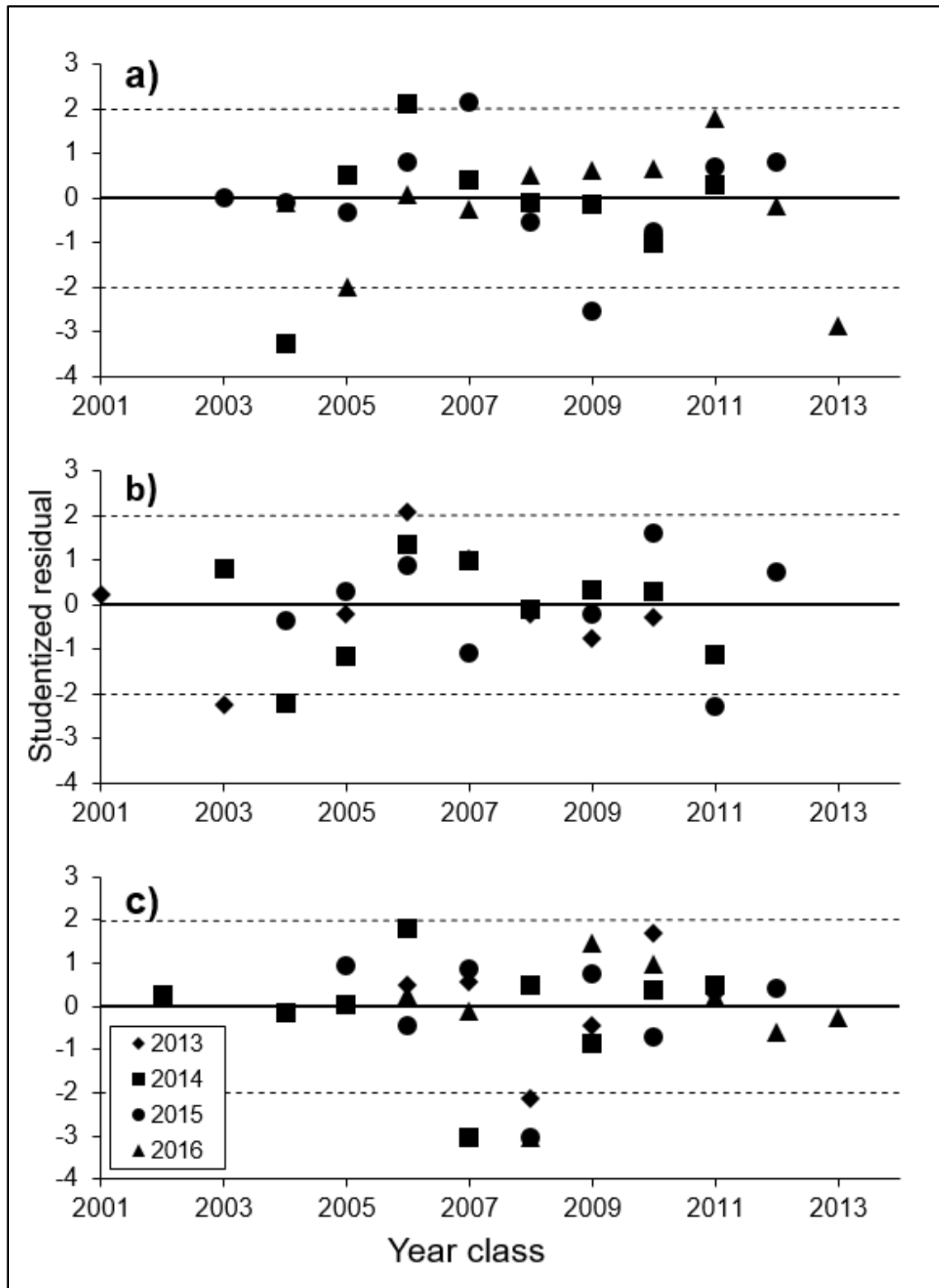


Figure 12. Studentized residuals from weighted catch-curve regressions indicating year-class strength of Shoal Bass in (a) Big Creek, (b) Chattahoochee River, and (c) Chestatee River. Studentized residuals exceeding ± 2 SD (dashed lines) were considered strong and weak year-classes, respectively. Symbols indicate residuals calculated over different sampling years.

Table 7. Results of principal component analysis (PCA) used to reduce the number of inter-correlated environmental variables considered in linear models of recruitment strength. The highest-loading variable from any axis explaining at least 10% of the variance in each system's dataset was included. Reported are the PCA axis number, axis eigenvalue, and the % of variation explained by each axis, along with the variably most highly correlated to each axis and its correlation coefficient (*r*) to the axis.

Location	Axis	Eigenvalue	% of		<i>r</i>
			variation	Highest loading variable	
Big Creek	1	13.82	49.35	Summer SD of discharge	0.95
	2	5.79	20.69	Spring min. discharge	-0.81
	3	3.39	12.12	Fall cumulative growing degree-days	-0.77
Chestatee River	1	13.98	49.93	Fall min. discharge	0.96
	2	5.58	19.94	Spring min. discharge	-0.75
	3	3.68	13.13	Spring avg. growing degree-days	-0.90
Chattahoochee River	1	14.05	50.17	Fall min. discharge	0.96
	2	5.92	21.13	Winter SD of discharge	0.75
	3	3.72	13.27	Summer cumulative growing degree-days	-0.73

Table 8. Results of univariate linear models relating catch-curve residuals representing Shoal Bass (*Micropterus catarractae*) recruitment strength in three systems of the upper Chattahoochee River basin to a subset of environmental variables obtained from principal component analysis. Models were considered significant at $P \leq 0.05$ (**bold**).

Location	Variable	Estimate	SE	df	<i>P</i>	<i>R</i> ²
Big Creek	Summer SD discharge	-0.27	0.07	1, 26	< 0.01	0.38
	Spring min. discharge	-0.36	0.22	1, 26	0.11	0.09
	Fall cumulative growing degree-days	3.49	1.60	1, 26	0.04	0.15
Chestatee River	Fall min. discharge	0.17	0.16	1, 28	0.31	0.04
	Spring min. discharge	0.36	0.25	1, 28	0.17	0.07
	Spring avg. growing degree-days	1.16	2.49	1, 28	0.65	0.01
Chattahoochee River	Fall min. discharge	-0.16	0.18	1, 23	0.39	0.03
	Winter SD discharge	0.55	0.26	1, 23	0.04	0.16
	Summer cumulative growing degree-days	3.91	3.70	1, 23	0.30	0.05

Objective 2a – Population Size

Numbers of phenotypic Shoal Bass captured per sampling day in Big Creek varied from 22 to 131, and the number of recaptured individuals varied from 4 to 38 (Table 9). Mean TL of captures was usually lower than mean TL of recaptured fish because tagged fish grew between initial capture and subsequent recaptures across primary periods. Point estimates of *N* in Big Creek ranged from 219-

348, and overlapping 95% CI's indicated that estimates were similar across all sampling seasons. Abundance in Big Creek was largely driven by young fish, as 78% (316 of 408) of unique PIT-tagged individuals had max age estimates between 0-2 years, compared to only 9% (36 of 408) having max ages of ≥ 7 years.

Table 9. Capture-mark-recapture data for Shoal Bass (*Micropterus cataractae*) in Big Creek, Roswell, Georgia, including date sampled, number of fish captured, mean total length (TL; mm) of captures, number of fish recaptured, mean TL of recaptures, and Huggins' closed-captures estimates of abundance (N) and associated 95% confidence intervals (CI; L = lower and U = upper).

Date	n captured	Mean capture TL	n recaptured	Mean recapture TL	N est.	LCI	UCL
20 May 2014	22	212	NA	NA	–	–	–
22 May 2014	44	208	4	300	245	125	579
17 Oct. 2014	74	130	5	250	–	–	–
18 Oct. 2014	81	116	27	142	253	200	347
13 May 2015	53	168	19	188	–	–	–
15 May 2015	67	184	38	211	219	164	325
16 May 2016	131	161	25	260	–	–	–
19 May 2016	69	181	35	207	348	276	470

Objective 2b – Movement

Eight adult Shoal Bass were sampled on 20 May 2014 and implanted with acoustic transmitters (Table 10). All tagged fish had between 2 and 108 detection days at a given SUR, with more daily detections at the downstream SUR in the winter months (Figure 13). Tagged fish were occasionally detected at both SUR locations within a given day, with tagged fish averaging 7.4 days (range: 1–18) wherein they were detected at both SURs. Daily percent residence was highest at the upstream SUR from late August to mid-October 2014 (max of 50.0%), whereas highest percent residence at the downstream SUR occurred from mid-October through late December 2014 (max of 62.5%; Figure 14). Daily percent residence at the upstream SUR was significantly and positively correlated with the three water temperature variables ($r = 0.49$ to 0.59 ; $P < 0.0001$). Upstream residence was significantly negatively correlated with the standardized difference in discharge between the two rivers ($r = -0.30$; $P < 0.0001$) and discharge in Big Creek ($r = -0.24$; $P = 0.0009$; Table 11). Daily percent residence at the downstream SUR was significantly and negatively correlated with the three water temperature variables ($r = -0.47$ to -0.58 ; $P < 0.0001$), whereas other variables were much less, and non-significantly, correlated ($|r| < 0.11$; $P \geq 0.1105$).

Table 10. Summary of adult Shoal Bass (*Micropterus cataractae*) in Big Creek, Roswell, Georgia that were equipped with acoustic transmitters. Summary includes total length (TL) and weight (g) of each fish; daily detections at each submersible ultrasonic receiver (SUR) location (US = upstream; DS = downstream); number of days with detections at both SURs; year resampled with electrofishing in shoals of Big Creek (May 20XX); and month of harvest from angler reports.

Freq. (khz)	Interval (ms)	Ping code	TL (mm)	Weight (g)	US SUR detect.	DS SUR detects.	Both SURs	Resample shoals	Harvest month
71	890	3-6-5	303	357	108	46	16	16	–
72	880	3-6-6	405	1048	37	22	9	15, 16	–
73	910	4-4-7	344	562	3	46	1	–	Feb. 2015
74	900	4-4-8	330	436	2	2	1	15	–
75	930	4-8-8	428	1073	9	35	6	–	–
76	920	5-5-5	331	491	2	2	1	–	–
77	950	6-7-7	429	1202	35	70	18	15	–
78	940	6-7-8	374	692	25	15	7	15	April 2016

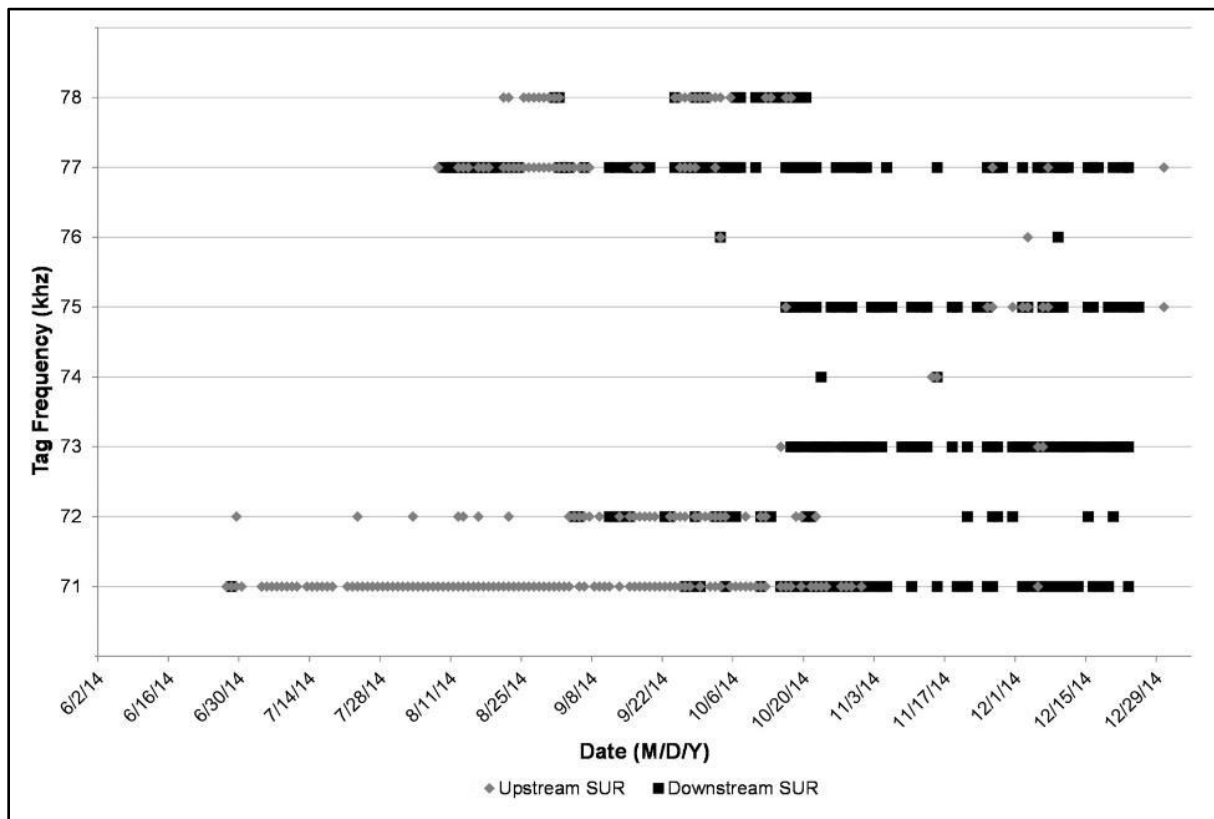


Figure 13. Abacus plot depicting daily detections of tagged adult Shoal Bass (*Micropterus cataractae*) at upstream and downstream submersible ultrasonic receiver (SUR) locations in Big Creek, Roswell, Georgia (see Figure 4 for locations).

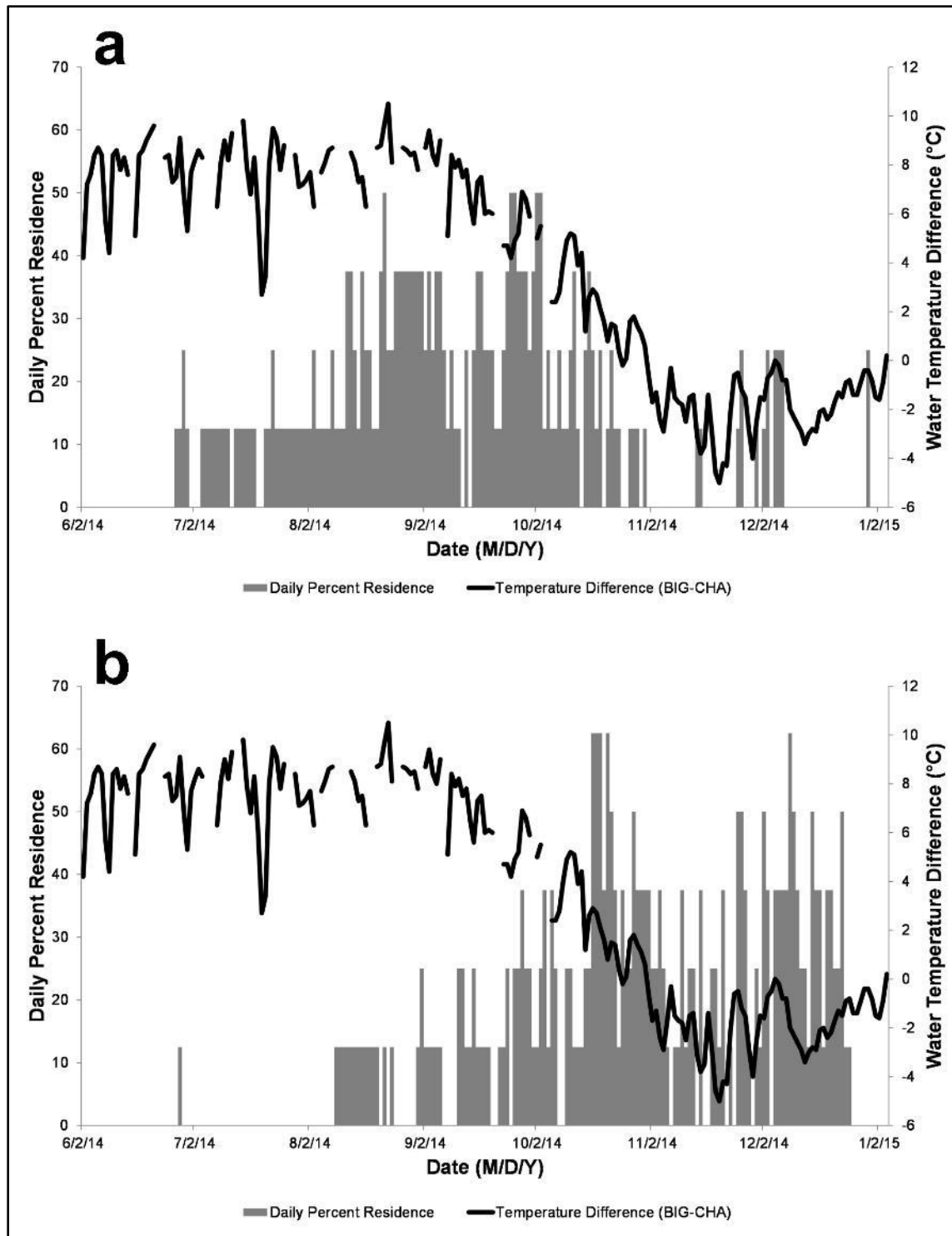


Figure 14. Daily percent residence of tagged adult Shoal Bass (primary y-axis) at (a) upstream and (b) downstream submersible ultrasonic receiver (SUR) locations in Big Creek, Roswell, Georgia. The difference in water temperature (°C; Big Creek temp. minus Chattahoochee River temp.; secondary y-axis) was significantly correlated with daily percent residence at each site (upstream SUR $r = 0.59$, downstream SUR $r = -0.58$). Water temperature differences < 0 °C indicate relatively warmer temperatures in the mainstem Chattahoochee River.

Table 11. Correlation analysis of daily percent residence of Shoal Bass (*Micropterus cataractae*) in Big Creek, Roswell, Georgia, at upstream and downstream submersible ultrasonic receiver (SUR) locations with environmental variables. Table includes sample size (*n*) used to calculate correlations, Pearson's product-moment correlation coefficients (*r*) between daily percent residence with environmental variables, and the resulting *P*-values ≤ 0.05 were considered significant (**bold**).

Location	Environmental variable	<i>n</i>	<i>r</i>	<i>P</i> -value
Upstream SUR	Big Creek water temp. (°C)	192	0.5678	< 0.0001
	Chattahoochee River water temp. (°C)	170	0.4932	< 0.0001
	Temp. difference (Big - Cha.;°C)	170	0.5851	< 0.0001
	Big Creek discharge (m ³ /s)	192	-0.2373	0.0009
	Chattahoochee R. discharge (m ³ /s)	192	0.0985	0.1739
	Standardized discharge difference (Big - Cha.)	192	-0.3027	< 0.0001
	Bull Sluice elevation (m)	186	-0.0389	0.5986
Downstream SUR	Big Creek water temp. (°C)	207	-0.5828	< 0.0001
	Chattahoochee River water temp. (°C)	182	-0.4688	< 0.0001
	Temp. difference (Big - Cha.;°C)	182	-0.5751	< 0.0001
	Big Creek discharge (m ³ /s)	207	-0.0234	0.7374
	Chattahoochee R. discharge (m ³ /s)	207	-0.0578	0.4085
	Standardized discharge difference (Big - Cha.)	207	0.0368	0.5977
	Bull Sluice elevation (m)	199	0.1135	0.1105

Supplemental location data provided inferences on movement and fates of tagged fish. Four of the eight (50%) tagged fish were recaptured in the upstream 1 km of shoal habitats during subsequent backpack electrofishing surveys in May 2015, and two were recaptured in the shoals in May 2016. During an opportunistic active-tracking survey on 15 October 2014, we observed a tagged fish (71 khz) situated within the visible current seam formed by the confluence of Big Creek and the Chattahoochee River. Another fish (78 khz) was positioned in Big Creek just upstream of the confluence near the downstream SUR on the same day.

Two anglers reported harvest of tagged fish (73 khz caught on 21 February 2015 and 78 khz on 07 April 2016). Both fish were caught in Big Creek by anglers using live bait while fishing near the confluence of Big Creek and the Chattahoochee River.

Discussion

Objective 1a – Genetic Diversity

Dakin et al. (2015) used microsatellites to identify two pure Smallmouth Bass, one F1 Shoal Bass x Smallmouth Bass hybrid and 25 pure Shoal Bass in a 2005 sample from Big Creek. Ten years later, our results demonstrated that the invasion of non-native Smallmouth Bass into Big Creek substantially effected the genetic integrity of the Shoal Bass population. Our sample from Big Creek contained an abnormally high percentage (76%) of non-native and hybrid individuals and an abnormally high genomic composition (23%) of non-native alleles. Noticeably lower percentages of hybrid individuals (16-18%) and overall genomic composition of non-native alleles (1-7%) have been documented in Shoal Bass populations of the lower Flint River and the Chipola River (Alvarez et al. 2015; Tringali et al. 2015b). Backcrossing of Smallmouth Bass hybrids appeared unidirectional towards Shoal Bass, indicating that fleeting opportunity exists to conserve the genetic integrity of the population. Shoal Bass in Big Creek have been hybridizing primarily with non-native Smallmouth Bass, but hybridization with non-native Alabama Bass was also detected.

The diminished number of pure Shoal Bass may represent the imminent loss of unique genetic diversity harbored in the Big Creek population (*see* Dakin et al. 2015), in the absence of conservation intervention. One such action could be supplemental stocking of pure, hatchery-reared Shoal Bass of a similar genetic stock as those found in Big Creek (Taylor 2017). In Texas, stocking of Guadalupe Bass successfully reduced introgression between native Guadalupe Bass (*M. treculii*) and non-native Smallmouth Bass without depressing native genetic diversity (Fleming et al. 2015). Supplemental stocking of genetically pure Shoal Bass in Big Creek could be used to replicate the natural genetic composition and diversity of Shoal Bass populations in the UCRB by using remaining genetically pure Shoal Bass from Big Creek as broodstock, along with potential supplementation of additional genetically pure Shoal Bass from the Chestatee and Chattahoochee rivers. Efforts to characterize and monitor the status of the Smallmouth Bass population in the Chattahoochee River upstream of Morgan Falls Dam, including the extent of their movement into, and use of, Big Creek would also be beneficial. If Smallmouth Bass become established in the mainstem Chattahoochee River upstream of Morgan Falls Dam, this could create increased propagule pressure into Big Creek and drive species swamping towards the non-native Smallmouth Bass genome. Additional study of the invasion of Smallmouth Bass and subsequent hybridization in Big Creek could provide novel insights into the mechanisms causing Shoal Bass population declines in tributary streams throughout the Chattahoochee River basin (Taylor and Peterson 2014; Sammons et al. 2015).

Measures of genetic diversity for pure Shoal Bass from the Chestatee and Chattahoochee rivers were similar to measures reported for relatively robust Shoal Bass populations in the upper Flint River, lower Flint River, and Chipola River (Taylor 2017). Our point estimates of N_e (93.8–197.4) for the combined Chestatee and Chattahoochee river population represent some of the first N_e estimates for a Shoal Bass population. General conservation guidelines for N_e estimates state that $N_e = \sim 50$ is adequate for short-term conservation, whereas $N_e = \sim 500$ allows enough genetic variability to maintain long-term evolutionary potential (Hallerman 2003). Using similar methodologies, Tringali et al. (2015b) reported point estimates of N_e in the relatively isolated, but sustainable Shoal Bass

population in the Chipola River, Florida, ranging from 110.4–131.4. Because of concern surrounding the low estimates of effective size and the uncertainty around these estimates, we follow Tringali et al. (2015b) in suggesting further studies to better assess and monitor genetic diversity and population sizes of Shoal Bass in the Chestatee and Chattahoochee rivers. However, the detection of Shoal Bass hybridization with non-native Alabama Bass in both rivers is cause for more immediate conservation concern, as our results from Big Creek illustrate that invasion and subsequent introgression of Shoal Bass populations can progress quickly. We encountered phenotypic Alabama Bass at all sites during our sampling on both rivers, but did not include those individuals in our genotyping; thus, hybridization rates are likely higher than inferred from our collections. Immediate investigations are warranted to determine the upstream extent of Alabama Bass invasion and quantify hybridization rates in both rivers.

Objective 1b – Age and Mortality

Because fishes are ectothermic, temperature-related differences in life histories are commonly documented across latitude and elevation gradients (Coutant 1976; Conover 1992; Kennedy et al. 2003). Compared to other studied populations situated in lower elevations and latitudes, Shoal Bass in the UCRB have pronounced differences in longevity, annual mortality, and growth. We estimated Shoal Bass ages up to 12 years in all three stream systems sampled for this study, compared to rare estimates of 10-11 years in the Flint and Chipola rivers (Sammons and Gocłowski 2012; Ingram and Kilpatrick 2015; Woodside et al. 2015), suggesting that Shoal Bass populations in the UCRB live longer. Coinciding with differences in longevity, Shoal Bass populations in the UCRB also experienced noticeably lower annual mortality (18-24%) compared to similarly-derived estimates of 40-69% in the Flint and Chipola rivers (Sammons and Gocłowski 2012; Ingram and Kilpatrick 2015; Woodside et al. 2015). Furthermore, growth models constructed with the resulting length-at-age data (Taylor 2017; Long et al. *in review*) suggest that Shoal Bass in the UCRB grow slower and attain shorter maximum lengths compared to populations in more southern latitudes and lower elevations (Sammons and Gocłowski 2012; Ingram and Kilpatrick 2015; Woodside et al. 2015; Taylor 2017; Long et al. *in review*). Finally, results from Long et al. (*in review*) suggest that the scale-based age estimates used in this study may have underestimated age for older fish, a phenomenon commonly observed in scale-based aging studies (Maceina et al. 2007); thus, differences found between the UCRB and other populations would only be strengthened if more accurate aging methods were employed.

These life history differences may warrant population-specific management and conservation strategies. For example, Shoal Bass in the UCRB reach a harvestable size (355 mm TL) at approximately age-7, compared to ages 4 or 5 elsewhere (Sammons and Gocłowski 2012; Woodside et al. 2015; Taylor 2017; Long et al. *in review*). Such differences in the age of harvested fish could differentially affect population responses to exploitation. Because fishing pressure for Shoal Bass in the UCRB is unknown, creel surveys to assess angler effort and harvest are warranted, along with an evaluation of how harvest-limit adjustments could influence these populations.

Objective 1c – Recruitment

Inconsistency in recruitment variability among the three rivers suggests that watershed-specific factors are influential. Two previous studies provide contrasting conclusions about Shoal Bass recruitment, similar to our results. Low variation in recruitment in the upper Flint River suggests that the environment is either stable or that the environment exerts little influence (Sammons and Goclowski 2012), but variable recruitment in the Chipola River has been attributed to poor year-classes during periods of high spring and summer discharge (Woodside et al. 2015). In our study, recruitment variation appeared to coincide with the amount of non-natural land cover in each watershed – from little variation in the relatively forested Chestatee River to high variation in the urbanized Big Creek. Negative relationships between recruitment and increased variation in summer discharge in Big Creek are likely linked to increased sedimentation and altered streamflow regimes associated with watershed urbanization. Sedimentation can deteriorate spawning substrate quality (Kemp et al. 2011), and larval black bass are vulnerable to downstream displacement during high discharge events (Harvey 1987). High flow events and increased variation in discharge during spawning season have been shown to negatively influence recruitment in fluvial populations of Smallmouth Bass (Lukas and Orth 1995; Smith et al. 2005), Largemouth Bass, and Suwanee Bass (*M. notius*; Bonvecchio and Allen 2005). To date, the effect of watershed land use on Shoal Bass populations is anecdotal, but has been implicated in Shoal Bass population declines in several tributaries to the middle Chattahoochee River (Stormer and Maceina 2008). Additional studies are warranted to identify the specific pathways through which land cover characteristics influence Shoal Bass recruitment strength, particularly in the Big Creek watershed where we observed the greatest variability in recruitment. Meanwhile, conservation actions to preserve forested watershed conditions, natural flow patterns, and shoal habitats in the UCRB will undoubtedly benefit overall stream health and Shoal Bass populations.

Our results also suggest that over-winter survival could be important for recruitment in Shoal Bass populations of the UCRB. Winter mortality has been documented to be important for recruitment in more northerly-distributed black bass populations, with growth-dependent effects evident (Oliver et al. 1979; Miranda and Hubbard 1994). Thus, conditions favorable to faster growth prior to the over-wintering period could be favorable for Shoal Bass recruitment in the UCRB (Conover 1992). In our catch-curve residual analysis, recruitment in Big Creek was positively related to cumulative growing degree-days in fall, a presumed growing period for age-0 Shoal Bass prior to the over-wintering period. Furthermore, recruitment in the Chattahoochee River was positively related to winter SD of discharge, which may also indicate an influence of winter temperature. Discharge in the upper Chattahoochee River during winter is generally a function of the number and magnitude of rain events, which temporarily elevate water temperatures (data available from USGS gauge 02330450); hence, the greater the number of winter rain events, the higher the SD of discharge and the warmer the water temperatures. Winters with above-average water temperatures, or even brief periods of elevated water temperatures, may confer improved over-winter survival of Shoal Bass in the UCRB by temporarily relieving metabolic demands on stored energy reserves and perhaps allowing foraging activity (see Fullerton et al. 2000). Furthermore, the slower growth and increased longevity we documented in Shoal Bass populations in the UCRB may reflect an adaptation to poor recruitment

driven by marginal temperature conditions, a phenomenon documented in other freshwater fishes (Conover 1992; Kennedy et al. 2003).

Objective 2a – Population Size

Estimation of local Shoal Bass abundance in Big Creek provided additional insight into the status and viability of the population. Throughout our study on Big Creek, point estimates of phenotypic Shoal Bass (≥ 70 mm TL) abundance fluctuated between 219-348 individuals within the 950-m reach of shoal habitats located downstream of Roswell Mill Dam. Large classes of age-0 and age-1 fish comprised the majority of fish marked and recaptured over the study, and mean TL of captures varied between 116-212 mm. In a similar-sized tributary of the Chattahoochee River, between 72-118 Shoal Bass (≥ 150 mm TL) inhabited the 650-m long Moffits Mill shoal complex of Little Uchee Creek (Stormer and Maceina 2008). However, over a two-year period following severe drought, abundance declined to 13-23 fish (≥ 150 mm TL; Stormer and Maceina 2008). More recent surveys indicate that the Shoal Bass population in Little Uchee Creek has suffered functional extirpation (Katechis 2015). Interestingly, these abundance estimates translate into similar densities as observed in the Chipola River, Florida, which harbored densities of approximately 100 Shoal Bass (≥ 150 mm TL) per river-kilometer (Woodside et al. 2015). These lines of evidence suggest that the relative isolation of tributary populations, such as those in Little Uchee Creek and Big Creek, increases the susceptibility of these populations to collapse by environmental or demographic stochasticity. The low abundance of older fish documented in our CMR study, coupled with the recruitment variability, further heightens concerns that the Shoal Bass population in Big Creek is vulnerable to functional extirpation in the near future.

Several insights from this CMR study can inform future population monitoring efforts, including potential tradeoffs in the effort required to collect data and the degree of accuracy and precision needed with abundance estimates to inform management. If CMR approaches are employed to monitor Shoal Bass abundance in the future, additional sampling events and increased sampling effort within each closure period would allow for more realistic model parameterizations and provide increased precision. CMR studies are effort-intensive and may not always be feasible, but resource managers interested in long-term monitoring of population trends may benefit from understanding how p (i.e., capture probability or detection) varies across individual (e.g., length) and environmental (e.g., substrate, flow velocity, depth, and water temperature) factors (see Price and Peterson 2010; Mollenhauer and Brewer 2017). A less-intensive monitoring option would be to use catch-per-unit effort (CPUE) as an index of abundance, but this index may be misleading when the assumption of constant p is violated (Hilborn and Walters 1992; Gwinn et al. 2011). If variation in p were quantified across a range of sampling conditions, CPUE could be adjusted to provide a more-reliable index of abundance (Hubert and Fabrizio 2007).

Objective 2b – Movement

Although Shoal Bass are considered shoal habitat specialists (Taylor and Peterson 2014; Sammons et al. 2015), our results demonstrate seasonal variation in habitat affinity wherein adults often resided in habitats near the confluence of Big Creek and the Chattahoochee River during the fall and winter months, suggesting importance of this connection interface and connectivity throughout the range.

Daily percent residence at each SUR location demonstrated that adult Shoal Bass transitioned out of the upstream 1-km shoal habitat beginning in mid-August, and took up residence in downstream portions of Big Creek, characterized by deeper and silt-laden habitats, as water temperatures cooled from mid-October through the end of the study in early January. Similarly, adult Shoal Bass in a fragmented section of the Chattahoochee River used deeper areas and less bedrock substrates in late fall compared to spring (Sammons and Early 2015), and 76% of adult Shoal Bass were sampled in pools during summer and fall in the Chipola River, Florida (Wheeler and Allen 2003). Recognition of seasonal variation in habitat use has important management and conservation implications for Shoal Bass. For example, if Shoal Bass typically occupy deeper water during the fall and winter, the combination of increased depth and decreased water temperature could drastically lower p when using conventional sampling gears, such as electrofishing.

This telemetry study also adds to a body of movement-related research on Shoal Bass, providing insight into how fragmentation affects Shoal Bass movement. In the interconnected mainstem shoal habitats of the upper and lower Flint River, Georgia, adult Shoal Bass moved an average of approximately 250–500 m/day (Gocłowski et al. 2013; Taylor and Peterson 2015) and movements of up to 200 km have been documented during the spring spawning season (Sammons 2015). In contrast, movement in fragmented portions of tributaries and mainstem rivers is much reduced. In a 1.15-km reach of Little Uchee Creek, Alabama, 3–4 m tall waterfalls bounded a population of Shoal Bass that had 75% of weekly movement observations ≤ 17 m/week (Stormer and Maceina 2009). In a 2-km portion of the mainstem Chattahoochee River bounded by an upstream dam and a downstream impoundment, Shoal Bass movement averaged 8–25 m/day and the downstream impoundment appeared to serve as a barrier to movement (Sammons and Early 2015). Our passive SUR detections suggested that adult Shoal Bass were relatively sedentary in Big Creek, as fish were rarely detected at both SUR locations (1 km apart) on the same day.

Among a number of isolated and fragmented tributary populations of Shoal Bass that have been studied, the population in the 2-km section of Big Creek is one of only a few that has persisted over the last decade. For example, several populations inhabiting Chattahoochee River tributaries in Alabama have suffered functional extirpation in recent years (Stormer and Maceina 2008; Katechis 2015). Many of these tributaries have dams that sever connectivity to mainstem rivers or have become disjunct from free-flowing mainstem habitats and now empty into impounded waters. We hypothesize that connectivity to a free-flowing mainstem river is important for the persistence of tributary populations. In connected habitats, fish from the mainstem are occasionally observed entering tributaries that support Shoal Bass populations (Sammons and Early 2015), suggesting that populations in the mainstem rivers could contribute to gene flow and growth of tributary populations. Furthermore, mainstem rivers may provide critical refuge from disturbances that occur in tributary systems. During a severe drought, tagged fish in Little Uchee Creek were unable to emigrate past natural barriers and suffered 87% mortality as discharge approached 0 m³/s (Stormer and Maceina 2009). Big Creek has had similarly low discharge levels (< 0.2 m³/s), yet fish likely had access to flowing waters in the mainstem river during drought conditions.

We did not directly observe tagged Shoal Bass in Big Creek entering the mainstem Chattahoochee River channel; however, evidence suggests that temporary or seasonal emigration into the Chattahoochee River is plausible. Although thermal barriers can limit fish movement (Caudill et al. 2013), the thermal barrier at the mouth of Big Creek appears to be seasonal, as temperatures were warmer in the thermally altered mainstem than in Big Creek during the winter months. Other black bass species have been documented to inhabit thermally altered, warmer waters during the winter months (Ross and Winter 1981; Cooke et al. 2004), further suggesting seasonal movement of Shoal Bass from Big Creek into the mainstem Chattahoochee River is plausible. More intensive studies could be undertaken to improve our understanding of Shoal Bass movement in and out of Big Creek.

Finally, reported harvest of tagged adults was quite high considering previous beliefs that the Shoal Bass population in Big Creek was relatively unknown and received little angling pressure. Two of eight (25%) tagged fish were harvested and reported. Although inference of angling pressure and attitudes is hindered by low sample size, it is important to note the potential effect of angler attitude on our results. In the well-known lower Flint River Shoal Bass fishery, catch-and-release is commonly practiced (Ingram and Kilpatrick 2015). However, via telephone discussions, we learned that neither angler was specifically targeting Shoal Bass, rather, they were targeting stocked trout for harvest. Therefore, the Shoal Bass population in Big Creek may not be widely known among local anglers, but the incidental catch and harvest of adults taking up seasonal residence near the confluence could have population-level effects. Low abundance of adult Shoal Bass, coupled with substantial angling access via the Vickery Creek Unit's trail systems, may justify the consideration of local harvest restrictions.

Conclusions

Shoal Bass populations in the UCRB represent a unique genetic stock within their native range (Taylor 2017). The Big Creek, Chestatee River, and Chattahoochee River populations examined in this study all exhibited increased longevity and markedly lower annual mortality than observed elsewhere across the species' native range. Among the three rivers sampled during this study, Shoal Bass recruitment was more variable with increased urban and agricultural land cover. Over-winter survival also appeared to be a pinch-point for recruitment of Shoal Bass populations in the UCRB, which may help explain the observed differences in life-history characteristics. These life history differences further underscore the value of conserving UCRB Shoal Bass populations towards maintain the diversity and adaptability of the species.

Measures of genetic diversity and estimates of N_e indicated that the populations in the Chestatee and Chattahoochee rivers are relatively stable in regards to short-term conservation, but may lose genetic variation and adaptability in the long-term. Thus, these two rivers represent the last strongholds for Shoal Bass in the UCRB. However, introgression with non-native Alabama Bass may pose a more immediate threat to conservation of the Shoal Bass populations in both rivers. Ensuring that genetically pure Shoal Bass are protected and maintained, along with their habitats in both rivers, would be a significant step towards the conservation of Shoal Bass, not only in the UCRB but across the species' range.

Shoal Bass in Big Creek represent one of four extant populations of Shoal Bass within the UCRB, and this population has harbored unique genetic diversity (Dakin et al. 2015). Following the illegal introduction of Smallmouth Bass into the study area, the Big Creek population has experienced some of the most elevated rates of introgressive hybridization yet documented for a Shoal Bass population. Few pure Shoal Bass were identified, and unidirectional backcrossing towards Shoal Bass suggests fleeting opportunity remains for genetic conservation. Variable recruitment coupled with low adult abundance heightens concerns that the population could be vulnerable to local extirpation caused by several years of poor environmental conditions, demographic stochasticity, or sudden anthropogenic disturbance. Finally, adult Shoal Bass in Big Creek used the upper 1 km of shoal habitats during the spring spawning season and into the summer months, and then transitioned downstream into deeper, slower habitats from late summer through winter. Adults appear vulnerable to incidental catch and harvest while residing near the confluence. Although we did not document emigration into the mainstem Chattahoochee River, emigration of adults appeared plausible, especially during the winter months. Although the connection interface between Big Creek and the Chattahoochee River is likely important refuge habitat, spawning activities appear to be confined to the 1 km of shoal habitats located downstream of Roswell Mill Dam – suggesting the breeding population persists in relative isolation.

Conservation of the Big Creek Shoal Bass population and its native genome will require non-trivial management action. Supplemental stocking of genetically pure Shoal Bass or transplanting of pure gravid adults may help bolster the Big Creek population during years of poor recruitment and alleviate genetic concerns such as inbreeding depression and introgression of non-native alleles

(Dakin et al. 2015; Porta and Long 2015). If stocking or transplanting is implemented, brood stock source is an important consideration because of documented population structure within the species (Taylor 2017) and because the unique life history traits documented in the Shoal Bass populations of the UCRB have a genetic basis in other fishes (Schultz et al. 1998; Conover et al. 2009). Selective removal of non-native congeners and hybrids may also help delay or prevent the onset of complete hybrid swamping of the native Shoal Bass genome. Finally, efforts to educate park visitors on the endemic Shoal Bass population in Big Creek and remnant shoal habitats they inhabit could benefit the population. First, anglers may develop an increased catch-and-release ethic, or be more receptive of increased harvest restrictions, if they learn that the local Shoal Bass population is of conservation interest (Cooke et al. 2016). In fact, such a unique fishery could be developed into a sustainable urban ecotourism destination for anglers (see Zwirn et al. 2005). Second, increased awareness of watershed impairments among anglers and the general public could bolster stakeholder engagement in conservation actions within the watershed (Cooke et al. 2016).

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NPS 636/144700, April 2018

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